

ORIGINAL RESEARCH

Annual variation in riverscape habitat use by a diadromous fish before oceanic migration

R. Futamura^{1,2} , K. Morita³ , Y. Kanno⁴ , A. Terui⁵ , A. Okuda⁶ & O. Kishida⁷ ¹Graduate School of Environmental Sciences, Hokkaido University, Takaoka, Tomakomai, Hokkaido, Japan²Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany³Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa, Chiba, Japan⁴Department of Fish, Wildlife, and Conservation Biology, and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA⁵Department of Biology, University of North Carolina at Greensboro, Greensboro, NC, USA⁶Tomakomai Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Takaoka, Tomakomai, Hokkaido, Japan⁷Wakayama Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Wakayama, Japan

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Correspondence

Ryo Futamura, Graduate School of Environmental Sciences, Hokkaido University, Takaoka, Tomakomai, Hokkaido 053-0035, Japan.

Email: rfutamurattg@gmail.com

Osamu Kishida, Wakayama Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Kozagawa, Higashimuro, Wakayama 649-4563, Japan.

Email: kishida@fsc.hokudai.ac.jp

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Introduction

Migration is a high-return and high-risk life history strategy that is prevalent among many animal taxa (Dingle & Drake, 2007). Although migratory animals gain large benefits such as significant growth and high reproductive success in the migratory habitat (Chapman et al., 2011; Sapir et al., 2011; Skov et al., 2013; White et al., 2014), they experience high mortality *en route* (Kinnison et al., 2003; Lok et al., 2015; Sogard, 1997). In particular, migration incurs disproportionate costs (e.g. predation) to smaller migratory individuals (migrants), resulting in higher mortality among smaller

Abstract

Many animals reap significant benefits from migration, yet they face high mortality rates during the journey. As the mortality during migration typically operates more strongly on smaller migratory individuals (migrants), small pre-migrants among migratory animals tend to grow better than larger ones prior to migration, enabling them to attain a larger body size. A common growth strategy for smaller pre-migrants is extending their growth period compared to larger ones. Although this tactic has been documented in previous studies, the landscape-scale habitat utilization that allowed smaller pre-migrants to stay longer prior to migration remains largely unknown. Here, we focused on two distinct riverscape habitats (nursery habitat and transitional habitat) and investigated where smaller pre-migrants of masu salmon (*Oncorhynchus masou*) stayed longer than larger ones prior to oceanic migration. We conducted an individual monitoring survey on their habitat utilization in two distinct migration years. We found that in 1 year, smaller pre-migrants stayed longer in the transitional habitat compared to the nursery habitat, whereas in the other year, they stayed longer in the nursery habitat compared to the transitional habitat. This suggests that smaller pre-migrants can adjust their duration of stay in each riverscape habitat. Our findings highlight the importance of conserving the entire pre-migration habitat to enhance the resilience of migratory animals in the face of rapid environmental changes.

migrants (i.e. size-selective mortality) during migration (Alerstam et al., 2003; Sogard, 1997). Thus, increased growth of smaller migrants prior to migration (pre-migrants) compared to larger ones can therefore help ameliorate their migration costs as it allows them to attain body size sufficient for migration (Futamura, Morita, Kanno, Kumikawa, et al., 2022; Nicieza & Brana, 1993; Sawyer et al., 2023). Indeed, the increased growth of smaller pre-migrants compared to larger ones is recognized as an adaptive pattern because smaller pre-migrants have higher ecological demand for growth (i.e. smaller pre-migrants should attain sufficiently large size prior to migration), but the growth increase prior to migration can incur

substantial energetic and ecological costs (R. Futamura, unpublished data). That is why smaller pre-migrants increase their growth, while larger pre-migrants do not need to.

