

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

Ryo Futamura

Hokkaido University Graduate School of Environmental Science: Hokkaido Daigaku Daigakuin Kankyo Kagakuin Chikyu Kankyo Kagaku Kenkyuin

Kentaro Morita

Hokkaido University: Hokkaido Daigaku

Yoichiro Kanno

Colorado State University

Shoji Kumikawa

Hokkaido University: Hokkaido Daigaku

Yuichi Matsuoka

Hokkaido University: Hokkaido Daigaku

Atsushi Okuda

Hokkaido University: Hokkaido Daigaku

Hiroshi Sugiyama

Hokkaido University: Hokkaido Daigaku

Hiroyuki Takahashi

Hokkaido University: Hokkaido Daigaku

Jiro Uchida

Hokkaido University: Hokkaido Daigaku

Osamu Kishida (✉ kishida@fsc.hokudai.ac.jp)

Hokkaido University <https://orcid.org/0000-0002-2663-8155>

Research Article

Keywords: anadromous fish, growth period, growth rate, life history, *Oncorhynchus masou*

Posted Date: March 2nd, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-279594/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at *Oecologia* on January 22nd, 2022. See the published version at <https://doi.org/10.1007/s00442-022-05111-0>.

Abstract

For migratory species, attaining enough large size before migration is a key mechanism of individuals for their success in risky migration. Since the smaller migrants suffer from high mortality during migration, prospective migrants with smaller size should grow better than larger ones before migration. To test this prediction, we investigated size-dependent patterns of the two growth mechanisms (i.e., growth rate and duration) of juvenile masu salmon (*Onchorynchus masou*) before their oceanic migration. Masu salmon exhibit a partial migratory strategy, in which single population consists of oceanic migrants and river-dwelling residents. Our individual mark-recapture survey and assessment of the river-descending timing by PIT-tag antenna-reader system revealed that patterns of growth rate in the pre-migration period and the timing of migration correspond with our predictions. For around half-year before outmigration (i.e., between after decision of migration and before start of migration), the prospective migrants showed the size-dependent growth rate, in which individuals with smaller size exhibited higher growth rate than those with larger size, but the residents showed the size-independent growth rate. In addition, the prospective migrants showed the size-dependent timing of outmigration, in which individuals with smaller size delayed the migration timing than those with larger size, to lengthen the duration of pre-migration period. These results suggest that size-selective mortality during migration has shaped size-dependent adjustment of the pre-migration growth in migratory masu salmon. Conditional changes in growth rate and duration of pre-migration period may be an adaptive tactic for the migratory animals.

Introduction

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

Migratory animals suffer varying degrees of mortalities en route due to energetic demands and risk of predation. Migrants begin their preparations for the long journey well before migration by adopting strategies to cope with the costs of migration. In particular, attaining sufficiently large body size prior to migration is critical for completing the risky migration because smaller individuals are more vulnerable to a multitude of stressors during migration (Koenings et al., 1993; Sogard, 1997; Zabel et al., 2002). This suggests that pre-migration growth is under natural selection, and hence it leads us to expect different growth patterns between migrants and non-migrants (Gillanders et al., 2015). In fact, average growth rates prior to migration are higher in migratory species compared to their non-migratory congeners (Chaplin & Chaplin, 1981) and in migratory individuals compared to non-migratory conspecifics within the same species (Metcalf et al., 1988; Olsson & Greenberg, 2004; Palmer & Dingle, 1986; Snyder,

1991; Yamamoto & Nakano, 1996). Because intensive growth inflicts physiological and ecological costs (Hector & Nakagawa, 2012), the faster growth of migrants before migration than residents represents an adaptive tactic of migratory individuals (Arendt, 1997; Roff, 1991).

However, growth tactics may not be uniform among migratory individuals because ecological demands vary according to their status. In particular, growth tactics before migration may depend on body size of migratory individuals. Because mortality is size-dependent and smaller migrants suffer higher risk of mortality en route (Alerstam et al., 2003), smaller prospective migrants should enhance their growth rate before migration. However, accelerated growth may incur behavioral and physiological costs (Arendt, 1997; Dmitriew, 2011). For example, more foraging activities needed for faster growth are intimately associated with increased risk of predation and competition (Nicieza & Metcalfe, 1999; Stoks et al., 2005). Thus, larger prospective migrants may be less incentivized to invest in body growth to ensure survival until migration commences. Alternatively, smaller prospective migrants may delay migration until they attain sufficiently large body size. Again, larger prospective migrants may be less incentivized to delay migration, since arriving at new habitat sooner allows them to exploit the new habitat and resources sooner and longer. Despite these plausible expectations, only a few research has investigated intraspecific variation in the pre-migration growth tactics (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 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) having profound ecological consequences through alternation of predator–prey interactions (Bolker et al., 2003; Rohr et al., 2015; Schmitz et al., 2004).

Some animal populations consist of both migratory and non-migratory (i.e., resident) individuals, and such partially migratory populations provide an ideal opportunity to test intraspecific variation in growth tactics in relation to the migration strategy. Masu salmon (*Oncorhynchus masou*) exhibits partial migration commonly in northern Japan (Kato 1991; Morita 2018). Adults spawn eggs in rivers, and some individuals complete their life entirely in the freshwater environment, but others migrate to the ocean after spending one or two years in the freshwater environment. Seaward migration occurs in spring, but juveniles make decisions to migrate as migrants or not by the previous autumn (Nagae et al., 1994; Tamate & Maekawa, 2002). This has been evidenced by the physiological studies (i.e., the prospective 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 in the river for reproduction, body length of migrants is several times larger than that of mature residents (Morita, 2018; Tamate, 2012), and migrants that have returned to the river are more reproductively successful than mature residents. However, the migrants suffer high mortality rates during migration (Miyakoshi et al., 2001; Morita et al., 2014). Importantly, mortality during the migration is typically size-selective where survival increases with body size until it reaches an asymptote at certain body size (Shimoda et al., 2003). Therefore, the ecological demands of smaller prospective migrations to grow are substantial. This allows us to make the following two

predictions on size-dependent growth patterns of prospective migrants. First, smaller prospective migrants enhance the growth rates than larger ones, but such a size-dependent pattern is weak at the best among residents. Second, smaller prospective migrants descend the river later in the migratory period than larger ones to grow more in the river before the ocean entry. To test these operational predictions, (1) we compared size-dependent patterns of growth rates between prospective migrants and residents during 6 months leading up to migration (i.e., fall to spring), and (2) we investigated whether body size of prospective migrants at early spring just prior to migration explains their timing of seaward migration.

