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Ecological studies on size-dependent growth tactics before migration in masu salmon (*Oncorhynchus masou*)

（サクラマスにおける回遊前のサイズ依存成長戦術に関する生態学的研究）

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A Dissertation Submitted to
Division of Biosphere Science,
Graduate School of Environmental Science
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Chapter 1

General Introduction

One of the most widespread and fascinating movement strategies in the animal kingdom is migration (Dingle and Drake 2007). A vast number of animals—mammals, birds, fish, insects, reptiles, amphibians, and planktons—conditionally or seasonally migrate between distinct habitats (Alerstam et al. 2003, Dingle and Drake 2007, Fudickar et al. 2021). Migration allows animals to gain substantial benefits at the migration destination habitats (i.e., huge growth, reproductive success and overwinter survival) (Gross et al. 1988, Dodson et al. 2013, Bauer and Hoye 2014, Fudickar et al. 2021). Although migration confers apparent benefits, it incurs a variety of costs which leads to high mortality (Roff 1988, Nøttestad et al. 1999, Brönmark et al. 2014, Lok et al. 2015). Thus, for the success of the migration, migratory animals should reduce high mortality costs which operates during migration (Alerstam et al. 2003, Hedenström 2008).

Many previous studies have documented that migratory animals have a variety of risk-reducing mechanisms to minimize the mortality costs during migration. For example, fishes, mammals, insects and birds migrate in large numbers (i.e., flocks, herds and shoals) to avoid predation and energy expenditure (Milner-Gulland et al. 2014, Furey et al. 2016). Many fishes, birds and insects migrate during the night to avoid the predation from the visual predators (Chapman et al. 2015b, Furey et al. 2016, Komal et al. 2017). Many birds usually migrate in the timing when the weather and wind condition is favorable to avoid energy expenditure (Liechti 2006). Some mammals migrate the landscape where predation risk is low (Hopcraft et al. 2014, Matthews et al. 2020). Although these studies have evidenced risk-reducing mechanisms of migration, only few studies have focused on its individual variation.

To minimize the mortality costs of migration, migratory animals should have evolved individual level risk-reducing mechanisms of migration. This is because the mortality costs are not uniform among individuals Large body of literature has reported the mortality costs during the migration vary among migratory individuals and they depends on the individual condition (Owen and Black 1989, Holtby and Healey 1990, Sogard 1997, Sillett and Holmes 2002, Kinnison et al. 2003, Tamate and Maekawa 2004a, Menu et al. 2005, Strandberg et al. 2010, Sergio et al. 2014, Oppel et al. 2015, Furey et al. 2015). Considering that mortality costs during migration operate differently among individuals, migratory animals should have risk-reducing tactics which depend on the conditions of the individuals (i.e., condition-dependent tactics).

In particular, such condition-dependent tactics against the selection on body size may be widely exist among migratory animals. Among various individual traits, body size is a key feature of the organisms and often assumed as a central element in the life-history evolution (Blanckenhorn 2000). Many studies on fishes, reptiles, mammals and birds have described that the mortality during migration operates stronger on individuals with smaller body size (i.e., size-selective mortality) (Healey 1982, Owen and Black 1989, Barlow and Boveng 1991, Sogard 1997, Bjorndal et al. 2003, Chaloupka and Limpus 2005, Zabel et al. 2005, Morrison et al. 2007, Strandberg et al. 2010, Sergio et al. 2014, Oppel et al. 2015, Flaten et al. 2016, Armstrong et al. 2018, Gregory et al. 2018, Jensen et al. 2018, Flávio et al. 2019). This suggests that size-selective mortality during migration is consistent among taxa and systems. Since migration has evolved repeatedly and independently (Dingle and Drake 2007), condition-dependent tactics to avoid size-selective mortality may be an critical component underlying the evolution of the migration strategies. Although studying condition-dependent tactics to avoid size-selective mortality can provide a fruitful perspective on the ecology and evolution of the migratory strategies, only few studies have studied it.

Condition-dependent tactics to avoid size-selective mortality during migration may exist before migration. For migratory animals, attaining a sufficiently large size before migration is necessary to avoid size-selective mortality during migration (Roff 1991). Arendt (1997) predicted that the migratory animals may accelerate the growth rate before migration to reach a sufficiently large size prior to migration (Arendt 1997). Actually, previous experimental studies that compared the growth rate of migratory type with non-migratory type during the pre-migration period support this prediction (Palmer and Dingle 1986, Wood and Foote 1990, Snyder 1991, Yamamoto and

Nakano 1996, Takami et al. 1998, Olsson and Greenberg 2004). However, these studies have assumed the growth pattern of migratory individuals (migrants) as uniform and thus has not focused on the individual variation in pre-migration growth. Since smaller migrants suffer higher mortality during migration, ecological demands of growth are higher in smaller migrants before migration. Considering acceleration of the growth rate before migration can incur behavioral and physiological costs (Metcalfe and Monaghan 2001, Hector and Nakagawa 2012), smaller migrants which needs to attain sufficient large size before migration may exhibit higher growth rate before migration than larger ones before migration. Alternatively, smaller migrants may delay migration until they attain sufficiently large body size. Similarly, larger 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, little ecological and evolutionary research has investigated such size-dependent growth tactics before migration. Studying size-dependent growth tactics as a condition-dependent tactics is important to deepen our understanding of the evolution and maintenance of the migration strategies. This is because such individual-level mechanisms may contribute to maximize the net benefits of the migration according to size condition before their migration trip, which may make a major contribution in the evolution and the maintenance of the migration as an adaptive strategy. Here, in this thesis, I conducted a series of studies on size-dependent growth tactics before migration using masu salmon (*Oncorhynchus masou*) as a study species.

Masu salmon is a partial migratory fish endemic to East Asia (Machidori and Kato 1984). Migrants emerge from the river bed of the river in early spring and stay in their river habitat for one or two years (Morita 2018). After staying in the river for one or two years, migrants descend the river to the ocean in spring after smoltification (i.e., morphological and physiological changes). The decision to migrate is made by the previous autumn, but migrants stay in the river for half a year additionally before the migration (Hirata et al. 1988, Nagae et al. 1994, Ugachi et al. 2023). In the resource-rich ocean, migrants grow to large sizes (>40 cm). Although the ocean has a great potential for growth, it is hazardous for migrants (i.e., the survival probability of oceanic migration is 0.1-10%) (Morita 2018). Importantly, size at the start of oceanic migration is thought by some to be a key factor affecting survival in the ocean (Miyakoshi et al. 2001, Shimoda et al. 2003, Miyakoshi 2006, but see Miyakoshi and Saitoh 2011). After migration, migrants return to the natal river to spawn. In contrast to migrants, residents stay in the river throughout their lives.

Using masu salmon, I conducted series of studies on size-dependent growth tactics before migration using a PIT-tag system in a small river in Hokkaido, northern Japan. In chapter 2, I tested whether masu salmon exhibit the growth patterns expected from the size-dependent growth tactics before migration (Futamura et al. 2022b). Specifically, I conducted a capture-mark recapture survey and PIT-tag antenna detection survey to test the following two predictions: (1) smaller eventual migrants exhibit a higher growth rate than larger migrant half year before migration (2) smaller eventual migrants stay longer (extend their stay) in the river. In chapter 3 and 4, I evaluated whether the size-dependent growth patterns obtained in chapter 2 is a growth tactic from the perspective of ecological demands for growth and costs of maximizing growth. In chapter 3, I investigated whether ecological demands for growth is greater in smaller migrants before migration (Futamura et al. 2022a). Specifically, I investigated whether migrants suffered size-selective mortality risk during descending the transitional habitat of the lower reaches of the river but river-dwelling residents in the uppermost reaches do not in the corresponding period by conducting capture-mark recapture survey and PIT-tag antenna detection survey. In chapter 4, I investigated the costs associated with higher growth rate and longer pre-migration period. By focusing on the tradeoff between growth and survival, I investigated whether the extension of stay in the river and acceleration of the growth rate incurs increased predation by investigating predation-caused wounds as a proxy of predation risk. In chapter 5, I investigated the behavioral process of one size-dependent growth tactic: the extension of the stay in the river by smaller eventual migrants (i.e., size-dependent migration departure) (Chapter 5). Specifically, I investigated where smaller migrants extended their stay in the river in the distinct riverscapes (nursery habitat and transitional habitat) over two migration years by tracking the individual movement using five PIT-antenna systems installed in the riverscape of the Horonai River. Finally, in chapter 6, I discuss the significance of this thesis in migration ecology.

Chapter 2

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

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, I investigated size-dependent patterns of growth rates and migration timing of juvenile masu salmon (*Oncorhynchus masou*) before their oceanic migration. I 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 my 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.

Introduction

Some animals compulsory or conditionally migrate between different habitats in particular life stages to improve their fitness (Gross et al. 1988, Dingle and Drake 2007, Newton 2010). Despite the apparent benefits of migration such as fast growth and high reproductive success (Nøttestad et al. 1999, McKinnon et al. 2010, Chapman et al. 2012), 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 (Sillett and Holmes 2002, Alerstam et al. 2003, Osterback et al. 2013, Lok et al. 2015). Migratory species have evolved life history strategies to cope with the risk of migration (Roff 1991, Furey et al. 2016).

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 and Williams 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 and Chaplin 1981) and in migratory individuals compared to non-migratory conspecifics (Palmer and Dingle 1986, Snyder 1991, Olsson and Greenberg 2004). 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 (Roff 1991, Arendt 1997).

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, Metcalfe and Monaghan 2001, Dmitriew 2011). 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, Schmitz et al. 2004, Rohr et al. 2015).

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 (Tamate 2012, Morita 2018), 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 (Miyakoshi et al. 2001, 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) I 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) I investigated whether body size of eventual migrants in early spring just prior to migration explained their timing of seaward migration.

Material and Methods

Study system

My 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 the ocean, and my study area was established in the uppermost 5.32 km part (hereafter called the survey area) (Fig. 2-1). I marked the 5.32 km survey area by 10 m increments to record fish locations. My survey area was established to encompass the portion of the river occupied by juvenile masu salmon (Fig. 2-1).

Capture-mark-recapture survey

I conducted a capture-mark-recapture survey throughout the survey area on five occasions: (1) autumn 2018 (3 –18 Sep-2018), (2) early spring 2019 (1 ‒5 Apr-2019), (3) autumn 2019 (7–11 Oct-2019), (4) early spring 2020 (18–26 Mar-2020), and (5) summer 2020 (25–26 Jun-2020). On each survey occasion, I 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). I 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. I 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. I 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, I identified the life history type of each individual based on behavioral evidence of outmigration. The criteria I 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, I recorded individual fish descending the river (i.e., migrants) using two types of devices installed downstream of the survey area (Fig. 2-1). 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. I 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 (23 Jul-2019), I 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 4 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, I 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, I 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.

I defined residents as individuals never detected by the antennas or captured by the trap. For analysis of body growth, I excluded individuals that had already matured in the autumn because maturity status may affect somatic growth rates (Rowe and Thorpe 1990). However, my preliminary analyses showed that including mature individuals did not affect results.

Statistical analysis

My 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, I 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). I 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, I 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 3-S1). The habitat effects (i.e., spatial variation in growth rates) were considered in two ways. First, I 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, my additional surveys using portable PIT antennas showed a majority of individuals stayed in the same 10-m section over several months (Futamura et al. *unpublished data*) and territoriality is common in stream-dwelling salmonids (e.g., Rodríguez 2002). Second, I 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 Table 3-S1 (i.e., two size traits [fork length or mass] × two periods [winter or spring] × 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, I investigated whether individual size at the capture survey in early spring explained the river-descending timing. I 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. I included section of capture in early spring as a covariate to account for varying distances of individuals to the PIT antenna system. I didn’t consider the interactive effects among body size, habitat section and year because my 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 2021).

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 2-S2). 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. 2-2; Fig. 2-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 (Table 2-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

($P < 0.001$) (Table 2-S3). As predicted, among the eventual migrants captured in early spring, smaller fish descended the river later than larger fish (Fig. 2-3; Fig. 2-S2).

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 my knowledge. My 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. 2-2; Fig. 2-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 I 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 ± 1SD] in April, May, June is 128.6 ± 9.1, 129.4 ± 9.20, 133.5 ± 8.6 mm, respectively; Fig. 2-4). This suggests a size threshold, above which migrants can better survive during the migration. In fact, my 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. 2022a). Hence, my 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 my 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 (Fig. 2-S3; Table 2-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. My two-year data support this idea. The significant effects of year and its interactions with initial size on the final size (Table 2-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 (Table 2-S3). 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. 2-3; Fig. 2-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, I 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 (Nakano and Murakami 2001, Baxter et al. 2005).

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.

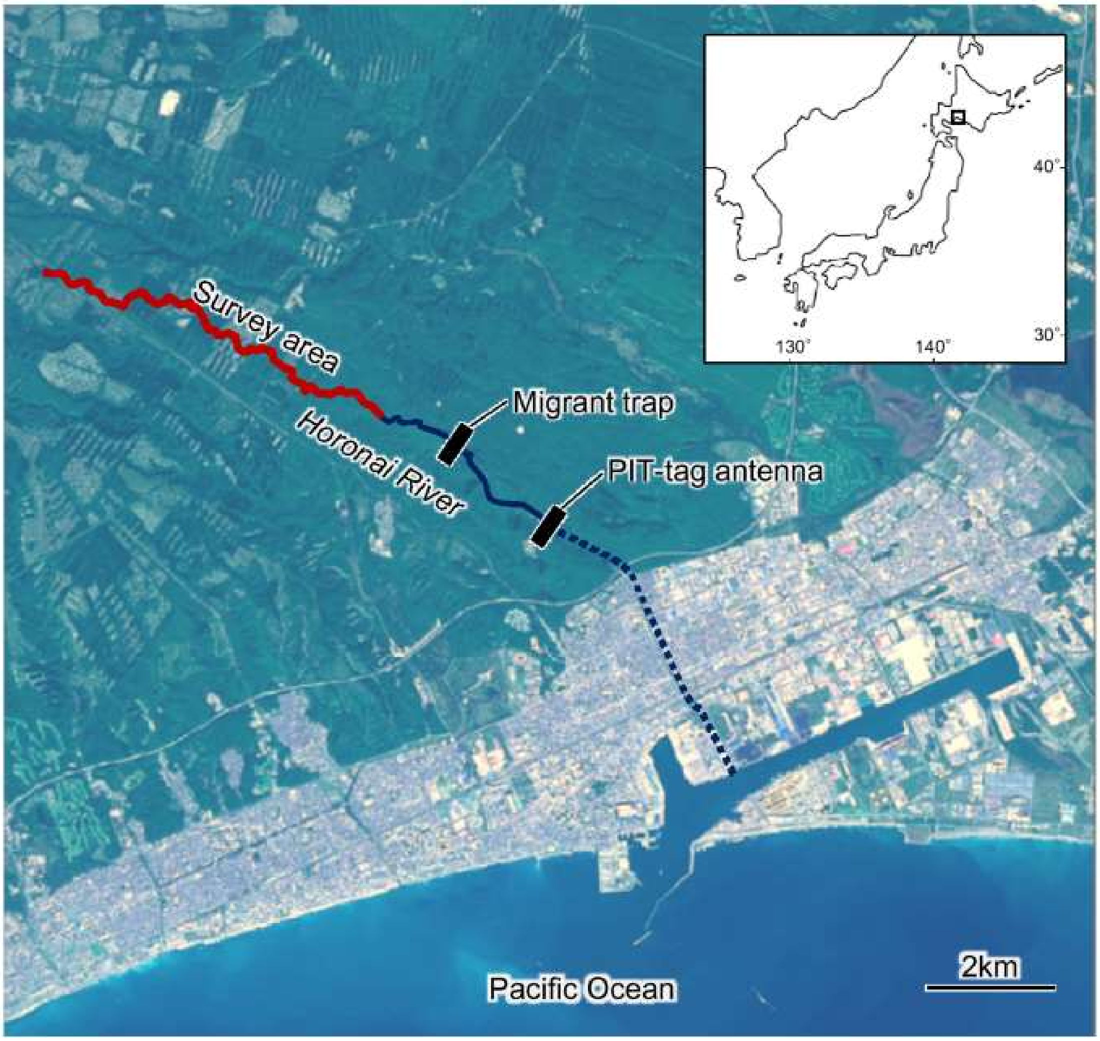

Fig. 2-1 The location of my survey area. This study was conducted at 5.3 km reach (as shown in red line) which corresponds to the primary distribution area of juvenile masu salmon in the Horonai River. The further downstream areas consist of the slow-flowing reaches where brown trout (*Salmo trutta*) 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.

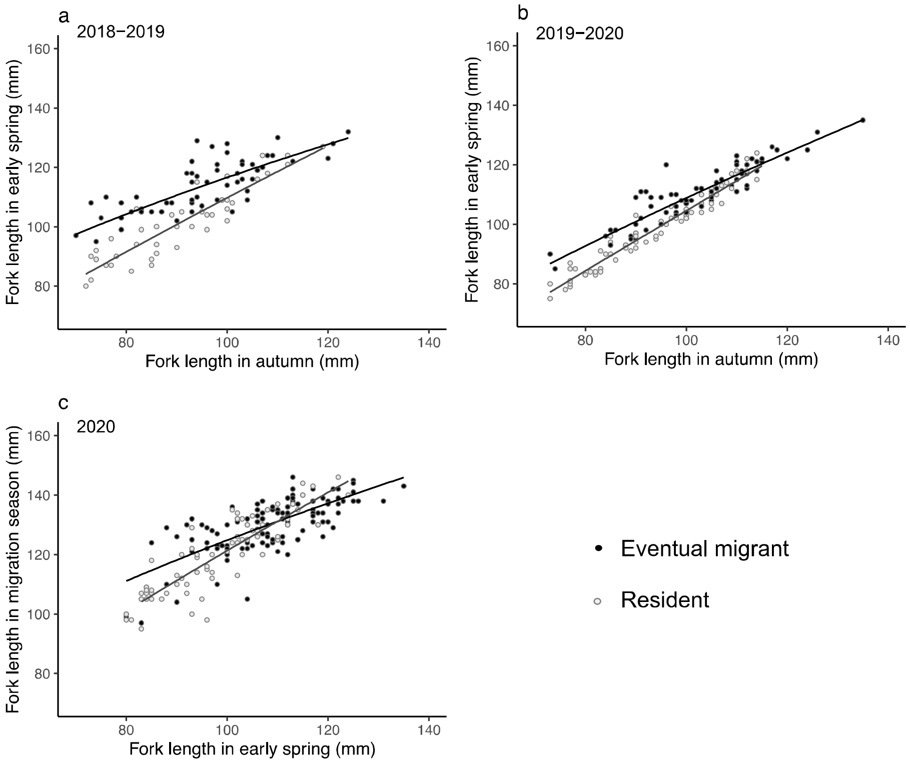

Fig. 2-2 Relationship between initial and final size (fork length) of masu salmon juveniles in the pre-migration periods. Shaded and open circles represent eventual migrants and residents, respectively. Regression lines are estimated after natural logarithmic transformation (i.e., $\ln(Y) = a \times \ln(X) + b \leftrightarrow Y = aX \times e^{b}$). 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 $Y = 0.50X \times e^{2.44}$, $P < 0.001$, adjusted $R^2 = 0.62$, for eventual migrants ($N = 60$); $Y = 0.81X \times e^{0.96}$, $P < 0.001$ adjusted $R^2 = 0.81$, for residents ($N = 41$); b $Y = 0.72X \times e^{1.38}$, $P < 0.001$, adjusted $R^2 = 0.83$, for eventual migrants ($N = 72$); $Y = 0.96X \times e^{0.21}$, $p < 0.001$, adjusted $R^2 = 0.94$, for residents ($N = 74$); c $Y = 0.52X \times e^{2.43}$, $P < 0.001$, adjusted $R^2 = 0.49$, for eventual migrants ($N = 117$); $Y = 0.82X \times e^{1.02}$, $P < 0.001$, adjusted $R^2 = 0.77$, for residents ($N = 74$)

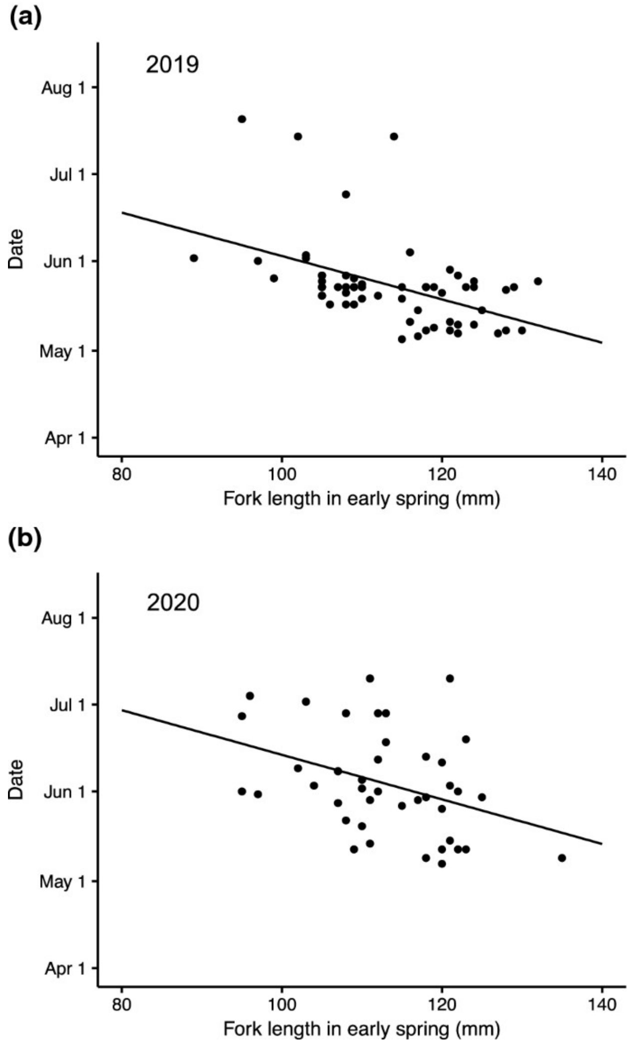

Fig. 2-3 Relation between the river-descending timing (date) and fork length at the early spring of the eventual migrants of masu salmon in a 2019 and b 2020. Regression lines: a $Y = -0.75X + 134.54$, $P < 0.001$, adjusted $R^2 = 0.20$ ($N = 60$); b $Y = -0.77X + 150.60$, $P = 0.015$, adjusted $R^2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