Delayed migration departure (i.e. longer stay in the pre-migration habitat) provides an extended temporal window for increased growth, allowing small pre-migrants to grow to a large size prior to migration (Bohlin *et al.*, 1996; Dermond *et al.*, 2019; Futamura, Morita, Kanno, Kumikawa, *et al.*, 2022; Sawyer *et al.*, 2023). Although this growth tactic of smaller pre-migrants has been documented in many studies of migratory fish, the behavioral process that leads to the delayed migration departure remains largely unknown. To the best of our knowledge, the only study on this topic is Sawyer *et al.* (2023), who showed that smaller pre-migrants of Coho salmon (*Oncorhynchus kisutch*) stayed longer in specific habitats (estuary and lower reaches of the river) than larger ones prior to oceanic migration (Sawyer *et al.*, 2023). Although pre-migrants may utilize other habitats such as upper reaches of the river prior to oceanic migration, it remains unknown whether they extend their stay in other habitats because their study focused exclusively on the lowermost reaches of the river and estuaries. Therefore, it remains unclear where smaller pre-migrants extend their stay in their entire habitat range prior to migration.

Typically, individuals are able to switch their habitats in response to the growth opportunities and risks in their current habitat (Bjørneraas *et al.*, 2012; Gilliam & Fraser, 1987; Guillemain *et al.*, 2000; Werner & Mittelbach, 1981). Considering that smaller pre-migrants need to attain larger size prior to migration, they may exhibit different behaviors that result in greater growth. Specifically, smaller pre-migrants may change the extent of their longer stay among habitats as potential for growth in local habitats may change in response to spatially fluctuating ecological factors (Caissie, 2006; Hansen & Closs, 2007; Jobling, 2002; Nemeth & Schuster, 2005). Revealing the habitat utilization of the smaller pre-migrants deepens our understanding of the mechanisms that maximize the benefits of the growth tactics and could also give us insights into the conservation of the migratory animals. Here, we investigated the habitat utilization patterns of masu salmon (*Oncorhynchus masou*) pre-migrants prior to oceanic migration.

Masu salmon is a partial migratory fish (i.e. a single population consists of migrants and residents) endemic to East Asia (Sahashi & Morita, 2024). Salmon fry emerge from the riverbed in spring and soon form a dominance hierarchy via their territorial behavior (Nakano, 1995; Nakano *et al.*, 1990; Sakata *et al.*, 2005). After 1 or 2 years of freshwater residency, individuals that adopt a migratory life history (migrants) descend the river in spring to migrate to the ocean (Kato, 1991). As masu salmon migrants make their decision to migrate by the last autumn before migration (Nagae *et al.*, 1994), they stay in the river as pre-migrants for at least half a year. Migrants typically spend 1 year in the ocean and return to the natal river for spawning (Sahashi & Morita, 2024). During oceanic migration, masu salmon migrants experience high mortality, which operates stronger on smaller ones (Miyakoshi, 2006; Miyakoshi *et al.*, 2001; Shimoda *et al.*, 2003). Meanwhile, freshwater residents stay in their nursery habitat in the river throughout their

lifetime (Sakata *et al.*, 2005). Importantly, a previous study in masu salmon migrants has shown that smaller pre-migrants delay the departure of oceanic migration compared to larger ones (Futamura, Morita, Kanno, Kumikawa, *et al.*, 2022). Here, we focused on the two distinct riverscape habitats where pre-migrants of masu salmon stay prior to oceanic migration: (1) nursery habitat where pre-migrants spend most of their time and (2) transitional habitat where pre-migrants pass through or stay temporarily to start their oceanic migration (Fig. 1). Typically, anadromous salmonids utilize the upper reach of the rivers as nursery habitat, and the middle and lower reaches as transitional habitats prior to oceanic migration (Welsh Jr *et al.*, 2001). 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 these habitats (Thorp *et al.*, 2006). Accordingly, we hypothesized that the degree to which smaller pre-migrants extend their stay differs among distinct riverscape habitats. To test this hypothesis, we conducted an individual monitoring survey using PIT-tags and an antenna system for two migration years, which also allowed us to investigate the annual variation of the size-dependent stay duration of pre-migrants in their riverscape habitats prior to oceanic migration.

