Journal of Ethology (2026) 44:87–96
https://doi.org/10.1007/s10164-025-00871-7

ARTICLE

Costs of size increase prior to oceanic migration inferred from predation-caused wounds in an anadromous fish

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Received: 18 July 2025 / Accepted: 14 October 2025 / Published online: 29 October 2025
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Abstract

Since the mortality during migration is typically greater among smaller individuals, migrants should adopt growth tactics to attain a large size before their migration trip. Size-dependent growth patterns represent such a case, where smaller pre-migrants exhibit rapid growth and delay the start of migration to attain a large body size. To understand factors that shape size-dependent growth patterns, revealing the costs associated with rapid growth and delayed migration is crucial, as size-dependent growth patterns cannot be solely explained by ecological demands of growth. We focused on the trade-off between growth and survival and investigated whether faster growth rates and longer pre-migration periods incurred higher predation risk in pre-migrants of masu salmon (*Oncorhynchus masou*). A capture-mark-recapture survey was conducted and predation-caused wounds as a proxy for predation risk were checked. Migrants that exhibited higher growth rate did not have higher probability of predation-caused wounds, but migrants that stayed longer in the river had higher probabilities of having predation-caused wounds, especially inflicted by piscivorous birds. This implies that smaller pre-migrants extend their stay in the river to attain larger size for surviving oceanic migration, although the extended stay in the river is costly in terms of increased predation risk.

Keywords Trade-off · Growth · Predation · Life-history · Variation · Individual · Salmonid

Introduction

Many animals migrate to complete their life cycle (Dingle and Drake 2007; Alerstam and Bäckman 2018). Although they benefit substantially from migration, they also suffer high mortality during migration (Alerstam et al. 2003). Notably, smaller migratory individuals (migrants) suffer higher mortality during 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 pre-migrants should adopt growth tactics aimed at reaching a sufficiently large size to survive migration (i.e., size-threshold) once they make their decision to migrate (Arendt 1997).

Previous research has documented potential growth tactics prior to migration (Arendt 1997). For example, studies on anadromous salmonids have demonstrated that smaller pre-migrants exhibit higher growth rates during their stay in the river and delay departure of oceanic migration (i.e., an extended pre-migration period) compared to their larger counterparts (Nicieza and Brana 1993; Bohlin et al. 1996;

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Sigourney et al. 2008; Dermond et al. 2019; Futamura et al. 2022a). This combination of higher growth rates in the river and extended stay in the river allow smaller pre-migrants “catch-up” to larger counterparts before oceanic migration (Futamura et al. 2022a). Given that smaller pre-migrants face stronger ecological demands for growth than larger ones in the river, these size-dependent growth patterns can be interpreted as life-history tactics to enhance their survival prospects. However, it is inappropriate to interpret these size-dependent growth patterns as life-history tactics solely on the basis of the ecological demands for growth. If faster growth rates and longer pre-migration periods do not incur any cost, maximizing size increment before oceanic migration should be beneficial for pre-migrants, regardless of body size. Therefore, costs associated with faster growth and longer pre-migration period should be a key factor in shaping this growth pattern as life-history tactics. However, these potential costs remain largely unexplored.

In this study, we addressed this knowledge gap by focusing on the trade-off between growth and survival (Stearns 1989). A trade-off between growth and survival exists where individuals attempting to achieve a larger size increment are subject to a higher mortality risk (Stearns 1989, 1992; Mangel and Stamps 2001). This growth-survival trade-off has been documented in previous studies that explored 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 associated with behaviors that individuals adopt to achieve a greater increment in size (Houston et al. 1993; Dmitriew and Rowe 2005). To achieve greater size increase, individuals need to either increase their foraging activity per unit of time or spend more time on their foraging (Werner and Anholt 1993; Damsgird and Dill 1998; Willette 2001). However, these behaviors are likely to increase encounters with predators (Lima and Dill 1990; Brown and Kotler 2004; Verdolin 2006).