Methods

Study system

Our study was conducted in the Horonai River, a small spring-fed stream (2–5 m wide) located in Hokkaido, Japan. The river is approximately 12 km long from its headwaters to the ocean, and our study area was established in the uppermost 5.32 km part (hereafter called the survey area) (Fig. 1). The survey area was marked every 10 m on the riverbank to record fish locations at this spatial resolution. Our survey area was established to encompass the portion of the river occupied by juvenile masu salmon (Fig. 1). Masu salmon was replaced by non-native brown trout (*Salmo trutta*) downstream of the survey area (Fig. 1).

Capture-mark-recapture survey 01-Jan-2008

We conducted a capture-mark-recapture survey throughout the survey area on five occasions; (1) autumn 2018 (3rd – 18th Sep-2018), (2) early spring 2019 (1st – 5th Apr-2019), (3) autumn 2019 (7th – 11th Oct-2019), (4) early spring 2020 (18th – 26th Mar-2020), and (5) summer 2020 (25th – 26th Jul-2020). On each survey occasion, we collected fish and recorded the section of capture (10-m scale) using a backpack electrofishing unit (300–400 V DC, model 12B, Smith-Root, Inc., Vancouver, WA, USA) and 3-mm mesh dipnets (width, 30 cm). 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). We examined whether fish had been previously marked by checking for and recording a PIT tag (12.0 mm × 2.12 mm, Oregon RFID, Inc) with a tag reader. Some of individuals without PIT tags were randomly marked by inserting tags in their abdominal cavity. Fish were then allowed to recover from anesthesia in a bucket with fresh river water, and were released to the section of capture alive. We tagged a total of 3513 individuals (680 in 2018 autumn, 695 in 2019 early spring, 1325 in 2019 autumn, and 813 in 2020 early spring).

Discrimination of life history types and investigation on migrants at seaward migration

Although decision of juveniles to migrate or not by half a year before the migrants descend the river (Nagae et al. 1994), determination of the life history types is difficult in the pre-migration period. For

example, although increase in concentration of smoltification-related hormone in the previous autumn is an indicator of prospective migrants, monitoring the physiological changes is unrealistic to apply for the survey on many individuals. So, in the present study, we identified the life history type of each individual by directly checking the outmigration of individuals.

In the Horonai River, masu salmon migrate to the sea from late April to early July. During the migration season of 2019 and 2020, we recorded individual fish descending the river (i.e., migrants) using two types of device installed downstream of the survey area (Fig. 1). A pair of PIT antennas was 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 (i.e., hereafter called the migrant trap).

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

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

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

Growth rate

To test for evidence of size-dependent growth patterns, we used daily absolute growth (gain per day) of fork length and body mass as a growth rate. Daily growth during winter period was calculated based on mark-recapture data between autumn and early spring for prospective migrants and residents. Daily growth of the prospective migrants in the spring period was based on body length and mass measurements between the mark-recapture survey at early spring and the trap survey in the river-descending season in 2020. Daily growth of the residents in the spring period was calculated based on mark-recapture data between early spring and summer in 2020.

Statistical analysis

To test the first prediction, we analyzed daily absolute growth of fork length and body mass in each period (i.e., winter or spring) using linear models, in which life history types (i.e., migrants and residents), individual size at the beginning of each period (i.e., autumn for the winter period and early spring for the spring period) and their interactions were considered as fixed predictor variables. In the analysis of daily growth in winter, we also considered the effect of the survey year and its interaction with other factors. In addition, we investigated spatial variation in growth rates in two ways. First, we tested if growth rates depended on the longitudinal position along the river by using the section of initial capture as a covariate. Except for the seaward migration, our additional surveys using portable PIT antennas showed a majority of individuals stayed in the same 10-m section over several months (*unpublished data*) and territoriality is a common feature in stream-dwelling salmonids (e.g., Rodriguez, 2002). Second, we modeled growth rates using sections as a random predictor to account for their spatial variation independent of the longitudinal position. In total, we analyzed eight models in Online Resource 1: Table 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, we investigated whether individual size at the capture survey at early spring explained the river-descending timing. We used a linear model with the river-descending timing as a response variable, and body size (fork length or body mass), year and section of capture as fixed predictor variables. We included section of capture at early spring as a covariate to account for varying distances of individuals to the PIT antenna system. We didn't consider the interactive effects among body size, habitat section and year because our preliminary analysis using a full model showed non-significant effects of their interactions. All statistical analysis was conducted in R version 3.6.1 using package "lme4".

Results

Analyses of daily growth in the pre-migration period supported the first prediction. The interaction term between body size and life history types were consistently significant across the eight models ($p < 0.001$; see Table S2 in Online Resource 1). Specifically, smaller prospective migrants exhibited higher growth rates in both fork length and body mass than larger ones, but size-dependent growth patterns were not evident in residents (Fig. 2; Online Resource 1: Fig. S1). Other predictors were also statistically significant

(Online Resource 1: Table S2). Importantly, year had significant interactions with other covariates, indicating that the individuals change their growth rate according to the year-specific conditions.