Materials and methods

Study system

Our 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. 1). We defined three distinct reaches in this river: upstream, middle and downstream (Fig. 1). The upstream 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. 1). This reach serves as the primary habitat for masu salmon. The middle reach (4.6–6.9 km from the river mouth) mainly consists of slow-flowing streams and artificial impoundments covering a total of 1.0 ha, and its water surface is mostly devoid of overhanging trees (Fig. 1). The lower reach (0–4.6 km 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.

We conducted a fish tracking survey in the upper and middle reaches of Horonai River as a pre-oceanic migration habitat. The upstream reach is the habitat where masu salmon pre-migrants initially stay until they start descending the river. In this reach, we have conducted a fish monitoring survey using PIT-tags (12.0 mm × 2.12 mm, Oregon RFID, Inc.) since 2018, which are distinguished at the 10-m scale survey section to record fish location (Futamura, Morita, Kanno, Kumikawa, *et al.*, 2022). The middle reach was defined as transitional habitat, as it is utilized after they leave the nursery habitat in the upstream reach. In this reach, masu salmon residents are rarely found (R. Futamura, unpublished data) and only pre-migrants seasonally utilize it as a transitional habitat. This landscape definition is appropriate not only for

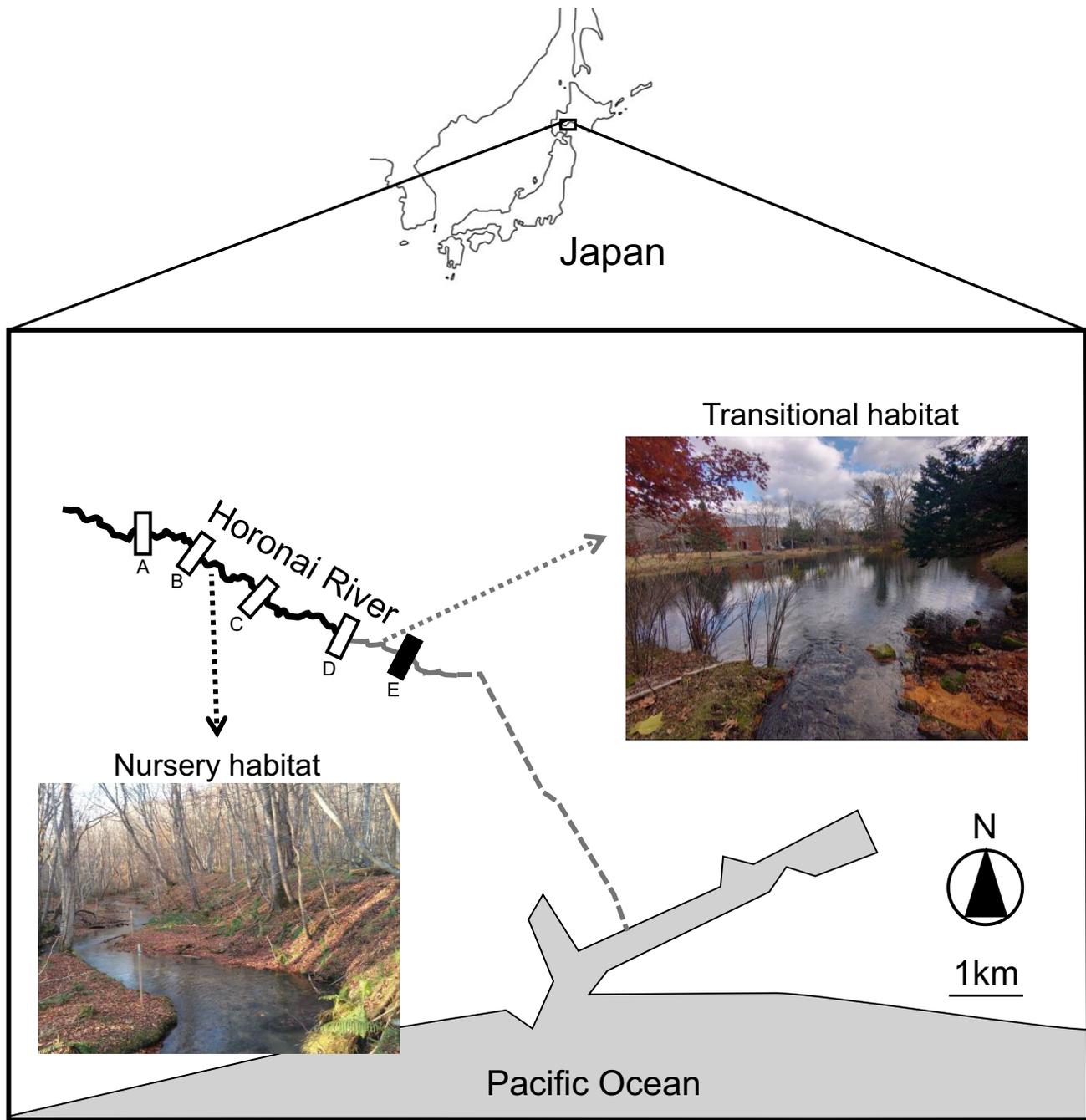


Figure 1 The map describing three distinct reaches of the Horonai River. The upstream reach of the Horonai River (between 6.9 km and 12 km from the river mouth) (black solid line) is the reach where pre-migrants of masu salmon spend most of their time prior to oceanic migration, and thus is defined as a nursery habitat. Four PIT-antennas were installed in the upstream reach (3890 m [A], 2480 m [B], 1030 m [C] and 20 m [D] from the lower most part of the upstream reach) (white box) to detect when migrants 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) (gray solid line), through which the pre-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) (gray dashed line), which is not included in our survey area.