Predation-caused wounds can be used as a proxy for predation risk. Predators might fail to eat the prey even after their initial attack on their target prey (Christensen et al. 1996; Hedenström and Rosén 2001). Such failed attacks can injure prey and result in a wound on prey body (i.e., predation-caused wounds) (Rennolds and Bely 2023). These predation-caused wounds can be found in wide range of animal taxa, including invertebrates (Barclay et al. 2024; Subasi et al. 2024), fish (Reimchen 1988, 1992; Davies et al. 1995; Polyakov et al. 2022), amphibians (Mott and Steffan 2014), reptiles (Martín and Salvador 1995), birds (Kepler 1967; Lyver 2000) and mammals (Visser et al. 2010). Because predation-caused wounds are the indicator of the past prey-predator interaction, this offers a unique opportunity to evaluate the predation risk, particularly in natural settings where observing prey-predator interaction is challenging. Here, we examined whether pre-migrants with a higher growth rate and longer growth period were subject to a higher predation risk before oceanic migration in masu salmon (*Oncorhynchus masou*) by investigating the frequency of predation caused wounds.

Masu salmon, an endemic salmonid to East Asia, commonly exhibit partial migration, with populations consisting of both river-dwelling residents and anadromous migrants (Kato 1991). Residents remain in the river throughout their lives (Nakano 1995; Sakata et al. 2005). In contrast, migrants typically spend the first 1–2 years in the river, during which they mostly stay in a limited habitat area in the upstream of the river, which serves as their nursery habitat. Subsequent to the stay at the nursery habitat, migrants descend the middle and lower reaches of the river (river corridor) towards the ocean in spring (i.e., between April and July) to begin oceanic migration (Kato 1991). Migrants travel the resource-rich, but high-risk ocean, a distance of more than 1000 km (from their natal river to the Sea of Okhotsk) (Machidori and Kato 1984). Finally, large-grown migrants return to their natal river to spawn (Morita 2018). Migrants, particularly smaller ones, face size-selective mortality during oceanic migration (Miyakoshi et al. 2001; Shimoda et al. 2003; Miyakoshi 2006). Notably, in masu salmon, we found size-dependent growth patterns among pre-migrants before oceanic migration, suggesting a growth tactic to avoid size-selective mortality during oceanic migration. Specifically, we found that smaller pre-migrants had exhibited higher growth rates during the half-year period before they started oceanic migration and descended the river later than larger ones in the same seasons (Futamura et al. 2022a).

In this study, we hypothesized that a faster growth rate and a longer river residency period of pre-migrants would be accompanied by increased predation risk in the river. More interpretively, we considered that these costs would result in the size dependence of growth rates and pre-migration periods. Specifically, the smaller pre-migrants would not survive the risky oceanic migration unless they attained larger sizes before oceanic migration. Therefore, they would accelerate growth rates and extend the pre-migration periods in the river, even if these growth tactics are accompanied by potentially higher costs. In contrast, the larger pre-migrants would not need to invest in additional size growth to prepare for risky oceanic migration and minimize these potential costs. Accordingly, we tested the following two predictions. First, pre-migrants that exhibited higher growth rates just before oceanic migration (i.e., period between early spring and start of oceanic migration) would be exposed to higher predation risk than those exhibiting lower growth rates. Second, pre-migrants that started oceanic migration later would be exposed to higher predation risk than those who started earlier. To test these predictions, we conducted a capture-mark-recapture survey in the pre-migration period and examined the frequency of the wounds due to predator attacks (i.e., hereafter called predation-caused wounds) as a proxy for predation risk (Fig. 1).

Materials and methods

Study system

Our study was conducted in a 12.2-km long spring-fed Horonai River (42°40′N, 141°35′E) located in Hokkaido, northern Japan (Fig. 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 by a natural riverbank and secondary deciduous forest. The uppermost reach is the primary nursery habitat of masu salmon residents and migrants (i.e., migrants stay from their emergence until the start of the river-descending). 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-moving and includes artificial impoundments and wetlands totaling 1.0 ha and a maximum depth of 2.5 m. This reach serves only as a river corridor, where river-descending masu salmon migrants pass through after leaving the nursery habitat in the uppermost reach. Masu salmon are rarely found in this reach except the river descending season (April to July) (Futamura et al., *personal observation*). Since this reach largely consists of artificial impoundments and wetlands, it appears favorable for piscivorous birds, which mainly forage in open waters where overhanging trees are sparse (Tojo 1996). In addition, brown trout (*Salmo trutta*) (<60 cm), which consumes masu salmon smolts, dominates in this reach (Futamura et al. 2022b). The lowermost reach (the lowermost 4.6 km section from the river mouth) flows through an urbanized landscape of Tomakomai City and is artificially straightened for flood control. Salmonid densities are low in this reach, which temporarily functions as a river corridor for masu salmon when they descend the river.