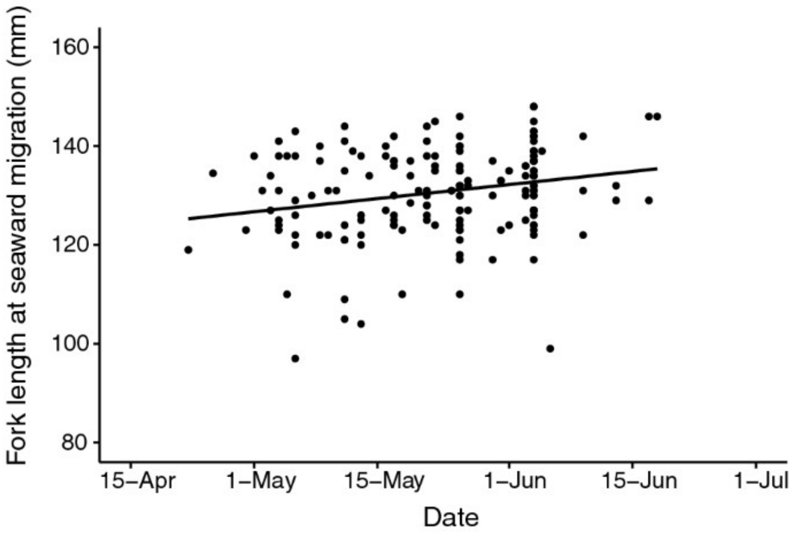

Fig. 2-4 Fork length at seaward migration in relation to date (i.e., timing of being captured by the migrant trap in the river-descending season of 2020). Slope of the regression line is significant but relatively weak (regression line: $Y = 0.18X + 123.87$, $p = 0.003$, adjusted $R^2 = 0.05$) ($N =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

Supplemental information 2-1:

Detailed information of the statistical analyses for the first prediction (i.e., smaller eventual migrants accelerated pre-migration periods)

Table 2-S1 Formulae of eight models used to test the first prediction

Model	Response variable	Fixed factor	Random factor
A	Ln (FL in ES)	Ln (FL in PA), *life history*, *year*, habitat section and their interactions	
B	Ln (BM in ES)	Ln (BM in PA), *life history*, *year*, habitat section and their interactions	
C	Ln (FL in ES)	Ln (FL in PA), *life history*, *year* and their interactions	*Habitat section*
D	Ln (BM in ES)	Ln (BM in PA), *life history*, *year* and their interactions	*Habitat section*
E	Ln (FL in MS)	Ln (FL in ES), *life history*, habitat section, their interactions and length of spring period	
F	Ln (BM in MS)	Ln (BM in ES), *life history*, habitat section, their interactions and length of spring period	
G	Ln (FL in MS)	Ln (FL in ES), *life history*, their interactions and length of spring period	*Habitat section*
H	Ln (BM in MS)	Ln (BM in ES), *life history*, their interactions and length of spring period	*Habitat section*

In each model, abbreviations PA, ES, MS, FL and BM stands for previous autumn, early spring, migration season, fork length and body mass. Continuous variables and categorical variables are shown in roman and italic, respectively.

Table 2-S2 Results of the eight models used to test first prediction

Model A	Fixed factor	Coefficient	Mean squares	F value	P value
	Ln (FL in PA)	0.43	2.56	1500.00	<0.0001
	Life history	-1.73	0.35	203.70	<0.0001
	Habitat section	-7.2×10^{-5}	1.3×10^{-3}	0.81	0.3689
	Year	-1.00	0.3	176.51	<0.0001
	Ln (FL in PA) × Life history	0.36	0.1	59.17	<0.0001
	Ln (FL in PA) × Habitat section	1.3×10^{-5}	3.0×10^{-4}	0.18	0.6748
	Life history × Habitat section	1.8×10^{-5}	6.9×10^{-4}	0.41	0.5251
	Ln (FL in PA) × Year	0.20	0.03	18.40	<0.0001
	Life history × Year	-0.16	0.01	3.63	0.0581
	Habitat section × Year	-1.0×10^{-4}	0.01	6.01	0.0149
	Ln (FL in PA) × Life history × Habitat section	-3.6×10^{-6}	9.7×10^{-4}	0.57	0.4511
	Ln (FL in PA) × Life history × Year	0.04	3.3×10^{-3}	1.93	0.1660
	Ln (FL in PA) × Habitat section × Year	2.4×10^{-5}	2.0×10^{-4}	0.13	0.7235
	Life history × Habitat section × Year	2.7×10^{-4}	4.3×10^{-4}	0.25	0.6160
	Ln (FL in PA) × Life history × Habitat section × Year	-5.8×10^{-5}	1.6×10^{-3}	0.95	0.3296
	Intercept	2.81			

Model B	Fixed factor	Coefficient	Mean squares	F value	p value
	Ln (BM in PA)	0.31	23.36	1164.92	<0.0001
	Life history	-1.06	3.11	155.17	<0.0001
	Habitat section	-1.6×10^{-4}	0.21	10.69	0.0012
	Year	-0.91	2.41	120.02	<0.0001
	Ln (BM in PA) × Life history	0.36	0.58	28.93	<0.0001
	Ln (BM in PA) × Habitat section	5.6×10^{-5}	2.7×10^{-3}	0.13	0.7163
	Life history × Habitat section	1.0×10^{-4}	0.05	2.72	0.1005
	Ln (BM in PA) × Year	0.31	0.25	12.70	0.0004
	Life history × Year	0.22	0.05	2.32	0.1289
	Habitat section × Year	7.5×10^{-5}	0	0.00	0.9990
	Ln (BM in PA) × Life history × Habitat section	-4.1×10^{-5}	0.05	2.29	0.1315
	Ln (BM in PA) × Life history × Year	-0.08	0.05	2.72	0.1003
	Ln (BM in PA) × Habitat section × Year	-3.8×10^{-5}	0.05	2.70	0.1020

	Life history × Habitat section × Year	4.1×10^{-5}	0.01	0.28	0.5963
	Ln (BM in PA) × Life history × Habitat section × Year	-1.2×10^{-5}	7.0×10^{-4}	0.03	0.8519
	Intercept	2.09			
Model C	Fixed factor	Coefficient	Mean squares	F value	p value
	Ln (FL in PA)	0.50	1.77	1163.94	<0.0001
	Life history	-1.43	0.06	41.31	<0.0001
	Year	-1.06	0.03	21.16	<0.0001
	Ln (FL in PA) × Life history	0.30	0.06	37.08	<0.0001
	Ln (FL in PA) × Year	0.22	0.03	18.14	<0.0001
	Life history × Year	0.30	9.0×10^{-4}	0.59	0.4423
	Ln (FL in PA) × Life history × Year	-0.06	8.0×10^{-4}	0.50	0.4809
	Intercept	2.44			
Model D	Fixed factor	Coefficient	Mean squares	F value	p value
	Ln (BM in PA)	0.48	12.29	847.93	<0.0001
	Life history	-0.73	0.46	31.99	<0.0001
	Year	-0.66	0.37	25.48	<0.0001
	Ln (BM in PA) × Life history	0.22	0.2	13.78	0.0003
	Ln (BM in PA) × Year	0.20	0.16	11.02	0.0010
	Life history × Year	0.30	0.03	2.13	0.1460
	Ln (BM in PA) × Life history × Year	-0.10	0.02	1.18	0.2794
	Intercept	1.61			
Model E	Fixed factor	Coefficient	Mean squares	F value	p value
	Ln (FL in ES)	0.70	1.31	647.42	<0.0001
	Life history	-0.64	0.01	6.77	0.001
	Habitat	6.9×10^{-5}	6.3×10^{-3}	3.11	0.0793
	Days of spring period	3.2×10^{-3}	0.15	74.36	<0.0001
	Ln (FL in ES) × Life history	0.11	0.02	7.78	0.0058
	Habitat × ln (FL in ES)	-1.6×10^{-5}	6.2×10^{-4}	0.30	0.5821
	Habitat × Life history	-1.0×10^{-4}	4.5×10^{-3}	2.24	0.1363
	Ln (FL in ES) × Life history × Habitat	2.4×10^{-5}	5.0×10^{-4}	0.23	0.6292
	Intercept	1.42			
Model F	Fixed factor	Coefficient	Mean squares	F value	p value

	Ln (BM in ES)	0.54	5.54	285.28	<0.0001
	Life history	-0.89	1.34	69.25	<0.0001
	Habitat	6.4×10^{-5}	8.0×10^{-4}	0.04	0.8386
	Days of spring period	0.01	1.45	74.70	<0.0001
	Ln (BM in ES) × Life history	0.29	0.25	13.08	0.0004
	Habitat × ln (BM in ES)	2.3×10^{-5}	0.01	0.55	0.4605
	Habitat × Life history	9.3×10^{-5}	0.1	5.37	0.0216
	Ln (BM in ES) × Life history × Habitat	-2.2×10^{-5}	3.4×10^{-3}	0.18	0.6740
	Intercept	1.10			
Model G	Fixed factor	Coefficient	Mean squares	F value	p value
	Ln (FL in ES)	0.65	1.07	528.06	<0.0001
	Life history	-0.90	0.02	9.36	0.0025
	Days of spring period	3.1×10^{-3}	0.12	59.14	<0.0001
	Ln (FL in ES) × Life history	0.17	0.01	7.04	0.0087
	Intercept	1.61			
Model H	Fixed factor	Coefficient	Mean squares	F value	p value
	Ln (BM in ES)	0.58	8.28	419.59	<0.0001
	Life history	-0.66	0.34	17.44	<0.0001
	Days of spring period	0.01	1.06	53.47	<0.0001
	Ln (BM in ES) × Life history	0.25	0.26	12.96	0.0004
	Intercept	1.00			

Abbreviations: PA (previous autumn), ES (early spring), FL (fork length), BM (body mass). Before the analyses, the categorical variables were transformed into dummy variables (i.e., converted to either 0 or 1). Specifically, I transformed life history (i.e., eventual migrant [0] and resident [1]) and year (i.e., autumn 2018–early spring 2019 [0] and autumn 2019–early spring 2020 [1]).

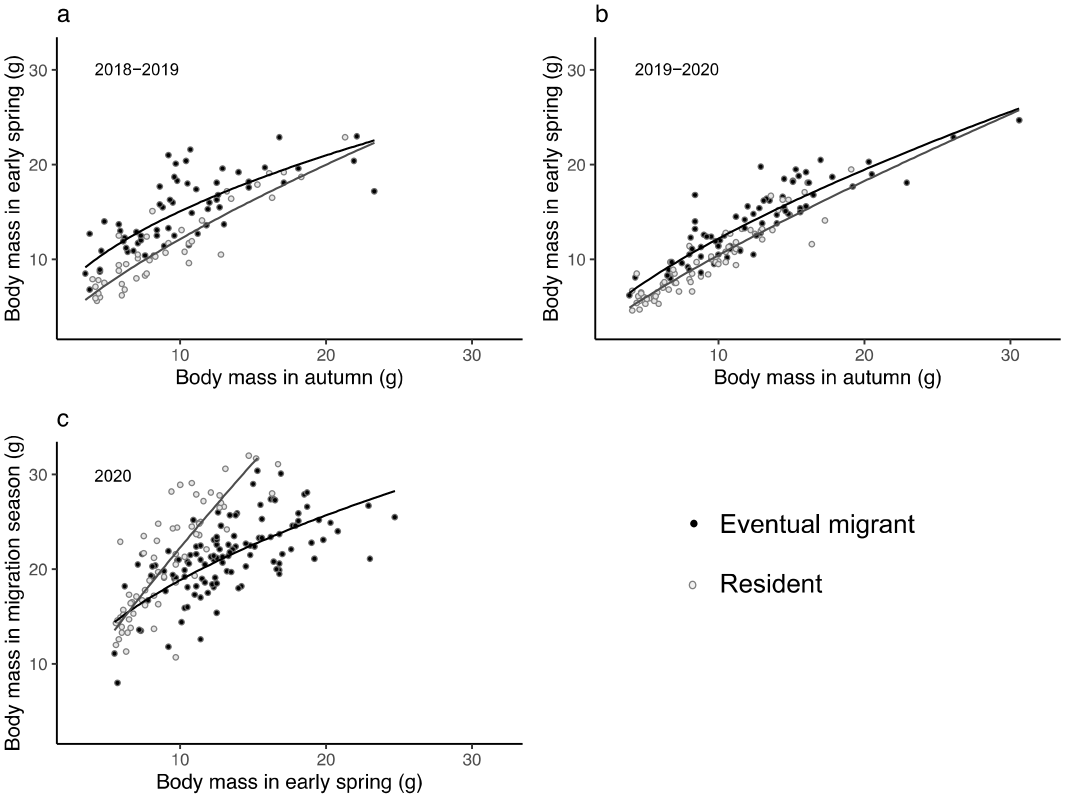

Fig. 2-S1 Relationship between initial size (body mass) and the subsequent size of eventual migrants (filled) and residents (open) of masu salmon juveniles during the pre-migration period. Regression lines are estimated after natural logarithmic transformation (i.e., $\ln(Y) = a \times \ln(X) + b \leftrightarrow Y = X^{a} \times e^{b}$). **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** $Y = X^{0.48} \times e^{1.62}$, $P < 0.001$, adjusted $R^2 = 0.60$, for eventual migrants (N=60); $Y = X^{0.71} \times e^{0.84}$, $p < 0.001$, adjusted $R^2= 0.80$, for residents (N = 41); **b** $Y = X^{0.68} \times e^{0.95}$, $P < 0.001$, adjusted $R^2 = 0.78$, for eventual migrants (N = 72); $Y = X^{0.81} \times e^{0.49}$, $P <0.001$, adjusted $R^2 = 0.86$, for residents (N = 74); **c** $Y = X^{0.45} \times e^{1.91}$, $P < 0.001$, adjusted $R^2 = 0.49$, for eventual migrants (N = 117); $Y = X^{0.83} \times e^{1.18}$, $P < 0.001$, adjusted $R^2 = 0.76$, for residents (N = 74)

As I predicted, compared to lighter residents, lighter eventual migrants at the beginning of pre-migration periods gained more weight at the end of pre-migration periods, but such a final mass difference between the life history types diminished with an increase in initial mass of individuals (**a**, **b**). However, although panel I showed a similar pattern in that the regression slope was less steep for the eventual migrants than for the residents, the eventual migrants gained less weight than the residents. This means that the eventual migrants increased comparatively more in length than in weight, i.e., the eventual migrants became slenderer just before the migration. However, I cannot exclude the possibility that the patterns were caused by the difference in the timing of measuring final mass between life history types. Final mass of the eventual migrants was measured when the migrants were caught at the migrant trap in the river-descending season (April to mid-June 2020), while that of the residents was measured at the capture survey held in summer (25 Jun-2020 or 26 Jun-2020). Other factors such as resource availability might have caused the different growth patterns between the life history types.

Supplemental information 2-2:

Detailed information of the statistical analyses for the second prediction (i.e., smaller eventual migrants descend the river later than larger ones)

Table 2-S3 Results of the two models predicting migration timing

	Fixed factor	Coefficient	Sum of squares	F value	P value
Fork length model	FL in ES	-0.65	5073.60	24.85	<0.0001
	Habitat section	0.00	1959.30	9.60	0.0026
	Year	13.76	4606.80	22.56	<0.0001
	Intercept	115.98			
Body mass model	BM in ES	-1.58	5545.20	26.91	<0.0001
	Habitat section	0.00	1336.90	6.49	0.0124
	Year	13.71	4571.60	22.18	<0.0001
	Intercept	66.86			

Abbreviations: ES (early spring), FL (fork length), BM (body mass). Before analysis, the “year” as a categorical variable was transformed to the dummy variables (i.e., 2019 [0] and 2020 [1])

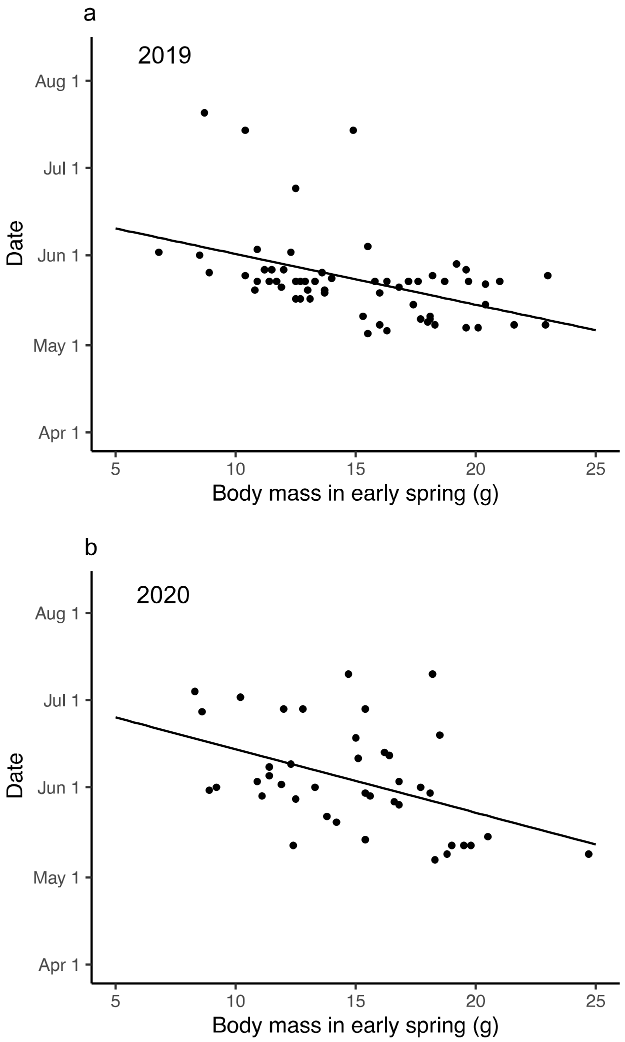

Fig. 2-S2 Relationship between the river-descending timing (date) and body mass (g) at the early spring of the eventual migrants in **a** 2019 and **b** 2020. Regression lines: **a** $Y = -1.75X + 75.93$, $P < 0.001$, adjusted $R^2 = 0.18$ ($N = 60$); **b** $Y = -2.18X + 95.99$, $P < 0.003$, adjusted $R^2 = 0.18$ ($N = 41$)

Supplemental information 2-3:
Statistical analysis of the complementary relationship between the effects of growth rate and period

Eventual migrants may not delay the start of migration to minimize the cost of delayed migration, if they grow well in winter. This hypothesis was tested in the analysis using the following model:

$$\text{River descending timing}_i \sim \text{Normal}(u_i)$$
$$u_i = \text{Intercept} + \text{Daily growth during the winter period}_i$$
$$+ \text{Fork length in previous autumn}_i + \text{Year}_i$$

Here, daily growth during the winter period was calculated as instantaneous growth rate (Lugert et al. 2016) (i.e. (ln [fork length in early spring] - ln [fork length in previous autumn]) / days between two surveys ×100).

Table 2-S4 Result of the analysis on the complementary relationship.

Fixed factor	Coefficient	Sum of squares	F value	P value
Fork length in autumn	-0.89	244.2	1.089	0.2992
Daily growth in winter period	-214.95	6153.4	27.449	<0.0001
Year	13.61	3301	14.725	0.0002
Intercept	154.11			

Before analysis, the “year” as a categorical variable was transformed to the dummy variables (i.e., autumn 2018–spring 2019 [0] and autumn 2019– spring 2020 [1])

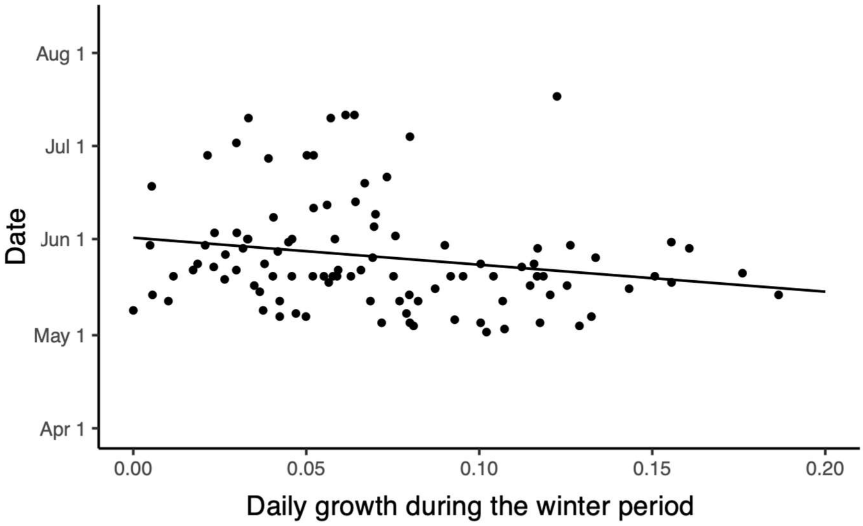

Fig. 2-S3 Relationship between the daily growth during the winter period and migration timing. Eventual migrants that grew faster in the winter period descended the river earlier. Regression line: $Y = -86.94 X + 61.43$, $P < 0.04$, adjusted $R^2 = 0.03$ ($N = 101$)

Chapter 3

Size-selective mortality occurs in smolts during a seaward migration, but not in river residents, in masu salmon (*Oncorhynchus masou*)

Abstract

Salmonid fish often experience size-selective mortality when descending the river (i.e., seaward migration). However, it is unknown whether size-selective mortality is specific to this life history (i.e., migrants), or is shared by an alternative life history (i.e., residents). In this study, I investigated the size-selective mortality patterns of masu salmon (*Oncorhynchus masou*) migrants and residents during the migration period (i.e., April to June) in the Horonai River, northern Japan. By conducting an individual-based study using PIT tags and antennas, I show that larger migrants more likely survived the seaward migration than smaller migrants, but size-dependent survival was not detected in river residents during the same period. These results suggest that size-selective mortality is specific to the river-descending migrants in masu salmon in their seaward migration period. I attribute this finding to the presence of piscivorous fishes (e.g., brown trout *Salmo trutta*) which occupy the migration corridor and consume masu salmon migrants, whereas such piscivorous fish do not occur in the river section farther upstream inhabited by residents.