River-descending timing was influenced significantly by body size (fork length model: $F_{1,97} = 24.85$, $p < 0.001$; body mass model: $F_{1,97} = 26.91$, $p < 0.001$), habitat section captured at early spring (fork length model: $F_{1,97} = 9.60$, $p = 0.003$; body mass model: $F_{1,97} = 6.49$, $p = 0.012$) and year (fork length model: $F_{1,97} = 22.56$, $p < 0.001$; body mass model: $F_{1,97} = 22.18$, $p < 0.001$). As predicted, of the prospective migrants captured at early spring, smaller fish descended the river later than larger fish (Fig. 3; Online Resource 2: Fig. 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 can shape size-dependent growth in the pre-migration period, but it has not been documented to our knowledge. Our study revealed that pre-migration growth rates and migration timing (i.e., growth duration) were both size-dependent in migratory masu salmon. In both winter and spring, smaller prospective migrants exhibited higher growth rates than larger ones, but residents did not show such a size-dependent growth pattern. In addition, of prospective migrants, smaller fish at early spring descended the river later than larger fish. As a result, body size at the time of seaward migration was remarkably constant throughout the river-descending season (i.e., fork length [mean \pm 1SD] in April, May, June are 128.6 ± 9.1 , 129.4 ± 9.20 , 133.5 ± 8.6 mm, respectively; Fig. 4). This suggests a size threshold, above which migrants can better survive during the migration. In fact, our additional investigation showed that the smallest 10% migrants (i.e., < 121 mm in fork length) suffered 31% higher mortality rates than larger migrants when they passed through the area downstream in which many large piscivorous salmonids inhabit (*unpublished data*). Hence, our results strongly suggest that the smaller prospective migrants need to accelerate growth or extend their growth period before migration to attain sufficiently large size for successful migration. In contrast, larger prospective migrants nearer to the threshold body size need not 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 the decision to optimize current and future needs that varies by individuals of based on body size and life history.

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. Small prospective migrants in the autumn may not delay migration to minimize the cost of delayed migration, if they grow well in winter. This hypothesis was supported by our additional analysis of the river-descending timing. Analysis using a linear model that considered daily growth rate in winter period, fork length at autumn and year as predictor variables showed significant negative effects of daily growth on the river-descending timing ($F_{1,97} = 9.77$, $p = 0.002$), indicating that prospective migrants with higher growth in the winter period

descended the river earlier. Such a growth-dependent pattern of the migration timing can represent an adaptive phenotypic plasticity (sense in Via et al. 1995) under unpredictable growth conditions (e.g., resource availability and temperature) in the pre migration period, which allows individuals to take full advantage of migration. If so, it should shape annual covariation between growth in winter and river-descending timing of migrants. Our two-year data support this idea. The significant effects of year and its interactions with individual size on the growth rates (Online Resource 1: Table S2) suggest that the prospective 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. The prospective migrants that grew better in winter (i.e., 2019–2020) started their migration earlier than those that grew less (i.e., 2018–2019). Future long-term monitoring is required to rigorously test whether annual variation in the winter growth rate predicts the river-descending timing of the 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 & Kishida, 2015). Individuals can achieve higher growth rates by increasing foraging activities (Damsgird & Dill, 1998; Sundström & Devlin, 2011). Increased foraging may lead to more profound ecological consequences by consuming more prey and also increasing the likelihood of encounter with predators (Biro et al., 2004; Kishida et al., 2011). Here, we found that smaller prospective 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 more strongly than the latter through more intensive and prolonged foraging in the river. Since juveniles of migratory salmonids often dominate the boreal streams, size distributions of prospective migrants may drive the abundance and individual growth of predators and prey. Hence, unravelling the behavioral mechanisms shaping the size-dependent growth is critical to identify the role of intraspecific growth variation in the dynamics of ecological community in the river and even in the adjacent ecosystem such as riparian forests (cf. Baxter et al., 2004, Nakano & Murakami, 2001).

The conditional changes in growth rates and duration of the prospective migrants may be adaptive tactics common in other migratory species. The comparative studies of milkweed bugs reported that average growth rates of migratory species before migration is higher than those of non-migratory species (Chaplin & Chaplin, 1981). This suggests that the migrants of 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 the lipids before migration (Metcalf & Furness, 1984; Rubolini et al., 2002; Skrip et al., 2015). In these species, lighter individuals may accumulate the 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 the migratory species can reveal a common mechanism maintaining individual growth variation and provide an insight into an evolution of migration.

Declarations

Acknowledgments

We thank Kotaro Takai, Tomoaki Sato, Susumu Igarashi, Makoto Odagiri, Ryohei Sugime, Muku Tsujino, Hisanori Okamiya, Yoshihiro Inoue, Aya Yamaguchi, Yuto Sasaki, Mari Kuroki, Ayaka Terada, Souta Minamiguchi, Kenya Matsui, Rin Uchida, Yutaka Okuzaki, Keisuke Atsumi, Moritz Lürig and Takehito Muto for their help in field work. We also greatly appreciate the support of Manabu Futamura and Nobuko Futamura. We thank Takashi Saitoh, Naoki Agetsuma and Itsuro Koizumi for helpful comments on our study.

Funding

This work was supported by a JSPS KAKENHI grant to OK (17H03725 and 20K21439), the Research Council of Norway project Global trout (no 287438) to KM and a Faculty Fellow grant by the Colorado Water Center to YK.

Conflicts of interest

The authors declare that they have no conflict of interest.

Ethics approval

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

Consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

All of the data analyzed in this study are available in the following site.

<https://www.dropbox.com/sh/xz6extqnb0zvew/AACROERscPKTQ41q6XcqxrMGa?dl=0>

Code availability

All of the R scripts are available in the following site.