Capture survey of migrants before river descending

Capture survey was conducted in the uppermost reach in spring 2020 (18–26 March 2020). We collected masu salmon using a backpack electrofishing unit (300–400 V DC, model 12B, Smith-Root, Inc., Vancouver, WA, USA) with 3 mm mesh dip nets (30 cm wide). Fish were anesthetized by diluted eugenol (FA-100 DS Pharma Animal Health Co., Ltd.) to measure their fork length (FL) (to the nearest 1 mm) and body mass (to the nearest 0.1 g) and to check for bodily wounds (see later). We examined whether fish had been previously identified by a PIT tag using a handheld reader. Individuals without a 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 in spring was 1495 and individuals having predation-caused

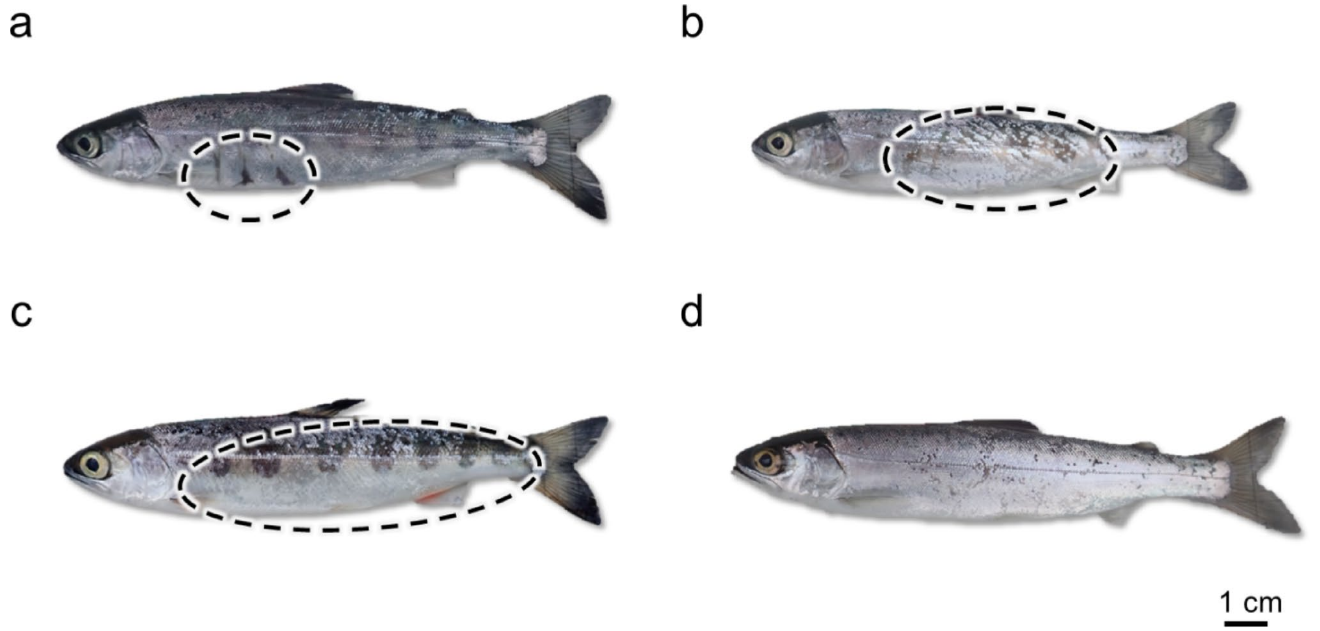

Fig. 1 Photograph of masu salmon migrants with wounds (a-c) and without wounds (d). **(a)** Individual with bill-shaped predation-caused wound (i.e., bill-shaped scar inflicted from either the ventral or dorsal side of the fish); **(b)** tooth-shaped predation-caused wound (i.e., several scars inflicted from the front or the back of the body); **(c)** non-identified predation-caused wound (i.e., large areas of missing scales). **(d)** Individual with no wounds. Dotted circles indicate the wounds on the fish body