Introduction

Some populations of freshwater fish species are made of residents and migrants, the latter of which move long distances to the sea in early life stages (Jonsson and Jonsson 1993, Brönmark et al. 2014). Despite apparent benefits such as rapid growth and subsequent reproductive success, migration is accompanied by various ecological and physiological costs which result in high mortality rates (Alerstam et al. 2003) . Because the vulnerability to environmental stressors (e.g., predation and starvation) is negatively correlated with body size of individuals, the mortality during the migration operates size-selectively in which smaller individuals suffer higher mortality rates than larger individuals in most cases (Sogard 1997, Brodersen et al. 2008, Tucker et al. 2016, Goatley and Bellwood 2016). This seems to be common in migratory fish, including anadromous salmonids (Sogard 1997, Alerstam et al. 2003, Chaput et al. 2019) even though the positive-size effects on survival may not be consistent across size ranges (Jonsson et al. 2016, 2017).

Anadromous salmonid fishes leave the natal freshwater habitat to attain larger body size in the resource-rich ocean. Numerous studies have documented that body size at the onset of migration (i.e., smolt size) determines survival during migration (Ward and Slaney 1988, Holtby et al. 1990, Koenings et al. 1993, Shimoda et al. 2003, Flaten et al. 2016, Gregory et al. 2018). Large proportions of mortality occur in the early phase of the migration; that is, mortality occurs in the river corridor before migrants reach the ocean (Chittenden et al. 2010, Welch et al. 2011, Melnychuk et al. 2014, Flávio et al. 2020). In particular, several studies have investigated size-dependent mortality patterns when migrants descend the river (i.e., prior to the ocean entry) (Zabel et al. 2005, Davidsen et al. 2009, Brown et al. 2013, Flávio et al. 2021). Although these studies have shown that migrants suffer high mortality rates and mortality is size-selective during the seaward migration, none have compared them to mortality of resident fish during the same period to discern whether size-selective mortality is unique to migrants or shared by river residents. Because the size-selective mortality often operates on river-dwelling juvenile salmonids (Good et al. 2001, Hurst and Conover 2003, Miyakoshi et al. 2003, Xu et al. 2010), both residents and migrants may suffer size-selective mortality.

Using a masu salmon (*Oncorhynchus masou*) population expressing migratory and resident life history forms, I investigated the magnitude of the size-selective mortality during seaward migration relative to that in resident individuals. Masu salmon is a partial migratory fish endemic to East Asia (Kato 1991, Morita 2018). I conducted two studies in the Horonai River, a small stream in Hokkaido, Japan. First, to test whether smaller migrants suffer greater mortalities than larger migrants, I investigated the relationship between individual body size and success of migrants to pass through a migration corridor downstream on their way to the sea, by using passive integrated transponder (PIT) tags and an antenna array system. Second, to examine the association between size-selective mortality and seaward migration, I investigated whether the survival of the residents in the upstream area (i.e., primary habitats for the juvenile masu salmon) depends on individual size in the same period, by conducting a capture-mark- recapture survey.

Material and Methods

Life history forms of masu salmon

Masu salmon populations harbor two life-history forms, anadromous migrants and river-dwelling residents (Kato 1991). Whereas residents stay in the river entirely, the freshwater residency of the anadromous migrants is limited to their early life stage for typically one or two years. During smoltification, the migrants descend the river between April and July (i.e., migration period) to begin oceanic migration. The migrants spend one year in the resource-rich ocean, and they consequently grow much faster and attain larger body size than river-dwelling residents. The age-2+ or age-3+ migrants then return to their natal rivers for spawning.

Study site

I conducted this study in the Horonai River, a small spring-fed stream (2–5 m wide) located in Hokkaido, Japan. The river is approximately 12.2 km long from its headwaters to the ocean, and the uppermost 5.3 km area (i.e., located between 6.9 km and 12.2 km from the river mouth, reach A in Fig. 3-1) is the primary habitat of masu salmon (i.e., both rearing and spawning habitats of residents and migrants). In reach A, a long-term fish monitoring project has been conducted so that salmonid fish including masu salmon were marked with PIT-tags. The farther downstream river habitat is distinctively different. The reach located between 4.6 and 6.9 km from the river mouth is slow-flowing (reach B in Fig 3-1) where piscivore fish species such as non-native brown trout (*Salmo trutta*) and native white-spotted charr (*Salvelinus leucomaenis*) occupy. The farthest downstream reach (4.6 km section from the river mouth) (reach C in Fig. 3-1) is located in an urbanized landscape and is highly altered with concrete revetment, which harbors few salmonids and function only as a migration corridor.

Study 1: Size-selective mortality of migrants in the seaward migration

To examine the size-selective mortality of migrants descending the river, I conducted a field survey in a 1.1 km section (hereafter called "the migrant-survey section") located in the piscivore-dominating reach B (Fig. 3-1). I investigated the success of migrants to survive and pass through the migrant-survey section from April to July 2020.

I captured migrants at the onset of their seaward migration by installing a fyke-net type trap (hereafter called the migrant trap) placed where the river narrows (50 cm wide) just below a cascade (70 cm high) at the uppermost boundary of the migrant-survey section. The survey using migrant trap was operated from 4 Apr-2020 to 24 Jul-2020 and was checked three times daily (i.e., morning [4:00], evening [16:00], night [22:00]). Trapped fish were anesthetized using eugenol (FA-100 DS Pharma Animal Health Co., Ltd.) and their fork length (precision of 1 mm) and weight (precision of 0.1 g) were measured. Additionally, I checked whether the individual fish had a PIT-tag (12.0 mm × 2.12 mm, Oregon RFID, Inc) using a PIT-tag reader. In this river, masu salmon have been tagged with PIT-tags for the long-term fish monitoring project held in the reach A. When the fish had a PIT-tag, I recorded the ID of the PIT-tag. If the fish had no PIT-tag, I inserted a PIT-tag in their abdominal cavity. I also examined morphological signs of migration (smoltification), including silver-colored body and an accumulation of black pigments along the outer edges of the dorsal and caudal fins (Quinn 2018). After these handling processes, fish were put in buckets filled with fresh river water until full recovery from anesthesia. After recovery, they were released to the pool habitat just below the trap and thus allowed to resume seaward migration. In the recovery time, 13 % of fish died. Such a relatively high mortality at the handling processes was perhaps due to relatively low resistance of migrants to stress factors since very few residents died in the other survey (ca 1–2%, Futamura, *unpublished data*). Using size data of the dead fish, I tested size-dependent handling mortality as a possible confounding mechanism (see below).

I monitored which migrants successfully passed through the lowermost boundary of reach B, using the PIT-antenna system (hereafter, PIT-antenna) installed there. A pair of PIT-antenna was installed at a location where river width spanned 330cm (19–33cm deep). In total, 261 individuals were detected at the paired antenna, among which 218 (84%) were detected at both antenna and 43 (16%) were detected only at either upper or lower antenna. The incomplete detection probably occurred because the other paired antenna failed to detect the passage of migrants with PIT-tags. Using the complete and incomplete detections, I tested size-dependent detectability as another possible confounding mechanism (see below).

Study 2: Size-selective mortality of residents

To investigate the size-selective mortality of residents, I conducted a capture-mark-recapture survey in the 5.3 km primary habitat of juvenile masu salmon in the Horonai River (reach A in Fig. 3-1; hereafter called resident-survey section). I conducted sampling three times; the first occasion (just before the seaward migration period in March 2020), second occasion (after the seaward migration period in June 2020) and third occasion (three months after the migration period in October 2020).The three survey occasions were necessary to infer the survival rate during the migration period because survival and recapture probabilities cannot be individually inferred in the last sampling interval in Cormack-Jolly-Seber (CJS) models. On all occasions, I used a backpack electrofishing unit (300–400 V DC, model 12B, Smith-Root, Inc., Vancouver, WA, USA) and 3–mm mesh dipnets (width, 30 cm) to collect fish. Captured fish were fully anesthetized by eugenol (FA-100 DS Pharma Animal Health Co., Ltd.) to measure their fork length (nearest 1 mm) and body weight (nearest 0.1 g). Because of the ongoing long-term fish monitoring project of individually tagged fish, I examined whether fish already had a PIT-tag and recorded its ID by a PIT-tag reader. All untagged fish were tagged with a PIT-tag. Fish were then allowed to recover from anesthesia in a bucket with fresh river water and were released alive to where they had been collected (10 m precision).

Statistical analysis of study 1

Logistic regression was used to investigate whether survival probability during the seaward migration depended on fork length (FL), timing of migration (date), and tagging (recap) at the onset of the migration:

$$y_i \sim \text{Bernoulli}\ (q_i)$$

$$\text{logit}(q_\text{i}) = \gamma_0 + \gamma_1 \times \text{recap[i]} + \gamma_2 \times \text{date[i]} + \gamma_3 \times \text{FL[i]}$$

The response variable was the detection at the lowermost antenna, where $y_i = 1$ if individual i was detected and 0 otherwise. Fork length was measured when individuals were captured and released at the migrant trap. Timing of migration was the number of days since 1 Apr-2020. Tagging effect was included as a binary predictor (0 = newly tagged at the migrant trap, and 1 = previously tagged during a mark-recapture survey). Timing of migration and fork length were included in the same model because they were not highly correlated with each other (Pearson's correlation: r = 0.08, p = 0.06). Prior to the analysis, fork length and timing of migration were mean-standardized and a unit change in these continuous predictors corresponded to their SD. Furthermore, I conducted an additional analysis to investigate the size-selective mortality of migrants. Specifically, I tested whether variance in body size is significantly different between migrants captured at the migrant trap and migrants detected at the PIT-antenna. Such a difference would lend additional support for the presence of size-selective mortality during migration.

I considered two alternative mechanisms that might confound interpretations of results. As the first confounding mechanism, I considered possible size-selective mortality due to handling effects (e.g., anesthesia, measurement, tagging). The smaller migrants might have suffered higher mortality rates than larger ones due to handling stresses. To examine the alternative mechanism, I used data of handling survival (i.e., 13 % of fish died in the handling process). In the analysis, I investigated whether timing of migration (date), fork length (FL) and tagging (recap) affected the survival at the handling process (handling survival) using logistic regression:

$$y_i \sim \text{Bernoulli}\ (p_{ai})$$

$$logit(p_\text{ai}) = \beta_{ao} + \beta_{a1} \times \text{date[i]} + \beta_{a2} \times \text{FL[i]} + \beta_{a3} \times \text{recap[i]}$$

The response variable was the handling survival, where $y_i = 1$ if individual i survived and 0 otherwise. Timing of migration was the number of days between 1 Apr-2020 and the day on which the individual was caught by the migrant trap. Tagging effect was included as a binary predictor (1= newly tagged at the migrant trap, and 0 = previously tagged during a mark-recapture survey). Prior to the analysis, fork length and timing of migration were mean-standardized, and a unit change in these continuous predictors corresponded to their SD.

As a second confounding mechanism, I considered the possible size-dependent detectability by the PIT-antenna. Detectability of PIT-tags might have been higher in the larger migrants than smaller ones (Saboret et al. 2021). To examine the alternative mechanism, I used data of the complete and incomplete detections by the PIT-antenna. Specifically, I investigated whether timing of migration (date), fork length (FL) and tagging (recap) affected the detection of the PIT-antenna using logistic regression:

$$y_i \sim \text{Bernoulli}\ (p_{bi})$$

$$logit(p_{bi}) = \beta_{b0} + \ \beta_{b1} \times \text{date[i]} + \beta_{b2} \times \text{FL[i]} + \beta_{b3} \times \text{recap[i]}$$

The response variable was the detection, where $y_i = 1$ if individual i was detected at both upper and lower antenna and 0 if detected at either upper or lower antenna. Timing of migration was the day on which the individual was caught by the migrant trap (the number of days between 1 Apr-2020). Tagging effect was included as a binary predictor (1= newly tagged at the migrant trap, and 0 = previously tagged during a mark-recapture survey). Prior to the analysis, fork length and timing of migration were mean-standardized, and a unit change in these continuous predictors corresponded to their SD.

Statistical analysis of study 2

Survival of residents between the first sampling occasion (i.e., March) and the second occasion (i.e., June) were inferred using the state-space approach of a Cormack-Jolly-Seber (CJS) model (Kéry and Schaub 2012). The CJS analysis was conducted to evaluate whether survival and probability of residents depended on body size between March and June to match with the migratory period. The model assumed that individual i may survive from survey t to survey t+1 with a probability equal to $\varphi_{i,t}$, which depended on fork length (FL):

$$z_{i,t+1} \mid z_{i,t} \sim Bernoulli\ (z_{i,t}\ \varphi_{i,t})$$

$$logit\ (\varphi_{i,t}) = \alpha_{\varphi} + \beta_{\varphi} \times FL_{i,t}$$

The latent state variable was binary, where $z_{i,t}$ = 1 if individual i was alive on survey t, and 0 otherwise. The latent state could be only imperfectly observed because electrofishing could not capture all individuals that were alive. Capture probability, $p_{i,t}$, was incorporated and this was assumed again to depend on fork length of individual *i* at sampling *t*:

$$y_{i,t} \mid z_{i,t} \sim Bernoulli\ (z_{i,t}\ p_{i,t})$$

$$logit\ (p_{i,t}) = \alpha_p + \beta_p \times FL_{i,t}$$

Observed data, $y_{i,t,}$, recorded the capture history, where $y_{i,t} = 1$ if individual i was captured on survey t, and 0 otherwise. Survival and capture probabilities cannot be inferred individually in the last sampling interval (i.e., July-October here) in the CJS framework (Kéry and Schaub 2012).

Model fitting

The logistic regression (study 1) and CJS analyses (study 2) were conducted in the Bayesian framework using a Markov Chain Monte Carlo (MCMC) method in Program JAGS (Plummer 2017) called from R (R Core Team 2021) with the *jagsUI* package. Uninformative priors were used for all parameter estimates. Posterior samples of the parameters were obtained by taking every 5th sample from 5,000 iterations of three chains after discarding 3,000 iterations as a burn-in period. Model convergence was checked by confirming that the R-hat statistic was less than 1.1 for all the parameters (Gelman and Hill 2006). Effects of predictors on survival during the seaward migration and in river residency were considered statistically significant when their 95% credible intervals (CI) did not overlap zero. I calculated odds ratios by exponentiating posterior mean effect sizes of continuous predictors and interpreted them as a change in odds of survival and capture with a 1 SD change in the predictors due to the mean standardization of the continuous predictors.

Result

Study 1: Size-selective mortality of migrants in the seaward migration

In the migrant trap at the uppermost boundary of the migrant-survey section in reach B, I captured a total of 578 fish, among which 179 had PIT-tags already (1%, 19% and 11% individuals were tagged in spring 2019, autumn 2019 and spring 2020, respectively), 399 were tagged anew, and 77 died in the handling processes (71% of fish that died were newly tagged). Thus, 501 fish were used for survival analysis of migrants during the seaward migration. All of these fish expressed external morphological characteristics of migrants (i.e., smolts). The PIT-antenna system at the lowermost boundary of the migrant-survey section detected 261 (see summary in Fig. 3-S1).

Survival probability of migrants depended on body size during the seaward migration (Fig. 3-2 (a)) (Table 3-1). The mean effect of body size on survival (γ_3) was 0.37 (95% CI: 0.18–0.57) and the odds ratio was 1.45, indicating that fish were 1.45 times more likely to survive as fork length increased by 10 mm (1 SD). The tagging also affected the survival of the migrants. The mean tagging effect on survival (γ_1) was 0.55 (95% CI: 0.16–0.95). This result indicated that survival of the migrants previously tagged during a mark-recapture survey was higher than migrants newly tagged at the migrant trap. Date of migration also affected the survival. The mean date effect on survival (γ_2) was -0.21 (95% CI: -0.4 and -0.02), indicating that the survival of the earlier migrants was higher. The posterior mean survival probability was 0.48 (95% CI: 0.43–0.53).

The fork length (mean ± 1SD) of the migrants captured at the migrant trap and those that successfully passed through the migrant-survey section was 132.5 ± 9.9 mm (n = 501) and 133.9 ± 8.1 mm (n = 261), respectively. The variance of the fork length significantly differed between them (i.e., test for equality of variance, $F_{260, 500} = 1.38$, p = 0.004), providing yet another evidence of size-selective mortality.

The analyses for the confounding factors indicated that the two alternative mechanisms causing an apparent pattern of size-selective mortality were unlikely to operate (Fig. 3-S3, 2-S4). The mean fork length effect on handling survival (β_{a2}) was -0.22 and its 95% CI ranged -0.49 and 0.04 (i.e., details of statistical results were in Table 2-S1), suggesting that larger migrants were more likely to die than smaller migrants, even though the size effect was marginal (Fig. 3-S3). The effect of the mean fork length on detection (β_{b2}) was -0.29 but its 95% CI ranged -0.65 and 0.06 (i.e., details of statistical result were in Table 3-S2). It indicates that smaller migrants were more likely to be detected by the PIT-antenna than larger migrants, even though the size effect was marginal again (Fig. 3-S4).

Study 2: Do size-selective mortality operate for residents

In the first survey, I captured (newly tagged or recaptured) 1512 fish and released 1498 fish (i.e., 14 individuals died in the measurement [handling mortality rate was 1%]). Among the released 1498 fish with PIT-tags, 143 were trapped by the migrant trap in the first study and, hence, they were identified as migrants descending the river in the seaward migration period. Furthermore, I excluded 509 fish from the analyses because they were outside the body size range of migrants (FL: 95–164 mm) (i.e., larger or smaller than migrants in the first survey). Among the remaining 846 fish, 201 were recaptured in the second capture survey. These 201 fish were identified as residents because they remained in the river after the migration period. Consequently, the remaining 645 fish belonged to one of the following three groups: (1) residents that died in the interval between the first and second occasions; (2) residents that were not recaptured but alive; (3) the prospective migrants that died in the interval between the first and second surveys (i.e., the prospective migrants failed to reach the migrant trap placed at the downstream area). Because the 645 unrecaptured fish included residents that died in the survey interval (i.e., category (1)), I can test the size-selective mortality of residents by examining whether survival rate in the migration period (i.e., period between first and second survey) depends on size at the first survey. The detailed information of the categorization of fish was summarized in Fig. 3-S2.

In contrast to migrants, survival probability of residents in resident-survey section (i.e., reach A) did not depend on body size between March and July (Fig. 3-2 (b)) (Table 3-2). The mean effect of body size on survival ($\beta_{\varphi1}$) was 0.14, but its 95% CI ranged -0.02 and 0.30, and overlapped zero. The posterior mean survival probability ($\alpha_{\varphi1}$) was 0.37 (95% CI: 0.32–0.42).

Capture probability of residents in July increased significantly with body size (Table 3-2). The mean body size effect on capture (β_{p1}) was 0.28 (95% CI: 0.03–0.56), and an odds ratio suggested that fish were 1.32 times more likely to be captured by electrofishing as fork length increased by 15 mm (1 SD). The posterior mean capture probability (α_{p1}) was 0.64 (95% CI: 0.55–0.72).

Discussion

I investigated whether masu salmon migrants suffered size-selective mortality in the seaward migration period. In the first study, I found that smaller migrants experienced higher mortality rates than larger migrants *en route* to the sea (Fig. 3-2 (a)). The size-selective mortality was unlikely to be caused by the handling effects such as anesthesia, measurement, and insertion of PIT-tag, because the survival of larger migrants in the handling process tended to be lower than the smaller ones (Fig 3-S3). In addition, size-dependent detectability of PIT-tags was excluded as a confounding factor, because detection probability of larger migrants was marginally lower than that of smaller migrants (Fig. 3-S4). These suggest that natural mortality factors strongly selected out small migrants in their seaward migration. Although previous studies on other salmonids have documented size-selective mortality of migrants during the seaward migration (Davidsen et al. 2009, Brown et al. 2013, Thompson and Beauchamp 2014, Flávio et al. 2021), it remains unknown whether seaward migration is the particular life history event in which the size-selective factor operate. In the second study, I showed that size-selective mortality did not operate on the residents during the seaward migration period, suggesting size-selective pressure operates only on migrants that pass through the predator rich migration corridor before seaward migration (Fig. 3-2 (b)). Thus, my study provides the first comparative evidence that selection acts on body size differently between life history forms in the same river.