<https://www.dropbox.com/sh/xz6extqnb0zvew/AACROERscPKTQ41q6XcqxrMGa?dl=0>

References

- Alerstam, T., Hedenstrom, A., & Akesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, *103*, 247–260. <https://doi.org/10.1034/j.1600-0706.2003.12559.x>
- Arendt, J. D. (1997). Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology*, *72*, 149–177. <https://doi.org/10.1086/419764>
- Bassar, R. D., Marshall, M. C., López-Sepulcre, A., Zandonà, E., Auer, S. K., Travis, J., Pringle, C. M., Flecker, A. S., Thomas, S. A., & Reznick, D. N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 3616–3621. <https://doi.org/10.1073/pnas.0908023107>
- Baxter, C. V., Fausch, K. D., Murakami, M., & Chapman, P. L. (2004). Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, *85*, 2656–2663. <https://doi.org/10.1890/04-138>
- Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2004). Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*, 2233–2237. <https://doi.org/10.1098/rspb.2004.2861>
- Bohlin, T., Dellefors, C., & Faremo, U. (1996). Date of smolt migration depends on body-size but not age in wild sea-run brown trout. *Journal of Fish Biology*, *49*, 157–164. <https://doi.org/10.1111/j.1095-8649.1996.tb00012.x>
- Bolker, B., Holyoak, M., Krivan, V., Rowe, L., & Schmitz, O. J. (2003). Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology*, *84*, 1101–1114. [https://doi.org/10.1890/0012-9658\(2003\)084\[1101:CTAESO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1101:CTAESO]2.0.CO;2)
- Chaplin, S. B., & Chaplin, S. J. (1981). Comparative growth energetics of a migratory and nonmigratory insect: the milkweed bugs. *The Journal of Animal Ecology*, *50*, 407–420. <https://doi.org/10.2307/4063>
- Chapman, B. B., Brönmark, C., Nilsson, J. Å., & Hansson, L.A. (2011). The ecology and evolution of partial migration. *Oikos*, *120*, 1764–1775. <https://doi.org/10.1111/j.1600-0706.2011.20131.x>
- Chapman, J. W., Bell, J. R., Burgin, L. E., Reynolds, D. R., Pettersson, L. B., Hill, J. K., Bonsall, M. B., & Thomas, J. A. (2012). Seasonal migration to high latitudes results in major reproductive benefits in an insect. *Proceedings of the National Academy of Sciences*, *109*, 14924–14929. <https://doi.org/10.1073/pnas.1207255109>
- Damsgird, B., & Dill, L. M. (1998). Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch*. *Behavioral Ecology*, *9*, 26–32. <https://doi.org/10.1093/beheco/9.1.26>

Dingle, H., & Drake, V. A. (2007). What is migration? *BioScience*, *57*, 113–121.

<https://doi.org/10.1641/B570206>

Dmitriew, C. M. (2011). The evolution of growth trajectories: what limits growth rate? *Biological Reviews*, *86*, 97–116. <https://doi.org/10.1111/j.1469-185X.2010.00136.x>

Furey, N. B., Hinch, S. G., Bass, A. L., Middleton, C. T., Minke-Martin, V., & Lotto, A. G. (2016). Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. *Journal of Animal Ecology*, *85*, 948–959. <https://doi.org/10.1111/1365-2656.12528>

Gillanders, B. M., Izzo, C., Doubleday, Z. A., & Ye, Q. (2015). Partial migration: Growth varies between resident and migratory fish. *Biology Letters*, *11*, 20140850. <https://doi.org/10.1098/rsbl.2014.0850>

Gross, M. R., Coleman, R. M., & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science*, *239*, 1291–1293. <https://doi.org/10.1126/science.239.4845.1291>

Hector, K. L., & Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology*, *81*, 583–593. <https://doi.org/10.1111/j.1365-2656.2011.01942.x>

Kato, F. (1991). Life histories of masu and amago salmon (*Oncorhynchus masou* and *O. rhodurus*). In C. Groot, & I. Margolis (Eds.), *Pacific Salmon Life Histories* (pp. 448–520). UBC Press.

Kishida, O., Trussell, G. C., Ohno, A., Kuwano, S., Ikawa, T., & Nishimura, K. (2011). Predation risk suppresses the positive feedback between size structure and cannibalism. *Journal of Animal Ecology*, *80*, 1278–1287. <https://doi.org/10.1111/j.1365-2656.2011.01871.x>

Koenings, J., Geiger, H.J., & Hasbrouck, J.J. (1993). Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*, 600-611. <https://doi.org/10.1139/f93-069>

Lok, T., Overdijk, O., & Piersma, T. (2015). The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters*, *11*, 20140944. <https://doi.org/10.1098/rsbl.2014.0944>

McKinnon, L., Smith, P. A., Nol, E., Martin, J. L., Doyle, F. I., Abraham, K. F., Gilchrist, H. G., Morrison, R. I. G., & Bêty, J. (2010). Lower predation risk for migratory birds at high latitudes. *Science*, *327*, 326–327. <https://doi.org/10.1126/science.1183010>

Metcalfe, N. B., & Furness, R. W. (1984). Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behavioral Ecology and Sociobiology*, *15*, 203–206. <https://doi.org/10.1007/BF00292976>