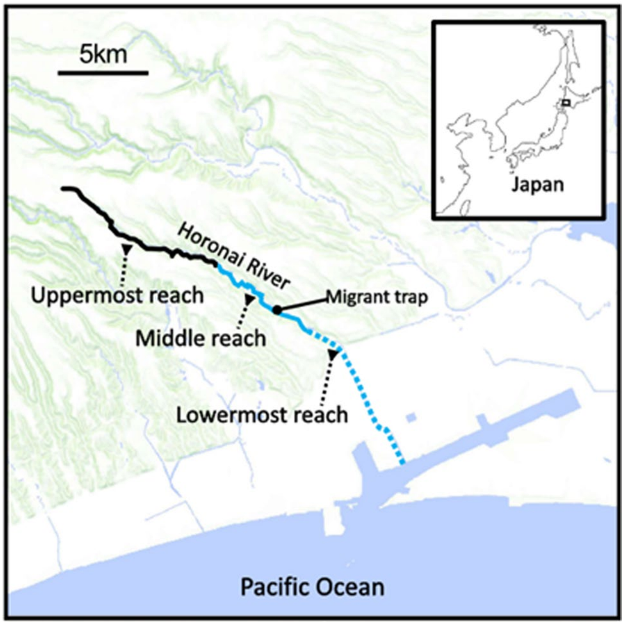

Fig. 2 Map of the Horonai River. The Horonai River consists of three distinct reaches. Uppermost reach (6.9–12.2 km from the river mouth (black solid line) is the primary habitat of masu salmon residents and migrants before descending the river, where they have a nursery habitat. Middle reach (4.6–6.9 km from the river mouth) (blue solid line) is the river corridor of the migrants, where they pass by during river-descending. 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) flows through the urbanized landscape of Tomakomai City and temporally serves as a river corridor. The map is based on the digital map published by the Geospatial Information Authority of Japan

wounds were not found on this occasion. These fish did not exhibit visual signs of smoltification and both pre-migrants and thus residents were tagged.

Capture survey on the river-descending migrants

We captured migrants at the onset of oceanic migration by operating a fyke-net type trap in the middle reach (5.7 km from the river mouth) from 4 April to 24 July 2020 (Fig. 2). Captured fish were anesthetized and were measured for fork length (nearest 1 mm) and body mass (nearest 0.1 g). We also examined whether fish had been previously identified by a PIT tag using a handheld reader and the tag was inserted into the abdominal cavity through a small incision made with a clean scalpel if not tagged. Fish were then allowed to recover from anesthesia and released to a pool just below the migrant trap. Importantly, we also checked for visual signs of smoltification (i.e., silvery body coloration and black pigmentation on the tip of the dorsal fin) and then photograph was taken. A waterproof digital camera (TG-5, Olympus Co., Tokyo, Japan) was used to take photographs and document predation-caused 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 downstream of the trap. Detailed information on the migrant trap survey is described in Futamura et al. (2022b).

Using the photographs taken during the migrant trap survey, we examined whether wounds were inflicted by predators (predation-caused wounds) or not (handling-caused wounds). Three categories of predation-caused wounds were identified based on their characteristics. First, bill-shaped scars inflicted from either the ventral or dorsal side were identified as avian wounds (Fig. 1a) (Reimchen 1988; Davies et al. 1995; Kortan et al. 2008). Second, a series of tooth-shaped scars inflicted from the front, or the back of the body were identified as those caused by piscivorous fish (Fig. 1b) (Reimchen 1988, 1991, 1992). Third, when we could not attribute scars to having been inflicted by either a bill or tooth, they were recorded as non-identified predation-caused wounds. The classification was done by a single observer who is skilled at identifying the fish wounds. The categorization of predation-caused wounds is also reasonable in terms of predator type of masu salmon pre-migrants, as piscivorous fish and birds are the main natural predators (Okado and Hasegawa 2024). Other wounds, such as large areas of missing scales or single linear scar, were classified as handling-caused wounds (i.e., capturing the fish by migrant trap and subsequent handling for measurement) (Fig. 1c). We are confident in our ability to identify the wound types (see Supplemental Information 1).

Definition of growth rate and pre-migration period

To test whether higher growth rates before migration and longer pre-migration periods incurred higher predation risk, we quantified two growth metrics (growth rate and growth period). Since migrants utilize uppermost reach before descending the river and thereafter middle reach two growth metrics are an inclusive metric of growth achieved in two riverscapes, but it is more likely to be achieved in middle reach as pre-migrants start descending the river just after the early spring capture survey (Futamura et al. 2025). As a metric of growth rate, we used relative growth rate adjusted for body size, because growth rate and predation highly depend on body size (Lugert et al. 2016). Relative growth rate was calculated from the residuals of the following model:

$$\textit{Relative growth rate} = \ln\ (\mathrm{FL\ migration})\ \sim\ \ln\ (\mathrm{FL\ early\ spring})\ +\ \Delta\,\mathrm{t}$$

where $\mathrm{FL}_{\mathrm{migration}}$ is the size at the migrant trap survey, $\mathrm{FL}_{\mathrm{early\ spring}}$ is the size in the early-spring capture-mark-recapture survey and Δt as elapsed dates between the two surveys. As a metric of the pre-migration period, we used the capture date at the migrant trap survey, which serves as an end-point of the pre-migration period. Both size measurements were natural log-transformed to account for non-linearity of growth (Lugert et al. 2016).