The contrasting pattern of size-selective mortality between migrants and residents is perhaps due to differences in the strength of mortality pressure between the life history types. In general, smaller individuals are more vulnerable to various mortality factors than larger individuals (Werner and Gilliam 1984, Garvey et al. 2004). The size-selective mortality is likely to emerge in a habitat dominated by large predators (Kishida et al. 2011, Takatsu and Kishida 2015, Hasegawa et al. 2021). In fact, as commonly seen in many river systems, the downstream area of the Horonai River, including the migrant-survey section, is inhabited by various large piscivores such as non-native brown trout (*Salmo trutta*) and native white-spotted charr (*Salvelinus leucomaenis*). In contrast, these piscivores are not common in the upstream area (i.e., reach A) (Futamura et al., *personal observation*). These piscivores might have consumed smaller migrants more frequently. Especially, predation by the brown trout can be severe. Brown trout is the most abundant fish in the slow-flowing reach of the downstream area (i.e., reach B) and attain large size (i.e., maximum 70 cm in fork length) (Jensen et al. 2008). My preliminary observations showed that brown trout accounts for 68% of the fish community and large individuals (> 40 cm in fork length) are commonly present in the slow-flowing reach (Futamura and Furusawa, *personal communication*). Actually, I found a consumed masu salmon migrant from the gut contents of a brown trout individual with typical size (FL: 297 mm) in the seaward migration period (Fig. 3-3).

Masu salmon migrants might avoid the size-selective mortality in the seaward migration by size-dependent growth mechanisms in the pre-migration period. Juvenile masu salmon make ‘decisions’ to migrate or not by autumn (Nagae et al. 1994). After the decisions, the prospective migrants stay in the river until the next spring when migration occurs (i.e., May to July). In my latest study, I found that smaller prospective migrants exhibited higher growth rates in the pre-migration period (i.e., growth rate between the previous autumn to spring) than larger ones (Chapter 2) (Futamura et al. 2022b). Interestingly, residents did not show such a size-dependent growth pattern in the same period. Furthermore, I also found that smaller migrants delayed the migration timing to catch up with growth and attain larger body size(Chapter 2) (Futamura et al. 2022b). This size-dependent growth pattern in the prospective migrants can be interpreted as adaptive tactics to increase survival of the migrants under the size-selective mortality pressures in the seaward migration as well as in the ocean.

An alternative mechanism of masu salmon migrants to survive the size-selective mortality in the seaward migration have been hypothesized. For example, masu salmon migrants are known to descend rivers in schools (Munakata 2012). In salmonids, this schooling is known as an adaptive behavior to increase survival under strong predation pressure in the risky seaward migration (Furey et al. 2016). In fact, in the seaward migration period, I sometimes observed fish schools formed by several masu salmon migrants in the downstream area of the Horonai River where piscivores such as brown trout dominated (Futamura et al., *personal observation*). If the piscivores are major factors of the size-selective mortality, the masu salmon migrants may exhibit size-dependent schooling behavior in their seaward migration. That is, smaller migrants are expected to form larger school sizes. Such a behavioral hypothesis warrants further investigations.

In summary, I found size-selective mortality in masu salmon migrants during the seaward migration in a natural river. Future studies should elucidate the mechanisms underlying the size-selective mortality and investigate the prevalence of the size-selective mortality across geographic populations of masu salmon. Such studies will provide significant insights into geographic variation of life history strategies in masu salmon.

Table 3-1 Summary of the parameters of the model predicting survival of masu salmon migrants. The mean survival (γ_0) is shown in probability scale (i.e., non-logit scale), whereas other factors are shown in logit scale.

	Mean	SD	2.5% quantile	50% quantile	97.5% quantile	Odds ratio
Mean survival (γ_0)	0.48	0.03	0.43	0.48	0.53	NA
Recapture (γ_1)	0.55	0.21	0.16	0.55	0.95	1.73
Release date (γ_2)	-0.21	0.1	-0.4	-0.21	-0.02	0.81
Fork length (γ_3)	0.37	0.1	0.18	0.37	0.57	1.45

Table 3-2 Summary of the parameters of survival of masu salmon residents. The mean survival ($\alpha_{\varphi 1}$) and mean recapture (α_{p1}) are shown in probability scale (i.e., non-logit scale), whereas other factors are shown in logit scale.

	Mean	SD	2.5% quantile	50% quantile	97.5% quantile	Odds ratio
Mean survival ($\alpha_{\varphi 1}$)	0.37	0.03	0.32	0.37	0.42	NA
Fork length effect on survival ($\beta_{\varphi 1}$)	0.14	0.08	-0.02	0.14	0.3	1.15
Mean recapture (α_{p1})	0.64	0.04	0.55	0.64	0.72	NA
Fork length effect on recapture (β_{p1})	0.28	0.14	0.03	0.28	0.56	1.32

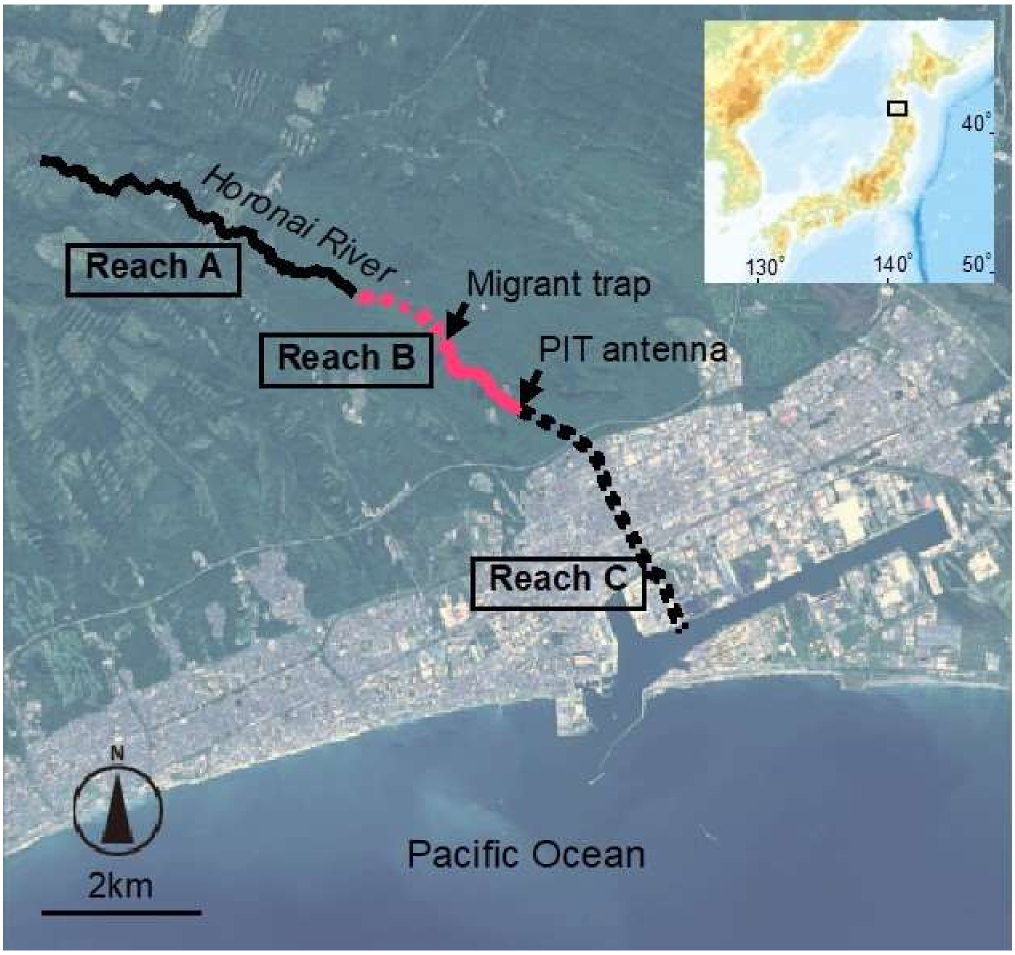

Fig. 3-1 Map of the Horonai River, 12 km long. The reach located between 6.9 km and 12.2 km from the river mouth (reach A: solid black line) is the primary habitat of masu salmon (i.e., habitat of residents and prospective migrants), where the *study 2* (i.e., resident-survey) was conducted. River habitat farther downstream is distinctively different. The reach located between 4.6 and 6.9 km from the river mouth is slow-flowing (reach B: solid and broken red line) where large piscivorous fish species occupy and the *study 1* (i.e., migrant-survey) was conducted. The river habitat farthest downstream (reach C: 4.6 km section from the river mouth) located in an urbanized landscape (broken black line). This map is based on the digital map published by the Geospatial Information Authority of Japan.

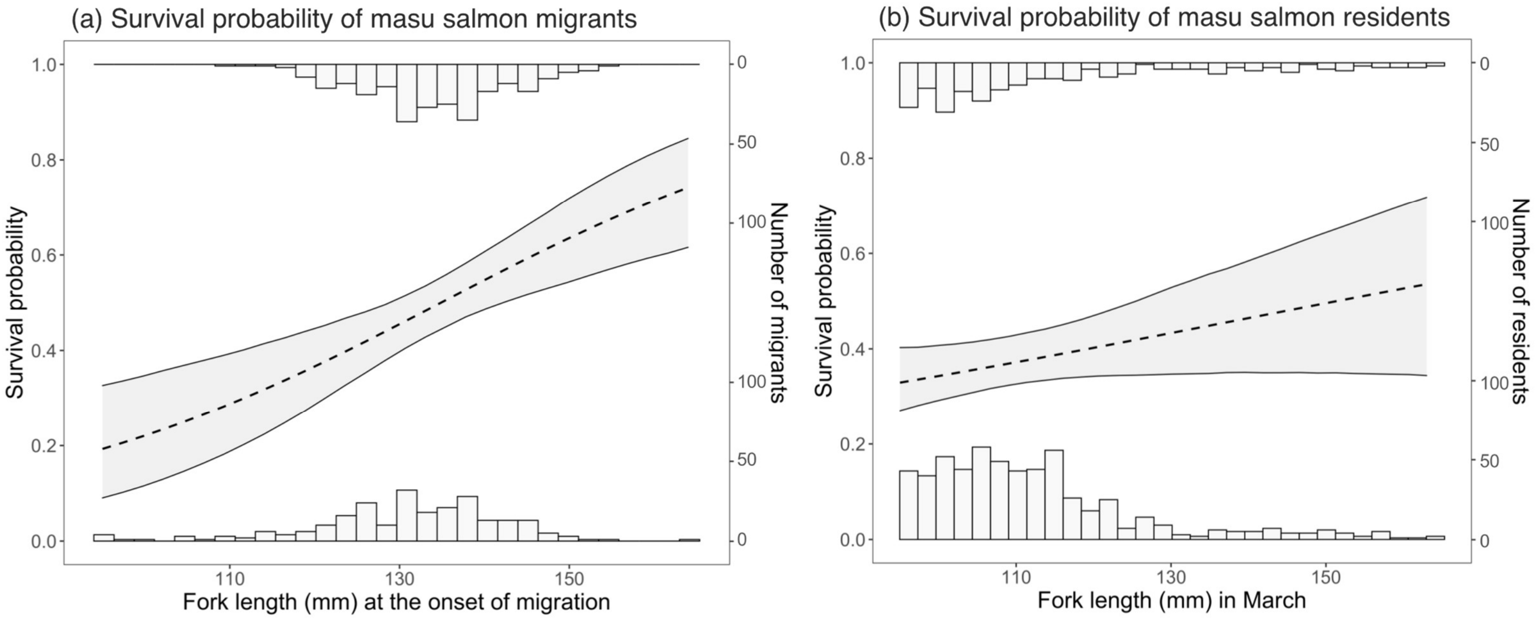

Fig. 3-2 Survival probability of masu salmon migrants and residents across the range of fork length. (a) Survival probability of masu salmon migrants in the passage through the migrant-survey section. The histograms show the number of individuals released below the migrant trap: the migrants successfully passed the PIT-antenna (y=1) and otherwise (y=0). Dotted lines indicate posterior mean responses and solid lines bound 95% credible intervals. (b) Survival probability of masu salmon residents from March to June across the range of fork lengths of migrants in March. Dotted lines indicate posterior mean responses and solid lines bound 95% credible intervals. The histograms show the number of individuals that were alive after the migration season (y=1) and otherwise (y=0).

Fig. 3-3 A brown trout and a consumed masu salmon migrant. The masu salmon migrant (Fork length [FL]:134mm) was found in the gut contents of this brown trout (FL: 297mm) caught in the migrant trap on 27 Apr-2020

Supplemental information 3-1: Details of the number of individuals.

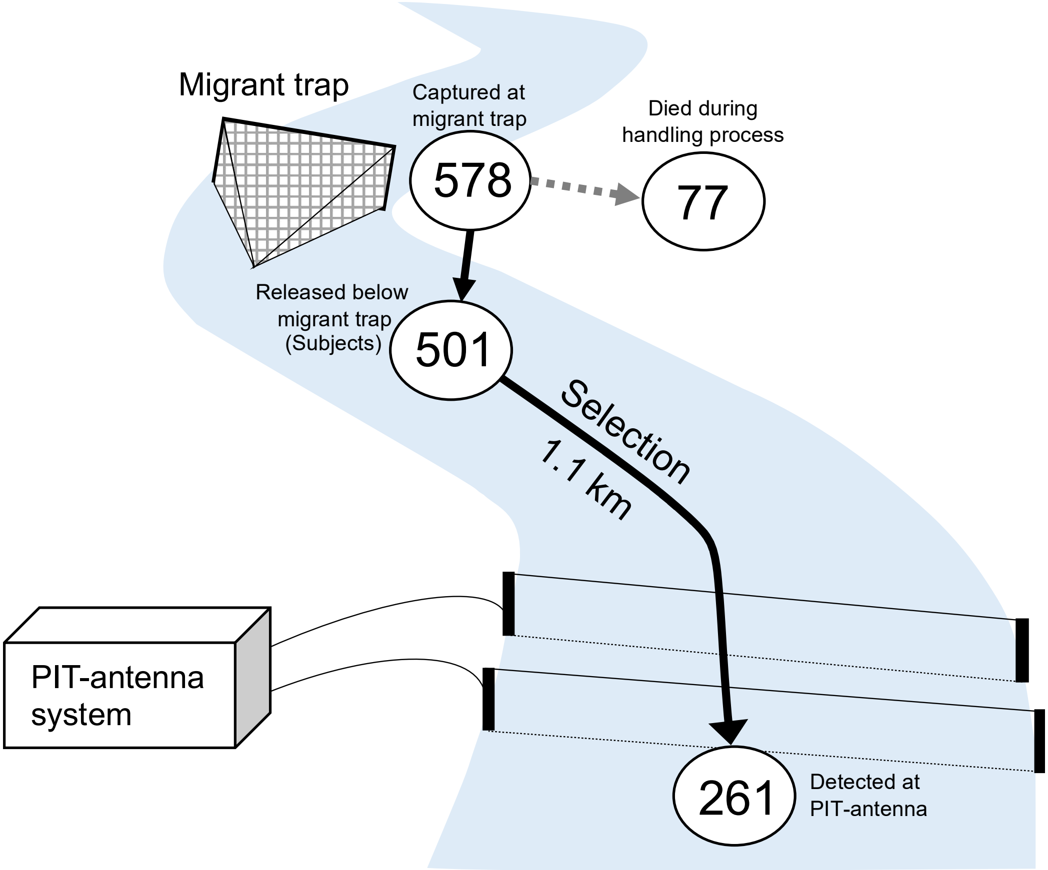

Fig. 3-S1 Categorization of fish in the *study 1*. At the migrant survey, 578 were caught (i.e., 173 were recaptured), among which 77 died. Thus, released 501 migrants were the focal subjects that experienced the possible selection in the 1.1 km section. As a result, 261 were detected at the downstream PIT-antenna (i.e., passing the survey section alive).

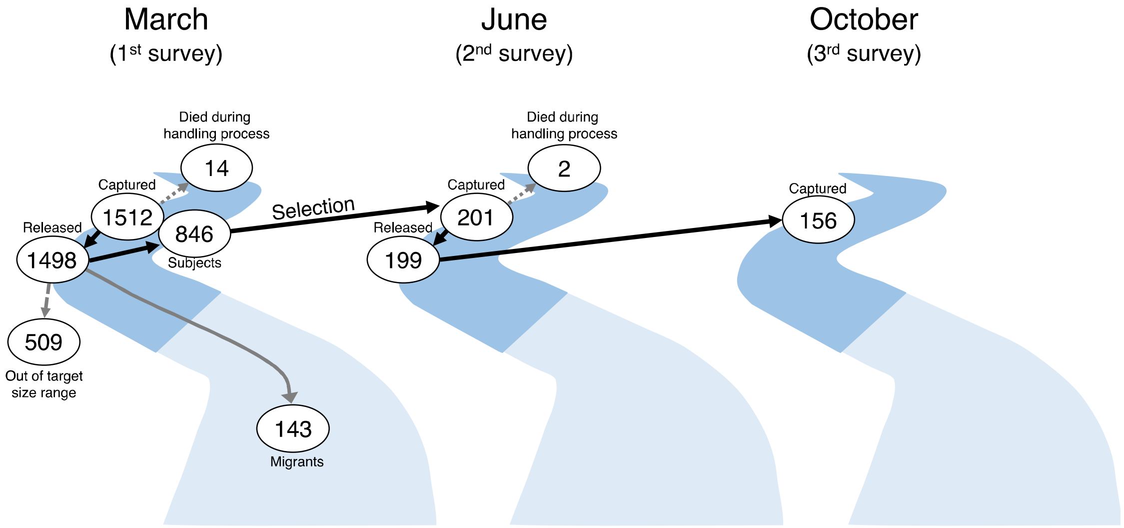

Fig. 3-S2 Categorization of fish in the *study 2.* At the spring survey I caught (recaptured or newly tagged) 1512 fish, among which 14 died. Among the released 1498 fish, 143 were excluded from the analysis as migrants because they were caught in the migrant survey. I excluded 509 fish that were out of the size range of migrants (i.e., larger or smaller than migrants captured at the migrant trap) from the analysis. Thus, the left 846 individuals were focal subjects (i.e., 1498-143-509 = 846). Among these individuals, 201 were recaptured at the June survey (2 died), and 156 were recaptured October survey.

Supplemental information 3-2: **Analyses of the possible confounding factors.**

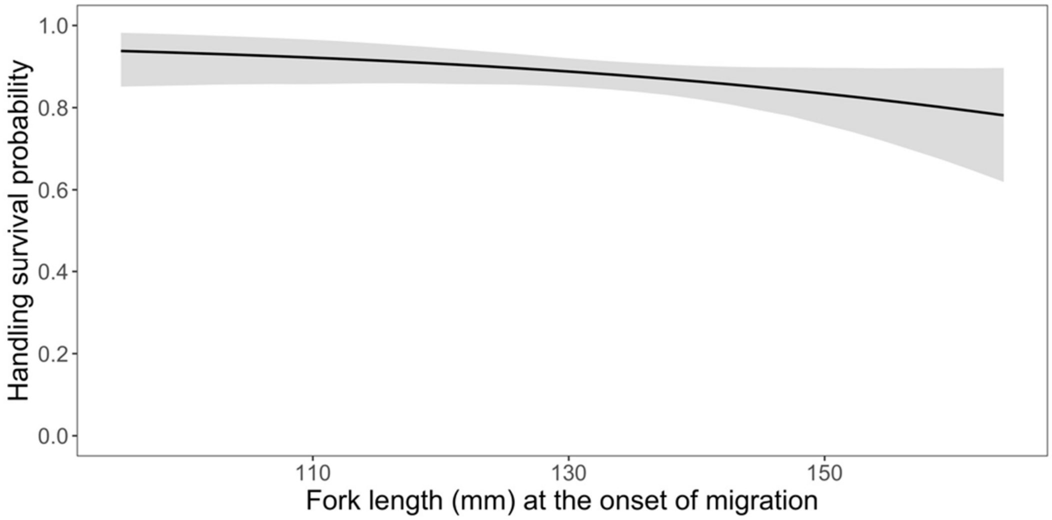

Fig. 3-S3 Probability of survival after handling against fork length. Solid lines are posterior mean responses and grey shades are 95% credible intervals. The survival probability of larger migrants in the handling process tended to be lower than the smaller ones, even though the size effect was marginal.

Table 3-S1 Summary of the parameters of the handling survival. The mean handling survival (β_{a0}) is shown in probability scale (i.e., non-logit scale), whereas other factors are shown in logit scale.

	Mean	SD	2.5% quantile	50% quantile	97.5% quantile	Odds ratio
Mean survival (β_{a0})	0.88	0.02	0.85	0.88	0.91	NA
Release date (β_{a1})	-0.82	0.16	-1.13	-0.81	-0.52	0.59
Fork length (β_{a2})	-0.22	0.14	-0.49	-0.22	0.04	1.04
Recapture (β_{a3})	0.35	0.29	-0.2	0.34	0.92	2.51

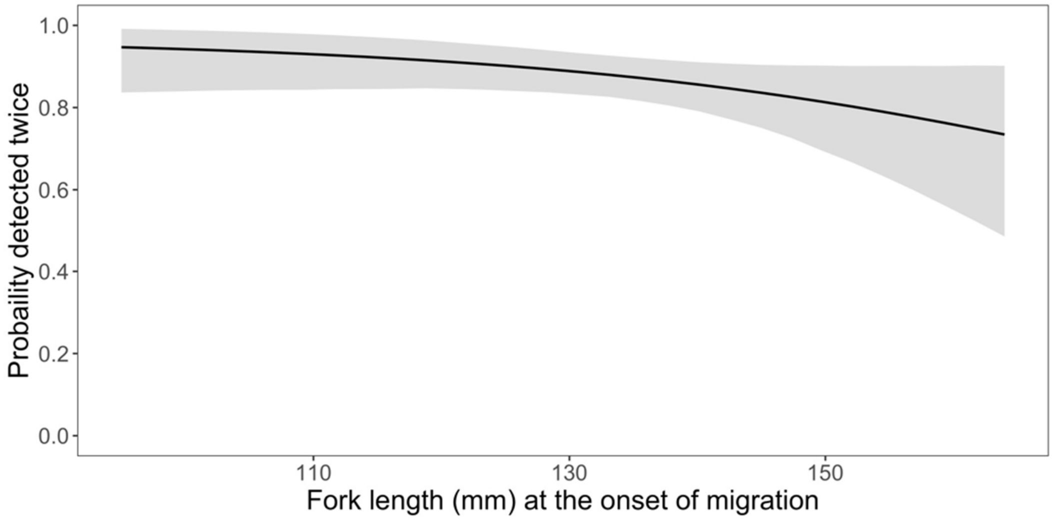

Fig. 3-S4 Probability of fish detected twice at the paired PIT-antenna against fork length. Solid lines are posterior mean responses and grey shades are 95% credible intervals. The detection probability of larger migrants was marginally lower than that of smaller migrants.