- Metcalfe, N. B., Huntingford, F. A., & Thorpe, J. E. (1988). Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, *57*, 463-474. <https://doi.org/10.2307/4918>
- Metcalfe, N. B., Fraser, N., & Burns, M. D. (1998). State-dependent shifts between nocturnal and diurnal activity in salmon. *Proceedings of the Royal Society B: Biological Sciences*, *265*, 1503–1507. <https://doi.org/10.1098/rspb.1998.0464>
- Miyakoshi, Y., Nagata, M., & Kitada, S. (2001). Effect of smolt size on postrelease survival of hatchery-reared masu salmon *Oncorhynchus masou*. *Fisheries Science*, *67*, 134–137. <https://doi.org/10.1046/j.1444-2906.2001.00209.x>
- Morita, K., Tamate, T., Kuroki, M., & Nagasawa, T. (2014). Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish. *Journal of Animal Ecology*, *83*, 1268-1278. <https://doi.org/10.1111/1365-2656.12240>
- Morita, K. (2018). Ocean Ecology of Masu (Cherry) Salmon. In R. Beamish (Eds.), *Ocean Ecology of Pacific Salmon and Trout* (pp 697-730). American Fisheries Society.
- Nagae, M., Fuda, H., Hara, A., Saneyoshi, M., & Yamauchi, K. (1994). Changes in serum concentrations of immunoglobulin M (IgM), cortisol and thyroxine (T₄) during smoltification in the masu salmon *Oncorhynchus masou*. *Fisheries Science*, *60*, 241–242. <https://doi.org/10.2331/fishsci.60.241>
- Nakano, S., & Murakami, M. (2001). Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences*, *98*, 166-170. <https://doi.org/10.1073/pnas.98.1.166>
- Newton, I. (2010). *The migration ecology of birds*. Elsevier.
- Nicieza, A. G., & Metcalfe, N. B. (1999). Costs of rapid growth: the risk of aggression is higher for fast-growing salmon. *Functional Ecology*, *13*, 793-800. <https://doi.org/10.1046/j.1365-2435.1999.00371.x>
- Nøttestad, L., Giske, J., Holst, J. C., & Huse, G. (1999). A length-based hypothesis for feeding migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*, 26–34. <https://doi.org/10.1139/f99-222>
- Olsson, I. C., & Greenberg, L. A. (2004). Partial migration in a landlocked brown trout population. *Journal of Fish Biology*, *65*, 106–121. <https://doi.org/10.1111/j.0022-1112.2004.00430.x>
- Osterback, A. M. K., Frechette, D. M., Shelton, A. O., Hayes, S. A., Bond, M. H., Shaffer, S. A., & Moore, J. W. (2013). High predation on small populations: avian predation on imperiled salmonids. *Ecosphere*, *4*, 1–21. <https://doi.org/10.1890/ES13-00100.1>

- Palmer, J. O., & Dingle, H. (1986). Direct and correlated responses to selection among life-history traits in milkweed bugs (*Oncopeltus fasciatus*). *Evolution*, *40*, 767-777. <https://doi.org/10.2307/2408461>
- Quinn, T. P. (2018). *The behavior and ecology of Pacific salmon and trout*. University of Washington press.
- R Core Team. 2019. "R: A Language and Environment for Statistical Computing." <https://www.r-project.org/>.
- Rodriguez, M. A. (2002). Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology*, *83*, 1-13. <https://doi.org/10.2307/2680115>
- Roff, D. A. (1991). Life history consequences of bioenergetic and biomechanical constraints on migration. *American Zoologist*, *31*, 205-215. <https://doi.org/10.1093/icb/31.1.205>
- Rohr, J. R., Civitello, D. J., Crumrine, P. W., Halstead, N. T., Miller, A. D., Schotthoefer, A. M., Stenoien, C., Johnson, L. B., & Beasley, V. R. (2015). Predator diversity, intraguild predation, and indirect effects drive parasite transmission. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 3008–3013. <https://doi.org/10.1073/pnas.1415971112>
- Rowe, D. K., & Thorpe, J. E. (1990). Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L., parr. *Journal of Fish Biology*, *36*, 643–658. <https://doi.org/10.1111/j.1095-8649.1990.tb04319.x>
- Rubolini, D., Pastor, A. G., Pilastro, A., & Spina, F. (2002). Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. *Journal of Avian Biology*, *33*, 15-22. <https://doi.org/10.1034/j.1600-048X.2002.330104.x>
- Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, *7*, 153–163. <https://doi.org/10.1111/j.1461-0248.2003.00560.x>
- Shimoda, K., Naito, K., Nakajima, M., Sasaki, Y., Misaka, N., & Imada, K. (2003). Marine survival and growth of masu salmon *Oncorhynchus masou*, in relation to smolt size. *NIPPON SUISAN GAKKAISHI*, *69*, 926–932. <https://doi.org/10.2331/suisan.69.926> [In Japanese with English summary.]
- Sillett, T. S., & Holmes, R. T. (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, *71*, 296–308. <https://doi.org/10.1046/j.1365-2656.2002.00599.x>
- Skrip, M. M., Bauchinger, U., Goymann, W., Fusani, L., Cardinale, M., Alan, R. R., & McWilliams, S. R. (2015). Migrating songbirds on stopover prepare for, and recover from, oxidative challenges posed by long-distance flight. *Ecology and Evolution*, *5*, 3198–3209. <https://doi.org/10.1002/ece3.1601>

- Snyder, R. J. (1991). Migration and life histories of the threespine stickleback: evidence for adaptive variation in growth rate between populations. *Environmental Biology of Fishes*, 31, 381–388. <https://doi.org/10.1007/BF00002363>
- Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of marine science*, 60, 1129-1157.
- Stoks, R., De Block, M., Van De Meutter, F., & Johansson, F. (2005). Predation cost of rapid growth: behavioural coupling and physiological decoupling. *Journal of Animal Ecology*, 74, 708–715. <https://doi.org/10.1111/j.1365-2656.2005.00969.x>
- Sundström, L. F., & Devlin, R. H. (2011). Increased intrinsic growth rate is advantageous even under ecologically stressful conditions in coho salmon (*Oncorhynchus kisutch*). *Evolutionary Ecology*, 25, 447–460. <https://doi.org/10.1007/s10682-010-9406-1>
- Takatsu, K., & Kishida, O. (2015). Predator cannibalism can intensify negative impacts on heterospecific prey. *Ecology*, 96, 1887–1898. <https://doi.org/10.1890/14-1616.1>
- Tamate, T. (2012). A concise review of geographic variation in adult body size in anadromous masu salmon, *Oncorhynchus masou*. *Environmental Biology of Fishes*, 94, 527–532. <https://doi.org/10.1007/s10641-009-9552-x>
- Tamate, T., & Maekawa, K. (2002). Individual growth and phase differentiation of lacustrine masu salmon, *Oncorhynchus masou*, under artificial rearing conditions. *Ichthyological Research*, 49, 397–400. <https://doi.org/10.1007/s102280200061>
- Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., & Van Tienderen, P. H. (1995). Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology & Evolution*, 10(5), 212-217. [https://doi.org/10.1016/S0169-5347\(00\)89061-8](https://doi.org/10.1016/S0169-5347(00)89061-8)
- Yamamoto, S., & Nakano, S. (1996). Growth and development of a bimodal length-frequency distribution during smolting in a wild population of white-spotted charr in northern Japan. *Journal of fish biology*, 48(1), 68-79. <https://doi.org/10.1111/j.1095-8649.1996.tb01419.x>
- Zabel, R. W., & Williams, J. G. (2002). Selective mortality in Chinook salmon: what is the role of human disturbance?. *Ecological Applications*, 12, 173-183. [https://doi.org/10.1890/1051-0761\(2002\)012\[0173:SMICSW\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0173:SMICSW]2.0.CO;2)