Statistical analysis

To assess the effects of relative growth rate and pre-migration period on the frequency of predation-caused wounds, we conducted our analysis in two steps. First, we assessed the association between these variables and frequency of predation-caused wounds by combining all wound types (i.e., bill-shaped, tooth-shaped, or not-identified). Second, we investigated the association between these variables and frequency 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 individually in separate models because of the sample size disparities (i.e., $N = 119$ for growth rate analysis, and $N = 578$ for pre-migration period analysis) (Table S1). The growth period and relative growth rate were not significantly correlated with each other (Pearson's $r = -0.03$). For the growth rate analysis, generalized linear model (GLM) with a binomial distribution and logit-link function (i.e., logistic regression) was employed to examine whether the frequency 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 frequency 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 dropped. Overall, we used six models on the analysis of the predation-caused wounds (i.e., three injury status [predation-caused wound types combined, bill-shaped, and tooth-shaped] × two growth metrics [growth rate and pre-migration period]). In all models, the significance of the independent variables was evaluated by a likelihood ratio test which was performed by using the maximum likelihood method. All statistical analysis was performed using R ver. 4.3.1 (R Core Team 2024).

Results

A total of 578 masu salmon migrants were captured in the migrant trap between 14-April and 16-June 2020 and were used for the analysis of the pre-migration period. Of the 578 migrants in the migrant trap, 111 masu salmon had predation-caused wound, among which 52 had bill-shaped wounds, 24 had tooth-shaped wounds, 4 had both types of wounds and 31 had non-identified wounds (Table S1). We also caught 25 brown trout, 8 rainbow trout (*Oncorhynchus mykiss*) and 7 white-spotted char (S*alvelinus leucomaenis*), among which 4 brown trout had predation-caused wound (3 had bill-shaped wound and 1 had tooth-shaped wound), 1 white-spotted char had predation-caused wound (bill-shaped wound). Of migrants captured in the trap survey, 119 had been previously captured in the early-spring capture-mark-recapture survey and were used for the analysis of the relative growth rate (Table S1).

The frequency of predation-caused wounds, regardless of their cause, tended to increase with the relative growth rate but was not significant (Table 1) (Fig. 3a). The relative growth rate in spring was not significantly related to the frequency of bill-shaped predation-caused wound or tooth-shaped predation-caused wound (Table 1) (Fig. 4a and c). The frequency of migrants with predation-caused wounds, regardless of its cause, significantly increased with the pre-migration period (Fig. 3b) (Table 1) and with the fork length (Table 1). Importantly, the probability of migrants having predation-caused wounds was 17% (6/34) in April,17% (69/404) in May and 26% (36/140) in June. The frequency of migrants with bill-shaped predation-caused wounds also significantly increased with the pre-migration period (Fig. 4b) (Table 1) and with the fork length (Table 1). However, the frequency of migrants with tooth-shaped wounds was not significantly related to either the pre-migration period (Fig. 4d) (Table 1) or the fork length (Table 1).

Discussion

Our result did not support the hypothesis that faster growth in the pre-migration period caused greater predation risk. To the contrary, timing of migration start (i.e., date of capture at migrant trap) was significantly associated with the frequency of wounds. Although the timing of migration departure did not explain the frequency of the tooth-shaped wound, the probability of inflicting bill-shaped predation-caused wound was higher in migrants with delayed migration start. These results suggest that masu salmon pre-migrants that initiated oceanic migration later were exposed to higher predation risk mainly by the avian predators. This implies that smaller pre-migrants stayed longer in the river to attain a large size for surviving the oceanic migration despite the increased predation risk in the river. In contrast, larger pre-migrants opted to leave the river sooner and avoided the predation risk. Importantly, this interpretation is valid under the following assumption: predation risk in the ocean and lower river reaches is either constant or increases over time. While we could not measure predation risk in the ocean, this