the methodological reason of our individual monitoring approach, but also in terms of environmental differences between the two reaches. For example, the predator and prey community differ 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 upstream 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 dominate in the upstream reach.

Capture-mark-recapture survey

We conducted a capture-mark-recapture survey throughout the upstream reach in autumn 2020 (October 2–9, 2020), spring 2021 (April 2–4, 2021), autumn 2021 (September 30–October 4, 2021) and spring 2022 (April 1–7, 2022). On each survey occasion, we collected 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 upstream reach. Collected fish were anesthetized with diluted phenoxyethanol (Wako Pure Chemical Industries, Ltd., Osaka, Japan) at a concentration of 1/1000 and measured their fork length (FL) (nearest 1 mm) and body mass (BM) (nearest 0.1 g). We also examined whether fish had been previously marked by checking for a PIT tag (12.0 mm × 2.12 mm, Oregon RFID, Inc). All individuals larger than 60 mm without PIT tags were tagged. The tag was inserted into the fish's abdominal cavity through a small incision made with a clean scalpel. The PIT tagging typically took less than 5 s. After each procedure, the fish were allowed to recover from anesthesia and were released back into the 10-m river section of their 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). The handling mortality rate during the capture-mark-recapture survey was 1.1% (86/7781).

Detection of the stay in pre-migration riverscape habitats

To record the period of the stay by pre-migrants in the nursery habitat and transitional habitat, we used five fixed PIT-tag antennas installed in the Horonai River, of which four were installed in nursery habitat (antenna A–D in the upstream reach) to detect the onset of river-descending and one in the transitional habitat (antenna E in the middle reach) (Fig. 1). The detection probabilities of PIT antennas B, C and D were 69% (47/68), 92% (133/145) and 96% (315/328), respectively. Using the data obtained from the PIT antennas, we determined the elapsed days between April 1 and the start of river-descending as the period of stay in the nursery habitat and the elapsed days between the start of river-descending and the start of oceanic migration as the period of stay in the transitional habitat.