Figures

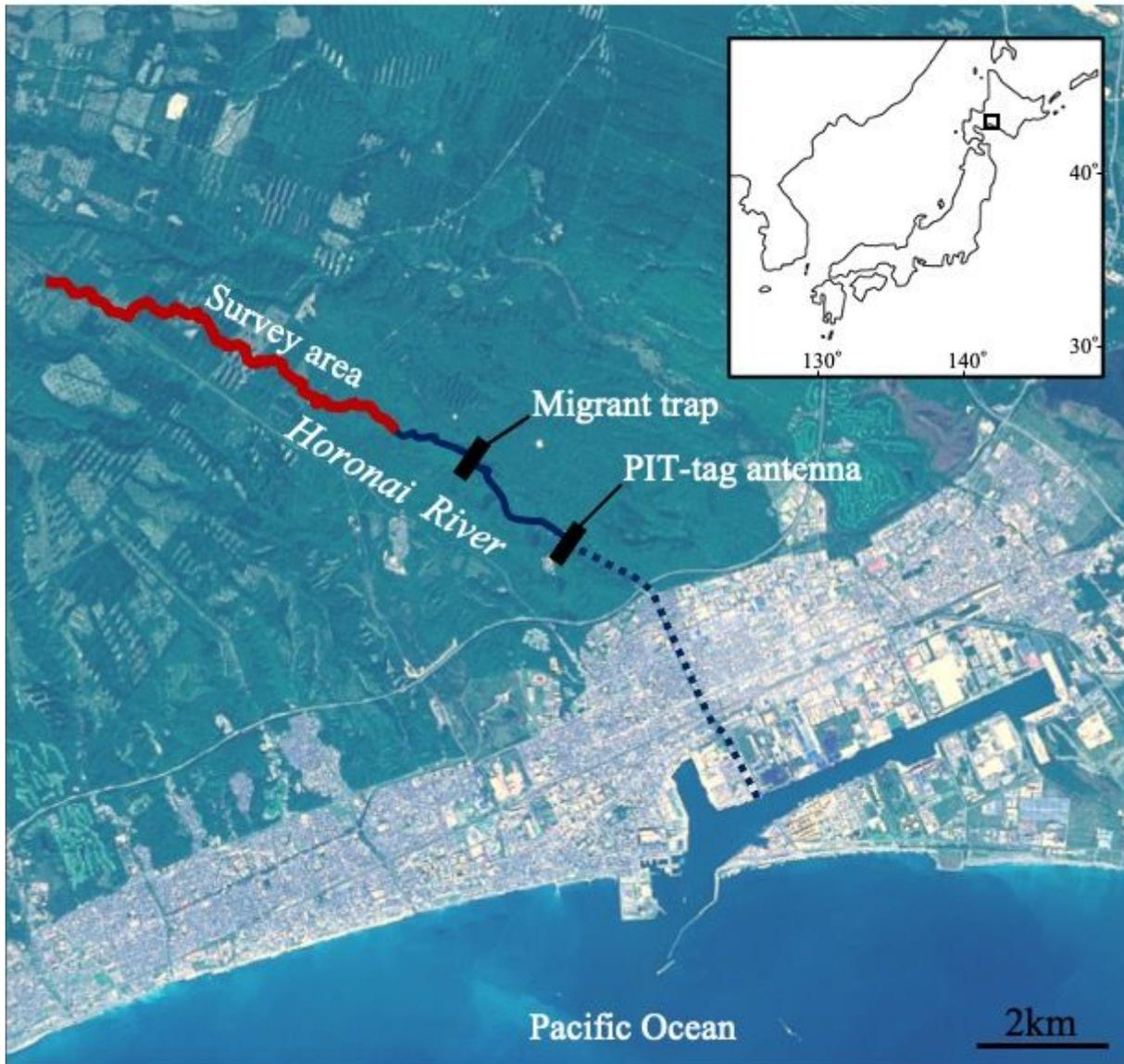


Figure 1

The location of our survey area. This study was conducted at 5.3 km reach (as shown in red line) which corresponds to the primary distribution area of juvenile masu salmon in the Horonai River. The further downstream areas consist of the slow-flowing reaches where brown trout (*Salmo trutta*) dominate (as shown in blue lines) and the fast-flowing reaches due to the past straitened river modification with concrete revetment, in which very few fish inhabit (as shown in dotted blue lines). The migrant trap and PIT-tag antenna was installed 1.2 km and 2.3 km downstream from the survey area, respectively. This map is based on the Digital Map (Aerial image map) published by Geospatial Information Authority of Japan. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