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

Model formulae	Independent variable	Estimates	Std. Error	Z value	*P* value
Frequency of predation-caused wound (regardless of cause) ~ Intercept + Relative growth rate					
	Intercept	−1.64	0.25	−6.45	**< 0.001**
	Relative growth rate	9.71	6.94	1.40	0.162
Frequency of bill-shaped predation-caused wound ~ Intercept + Relative growth rate					
	Intercept	−2.30	0.32	−7.17	**< 0.001**
	Relative growth rate	4.64	8.60	0.54	0.586
Frequency of tooth-shaped predation-caused wound ~ Intercept + Relative growth rate					
	Intercept	−4.39	0.94	−4.69	**< 0.001**
	Relative growth rate	22.94	22.41	1.02	0.306
Frequency of predation-caused wound (regardless of cause) ~ Intercept + Pre-migration period + Fork length					
	Intercept	−8.83	2.02	−4.37	**< 0.001**
	Pre-migration period	1.96×10^{-2}	9.30×10^{-3}	2.10	**0.035**
	Fork length	3.46×10^{-2}	1.12×10^{-2}	2.91	**0.003**
Frequency of bill-shaped predation-caused wound ~ Intercept + Pre-migration period + Fork length					
	Intercept	−12.73	2.82	−4.53	**< 0.001**
	Pre-migration period	4.44×10^{-2}	1.33×10^{-2}	3.32	**< 0.001**
	Fork length	3.10×10^{-2}	1.58×10^{-2}	1.96	**0.045**
Frequency of tooth-shaped predation-caused wound ~ Intercept + Pre-migration period + Fork length					
	Intercept	−6.40	3.51	−1.82	0.068
	Pre-migration period	1.42×10^{-2}	1.62×10^{-2}	−0.88	0.379
	Fork length	4.02×10^{-2}	2.14×10^{-2}	1.88	0.060

Estimates of independent variables are shown on the logit scale

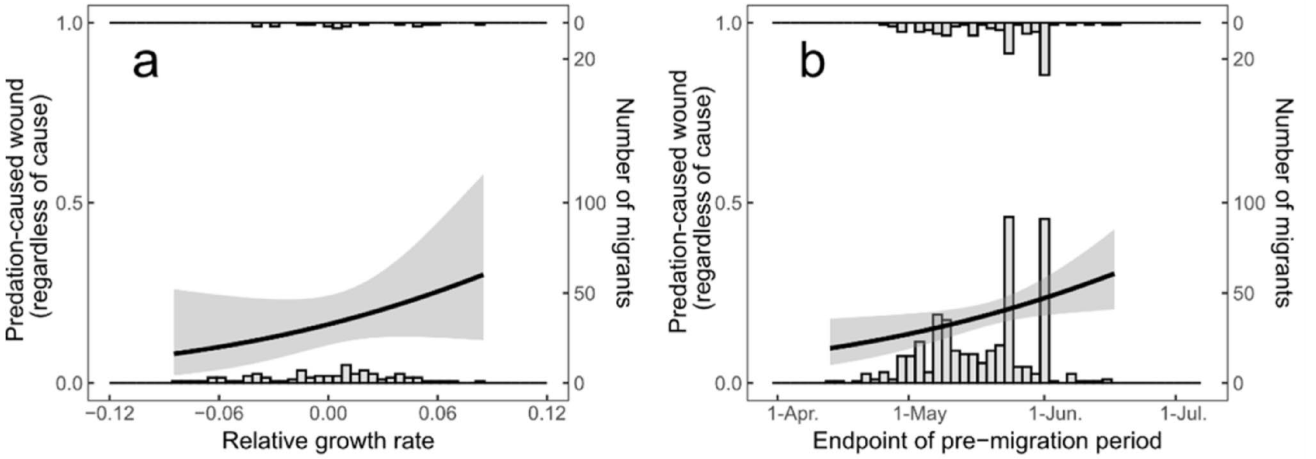

Fig. 3 Frequency of predation-caused wounds regardless of the causes in relation to **(a)** relative growth rate and **(b)** endpoint of pre-migration period (i.e., date of capture in migrant trap). Regression line was predicted by logistic regression (see Table 1 for estimates). Shaded area represents the 95% confidence interval of the fitted regression. The second Y-axis shows the number of individuals with wounds (y = 1) and without wounds (y = 0)

assumption holds at least during the passing of the lowermost reaches of this river (Futamura et al. 2022b).