Four PIT-antennas in the upstream reach (antenna A–D) were installed at the location where 3890 m, 2480 m, 1030 m and 20 m from the lowermost part of the upstream reach (10.1 km, 9.4 km, 7.9 km and 6.9 km from the river mouth) (Fig. 1). When descending the river, the pre-migrants with PIT tags pass through and are detected by one to four of the four antennas installed in the nursery habitat. Therefore, we defined the timing of the first detection by any of the four antennas as the start of river-descending.

The use of four antennas in the uppermost reach is better suited for accurately recording the onset of river-descending as each pre-migrant has their respective natal habitat throughout the uppermost reach. Using the fixed PIT-antenna system to detect the start of river-descending of pre-migrants is reasonable because salmonids typically stay in a limited habitat area (Rodríguez, 2002). Actually, our long-term monitoring on the movement of masu salmon pre-migrants in Horonai River has shown that they remain in their nursery habitat until they start river-descending in spring (R. Futamura, unpublished data).

One antenna in the transitional habitat (antenna E in the middle reach) was installed at a location 5.7 km from the river mouth (Fig. 1). We identified fish that passed through this antenna as pre-migrants. We also used the timing at which each pre-migrant passed through this antenna to quantify their period of stay in the transitional habitat. Specifically, we 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 pre-migrants and measure their period of stay in the transitional habitat is reasonable for the following two reasons. First, previous research (Futamura, Morita, Kanno, & Kishida, 2022) revealed that almost all masu salmon passing through this antenna exhibited morphological characteristics of sea-run migratory fish (i.e. smoltification). This indicates that only ocean-bound migratory fish (pre-migrants) are detected at this antenna. Additionally, this antenna rarely detected masu salmon that were tagged in the upstream reach, except during the river-descending season from April to June.

Capture survey of pre-migrants by migrant trap

During the season of the river-descending (April to June) in 2021 and 2022, we randomly captured river-descending pre-migrants using a migrant trap installed 5.7 km from the river mouth, positioned just 10 m below the fixed PIT-antenna in the transitional habitat (Fig. 1). This trap is placed where the river narrows below a cascade (50 cm in height). We checked the trap at least twice daily from April 1 to July 15 to see if any fish had been captured. If fish were captured in the trap, we 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 using a handheld PIT tag reader. After completing all measurements, fish were allowed to recover from anesthesia in a bucket filled with fresh river water, and then released into a pool just below the migrant trap.

Statistical analysis

We used linear models with a Gaussian distribution to examine the effect of body size on the stay duration in nursery and transitional sections. The response variable of our model is the duration of stay in each habitat (either nursery or transitional), whose expected value was related to linear predictors of fork length in early spring, year (2021 or 2022) and their interaction. Fork length in early spring was natural log transformed before the analysis. Year was included in the analysis also to consider the annual variation of the behavior of smaller pre-migrants. Although we conducted a capture-mark-recapture survey multiple times, individuals captured just before oceanic migration (i.e. early spring survey) were only used for the analysis. The underlying assumption in our model is that there is a positive correlation between growth and the duration of the stay in each habitat. Our supplementary analysis validated this assumption (see Appendix S1 for detail). All statistical analyses were performed using R version 4.1.2 (R Core Team, 2024).

Results

In the 2-year migration season (2021 and 2022), a total of 466 masu salmon pre-migrants (157 [2021] and 309 [2022]) were detected at any of the four PIT-antennas in the upstream reach (after leaving the nursery habitat) and then detected at the PIT antenna in the middle reach (beginning oceanic migration). The fork length of pre-migrants in early spring (mean \pm 1 SD) was 115.06 ± 11.42 mm in 2021 and 110.40 ± 11.22 mm in 2022, suggesting that 2022 had smaller pre-migrants than 2021. Pre-migrants were detected at one of the four PIT-antennas in the upstream reach (left their nursery habitat) between April 5 and May 30 in 2021 and between April 8 and May 27 in 2022. Pre-migrants were detected at the PIT antenna in the middle reach between April 17 and August 10 in 2021 and April 15 and July 5 in 2022. The period of stay in the transitional habitat (mean \pm 1 SD) was 26.83 ± 16.21 days in 2021 and 23.87 ± 16.85 days in 2022. Among pre-migrants detected at the PIT-antennas in the two

reaches, 207 were captured in the migrant trap (46 [2021] and 161 [2022]). As 466 pre-migrants were detected by the PIT antenna at the middle reach, this indicates that the capture efficiency of the migrant trap was 44% (207 out of 466). The fork length (\pm 1 SD) at the migrant trap was 132.87 ± 11.47 mm in 2021 and 137.66 ± 11.30 mm in 2022.