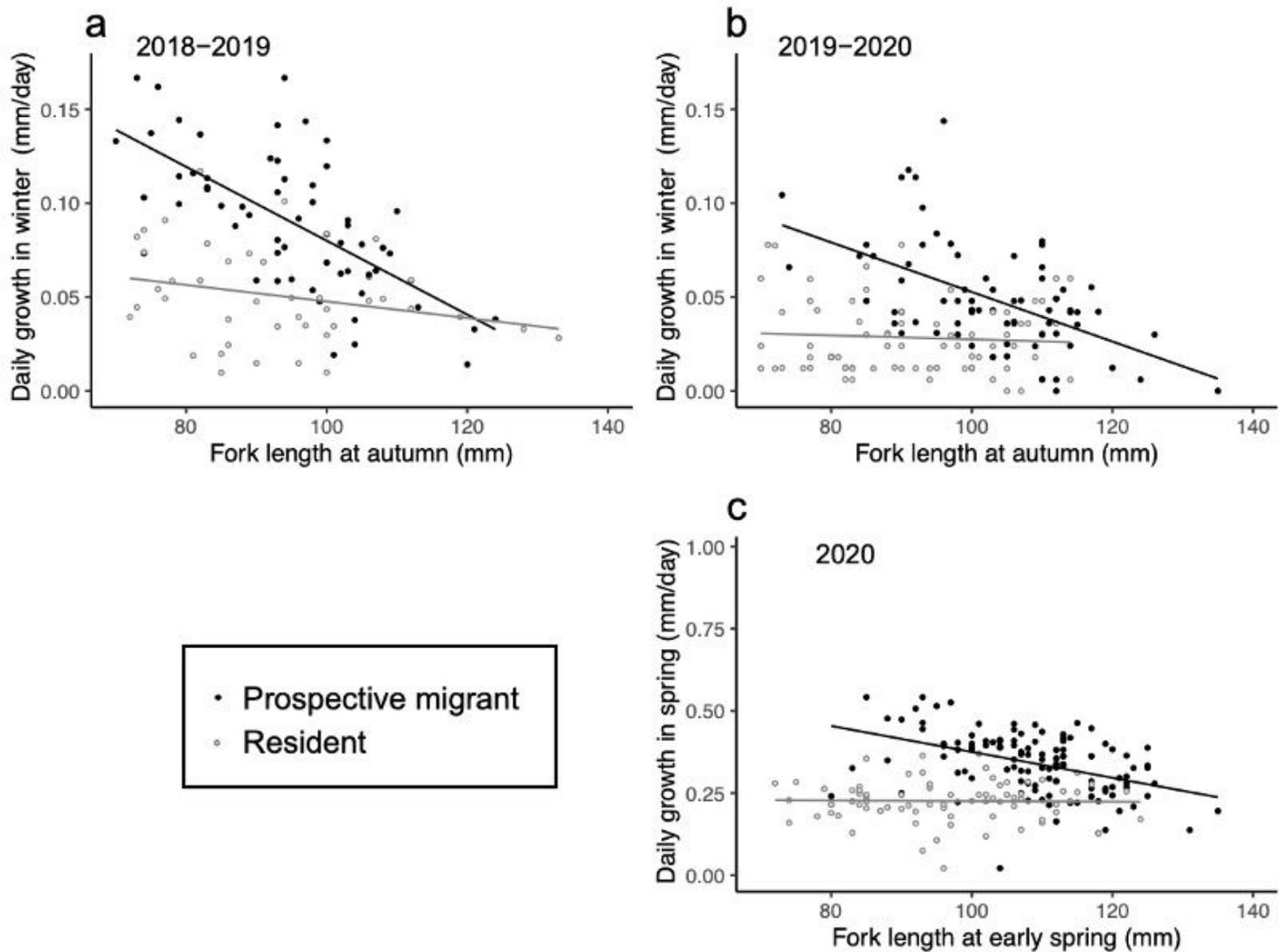


Figure 2

Relationship between size (fork length) and the subsequent growth rate of prospective migrants (black) and residents (grey) of masu salmon juveniles. (A) Daily growth in winter period (2018–2019); (B) daily growth in winter period (2019–2020); (C) daily growth in spring period (2020). Regression lines; (A) $Y = -2.0 \times 10^{-3}X + 0.28$, $p < 0.001$, Adjusted $R^2 = 0.43$, for prospective migrants; $Y = -5.3 \times 10^{-4}X + 0.10$, $p = 0.025$, Adjusted $R^2 = 0.08$, for residents; (B) $Y = -1.3 \times 10^{-3}X + 0.18$, $p < 0.001$, Adjusted $R^2 = 0.28$, for prospective migrants; $Y = -1.1 \times 10^{-4}X + 0.04$, $p = 0.542$, Adjusted $R^2 = -0.008$, for residents (C); $Y = -3.9 \times 10^{-3}X + 0.77$, $p < 0.001$, Adjusted $R^2 = 0.19$, for prospective migrants; $Y = -1.0 \times 10^{-4}X + 0.24$, Adjusted $R^2 = -0.01$, $p = 0.856$, for residents.