Table 3-S2 Summary of the parameters of the PIT-antenna detectability. The mean detectability (β_{b0}) is shown in probability scale (i.e., non-logit scale), whereas other factors are shown in logit scale.

	Mean	SD	2.5% quantile	50% quantile	97.5% quantile	Odds ratio
Mean detectability (β_{b0})	0.88	0.03	0.83	0.88	0.93	NA
Release date (β_{b1})	0.96	0.19	0.61	0.96	1.35	2.61
Fork length (β_{b2})	-0.29	0.18	-0.65	-0.29	0.06	0.75
Recapture (β_{b3})	-0.28	0.4	-1.06	-0.28	0.51	0.76

PIT-antenna detectability was marginally lower for larger individuals. This result might be of the size-dependent swimming speed of migrant.

Chapter 4

Predation-caused wounds of masu salmon (*Oncorhynchus masou*) migrants reveal costs of attaining larger size before migration

Abstract

Since smaller migrants suffer higher mortality en route to their destination, migrants are predicted to adopt adaptive growth tactics to attain large size before migration. The size-dependent growth patterns represent such a case, in which smaller migrants exhibit rapid growth and delayed start of migration (extended pre-migration period) to attain large body size. To confirm the adaptiveness of these size-dependent growth patterns, it is crucial to explore the costs associated with rapid growth and delayed migration start, since the adaptiveness of the size-dependent growth patterns cannot be solely explained by ecological demands of rapid growth and late migration start. However, the potential costs remain largely unknown. Here, I focused on the trade-off between growth and survival, and investigated whether faster pre-migration growth rate and longer pre-migration period incurs higher predation risk in masu salmon (*Oncorhynchus masou*) which exhibit the size-dependent growth patterns. In the capture-mark-recapture survey examining predation-caused wound as a proxy for predation risk, I found a non-significant effects of growth rate but significant positive effects of timing of migration start on the occurrence of predation-caused wounds. In particular, the migrants that stayed longer in the river had higher probability of having predation-caused wounds, especially inflicted by piscivorous birds. This result suggests that size-dependent departure to oceanic migration in masu salmon is an adaptive tactic that has been shaped and maintained at least partly by the trade-off between growth and survival in the pre-migration period.

Introduction

Many animals migrate to complete their life cycle (Dingle and Drake 2007, Alerstam and Bäckman 2018). Although migratory animals benefit substantially from migration, they suffer high mortality during migration (Alerstam et al. 2003). Notably, smaller migratory individuals (migrants) suffer higher mortality during such a risky migration trip (Sogard 1997, Alerstam et al. 2003, Oppel et al. 2015, Tucker et al. 2016, Gregory et al. 2019, Simmons et al. 2022). Thus, attaining large size before migration is critical for successful migration (Roff 1991). This suggests that migrants should adopt adaptive growth tactics to attain sufficiently large size (i.e., size threshold) at the onset of migration (Arendt 1997).

Indeed, previous research has documented potential adaptive growth tactics just prior to migration. For instance, smaller migrants exhibited higher growth rates and a delayed start to migration (i.e., an extended pre-migration period) compared to their larger counterparts (Nicieza and Brana 1993, Bohlin et al. 1996, Dermond et al. 2019, Futamura et al. 2022b). This combination of higher growth rates and extended pre-migration periods allow smaller migrants to achieve a greater size increment during the pre-migration period, enabling them to surpass the size threshold at the onset of migration. Given that smaller migrants face stronger ecological demands than larger ones, these size-dependent growth patterns can be interpreted as adaptive life history tactics. However, it's important to note that the adaptiveness of this growth pattern cannot be solely explained by the size-dependent ecological demands of growth placed on smaller migrants. If a faster growth and longer pre-migration period do not incur any costs, maximizing size increment before migration should be adaptive for migrants, regardless of body size. Therefore, to affirm the adaptive significance of the size-dependent growth pattern, it's necessary to uncover the costs associated with faster growth and longer pre-migration period of migrants. However, these potential costs remain largely unexplored. In this study, I addressed this issue by focusing on the trade-off between growth and survival (Stearns 1989).

The trade-off between growth and survival is characterized by a positive correlation between size increment and mortality, where individuals who achieve a larger size increment are subject to a higher risk of mortality (Stearns 1989, 1992, Mangel and Stamps 2001). This growth-survival trade-off has been documented in previous studies that have explored both the genetic and plastic variation in growth rates among individuals (Anholt and Werner 1995, Gotthard 2000, Munch and Conover 2003, Biro et al. 2004). One well-known cause of this trade-off is the increased predation risk that comes with behaviors that enable individuals to achieve a larger size increment (Houston et al. 1993, Dmitriew and Rowe 2005). To achieve larger size increment, individuals need to either increase their foraging activity or extend their foraging time (Werner and Anholt 1993, Damsgird and Dill 1998, Willette 2001), but these behaviors likely increase the likelihood of encountering predators (Lima and Dill 1990, Brown and Kotler 2004, Verdolin 2006). In this study, I sought to confirm whether the same processes operate during the pre-migration period of migrants. I examined whether migrants with a higher growth rate and longer growth period are subjected to a higher predation risk before migration. This was done by investigating the wounds caused by predator attacks on masu salmon (*Oncorhynchus masou*) migrants.

Masu salmon, endemic to East Asia, commonly exhibit partial migration, with populations consisting of both anadromous migrants and river-dwelling residents (Kato 1991). Residents remain in their natal river throughout their lives (Nakano 1995b, Sakata et al. 2005). In contrast, migrants spend the first 1-2 years in the nursery habitat of the river and descend the river in spring (i.e., between April and July) to begin oceanic migration (Kato 1991). After spending a year in the resource-rich but high-risk ocean, migrants return to their natal river to spawn (Morita 2018). Migrants, particularly smaller ones, face the size-selective mortality in the migration area, which includes the lowermost reaches of the river and the ocean (Miyakoshi et al. 2001, Miyakoshi 2006, Futamura et al. 2022a). Notably, I found size-dependent growth patterns among masu salmon migrants before migration, which can be interpreted as an adaptive tactic to avoid size-selective mortality during migration: smaller migrants exhibit higher growth rates for half a year before they start oceanic migration and descend the river later than larger ones (Futamura et al. 2022b). Here, I hypothesized that when smaller migrants exhibit higher growth rate and longer pre-migration period, they are subjected to predation pressure. This is likely to be true when descending the transitional habitats of the river, which ranges from the middle reaches to the lower reaches, where larger piscivorous fish and birds are more abundant than in the nursery habitat (i.e., upper reach). Thus, if migrants forage more actively and stay longer in the transitional habitat, they can face increased predation risk. Therefore, I made the following two predictions. First, masu salmon migrants that exhibit higher growth rates just before oceanic migration (i.e., period between early spring and start of oceanic migration) are subjected to higher predation risk. Second, masu salmon migrants that onset oceanic migration later are subjected to higher predation risk. To test these predictions, I conducted a capture-mark-recapture survey on masu salmon migrants in the pre-migration period and examined the presence of the wound due to predator attacks (i.e., hereafter called predation-caused wound) as a proxy for predation risk (Fig. 4-1) (Reimchen 1988, 1992, Davies et al. 1995, Polyakov et al. 2022).

Material and Methods

Study system

My study was conducted in a 12.2 km long spring-fed stream, Horonai River (42°40′N, 141°35′E) located in Hokkaido, northern Japan (Fig. 4-2). This river is composed of three distinct reaches. The uppermost 5.3 km reach (6.9–12.2 km from the river mouth) is characterized with natural riverbank and secondary deciduous forest. The uppermost reach is the primary habitat of masu salmon residents and migrants before descending the river. In this reach, masu salmon have been marked with a PIT-tag (12.0 mm × 2.12 mm, Oregon RFID, Inc) for an ongoing fish monitoring project since 2018. The middle river reach (4.6–6.9 km from the river mouth) is slow-flowing, which includes the artificial impoundments and wetland area of total 1.0 ha and a maximum depth of 2.5 m. This reach is utilized as a transitional habitat by masu salmon. In the middle reach, piscivorous fish brown trout (*Salmo trutta*) account for the 70 % of the fish (Futamura et al. *unpublished data*) and water birds such as Great Egret (*Ardea alba*) and Common Merganser (*Mergus merganser*) are often observed (Futamura et al. *personal observation*). Since this reach largely consists of artificial impoundments and wetland area, it seems favorable for piscivorous birds, which mainly forage in wetlands where tree overhung is sparce (Tojo 1996). The lowermost reach (the lowermost 4.6 km section from the river mouth) flows through the urbanized landscape of Tomakomai

City, which harbors only few salmonids and function as a transitional habitat of masu salmon.

Capture-mark recapture survey on migrants before river-descending.

I conducted a capture-mark-recapture survey in the uppermost reach in spring 2020 (18–26 Mar-2020). I collected masu salmon using a backpack electrofishing unit (300–400 V DC, model 12B, Smith-Root, Inc., Vancouver, WA, USA) with 3 mm mesh dipnets (30 cm wide). Fish were anesthetized by diluted eugenol (FA-100 DS Pharma Animal Health Co., Ltd.) to measure their fork length (FL) (nearest 1 mm) and body mass (nearest 0.1 g) and to check for bodily wounds (see later). I also examined whether fish had been previously identified by a PIT tag using a handy PIT-tag reader. Individuals without the PIT tag > 60 mm were tagged in this survey. The tag was inserted into the abdominal cavity through a small incision made with a clean scalpel. Fish were then allowed to recover from anesthesia and were released within 10 m of original capture. The number of masu salmon captured and identified by PIT tag was 1495 and individuals having predation-caused wounds was not found at this occasion.

Capture survey on the river-descending migrants

I conducted a migrant trap survey in the middle reach of Horonai River to capture the migrants at the onset of oceanic migration by installing a fyke-net type trap at the middle reach (5.7 km from the river mouth) from 04 Apr to 24 Jul, 2020 (Fig. 4-2). Captured fish were anesthetized using eugenol (FA-100 DS Pharma Animal Health Co., Ltd.), then measured for fork length (nearest 1 mm) and weight (nearest 0.1 g). After measurement, I checked the visual signs of smoltification (i.e., morphological signs of migration) and then took a photograph. A waterproof digital camera (TG-5, Olympus Co., Tokyo, Japan) was used to take the photographs to check for predation wounds. Then, fish were held in a bucket filled with fresh river water to allow recovery from anesthesia and were released to the pool habitat just below the trap. Detailed information on migrant trap survey is described in Futamura et al. (2022b).

Using the photographs taken in the migrant trap survey, I examined whether migrant had wounds inflicted by the predators (predation-caused wound) and wound not inflicted by predators (handling wound). Three categories of predation-caused wounds were identified based on their characteristics. First, the bill-shaped scar inflicted from either the ventral or dorsal side was identified as a bill-shaped predation-caused wound (Fig. 4-1a) (Reimchen 1988, Davies et al. 1995, Kortan et al. 2008). Bill-shaped predation-caused wound is inflicted by avian predators that attack the fish by their sharp bill. Second, several scars inflicted from the same direction on the fish's body was identified as tooth-shape predation-caused wound (Fig. 4-1b) (Reimchen 1988, 1991, 1992). Tooth-shaped wound is inflicted by the attack of piscivorous fish with a sharp tooth. Third, scar that is stripped over a certain direction, but undefinable to determine whether it is inflicted by either bill or tooth was identified as non-identified predation-caused wound. If migrant had either of the predation-caused wound, I defined that migrant had a predation-caused wound. Other wounds, such as large areas of missing scales or single linear scar, were classified as handling wounds (Fig. 4-1c). These are presumably inflicted during handling processes (i.e., capturing the fish by migrant trap and measurement).

The identification of the wound type based on the scar characteristics is difficult because scar patterns are sometimes unclear. This raises the concern that my categorization of the wound type might be incorrect. However, this concern is not justified, as the occurrence patterns of handling wounds and predation-caused wound were inconsistent. Although I observed a positive relationship between the timing of migration start and the occurrence of predation-caused wounds (see Result), the relationship between migration timing and the occurrence of handling wounds was negative (Fig. 4-S1) (Table. 4-S2) (see Online Resource 4-1 for detail).

Definition of growth rate and pre-migration period

To test whether higher growth rate before migration and longer pre-migration period incurs increased predation risk, I first defined growth rate before migration and pre-migration period using the data obtained from the capture-mark-recapture survey in early spring and migrant trap survey. As a metric of growth rate, I used relative growth rate adjusted for body size, because growth rate and predation effects highly depend on body size (Lugert et al. 2016). Relative growth rate was calculated from the residuals of the following linear model: $\ln(FL_{\text{migration}}) \sim \ln(FL_{\text{early spring}}) + \Delta t$, in which $FL_{\text{migration}}$ is the size at the migrant trap survey, $FL_{\text{early spring}}$ is the size at early spring capture-mark-recapture survey and Δt as elapsed date between two surveys. As a metric of the pre-migration period, I used the capture date at the migrant trap survey, which serves as an endpoint of the pre-migration period.

Statistical analysis

To assess the effects of relative growth rate and pre-migration period on the occurrence of predation-caused wounds, I conducted my analysis in two procedures. First, I assessed the association between these variables and occurrence of predation-caused wounds regardless of their cause (i.e., bill-shaped, tooth-shaped, or not-identified). Then, I investigated the association between these variables and occurrence of each type of predation-caused wounds (bill-shaped and tooth-shaped). The effect of relative growth rate and pre-migration period on predation-caused wounds were analyzed in separate models because of the sample size disparities (i.e., sample size for growth rate analysis is $n = 119$, sample size for pre-migration period analysis is $n = 578$). This method is relevant because growth period and relative growth rate did not exhibit significant correlation (Pearson's r correlation, $r = -0.03$, $P = 0.780$). For the growth rate analysis, generalized linear model (GLM) with a binominal distribution and logit-link function (i.e., logistic regression) was employed to examine whether the occurrence of the predation-caused wound at the onset of migration was determined by relative growth rate in spring. Similarly, logistic regression was employed to examine whether the occurrence of the predation-caused wound at the migrant trap was affected by the pre-migration period and fork length at migrant trap. Because the interaction term pre-migration period × fork length did not improve the models in preliminary analyses, the interaction terms were not considered. Overall, I used six models on the analysis on the predation-caused wound (i.e., three injury status [predation-caused wound regardless of cause, bill-shaped, and tooth-shaped] × two growth mechanisms [growth rate and pre-migration growth period]). In all models, the significance of the independent variables was evaluated by likelihood ratio test which was performed by using the maximum likelihood method. All statistical analysis was performed using R ver. 4.3.1.

Result

A total of 578 masu salmon migrants were captured in migrant trap survey from 14-Apr to 16-Jun 2020. Among these, 51 had a bill-shaped wound, 24 had a tooth-shaped wound, 31 had a non-identified predation-caused wound, 186 had a handling wound, 1 had both bill-shaped predatory and handling wounds, 4 had both bill-shaped predatory and tooth-shaped predation-caused wounds, and 281 had no wound (unscathed) (Table 4-S1). These 578 individuals were subjected to the analysis on the pre-migration growth period. Of migrants captured in the migrant trap survey, 119 had been recaptured (previously captured in early spring capture-mark-recapture survey). The categorization of the recaptured 119 migrants is as follows: 10 had a bill-shaped wound, 2 had a tooth-shaped wound, 7 had a non-identified predation-caused wound, 32 had a handling wound, 1 had both bill-shaped predatory and handling wounds, and 67 had no wound (Table 4-S1). These 119 individuals were used for the analysis of the relative growth rate.

The occurrence of migrants with predation-caused wound, regardless of its cause, tends to increase with the relative growth rate, but was not significant (χ^2 = 2.07, *P* = 0.150) (Table 4-1) (Fig. 4-3a). The occurrence of migrants with neither bill-shaped predatory nor tooth-shaped predation-caused wounds were significantly related to the relative growth rate in spring (bill-shaped predation-caused wound: χ^2 = 0.30, P = 0.586; tooth-shaped predation-caused wound: χ^2 = 1.19, *P* = 0.276) (Table 4-1) (Fig. 4-3c; Fig. 4-3e).

The occurrence of migrants with predation-caused wounds, regardless of its cause, significantly increased with the pre-migration period (χ^2 = 5.76, *P* = 0.016) (Fig. 4-3b) and with the fork length (χ^2 = 10.31, *P* = 0.001) (Table 4-1). The occurrence of migrants with bill-shaped predation-caused wound also significantly increased with the pre-migration period (χ^2 = 12.13, *P* < 0.001) (Fig. 4-3d) and with the fork length (χ^2 = 4.02, P = 0.045) (Table 4-1). However, the occurrence of migrants with tooth-shaped wound was not significantly related with either the pre-migration period (χ^2 = 0.77, *P* = 0.381) (Fig. 4-3f) or the fork length (χ^2 = 3.67, *P* = 0.055) (Table 4-1).

Discussion

In many migratory species, small individuals at a certain timing before migration tend to grow faster and start migrating later than large individuals, which allows the small ones to reach a large size (i.e., threshold size) before they start risky migration (Nicieza and Brana 1993, Bohlin et al. 1996, Dermond et al. 2019, Futamura et al. 2022b). While the potential costs of faster growth and later migration explain why migrants don't all maximize these size-increment factors, these costs have not been directly investigated. This study, using masu salmon migrants, tested the hypotheses that faster growth and later migration start increase predation risk for migrants in the pre-migration period. My result could not prove the hypothesis that faster growth in the pre-migration period causes greater predation risk was not supported. To the contrary, timing of migration start (i.e., date of capture at migrant trap) related to the occurrence of wounds. In particular, although the timing of migration start did not explain the occurrence of the tooth-shaped wound, probability of inflicting bill-shaped predation-caused wound was higher in migrants with later migration start. These results suggest that masu salmon migrants that onset oceanic migration later were subjected to higher predation risk mainly by the avian predators before migration. As the occurrence of predation-caused wounds in migrants increased over time, it is possible that the higher probability of inflicting predation-caused wounds with late migration start is simply due to the later timing of the wound assessment (i.e., the day of capture in the migrant trap). However, this possible confounding factor is unlikely to be a problem for my conclusion. This is because all migrants, regardless of when they were captured, must pass through high predation risk areas such as the lower reaches of the river and coastal areas before they onset oceanic migration (Welch et al. 2011, Clark et al. 2016, Moore et al. 2021). If all migrants are exposed to at least the same predation risk during the passage through such risky areas, regardless of the timing, my conclusion that migrants with predator wounds at the time of capture are exposed to a higher predation risk before the start of oceanic migration remains valid.

My study reveals increased predation on migrants with longer pre-migration periods, particularly from piscivorous birds. This raises a further question: where and how are these migrants encountering this heightened predation risk before their journey? There are two potential hotspots for increased predation before migration: the nursery habitat where migrants remain until start of river-descending, and the transitional habitat during descending the river. A survey of masu salmon residents, which was held right after the river-descending season of migrants (25–26 Jun-2020), suggest the former hypothesis is unlikely. In the survey, the residents remaining in the migrants' nursery habitat (the uppermost river reach) exhibited no predation-caused wounds (i.e., total 509 residents had no predation-caused wounds) (Futamura et al., *unpublished data*). While I didn't directly observe predator attacks in the transitional habitat, this strongly suggests that migrants were facing increased predation risk during descending the river. This aligns with my frequent observations of piscivorous birds in the middle reaches of the Horonai River, lending support to the hypothesis. Notably, great egrets and common mergansers, rarely seen in the uppermost reach, were regularly present in the middle reaches during the river-descending season of migrants (Futamura et al., *personal observation*).

In general, individuals with faster growth are more vulnerable to predators because active foraging, which allows them to grow faster, also makes them more likely to be detected or encountered by predators (Lima and Dill 1990, Brown and Kotler 2004, Verdolin 2006). However, in my present study, I did not find any evidence of predation-related costs in migrants with higher growth rates. This does not necessarily mean that there are no costs associated with rapid growth before migration. While I focused on increased predation risk as a potential fitness cost of faster growth, other costs are also worth considering. For example, higher growth rates may incur physiological costs such as increased metabolic costs and impaired immune function (Stoks et al. 2006, Van Der Most et al. 2011). It is important to explore these potential long-term costs in order to fully understand the costs associated with rapid growth before migration.