The linear model showed that the period of stay in nursery habitat was influenced by year ($t = 2.89$, $P = 0.004$), the interaction between year and early spring size ($t = -2.72$, $P = 0.006$) but not by early spring size ($t = -0.59$, $P = 0.559$) (Table 1). These results indicate that a significant effect of fork length on habitat residence occurred only in 2021 (Fig. 2). The period of stay in transitional habitat was influenced by year ($t = -2.82$, $P = 0.005$), fork length in early spring ($t = -4.32$, $P < 0.001$) and their interaction term ($t = 2.77$, $P = 0.006$) (Table 1). This indicates that the significant effect of FL on habitat residence was only found in 2022 (Fig. 2). Together, these models indicate that smaller pre-migrants stayed longer than larger ones in the transitional habitat than in the nursery habitat only in 2021, whereas smaller pre-migrants stayed longer than larger ones in the nursery habitat than in the transitional habitat only in 2022 (Fig. 2). The same patterns of statistical significance were also found in the analyses using the alternative size factor, body mass (see Appendix S2). These results were consistent even when we excluded the small size pre-migrants from the 2022 data (i.e. individuals smaller than 83 mm) (Appendix S3).

Discussion

In this study, we monitored the river-descending behavior in masu salmon pre-migrants in two distinct riverscape habitats (nursery habitat and transitional habitat) over two consecutive migration years. We found that the degree of extended stay for smaller pre-migrants compared to larger ones varied between nursery habitat and transitional habitat in both years (Fig. 2). These results suggest that smaller pre-migrants can alter their extended-stay habitat choice. Interestingly, even though smaller pre-migrants altered their preferred extended-stay habitat each year, the habitat they stayed longer in differed between the two migration years. This suggests that the choice of extended

Table 1 Summary statistics of the linear model predicting the period of stay in riverscape habitats prior to migration

	Estimate	Standard error	T value	P value
Period of stay in nursery habitat ~ Intercept + Year + ln (Fork length in early spring) + Year ^a × ln (Fork length in early spring)				
Intercept	47.53	47.22	1.01	0.315
Year ^a	164.37	56.98	2.89	0.004
ln (Fork length in early spring)	-5.83	9.96	-0.59	0.559
Year × ln (Fork length in early spring)	-32.74	12.05	-2.72	0.007
Period of stay in transitional habitat ~ Intercept + Year + ln (Fork length in early spring) + Year ^a × ln (Fork length in early spring) + ln (Period of stay in nursery habitat)				
Intercept	301.02	63.46	4.74	<0.001
Year ^a	-215.91	78.57	-2.82	0.005
ln (Fork length in early spring)	-57.84	13.38	-4.32	<0.001
Year ^a × ln (Fork length in early spring)	44.80	16.19	2.77	0.006