Our study revealed increased predation on migrants with longer pre-migration periods, particularly from piscivorous birds. This raises a further question: where and how do these migrants encounter this heightened predation risk before their journey? There are two potential hotspots for increased predation before oceanic migration: the uppermost reach where migrants spend until the start of river-descending as a nursery habitat, and the middle reach which serves as a river corridor during descending the river. A survey of masu salmon residents, which was held right after the river-descending season of migrants (25–26 June 2020), indicates 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*). This suggests that pre-migrants were facing increased predation risk while descending the river. This also aligns with our observations

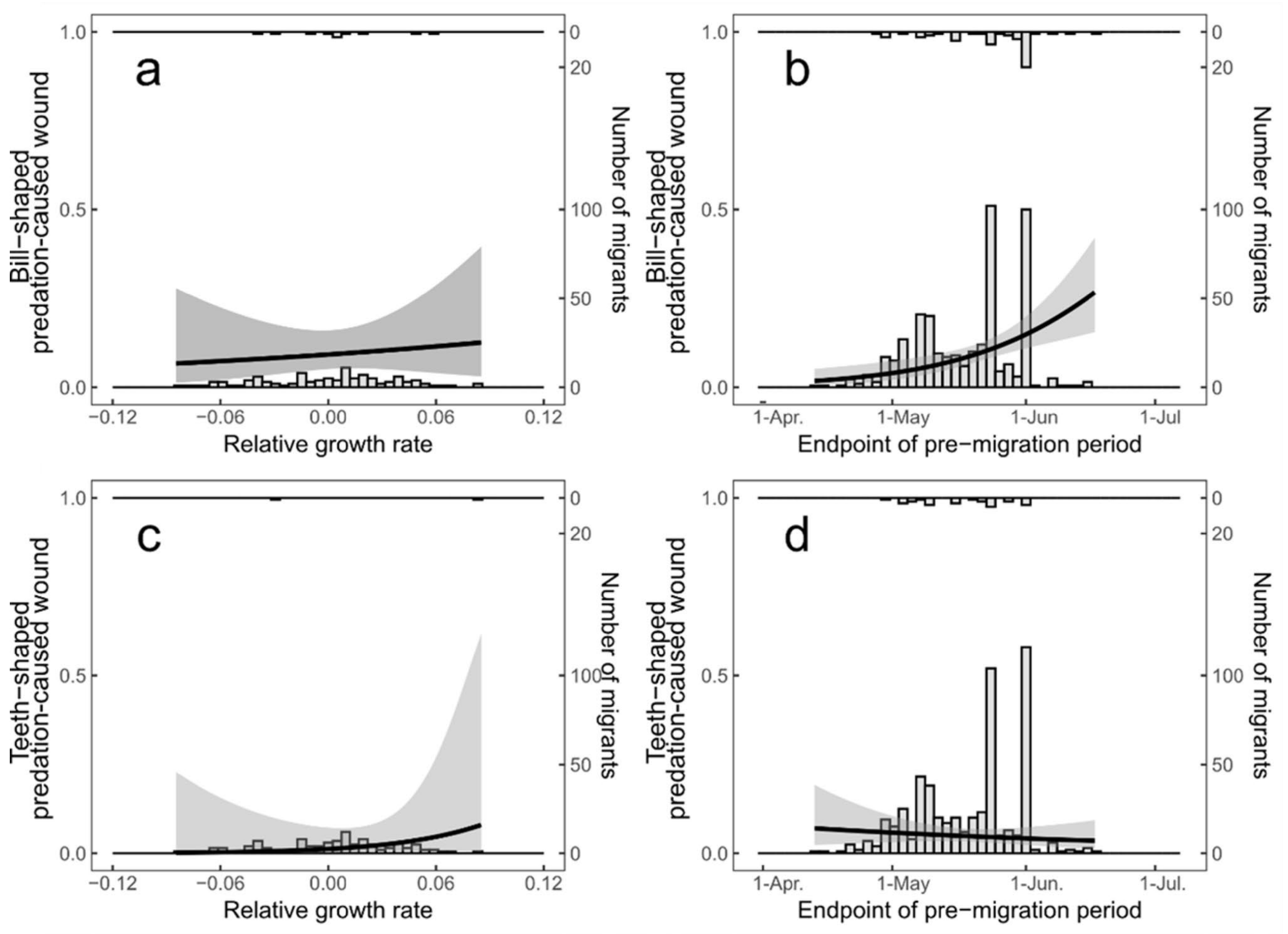

Fig. 4 Relationship between the relative growth rate, endpoint of pre-migration period and the frequency of two predation-caused wound types. Frequency of bill-shaped predation-caused wound in relation to **(a)** relative growth rate and **(b)** endpoint of pre-migration period; Frequency of tooth-shaped predation-caused wound in relation to **(c)** relative growth rate and **(d)** endpoint of pre-migration period. Regression line was predicted by logistic regression (see Table 1 for estimates). 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)

of piscivorous birds in the middle reaches of the Horonai River, lending support to the hypothesis. Notably, Great Egrets (*Ardea alba*) and Common Mergansers (*Mergus merganser*), rarely seen in the uppermost reach, were regularly present in the middle reach during the river-descending season of migrants (Futamura et al., *personal observation*). Although the middle reach is likely to be hazardous for pre-migrants, it harbours better growth conditions compared to uppermost reach in terms of water temperature, fish density and food availability (Futamura et al. 2025). Therefore, smaller pre-migrants would need to stay longer in the middle reached although they experience high predation risk.

There were two peak days of migration departure in the later season of migration, which both seem to be triggered by high water discharge (Fig. 3b). The first peak (25 May 2020) followed heavy rainfall, while the second (3 June 2020) resulted from a temporary suspension of water intake for public supply due to maintenance, which raised the water level (Futamura et al., *personal observation*). Since high discharge typically results in high water turbidity, high-water flow timing can be a favorable for salmon smolts to descend the river as they can ambush their visual predators (Hembrel et al. 2001). Indeed, 34% (200/578) of the fish migrated during the two peak days, suggesting that the masu salmon smolt responded to high-water flow also in our study system. Since many fish were caught in these peak days, this raises a concern that our interpretation of results is confounded by the data points of peak days. Although we analyzed the data excluding these outlier days, we obtained same results (Table S3), indicating the robustness of our interpretation.