Smaller individuals typically face heavier predation pressure (Sogard 1997, Van Kooten et al. 2007, Takatsu et al. 2017, Stige et al. 2019), and this holds true even for migrating species (Alerstam et al. 2003, Oppel et al. 2015, Gregory et al. 2019, Simmons et al. 2022). Actually, my previous study has provided the evidence of such size-selective mortality in migrants during descending the lower reaches of Horonai River (i.e., 1.1 km reach below migrant trap) (Futamura et al. 2022). However, my results contradicted this general pattern. Larger migrants showed a higher frequency of predation-caused wounds (Table 4-2). This trend mirrors a similar finding in a previous study on predation-caused wounds of three-spine stickleback (*Gasterosteus aculeatus*) (Reimchen 1988). This seemingly paradoxical result may be explained by predator handling abilities. While piscivorous birds and fish can attack and capture prey across a wide size range, their ability to consume certain larger prey is limited by their gape size ("gape-limited") (Moser 1986, Hambright 1991). Additionally, even with prey smaller than their gape, predators require time to handle and swallow them (Draulans 1987). This extended handling time provides larger migrants with a heightened chance of escape, even after initial capture. Consequently, larger migrants may inflict more predation-caused wounds due to these attempted predations.

My findings demonstrate that extending the pre-migration growth period incurs a fitness cost in the form of increased predation risk. This suggests that size-dependent pattens in onset of oceanic migration may be driven and maintained by the trade-off between growth and survival in the pre-migration period. However, this might not preclude the possibility that other mechanisms operate as costs of an extended pre-migration period. For example, a delay in the departure of migration likely results in decreased benefits of oceanic migration, because longer pre-migration period also translates to a shorter oceanic migration period. During oceanic migration, salmonids can significantly increase their size by consuming abundant prey, which ultimately benefits reproduction (Gross et al. 1988, Maekawa and Nakano 2002). Thus, to maximize resource gains, starting oceanic migration early can be crucial. Therefore, investigating such potential trade-off between oceanic growth and early departure, alongside predation costs, in masu salmon and other migratory species would be valuable in advancing our understanding of the factors that shape condition-dependent migration departure.

Table 4-1 Results of the logistic regression model predicting occurrence of predation-caused wound

Model formulae	Independent variable	Estimates	Std. Error	χ^2 value	P
Occurrence of predation-caused wound (regardless of cause) ~ Intercept + Relative growth rate					
	Intercept	-1.64	0.25		
	Relative growth rate	9.71	6.94	2.07	0.150
Occurrence of bill-shaped predation-caused wound ~ Intercept + Relative growth rate					
	Intercept	-2.30	0.32		
	Relative growth rate	4.64	8.60	0.30	0.586
Occurrence of tooth-shaped predation-caused wound ~ Intercept + Relative growth rate					
	Intercept	-4.40	0.94		
	Relative growth rate	22.94	22.41	1.19	0.276
Occurrence of predation-caused wound (regardless of cause) ~ Intercept + Pre-migration period + Fork length					
	Intercept	-9.66	2.07		
	Pre-migration period	2.23×10^{-2}	9.44×10^{-3}	5.76	0.016
	Fork length	3.77×10^{-2}	1.20×10^{-2}	10.31	0.001
Occurrence of bill-shaped predation-caused wound ~ Intercept + Pre-migration period + Fork length					
	Intercept	-12.73	2.82		
	Pre-migration period	4.44×10^{-2}	1.33×10^{-2}	12.13	< 0.001
	Fork length	3.10×10^{-2}	1.58×10^{-2}	4.02	0.045
Occurrence of tooth-shaped predation-caused wound ~ Intercept + Pre-migration period + Fork length					
	Intercept	-6.40	3.51		
	Pre-migration period	-1.42×10^{-2}	1.62×10^{-2}	0.77	0.381
	Fork length	4.02×10^{-2}	2.14×10^{-2}	3.67	0.055

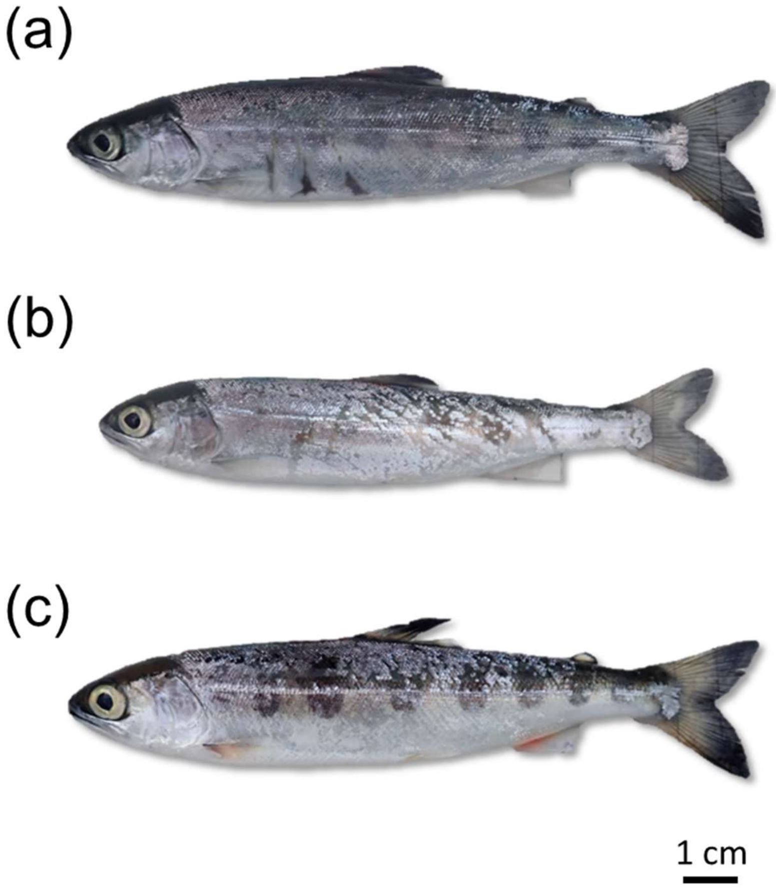

Fig. 4-1 Photograph of the masu salmon migrants with wounds. **(a)** Bill-shaped predation-caused wound (i.e., bill-shaped scar inflicted from either the ventral or dorsal side of the fish); **(b)** tooth-shaped predation-caused wound (i.e., several scars inflicted from the same direction on the fish's body); **(c)** handling wound (i.e., large areas of missing scales).

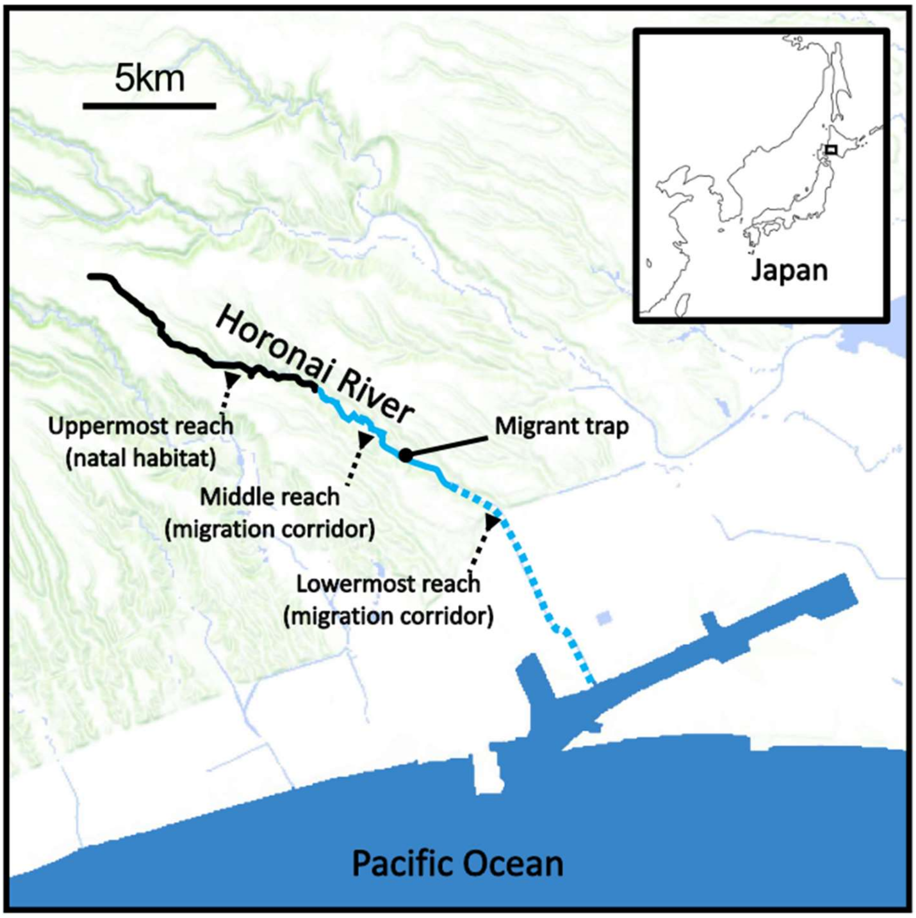

Fig. 4-2 Map of the Horonai River. The Horonai River consists of three distinct reaches. Uppermost reach (6.9–12.2 km from the river mouth (black solid line) is the primary habitat of masu salmon residents and migrants before descending the river, where they have a nursery habitat. Middle reach (4.6–6.9 km from the river mouth) (blue solid line) is the transitional habitat of the migrants. The migrant trap was installed at the midstream of Horonai River (place in which 5.7 km from the river mouth) (black dot) to capture river-descending migrants. Lowermost reach (4.6 km section from the river mouth) (blue break line) is also a transitional habitat of the migrants, which flows through the urbanized landscape of Tomakomai city. This map is based on the digital map published by the Geospatial Information Authority of Japan.

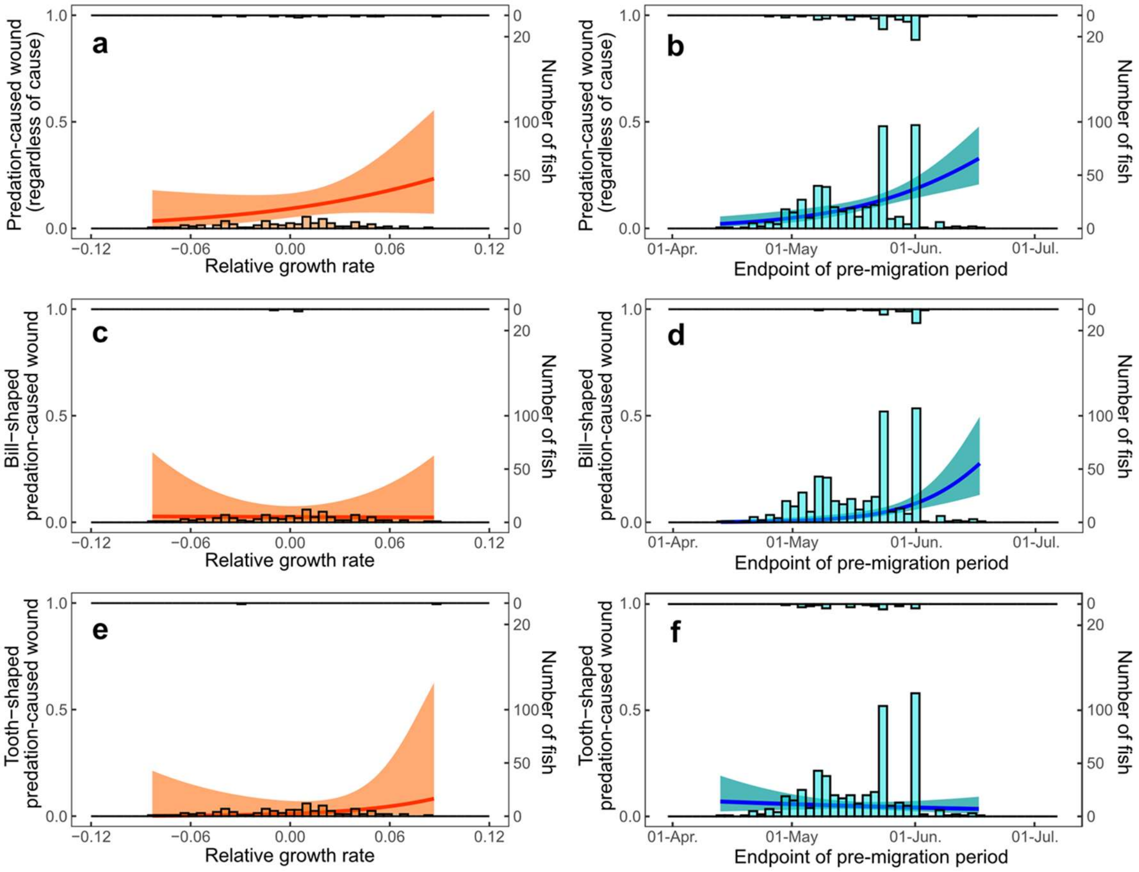

Fig. 4-3 Relationship between the relative growth rate, endpoint of pre-migration period and the occurrence of predation-caused wound. Regression line was predicted by logistic regression (see Table 1 for estimates). The shaded area represents the 95 % confidence interval of the fitted regression. The second Y-axis shows the number of individuals with wound (y = 1) and without wound (y = 0). Occurrence of predation-caused wound regardless of the causes in relation to **(a)** relative growth rate and **(b)** endpoint of pre-migration period (i.e., date of capture in migrant trap); Occurrence of bill-shaped predation-caused wound in relation to **(c)** relative growth rate and **(d)** endpoint of pre-migration period; Occurrence of tooth-shaped predation-caused wound in relation to **(e)** relative growth rate and **(f)** endpoint of pre-migration period.

Supplemental Information 4-1

Table 4-S1 Categorization of migrants

	Capture occasion		
	Migrant trap survey	Migrant trap survey & early spring capture survey	Total
Bill-shaped predation-caused wound	41	10	51
Tooth-shaped predation-caused wound	22	2	24
Non-identified predation-caused wound	24	7	31
Handling wound	154	32	186
Tooth-shaped predation-caused wound & handling wound	0	0	0
Bill-shaped predation-caused wound & handling wound	0	1	1
Bill-shaped predation-caused wound & tooth-shaped predator wound	4	0	4
Non identified predation-caused wound & handling wound	0	0	0
No wound (unscathed)	214	67	281
Total	459	119	578

Confirmation of the accuracy of the wound type classification

The identification of the wound type based on the scar characteristics is difficult because scar patterns are sometimes unclear. This raises the concern that my categorization of the wound type might be incorrect. To confirm this plausible problem is not in my case, I investigated the consistency of occurrence patterns between handling and predation-caused wounds. If my categorization was incorrect, the occurrence pattern should be correlated between the predatory and handling wounds. Specifically, I assessed whether occurrence of the handling wounds was positively affected by the date of capture in migrant trap, because effects of the date of capture in migrant trap on the occurrence of predation-caused wound was positive (see Results). Logistic regression was employed to assess whether the occurrence of the handling wound at the migrant trap was positively affected by the date of capture in migrant trap and size (fork length) at migrant trap. Interaction term between date of capture at migrant trap and fork length was not included in the model because of non-significant effects observed in preliminary analyses using full models.

The occurrence of migrants with handling wounds was negatively affected by the date of capture at migrant trap (χ^2 = 4.30, P = 0.038) (Fig. 4-S1) (Table S2) and positively affected by fork length at migrant trap (χ^2 = 6.40, P = 0.011) (Table S2). This indicates that the relationship between migration timing and the occurrence of handling wounds was negative, which contrasts to predation-caused wounds (see Results). This inconsistency between the occurrence patterns of handling and predation-caused wounds suggests my concerns regarding classification accuracy are warranted. The negative relationship between occurrence of the handling wounds and timing of start of migration may be due to the smaller sample size of the caught migrants in the later survey period, which allowed us to handle the fish more carefully.

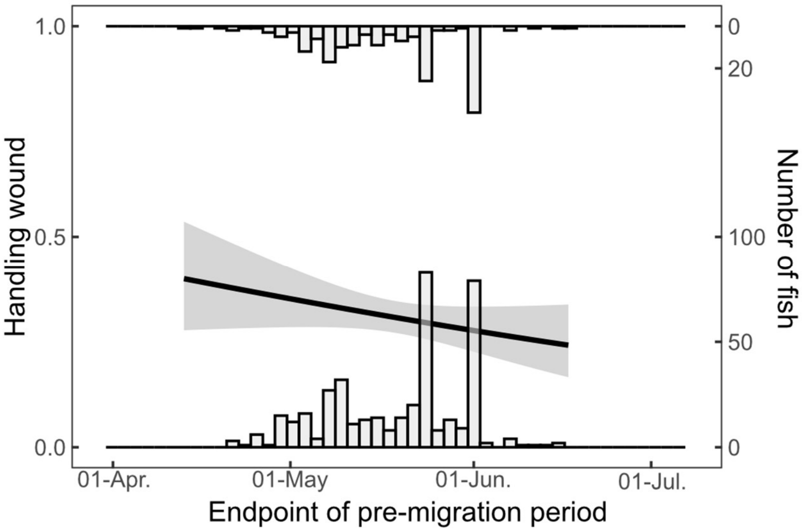

Fig.4-S1 The occurrence of handling wound in relation to date of capture in migrant trap (end point of pre-migration period). Regression line was predicted by logistic regression (see Table S1 for estimates). The shaded area represents the 95 % confidence interval of the fitted regression line. The second Y-axis shows the number of individuals with wound (y = 1) and without wound (y = 0).

Table 4-S2 Results of the logistic regression model predicting occurrence of handling wound

Model formulae	Independent variable	Estimates	Std. Error	χ^2 value	P
Occurrence of handling wound ~ Intercept + Pre-migration period + Fork length					
	Intercept	-1.75	1.57		
	Pre-migration period	-1.56×10^{-2}	7.55×10^{-3}	4.30	0.038
	Fork length	2.40×10^{-2}	9.64×10^{-3}	6.40	0.011

Chapter 5

Stay longer in nursery habitat or transitional habitat: flexible size-dependent behaviors of masu salmon (*Oncorhynchus masou*) migrants before oceanic migration.

Abstract

Although many animals gain substantial benefits by migration, they experience high mortality *en route*. Since the mortality during migration typically operates more strongly on smaller individuals, migratory animals exhibit size-dependent growth tactics before migration, wherein smaller migratory individuals (migrants) attain higher size increments than larger ones. A representative size-dependent growth tactics is the size-dependent migration departure, where smaller migrants delay the start of migration than larger ones. Although size-dependent migration departure has been documented in previous studies, the behavioral process behind this tactic is largely unknown. Here, I focused on two distinct pre-migration landscapes (nursery habitat and transitional habitat) and investigated where smaller masu salmon (*Oncorhynchus masou)* migrants stayed longer than larger ones by an individual monitoring survey across two years. I found that smaller migrants stayed longer than larger ones in the different riverscapes depending on the year. This suggests that smaller migrants may be capable of adjusting their duration of stay in each location in response to the environmental conditions. Studying the behavioral processes of other life history tactics and behavioral tactics by focusing on habitat use may enhance our understanding on how animals adapt to spatially and temporally variable environments.

Introduction

Migration is a high-return and high-risk life history strategy that is prevalent among many animal taxa (Dingle and Drake 2007). Although migratory animals gain large benefits such as significant growth and high reproductive success in the migratory habitat (Sapir et al. 2011, Chapman et al. 2011, Skov et al. 2013, White et al. 2014), they experience high mortality during their migration (Sogard 1997, Kinnison et al. 2003, Lok et al. 2015). In particular, the high mortality during migration represents strong size-selective characteristics, and thus, smaller migratory individuals (migrants) suffer higher mortality due to their high vulnerability to severe environmental stress compared to larger ones (Sogard 1997, Alerstam et al. 2003). To avoid size-selective mortality during migration, migratory animals exhibit size-dependent growth tactics during the pre-migration period, by which smaller migrants attain a larger size increment compared to larger ones before the migration (Nicieza and Brana 1993, Futamura et al. 2022b, Sawyer et al. 2023). Indeed, the size-dependent growth is acknowledged as an adaptive pattern because the ecological demand for growth is higher in smaller migrants than larger ones, but the enhancement of growth is costly. Smaller migrants have to grow more than larger ones to survive the migration, but attaining large size increment in the pre-migration period is costly (Chapter 4). That’s why the size-dependent growth is an adaptive tactic.

A representative example of the size-dependent growth tactics is the size-dependent migration departure, in which smaller migrants start migration later than larger ones (Bohlin et al. 1996, Dermond et al. 2019, Simmons et al. 2020, Futamura et al. 2022b). This allows smaller migrants to grow larger before they start migration. Although many studies have documented the size-dependent migration departures (Bohlin et al. 1996, Dermond et al. 2019, Simmons et al. 2020, Futamura et al. 2022b), the behavioral processes behind this tactic are still largely unknown. Studying the behavioral processes would deepen our understanding of the mechanisms that maximize the benefit of the growth tactics. It could also give us insights into ecological consequences of the growth tactics and the conservation of the migratory animals. In this study, I investigated where the size-dependent migration departure take place. In other words, I tried to answer the question: Where do smaller migrants stay longer than larger ones in the pre-migration habitats?

In this study, using anadromous salmonid masu salmon (*Oncorhynchus masou*) that exhibit size-dependent migration departure as a subject species, I examined where smaller migrants stay longer in the river before oceanic migration than larger individuals. I focused on the river landscape (riverscape) structure and divided it into two types: (1) nursery habitat where migrants spend most of their pre-migration period and (2) transitional habitat where migrants pass through or stay temporarily to start their migration (Fig.5-1). I used these two landscape types because many migratory animals such as migratory birds and fish use these two landscapes before migration, and the environmental conditions differ between the two landscapes. For anadromous salmonids, the upper reach of the rivers is the nursery habitat, and the middle and lower reaches are included in the transitional habitats. The hydrological and physical conditions such as river width, flow velocity, depth and substrate, and the biological conditions such as vegetation and animal species composition vary greatly across the reaches (Fig.5-1). I hypothesized that the degrees of extension of stay by small migrants differ between the distinctive riverscapes, since animal individuals generally utilize favorable locations in terms of growth potential and survival potential which are determined by the environmental conditions (Davies et al. 2012). To test this hypothesis, I conducted an individual monitoring survey using PIT-tags and an antenna system for two years. The two-years survey allowed us to also investigate the annual variation of the extension of pre-migration periods of smaller migrants in the landscapes.