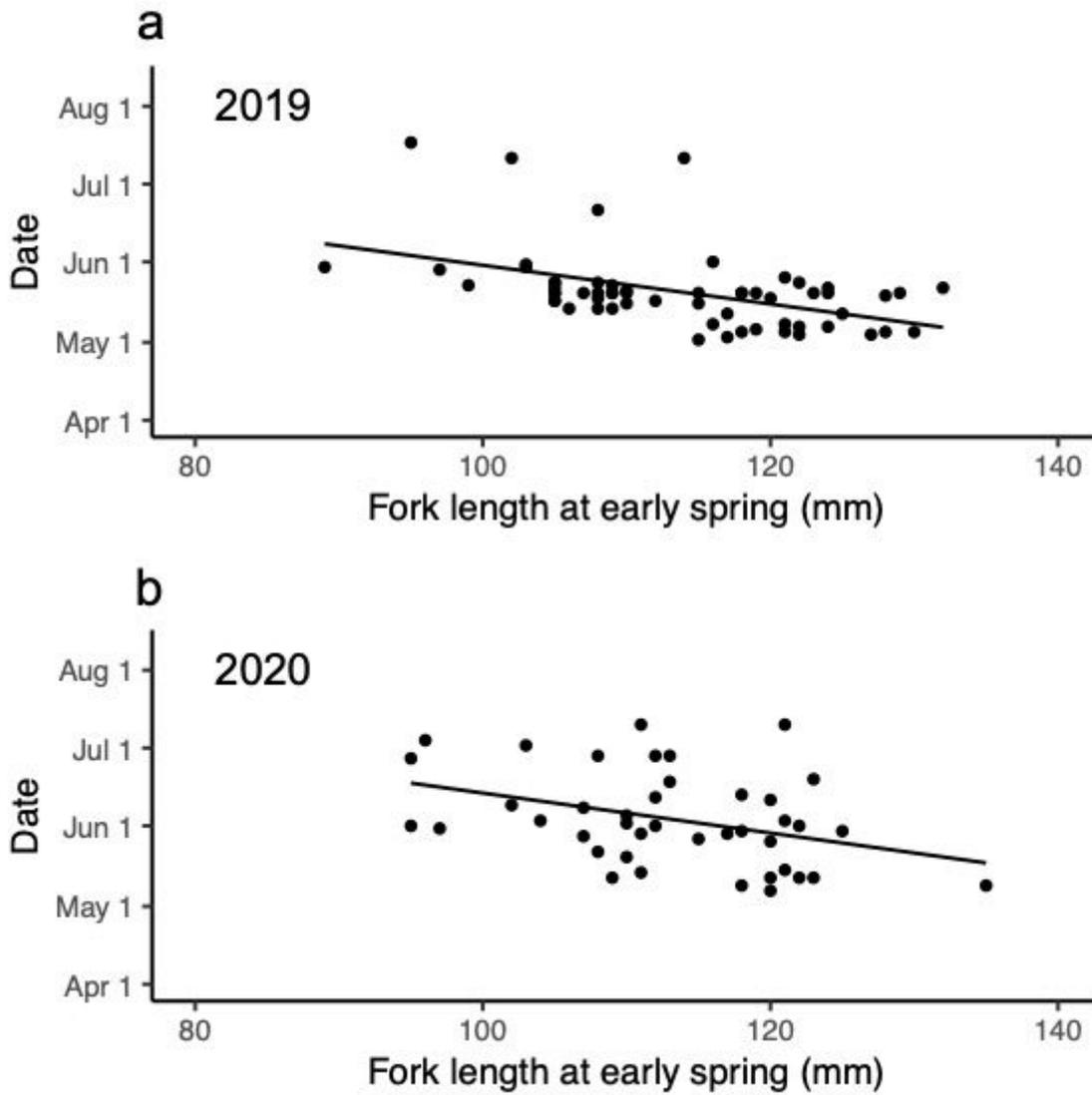


Figure 3

Relation between the river-descending timing (date) and fork length at the early spring of the prospective migrants in 2019 (a) and 2020 (b). Regression lines; (a) $Y = -0.75X + 108.54$, $p < 0.001$, Adjusted $R^2 = 0.20$; (b) $Y = -0.77X + 124.60$, $p = 0.015$, Adjusted $R^2 = 0.12$.

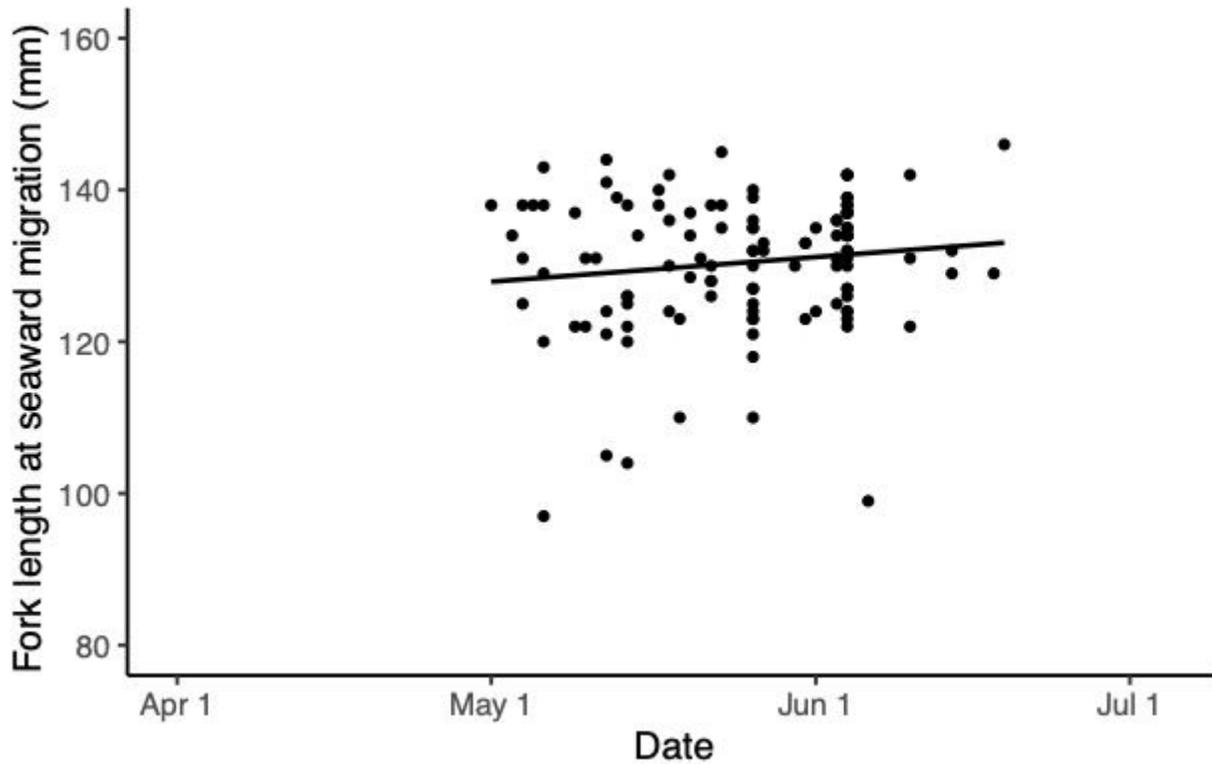


Figure 4

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 $R^2 = 0.05$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [ESM1.docx](#)
- [ESM2.docx](#)