In general, individuals with faster growth are more vulnerable to predation because active foraging to support faster growth also makes them more likely to be detected or encountered by predators (Lima and Dill 1990; Brown and Kotler 2004; Verdolin 2006). However, in our present study, we did not find statistically significant evidence of predation-related costs in pre-migrants with higher growth rates. This does not necessarily mean that there are no costs associated with rapid growth before oceanic migration. While we 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 to fully understand the costs associated with rapid growth before oceanic 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 similarly for migratory species (Alerstam et al. 2003; Oppel et al. 2015; Gregory et al. 2019; Simmons et al. 2022). In fact, our previous study provided evidence of such size-selective mortality in masu salmon migrants while descending the lower reaches (river corridor) of Horonai River (Futamura et al. 2022b). However, our results contradicted this general pattern. Larger migrants showed a higher frequency of predation-caused wounds (Table 1). This pattern 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 attacks.

Predation pressure is a major ecological factor driving life-history evolution but assessing the strength of selection in the field is challenging (Sih et al. 1985). In this study, we evaluated selection pressure due to predation using wounds and inferred one of the driving factors of condition-dependent life-history tactics. Since predation attempts are not always successful, injuries caused by predation have been observed in various prey species (reviewed in Rennolds and Bely 2023). By examining the relationship between the type and frequency of predation-caused wounds and individual traits, we may uncover unknown risk-reducing tactics against predation risk, as well as unknown traits which are susceptible to predation.

Our findings demonstrated that extending the pre-migration period incurs a mortality cost in the form of increased predation risk. 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 and might miss the optimal timing of migration. 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; Goto et al. 2025) and the timing of migration affect the ocean survival (Jonsson and Jonsson 2009; Iida et al. 2018). 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 life-history tactics.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10164-025-00871-7.

Acknowledgements We thank Yuichi Matsuoka, Shoji Kumikawa, Hiroshi Sugiyama, Hiroyuki Takahashi, Susumu Igarashi, Tomoaki Sato and Yuto Sasaki for their support in fieldwork. ChatGPT 4o was used to correct spelling and grammar. We also thank two anonymous reviewers for many insightful comments which improved our paper.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability All of the R script and data analyzed in this study are deposited in Figshare (https://doi.org/10.6084/m9.figshare.25638036).

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