Material and Methods

Study species

Masu salmon is a partial migratory (i.e., migrants and residents consists of the same population) fish endemic to East Asia (Morita 2018). After hatching, both masu salmon migrants and residents emerge from the riverbed in spring and soon they form a territory in the river individually (Nakano et al. 1990, Nakano 1995a, Sakata et al. 2005). After staying in the river for one or two years, migrants start to descend the river towards the ocean in the spring (Kato 1991). After entering the sea, they migrate in the ocean for one year and return to the natal river for reproduction. During oceanic migration, masu salmon migrants suffer size-selective mortality in which smaller ones experience higher mortality than larger ones (Miyakoshi et al. 2001, Shimoda et al. 2003, Miyakoshi 2006). Meanwhile, residents stay in their nursery habitat in the river for their lifetime (Sakata et al. 2005).

Study system

This study was conducted in Horonai River, a 12 km long spring-fed river located in Hokkaido, northern Japan (42°40'N, 141°35'E) (Fig. 5-1). This river has three distinct reaches: uppermost, middle, and lowermost reaches (Fig.5-1a). The uppermost reach (6.9–12.2 km from the river mouth) is least disturbed (i.e., natural riverbank remains) and flows through the secondary deciduous forest (Fig.5-1b). This reach serves as a primary habitat of masu salmon. In this reach, my research group has been conducting a long-term fish monitoring project using PIT-tags (12.0 mm × 2.12 mm, Oregon RFID, Inc) and this reach is divided individually into 10 m-section to record the location of the fish since 2018. The middle reach (4.6–6.9 km from the river mouth) mainly consists of slow-flowing stream and artificial impoundments in total 1.0 ha, of which water surface is mostly devoid of overhanging trees (Fig.5-1c). The lowermost reach (0–4.6 km reach from the river mouth) is characterized by a human-altered riverscape (i.e., riverbank is protected by concrete revetment) and flows through an urban area.

I conducted the individual monitoring study in the uppermost and middle reaches. Because my study subjects are the migrants with PIT-tags that originally lived in uppermost reach, I defined uppermost reach as a nursery habitat and middle reach as a transitional habitat. This landscape definition is appropriate not only in terms of the methodological reason of my individual monitoring approach, but also in terms of environmental differences between uppermost reach and middle reach. For example, predator and prey community is different between these reaches. In the middle reach, piscivorous fish, brown trout (*Salmo trutta*), are abundant and piscivorous birds such as Great Egret (*Ardea alba*) and Common Merganser (*Mergus merganser*) are often observed, but these are very few in the uppermost reach. While aquatic prey invertebrates that typically inhabit lentic water such as chironomids are abundant in the middle reach, those that typically inhabit flowing water such as Baetidae dominates in the uppermost reach.

Capture mark-recapture survey

I conducted a capture-mark recapture survey in the uppermost reach in autumn 2020 (2–9 Oct-2020), spring 2021 (2–4 Apr-2021), autumn 2021 (30 Sep–4 Oct-2021), and spring 2022 (1–7 Apr-2022). On each survey occasion, I collected the fish using a backpack electrofishing unit (300–400 V DC, model 12B, Smith-Root, Inc., Vancouver, WA, USA) with 3 mm mesh dipnets (30 cm wide) in each 10-m section in the uppermost reach. Collected fish were anesthetized with diluted phenoxyethanol to measure their fork length (FL) (nearest 1 mm) and body mass (BM) (nearest 0.1 g). I also examined whether fish had been previously marked by checking for a PIT tag. Individuals without PIT tags larger than 60 mm were tagged. The tag was inserted into the fish's abdominal cavity through a small incision made with a clean scalpel. After processes, the fish were allowed to recover from anesthesia and were released to each 10 m river section of the capture. The number of masu salmon captured and identified by the PIT tag in each survey was 2160 (autumn 2020), 1712 (spring 2021), 2302 (autumn 2021) and 1607 (spring 2022).

Detection of the stay in pre-migration riverscapes

To record period of the stay by migrants in the nursery habitat and transitional habitat, I used five fixed PIT-tag antennas installed in the Horonai River, among which four were installed in nursery habitat (antenna A-D in the uppermost reach) to detect the start of river-descending and one in the transitional habitat (antenna E in the middle reach) (Fig. 5-1). Using the data obtained from the PIT-antennas, I determined the day at the start of river-descending as endpoint of stay in the nursery habitat and the elapsed days between the start of river-descending and the start of oceanic migration as period of stay in the transitional habitat.

Four PIT-antennas in the uppermost reach (antenna A-D) were installed at the location where 20 m, 1030 m, 2480 m, and 3890 m from the lower most part of the uppermost reach (6.9 km, 7.9 km, 9.4 km, and 10.1 m from the river mouth) (Fig. 5-1). When descending the river, the migrants with PIT tags pass through and were detected by one to four of the four antennas installed in the nursery habitat. Therefore, I defined the timing of the first detection by either of the four antennas as the start of river-descending. Using the fixed PIT-antenna system to detect the start of river-descending of migrants is reasonable because salmonids typically stay in a limited habitat area (Rodríguez 2002). Actually, masu salmon migrants in Horonai River remained in their nursery habitat until they start river-descending in spring. This is because four PIT antennas installed in the uppermost reach rarely detected the downward movement of the migrants between autumn to early spring (before the season of river descending) (Futamura et al. *unpublished data*).

One antenna in the transitional habitat (antenna E in the middle reach) was installed at the location 5.7 km from the river mouth (Fig. 5-1). I identified fish that passed through this antenna as migrants. I also used the timing at which each migrant passed through this antenna to quantify their period of stay in the transitional habitat. Specifically, I calculated the difference between the day a fish passed this antenna and the day this fish started river-descending (i.e., the day it was first detected by the nursery habitat antennas) as the period of stay in the transitional habitat. Using this antenna to identify migrants and measure their period of stay in the transitional habitat is reasonable for the following two reasons. First, my previous research (Futamura et al. 2022a) revealed that almost all masu salmon passing through this antenna exhibited morphological characteristics of migratory fish (i.e., smoltification). Additionally, this antenna rarely detects masu salmon, which were tagged in the uppermost reach, except during the river-descending season from April to June. This suggests that the antenna is effectively detecting the migration behavior of the fish.

Capture survey of migrants by migrant trap

During the season of the river-descending (April to June) of 2021 and 2022, I randomly captured the river-descending migrants using the migrant trap installed in the location 5.7 km from the river mouth, just 10 m below the fixed PIT-antenna in the transitional habitat (Fig. 5-1). This trap is placed where the river narrows below a cascade (50cm in height). The trap was checked every day from early April to late June. If fish were captured in the trap, I collected the fish and anesthetized them using diluted phenoxyethanol, and measured size (fork length [nearest 1 mm] and body mass [nearest

0.1 g]). In addition, PIT tags were recorded (12.0 mm × 2.12 mm, Oregon RFID, Inc) using a handy-held PIT tag reader.

Statistical analysis

To identify where small migrants extended their stay and how it varied between years, I investigated how size-dependent patterns in which smaller migrants stay longer than larger ones varied across different riverscapes and years. Specifically, I separately applied linear models to the period of stay in nursery habitat and transitional habitat, respectively, with log-transformed fork length in early spring, year (2021 or 2022), and their interaction as a predictor variable. Importantly, if the interaction term between early spring size and year is significant in these two models and their sign is opposite each other, it means that the riverscape in which size-dependent patterns occurred between the two years are different.

In my study, I am operating under the premise that there is a positive relationship between the period of stay in a given riverscape and growth. This fundamental assumption is refuted if migrants do not achieve greater size increment where they stay longer. However, this assumption is valid because my data showed that the increase in size during the pre-migration period was positively correlated with the period of the stay in two pre-migration riverscapes (see Supplementary Information 5-1 for detail). All statistical analysis was conducted using R version 4.1.2 (R Core Team 2021).

Results

In the migration season of over two years (2021 and 2022), 453 masu salmon migrants (151 [2021] and 302 [2022]) were detected at either of the four PIT-antennas in the uppermost reach (left the nursery habitat) and then detected at the PIT antenna in the middle reach (started oceanic migration). Migrants were detected at either of the four PIT-antennas in the uppermost reach (left their nursery habitat) between 5-Apr and 30-May in 2021 and between 8-Apr. and 27-May in 2022. Migrants were detected at the PIT antenna in the middle reach between 17-Apr. and 10-Aug. in 2021 and 15-Apr. and 5-Jul. in 2022. The period of the stay (mean ± 1SD) in the transitional habitat was 34.00 ± 14.51 in 2021 and 23.54 ± 15.99 in 2022. Among migrants detected at the PIT-antennas in the two reaches, 201 were captured in the migrant trap (45 [2021] and 156 [2022]). The fork length (mean ± 1SD) at the migrant trap was 133.04 ± 11.53 mm in 2021 and 137.66 ± 11.40 mm in 2022.

Linear model showed that endpoint of stay in nursery habitat was influenced by year ($F_{1, 445} = 64.98$, $P < 0.001$), fork length in early spring ($F_{1, 445} = 23.23$, $P < 0.001$) and their interactions ($F_{1, 445} = 8.50$, $P = 0.004$). Similarly, period of stay in transitional habitat was influenced by year ($F_{1, 445} = 7.62$, $P = 0.006$), fork length in early spring ($F_{1, 445} = 13.18$, $P < 0.001$) and their interaction term ($F_{1, 445} = 8.93$, $P = 0.003$). The significant effects of interaction term between fork length and year in these two models and their sign is opposite each other indicate that the size-dependent pattern was more pronounced in the transitional habitat than in the nursery habitat in 2021, whereas size-dependent pattern was more pronounced in the nursery habitat than in the transitional habitat in 2022 (Table 5-1) (Fig. 5-2). Same patterns in statistical significance were also obtained in the analyses using the alternative size factor, body mass (see Supplemental Information 5-2 for detail).

Discussion

Although the size-dependent migration departure tactic is documented in various taxonomic groups (Bohlin et al. 1996, Dermond et al. 2019, Futamura et al. 2022b, Sawyer et al. 2023), its underlying behavioral process has been poorly studied. Here, I focused on the question: where do smaller migrants stay longer than larger ones before migration? To the best of my knowledge, the only study on this topic is Sawyer et al. (2023), which showed that smaller coho salmon (*Oncorhynchus kisutch*) migrants stayed longer duration in the estuary and lower reaches of the river than larger ones, as transitional habitat prior to oceanic migration (Sawyer et al. 2023). Although this study showed that smaller migrants extend their stay in the lowermost reaches as a part of transitional habitat, it remained unknown whether they extend their stay in the other locations because they focused exclusively on the lowermost reaches. In the present study, by monitoring the river-descending behaviors of masu salmon migrants across the two distinctive riverscapes over two years, I found that smaller migrants stayed longer than larger ones in the different riverscapes depending on the year. This indicates that the locations where smaller migrants stay longer to grow more before migration are not fixed. Rather, it suggests that they are capable of utilizing multiple locations to extend their stay in the rivers. Furthermore, my results imply that masu salmon exhibit a flexible adaptive behaviors in their river habitats. The annual variation in the riverscapes, where size-dependent patterns in the period of stay were observed, suggests that smaller migrants adjusted their duration of stay at each location in response to its environmental conditions in that location.

Given that masu salmon have a potential to flexibly change their stay in each location, what factors are involved in the extension of stay in the riverscapes? Because animals select locations with high growth potential or survival potential as a habitat (Morris 2003), the smaller migrants might have responded to environmental factors influencing the growth and survival potentials. For example, prey availability could influence the behavior of the migrants. In the study river, prey communities for masu salmon vary between the uppermost reach and middle reach. While prey invertebrates typically living in still water such as Chironomids are abundant in the middle reach where the water flow is slow or non-existent. On the other hand, invertebrates that typically inhabit flowing water such as Baetidae species are abundant in the uppermost reach where the water flow is continuous. The smaller migrants of masu salmon may adjust their duration of stay in each riverscape according to the annual variation in the abundance of these riverscape-specific invertebrates. Water temperature is another potential factor related to growth potential. My results showed that smaller migrants stayed longer in the nursery habitat than larger ones in 2022 but not in 2021 (Fig. 5-2). Given that water temperature in early spring positively affects the growth of salmonids (Simmons et al. 2020), this pattern might have been partially explained as a result of an adaptive response of smaller migrants to water temperature, since average water temperature in the winter of 2022 was 1.61 °C higher than in 2021 in the nursery habitat (Futamura et al. *unpublished data*). Predation risk is another possible factor affecting migrant behavior, because prey animals tend to avoid staying in high-risk landscapes (Gilliam and Fraser 2001, Hope et al. 2014, Matthews et al. 2020). Although piscivorous bird and fish mainly inhabit lower part of the river, including the middle reach, their abundance varies from year to year (Futamura et al., *personal observation*).

Therefore, smaller migrants may extend their stay in locations with low predation pressure.

Even if masu salmon have the ability to change their duration of stay based on the current environment, time constraints may prevent them from staying for extended periods. While a longer stay in the pre-migration habitat is beneficial for achieving a larger size before migration, there should be a limit to the extension of this stay. This is because a longer stay in the pre-migration habitat results in a shorter duration of ocean migration, leading to a decrease in the growth benefits gained during oceanic migration. In terms of riverscape structure, the duration of stay in the initial riverscape may influence that in the subsequent riverscape. Therefore, if smaller migrants extend their stay in the nursery habitat, they may not extend their stay in the transitional habitat, even if the environmental conditions there are favorable. Actually, my data supports this hypothesis as period of stay in nursery habitat negatively correlated with transitional habitat (Spearman's rank correlation, $R_{ho} = -0.48$, $P < 0.001$) (Fig. 5-3).

Future studies are needed to explore the hypothesis of stay adjustment of smaller migrants and the potential factors contributing to this flexible response. The success of these studies would shed light on the ecological implications of size-dependent growth tactics. By identifying the factors that influence the duration of stay for smaller migrants, I can enhance my predictions about where and when these smaller migrants fulfill their ecological roles, such as preying on other species and serving as prey for predators. This leads to gaining insight into how growth tactics drive the dynamics of trophic interactions in landscape structures.

My findings provide implications for the conservation of migratory animals. The conservation of migratory species is important because migratory species can provide diverse benefits to ecosystems and humanity (Bauer and Hoye 2014, McIntyre et al. 2015). However, migratory species are declining dramatically due to various human activities (Kirby et al. 2008, Limburg and Waldman 2009). In particular, loss and degradation of the pre-migration habitat is one of the major causes in the decline of migratory animals (Jeffres and Moyle 2012, McIntyre et al. 2015). To effectively conserve migratory animals, conservation efforts that considering their life-history is crucial (Levin and Lubchenco 2008). Since size-dependent migration departure occurred in different riverscapes between two survey years, I emphasize the need to the conserve both nursery habitat and transitional habitat. This is because sustaining both riverscapes as a part of habitat portfolio can increase the likelihood of smaller migrants reaching larger sizes, even in variable environments (Schindler et al. 2015). In particular, this initiative contributes to enhancing the resilience of migratory animals in the face of rapid environmental changes (Alley et al. 2003).

It may be quite common for locations where life history tactics and behavioral tactics are employed to change over time, since flexible behaviors have the potential to maximize benefits of such tactics. For instance, some migratory species exhibit size-dependent growth rates, with smaller individuals growing faster than larger ones. Due to this accelerated growth, smaller individuals reach larger sizes before migration (Nicieza and Brana 1993, Futamura et al. 2022b). If smaller migrants selectively use locations with high growth potential to boost their growth rate, the locations used by these smaller migrants during the pre-migration period may vary from year to year depending on annual changes in environmental conditions. In some taxa, males establish and defend mating territories to monopolize females, warding off other males as a reproductive tactic (Hinde. 1956, Clutton-Brock 1989, Avise et al. 2002, Perdigón Ferreira and Lüpold 2021). If males choose locations to establish their territories where they can easily detect the approach of other males and where there are fewer predators, the location of their territories is also likely to change over time. Therefore, studying the behavioral processes of life history tactics and behavioral tactics by focusing on space use will deepen our understanding on how animals behave under spatially and temporally variable environments.

Table 5-1 Summary statistics of the linear model predicting the period of stay in pre-migration riverscapes

	Estimate	Standard Error	T value	P value
Endpoint of stay in nursery habitat ~ Intercept + Year + Ln (fork length in early spring) + Year† × ln (fork length in early spring)				
Intercept	122.51	48.13	2.55	0.011
Year†	178.29	57.78	3.09	0.002
Ln (fork length in early spring)	-2.66	10.15	-0.26	0.794
Year × ln (fork length in early spring)	-35.62	12.22	-2.92	< 0.001
Period of stay in transitional habitat ~ Intercept + Year + Ln (fork length in early spring) + Year† × Ln (fork length in early spring)				
Intercept	319.76	65.01	4.92	< 0.001
Year†	-237.79	78.06	-3.05	0.002
Ln (fork length in early spring)	-61.76	13.71	-4.50	< 0.001
Year† × ln (fork length in early spring)	49.33	16.51	2.99	0.003

† Year was transformed into dummy variables before analysis (2021 [0] and 2022 [1]).

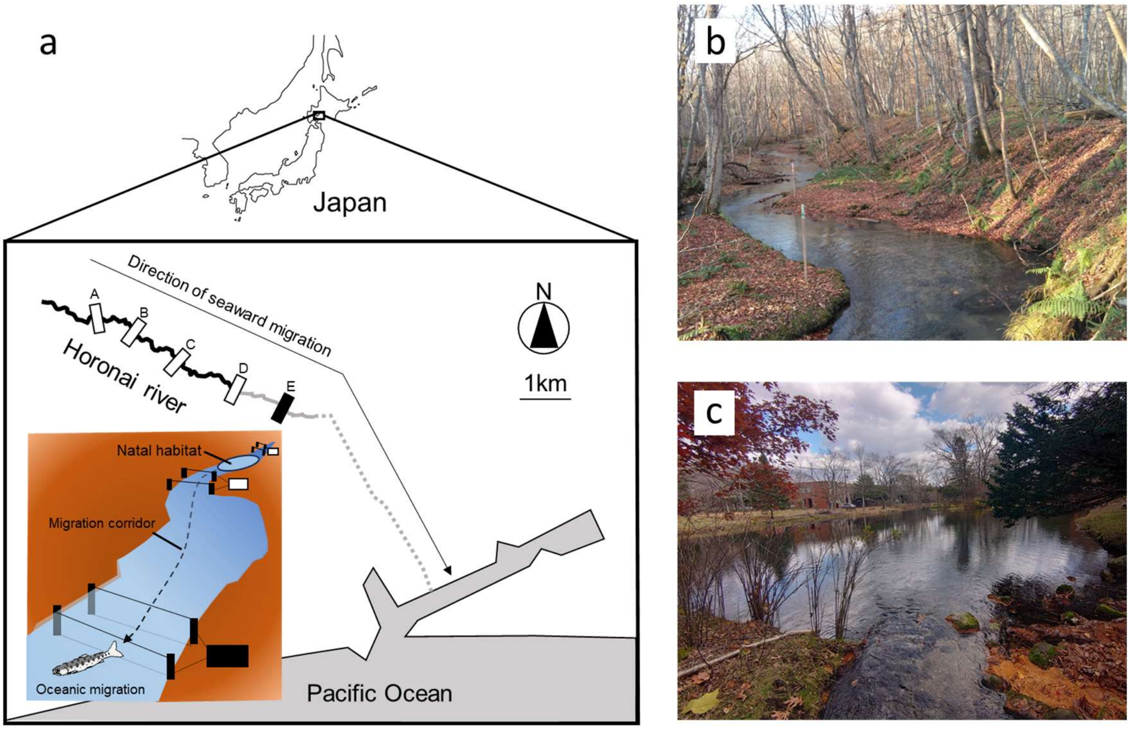

Fig. 5-1 The map describing three distinct reaches of Horonai River (a). The uppermost reach of the Horonai river (between 6.9 km and 12 km from the river mouth) (black solid line) is the reach where migrants spend most of time before migration, and thus defined as a nursery habitat. Four PIT-antennas were installed in the uppermost reach (3890 m [A], 2480 m [B], 1030 m [C], and 20 m [D] from the lower most part of the uppermost reach) (white box) to detect when migrant left the nursery habitat (i.e., started river-descending). The middle reach is located in the midstream of the river (the location between 4.6 km and 6.9 km from the river mouth) (grey solid line), through which the migrants pass during their river-descending, and thus, is defined as a transitional habitat. One PIT antenna was installed in the middle reach where 5.7 km from the river mouth (black box). The lowermost reach is located in the lowermost part of the river (4.6 km reach from the river mouth) (grey dashed line), which is not included in my survey area. Photograph taken in the representative riverscape of uppermost reach (b) and middle reach (c).