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

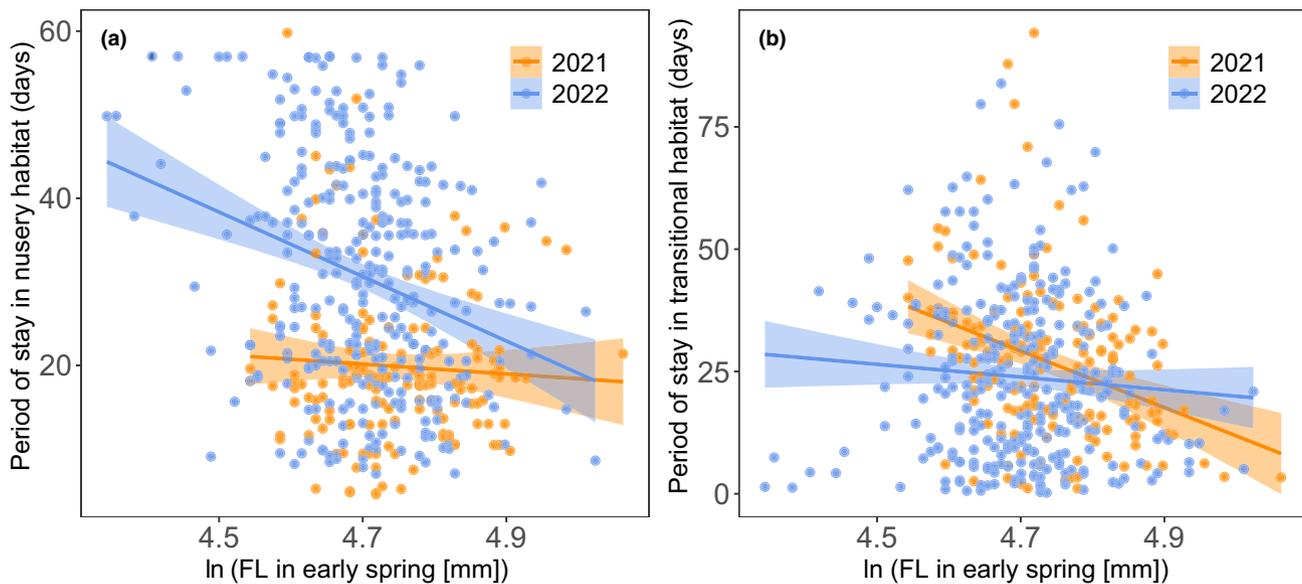


Figure 2 The relationship between fork length in early spring (mm) and period of stay in two riverscape habitats in 2021 (orange) and 2022 (blue). (a) Relationship between fork length in early spring and period of stay in the nursery habitat (elapsed date between April 1 and start of river-descending); (b) relationship between fork length in early spring and period of stay in transitional habitat (period of river-descending). Fork length was natural log-transformed before analysis. The regression line was fitted using linear regression. Shaded areas represent 95% CI.

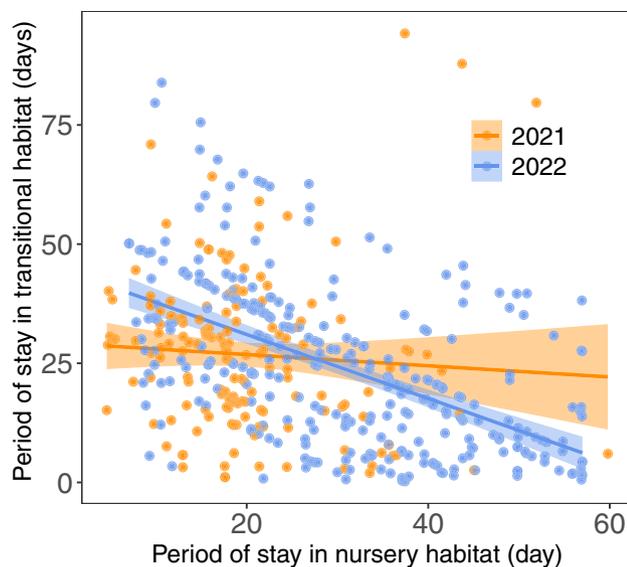


Figure 3 The relationship between the period of stay in nursery habitat and transitional habitat. The regression line was fitted using linear regression. Shaded areas represent 95% CI.

riverscape habitats by smaller pre-migrants is influenced by both spatial and annual factors.