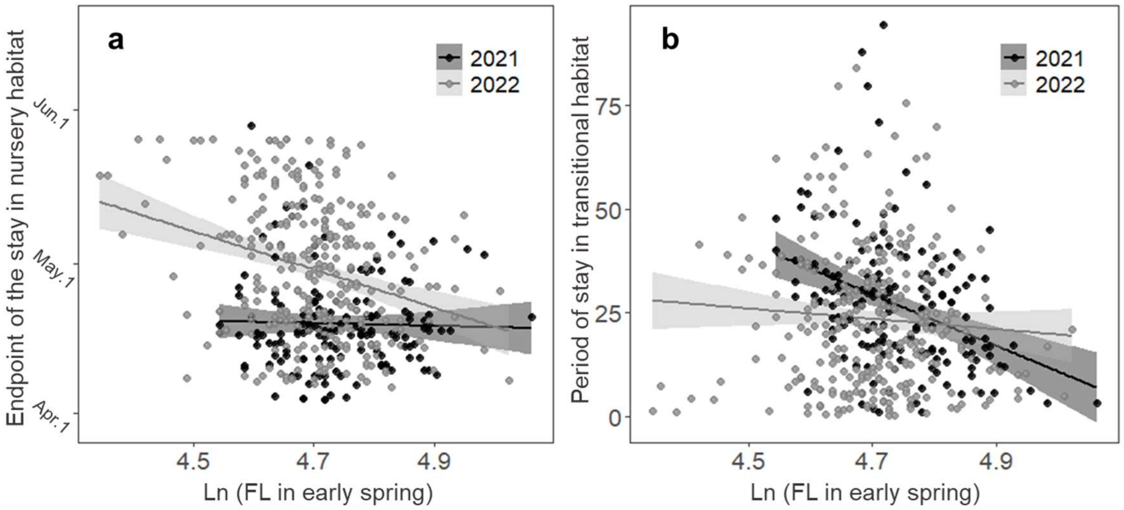

Fig. 5-2 The relationship between fork length in early spring (mm) and period of the stay in two pre-migration riverscape in 2021 (black) and 2022 (grey). (a) Relationship between fork length in early spring and endpoint of stay in the nursery habitat (timing of the start of river descending); (b) relationship between fork length in early spring and period of stay in transitional habitat (period of river-descending). Fork length was log-transformed before analysis. The regression line was fitted using linear regression. Shaded areas represent 95% CI.

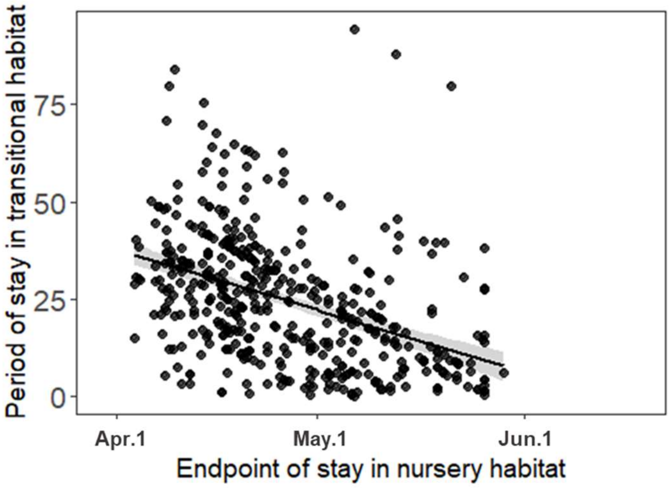

Fig.5-3 The relationship between endpoint of stay in nursery habitat and period of stay in transitional habitat. The regression line was fitted using linear regression. Shaded areas represent 95% CI.

Supplemental Information 5-1

Analysis of the assumption

In this study, I identified where small migrants extended their growth period and how it varied between years. This analysis is operated under the assumption that there is a positive relationship between the period of stay and growth in a given riverscape. This assumption is refuted if migrants do not achieve greater size increment where they stay longer. To verify my assumption, I examined whether period of the stay in two pre-migration riverscapes positively correlate with size increment. Specifically, I analyzed whether period of the stay in nursery habitat and transitional habitat and year positively influenced by size increment of two size factors (fork length and body mass) using linear model. Period of stay in nursery habitat and transitional habitat was log-transformed before analysis to improve normality and reduce heterogeneity. Interaction term was excluded from this analysis because it was not significant in the preliminary analysis using the full model including all variables including the interaction term. Size increment was the size differences between early spring (i.e., size at the capture survey in early spring) and onset of migration (i.e., size at migration trap). This was calculated for both size factors.

Size increment of fork length was positively influenced by start of river-descending ($F_{1, 197} = 138.16$, $P < 0.001$), period in river-descending ($F_{1, 197} = 175.21$, $P < 0.001$) and year ($F_{1, 197} = 22.93$, $P < 0.001$). Size increment of body mass was positively influenced by the start of river-descending ($F_{1, 197} = 93.81$, $P < 0.001$), period in river-descending ($F_{1, 197} = 145.78$, $P < 0.001$) and year ($F_{1, 197} = 11.90$, $P < 0.001$). These results indicates that increase in size during the pre-migration period positively correlated with the period of the stay in two pre-migration riverscape. (Table 5-S1) (Fig. 5-S1; Fig. 5-S2). Thus, my assumption is valid.

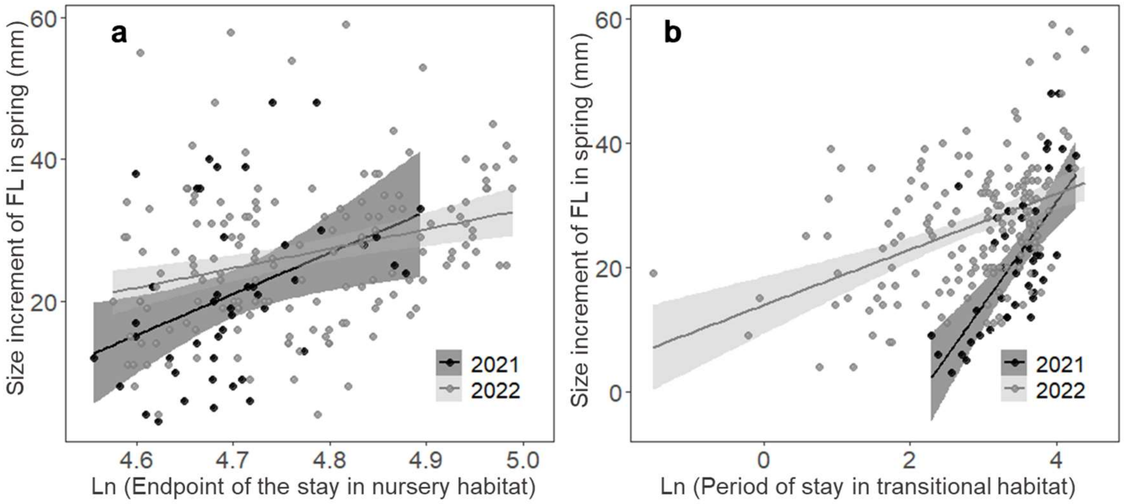

Fig. 5-S1 Size increment of fork length (FL) in relation to period of the stay in pre-migration riverscapes in 2021 (black) and 2022 (grey). (a) Relationship between endpoint of the stay in nursery habitat (start of river descending [day of the year since 1 Jan]) and size increment of FL; (b) relationship between duration of stay in transitional habitat (period of river-descending) and size increment of FL. Period of the stay in in two pre-migration riverscapes were log-normalized before analysis. The regression line was fitted using linear model. Shaded areas represent 95% CI.

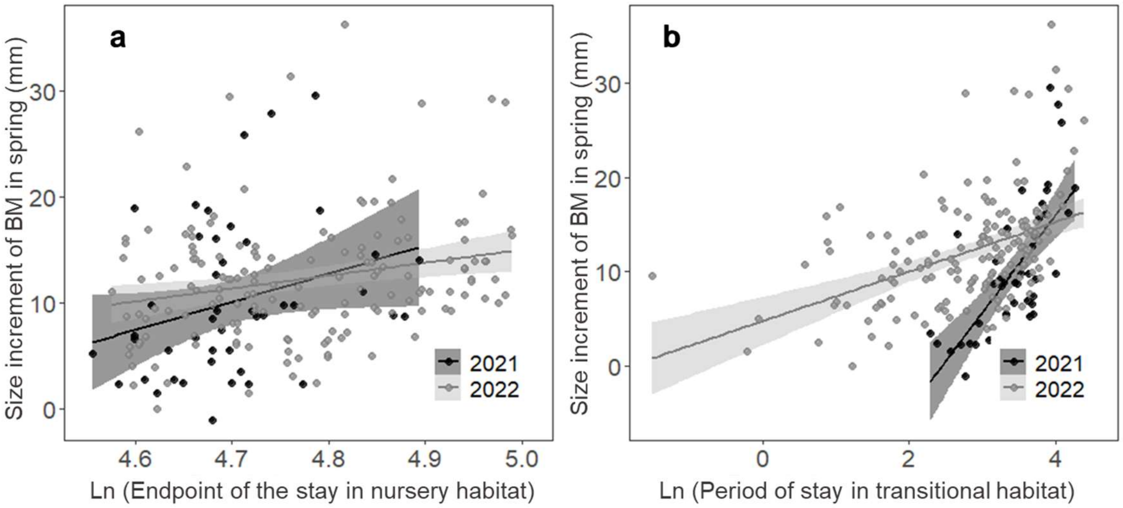

Fig. 5-S2 Size increment of fork length (BM) in relation to period of the stay in pre-migration riverscapes in 2021 (black) and 2022 (grey). (a) Relationship between the endpoint of the stay in nursery habitat (start of river descending [day of the year since 1 Jan]) and size increment of BM; (b) relationship between duration of stay in transitional (period of river-descending) and size increment in BM. Period of the stay in in two pre-migration riverscapes were log-normalized before analysis. The regression line was fitted using linear model. Shaded areas represent 95% CI.

Table 5-S1 Summary statistics of the linear model predicting size increment

	Estimate	Standard Error	T value	P value
Size increment of fork length~ Intercept + Year + Ln (period of stay in transitional habitat) + Ln (endpoint of stay in nursery habitat)				
Intercept	-314.06	27.09	-11.59	< 0.001
Year[†]	8.89	0.67	13.24	< 0.001
Ln (period of stay in transitional habitat)	6.38	1.33	4.79	< 0.001
Ln (endpoint of stay in nursery habitat)	64.81	5.51	11.75	< 0.001
Size increment of body mass~ Intercept + Year + Ln (period of stay in transitional habitat) + Ln (endpoint of stay in nursery habitat)				
Intercept	-160.09	16.54	-9.68	< 0.001
Year[†]	4.95	0.41	12.07	< 0.001
Ln (period of stay in transitional habitat)	2.81	0.81	3.45	< 0.001
Ln (endpoint of stay in nursery habitat)	32.60	3.37	9.69	< 0.001

[†] Year was transformed into dummy variables before analysis (2021 [0] and 2022 [1]).

Supporting Information 5-2

The results on the statistical analysis on body mass

Table 5-S2 Summary statistics of the linear model predicting the period of stay in pre-migration riverscapes

	Estimate	Standard Error	T value	P value
Endpoint of stay in nursery habitat~ Intercept + Year + Ln (body mass in early spring) + Year† * ln (body mass in early spring)				
Intercept	106.77	9.49	11.25	< 0.001
Year†	46.32	11.27	4.11	< 0.001
Ln (body mass in early spring)	1.16	3.48	0.33	0.740
Year†*ln (body mass in early spring)	-13.38	4.17	-3.21	0.001
Period of stay in transitional habitat ~ Intercept + Year + Ln (body mass in early spring) + Year† * Ln (body mass in early spring)				
Intercept	86.75	12.72	6.82	< 0.001
Year†	-47.22	15.11	-3.13	0.002
Ln (body mass in early spring)	-21.99	4.66	-4.72	< 0.001
Year†*ln (body mass in early spring)	15.93	5.59	2.85	0.005

† Year was transformed into dummy variables before analysis (2021 [0] and 2022 [1]).

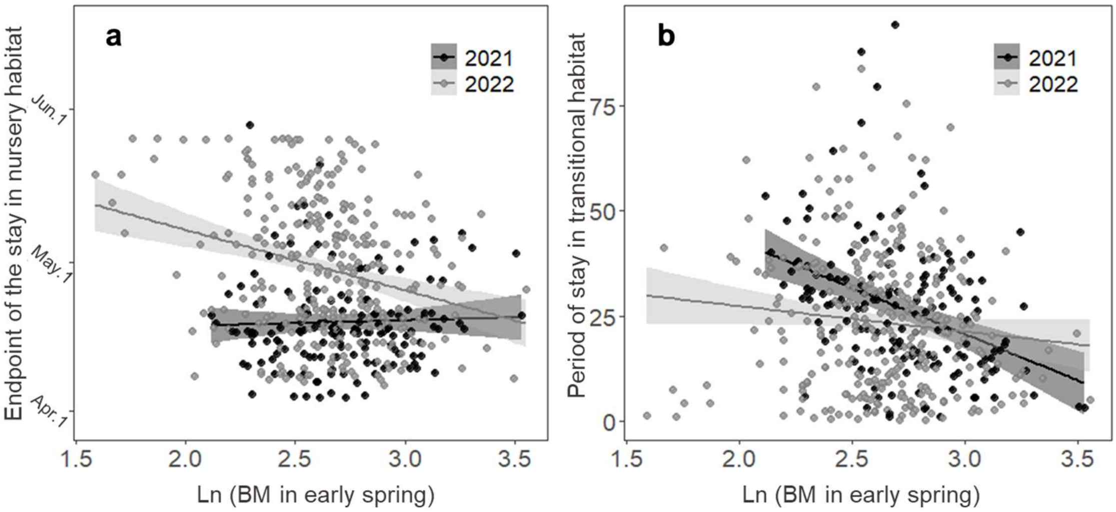

Fig. 5-S3 The relationship between body mass (BM) in early spring (g) and period of the stay in two pre-migration riverscapes in 2021 (black) and 2022 (grey). (a) Relationship between body mass in early spring and endpoint of stay in the nursery habitat (timing of the start of river descending); (b) relationship between body mass in early spring and duration of stay in transitional habitat (period of river-descending). Body mass was log-transformed before analysis. The regression line was fitted using linear regression. Shaded areas represent 95% CI.

Chapter 6

General Discussion

Migration is a high-risk and high-return life history strategy (Fudickar et al. 2021). Thus, migratory animals should evolve and maintain mechanisms to minimize the high cost of migration (Alerstam et al. 2003). Indeed, previous studies have shown that migratory animals adopt risk-reducing behavioral tactics to minimize the mortality costs of migration (Pavlov et al. 2000, Milner-Gulland et al. 2014, Hopcraft et al. 2014, Chapman et al. 2015a, Furey et al. 2016, Komal et al. 2017). However, these studies on the risk-reducing mechanisms of migration rarely focused on its condition-dependence. Here, I conducted a series of studies on size-dependent growth tactics as a condition-dependent tactics against migration by conducting a capture-mark recapture survey and individual tracking in masu salmon. First, I found a size-dependent growth pattern of migrants in both growth rate and pre-migration growth period expected from the size-dependent growth tactic (chapter 2). Specifically, I found that smaller migrants exhibited higher growth rate half a year before migration and extended their stay in the river longer than larger ones to attain a large body size before migration. Then, to affirm these growth patterns as a tactic, I assessed the ecological demands for growth in migrants (chapter 3) and costs associated with behaviors to maximize size increment (chapter 4). In chapter 3, I found that the growth demands of the smaller migrants are higher than larger ones before migration because smaller migrants suffered higher mortality in the lowermost reaches of the river, but residents did not exhibit such patterns. This indicates the ecological demands for growth is higher in smaller migrants before migration. In chapter 4, I identified the costs associated with behaviors to attain larger size increments before migration. In particular, I discovered that extension of the stay in the river incurs higher predation risk in the pre-migration habitat. These results indicate that the size-dependent growth patterns obtained in chapter 2 are adaptive. Finally, I investigated the behavioral process of one size-dependent growth tactics: size-dependent migration departure, where smaller migrants extend their stay in the river. I found that the size-dependent migration departure was occurring in different landscapes between two years suggesting that smaller migrants flexibly change the pre-migration landscape for a longer stay in response to environmental conditions in the natural habitats. These studies on size-dependent growth tactics of masu salmon migrants has advanced our knowledge on the risk-reducing mechanisms of the migratory animals, which has been rarely studied on an individual level.

It is well known that migratory animals employ pre-migration growth tactics to reach to a large size that could survive the prior to migration. Arendt (1997) predicted that the migratory animals may accelerate the growth rate before migration to reach a sufficiently large size prior to migration (Arendt 1997). Actually, previous studies that compared the growth rate of migratory type with non-migratory type during the pre-migration period support this prediction (Palmer and Dingle 1986, Wood and Foote 1990, Snyder 1991, Yamamoto and Nakano 1996, Takami et al. 1998, Olsson and Greenberg 2004). However, these studies ignored the individual variation. In chapter 2, I found the expected size-dependent growth pattern from size-dependent growth tactics in both growth rate and growth period by conducting a capture mark recapture survey in the natural river. This implies that there is an individual variation in pre-migration growth tactics before migration.

The size-dependent growth pattern in which smaller migrants grow better than larger ones should be driven by the ecological demands of the growth which are higher in smaller migrants. These ecological demands for growth are derived from size-selective mortality which operates more strongly on smaller migrants. In which location did size-selective mortality operate on migrants? Chapter 3 suggests that size-selective mortality occurred in the lower reaches of the river, as I found that masu salmon migrants suffered higher mortality in the lower reaches of the river, but residents in the upstream of the river did not during the corresponding period. Nevertheless, this does not negate the possibility that size-selective mortality may also occur in other locations. In general, salmonids face size-selective mortality in the estuaries and oceans (Holtby and Healey 1990, Sogard 1997, Kinnison et al. 2003, Tamate and Maekawa 2004b, Furey et al. 2015). In fact, while not demonstrated in my preliminary three-year data from the Horonai River (Futamura et al, *unpublished data*), evidence for size-selective mortality in masu salmon has been reported (Miyakoshi et al. 2001, Shimoda et al. 2003, Miyakoshi 2006). Thus, not only size-selective mortality pressures in migratory areas such as downstream reaches but also in estuaries and ocean may drive size-dependent growth patterns before migration.

To affirm size-dependent growth pattern as growth tactic, it’s necessary to uncover the costs associated with a faster growth and a longer pre-migration period of migrants. This is because maximizing size increment before migration should be adaptive for migrants, regardless of body size if there are no associated costs. In chapter 4, I focused on the trade-off between growth and survival and investigated the costs associated with longer pre-migration period and higher growth rate. I found that migrants with a longer pre-migratory period are subjected to higher predation risk, particularly from avian predators prior to migration. In contrast, I could not find the evidence that migrants exhibiting higher growth rates were subjected to higher predation risk. However, this does not negate the possibility that higher growth rate before migration incur costs. While I focused on increased predation risk as a potential fitness cost of faster growth, other costs, such as physiological costs including increased metabolic costs and impaired immune function are also worth considering (Stoks et al. 2006, Van Der Most et al. 2011). Indeed, these costs may be fatal for migrants because they physiologically prepare for oceanic migration during the pre-migration period (i.e., smoltification) (McCormick 2009). Thus, to further our understanding of the adaptiveness of the size-dependent patterns in growth rate, future studies should explore these potential long-term costs which can be associated with faster growth before migration.

To successfully employ pre-migration growth tactics in the natural habitats, migrants have to deal with the fluctuating environmental conditions. Chapter 4, which I examined where size-dependent migration departure occurred, suggests that smaller migrants adaptively adjust their duration of stay at each location in response to its environmental conditions in that location. Given that adaptability in behavior has the capacity to maximize the benefits of the growth tactics (Dmitriew 2011), it is postulated that smaller migrants also utilize locations favorable for growth to grow faster. In particular, smaller migrants may selectively use locations with high growth potential to boost their growth rate, which may fluctuate from year to year due to annual changes in environmental conditions. Future study testing this prediction may deepen our understanding of the adaptive behaviors behind the condition-dependent tactics of migration.

In this thesis, I demonstrated that masu salmon migrants employ size-dependent growth tactics before migration, as a condition-dependent tactics to reduce the risk of migration, by individual identification and tracking of many individuals using PIT-tag telemetry system. Based on my thesis, I propose two directions in future research to further enhance our understanding of migration. First, I suggest investigating whether migratory animals have other condition-dependent tactics. Size-dependent growth tactic before migration may not be the sole condition-dependent tactic against migration. Given that smaller migrants have higher ecological demands to reduce mortality risk, and behaviors to reduce the mortality risk can also lead to a decreased benefits gained in migration, migratory animals may employ size-dependent behavioral patterns in risk-reducing behaviors, where smaller migrants more likely to employ risk-reducing behaviors during migrating through risky landscapes, as condition-dependent behavioral tactic. For example, migratory animals may exhibit condition-dependent patterns in schooling, where smaller migrants are more likely to migrate in school as behavioral tactics. This is because the benefits of schooling can be greater for smaller migrants (i.e., reduce size-selective predation risk and swimming costs), whereas schooling can lead to a reduced prey availability per an individual (Pavlov et al. 2000, Liao 2007). Migratory animals may exhibit condition-dependent patterns in nocturnal migration, in which smaller migrants are more likely to migrate at night, as behavioral tactics. This is because nocturnal migration can avoid size-selective predation risk from the predators, while migrants cannot forage efficiently at night and may lose navigation of the migration route (Metcalfe et al. 1998). Testing these hypotheses on potential condition-dependent behavioral tactics in future studies are meaningful to identify the causes shaping individual variation in the behaviors of migratory animals and broaden our understanding on the risk-reducing mechanisms involved in the evolution and maintenance of migratory strategies. Second, I suggest investigating the prevalence of each discovered condition-dependent behavioral tactics and size-dependent growth tactics. By investigating the prevalence of each of condition-dependent tactics, we can identify the ecological context in which these tactics are being maintained. This will provide an insight into how migration has evolved and been maintained within a particular ecological context. Therefore, accumulating knowledge on the prevalence of various condition-dependent tactics of migration would shed light on why migration has been able to evolve repeatedly despite different ecological contexts. Overall, to conduct these future studies on condition-dependent tactics of migration, I emphasize that the prominent approach is individual identification and tracking of many individuals, as I did in my thesis.

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