Ecological theory predicts that animals select locations with high growth potential or survival potential as a habitat (Morris, 2003). Thus, smaller pre-migrants may have adjusted their period of stay in response to spatiotemporally fluctuating environmental factors that can influence growth and survival

potential. For example, prey availability could influence the foraging behavior of pre-migrants. In the study river, the abundance and types of prey communities vary between the upstream and middle reaches. Prey invertebrates, such as chironomids, are abundant in the middle reach, where water flow is slow or stagnant. On the other hand, baetids, which typically inhabit flowing water, are abundant in the upstream reach, where water flow is faster. Smaller pre-migrants of masu salmon may adjust their duration of stay in each riverscape habitat according to the annual variation in the abundance of these riverscape-specific invertebrates. Water temperature is another potential factor related to growth. Our results showed that smaller pre-migrants stayed longer in the nursery habitat than larger ones in 2022, but not in 2021 (Fig. 2). This pattern might be an adaptive response of smaller pre-migrants to water temperature as water temperature in early spring increases the growth of salmonids (Armstrong *et al.*, 2013; Simmons *et al.*, 2020). In support of this view, the average water temperature in the winter of 2022 was 1.61°C higher than in 2021 in the nursery habitat (R. Futamura, unpublished data). Predation risk is another possible factor affecting pre-migrant behavior, because prey animals tend to avoid areas with high predation risks (Gilliam & Fraser, 2001; Hope *et al.*, 2014; Matthews *et al.*, 2020). Although piscivorous birds and fish mainly inhabit the lower part of the river, including the middle reach, it is reasonable to assume that their abundance varies annually. Therefore, smaller pre-migrants may extend their stay in locations with low predation pressure. Overall, further long-term studies assessing the behavioral patterns of pre-migrants and environmental factors are needed to reveal whether smaller pre-migrants can flexibly adjust their duration of stay in each distinct habitat.

Even if masu salmon may have an ability to change their duration of stay based on the current environmental factors, time constraints may prevent them from staying longer. While a longer stay in the river is beneficial for achieving a larger size, there should be a limit to the length of stay. This is because a longer stay in the river results in a shorter duration of time spent in the ocean, leading to a decrease in the growth benefits gained during oceanic migration. In terms of riverscape habitat structure, the duration of stay in the initial riverscape habitat may influence that in the subsequent riverscape habitat. Therefore, if smaller pre-migrants extend their stay in the nursery habitat, they may not do so in the transitional habitat, even if the environmental conditions are favorable. Our data support this hypothesis as the period of stay in the nursery habitat was negatively correlated with the period in the transitional habitat (Fig. 3; Appendix S4). Time constraints might explain why smaller pre-migrants extended their stay in the nursery habitat but not in the subsequent transitional habitat in 2022.

Our 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 & Hoye, 2014; McIntyre *et al.*, 2015). However, migratory species are declining significantly due to various human activities (Kirby *et al.*, 2008; Limburg & Waldman, 2009). In particular, the loss and degradation of the pre-migration habitats are major causes of the decline of migratory animals (Jeffres & Moyle, 2012; McIntyre *et al.*, 2015). To effectively conserve migratory animals, conservation efforts that consider their life history are crucial (Levin & Lubchenco, 2008). As the delayed migration by the smaller pre-migrants occurred in different riverscape habitats across the two survey years, we emphasize the need to conserve both nursery habitat and transitional habitat. Sustaining both riverscape habitats as part of a habitat portfolio can increase the likelihood of smaller pre-migrants reaching larger sizes, even in variable environments (Schindler *et al.*, 2015). In particular, this strategy contributes to building resilience of migratory animals in the face of rapid environmental changes (Alley *et al.*, 2003).

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Author Contributions

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

Data Availability Statement

All data and R code used in this study are uploaded in Figshare (<https://doi.org/10.6084/m9.figshare.27826809.v1>).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Analysis of the assumption.

Appendix S2. Results on the statistical analysis on body mass.

Appendix S3. Results of the statistical analysis conducted on the data set excluding the smallest individuals (i.e., below 83 mm).

Appendix S4. Analysis on the complementary relationship on the stay of two pre-migration habitats.