



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

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Abstract Salmonid fish often experience size-selective mortality when descending the river (i.e., seaward migration). However, it is unknown whether size-selective mortality is specific to this life history (i.e., migrants), or is shared by an alternative life history (i.e., residents). In this study, we investigated the size-dependent mortality patterns of masu salmon (*Oncorhynchus masou*) migrants and residents during the migration period (i.e., April to June) in the

Horonai River, northern Japan. By conducting an individual-based study using PIT tags and antennas, we show that larger migrants more likely survived the seaward migration than smaller migrants, but size-dependent survival was not detected in river residents during the same period. These results suggest that size-selective mortality is specific to the river-descending migrants in masu salmon in their seaward migration period. We attribute this finding to the presence of piscivorous fishes (e.g., brown trout *Salmo trutta*) which occupy the migration corridor and consume masu salmon migrants, whereas such piscivorous fish do not occur in the river section farther upstream inhabited by residents.

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Introduction

Some populations of freshwater fish species are made of residents and migrants, the latter of which move long distances to the sea in early life stages (Jonsson and Jonsson 1993; Brönmark et al. 2014). Despite apparent benefits such as rapid growth and subsequent reproductive success, migration is accompanied by various ecological and physiological costs which result in high mortality rates (Alerstam et al. 2003). Because the vulnerability to environmental stressors (e.g., predation and starvation) is negatively correlated

with body size of individuals, the mortality during the migration operates size-selectively in which smaller individuals suffer higher mortality rates than larger individuals in most cases (Sogard 1997; Brodersen et al. 2008; Goatley and Bellwood 2016; Tucker et al. 2016). This seems to be common in migratory fish, including anadromous salmonids (Sogard 1997; Alerstam et al. 2003; Chaput et al. 2019) even though the positive size effects on survival may not be consistent across size ranges (Jonsson et al. 2016; 2017).

Anadromous salmonid fishes leave the natal freshwater habitat to attain larger body size in the resource-rich ocean. Numerous studies have documented that body size at the onset of migration (i.e., smolt size) determines survival during migration (Ward and Slaney 1988; Holtby et al. 1990; Koenings et al. 1993; Shimoda et al. 2003; Flaten et al. 2016; Gregory et al. 2018). Large proportions of mortality occur in the early phase of the migration; that is, mortality occurs in the river corridor before migrants reach the ocean (Chittenden et al. 2010; Welch et al. 2011; Melnychuk et al. 2014; Flávio et al. 2020). In particular, several studies have investigated size-dependent mortality patterns when migrants descend the river (i.e., prior to the ocean entry) (Zabel et al. 2005; Davidsen et al. 2009; Brown et al. 2013; Flávio et al. 2021). Although these studies have shown that migrants suffer high mortality rates and mortality is size-selective during the seaward migration, none have compared them to mortality of resident fish during the same period to discern whether size-dependent mortality is unique to migrants or shared by river residents. Because the size-selective mortality often operates on river-dwelling juvenile salmonids (Good et al. 2001; Miyakoshi et al. 2003; Hurst 2007; Xu et al. 2010), both residents and migrants may suffer size-selective mortality.

Using a masu salmon (*Oncorhynchus masou*) population expressing migratory and resident life history forms, we investigated the magnitude of the size-selective mortality during seaward migration relative to that in resident individuals. Masu salmon is a partial migratory fish endemic to East Asia (Kato 1991; Morita 2018). We conducted two studies in the Horonai River, a small stream in Hokkaido, Japan. First, to test whether smaller migrants suffer greater mortalities than larger migrants, we investigated the relationship between individual body size and success of migrants to pass through a migration corridor

downstream on their way to the sea, by using passive integrated transponder (PIT) tags and an antenna array system. Second, to examine the association between size-selective mortality and seaward migration, we investigated whether the survival of the residents in the upstream area (i.e., primary habitats for the juvenile masu salmon) depends on individual size in the same period, by conducting a capture-mark-recapture survey.

Material and methods

Life history forms of masu salmon

Masu salmon populations harbor two life history forms, anadromous migrants and river-dwelling residents (Kato 1991). Whereas residents stay in the river entirely, the freshwater residency of the anadromous migrants is limited to their early life stage for typically 1 year. During smoltification, the migrants descend the river between April and July (i.e., migration period) to begin oceanic migration. The migrants spend 1 or 2 years in the resource-rich ocean, and they consequently grow much faster and attain larger body size than river-dwelling residents. The age 2 or age 3 migrants then return to their natal rivers for spawning.

Study site

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

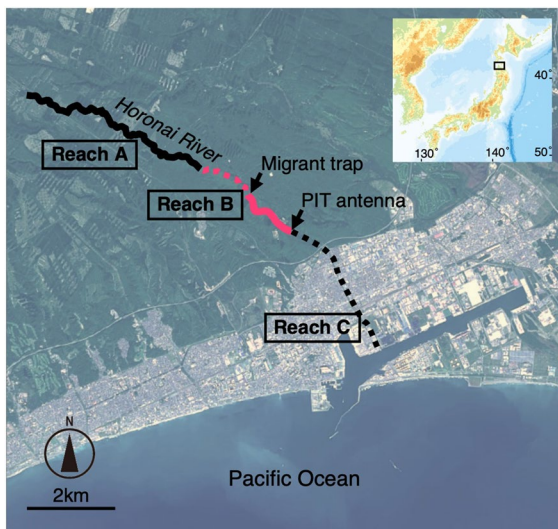


Fig. 1 Map of the Horonai River, 12 km long. The reach located between 6.9 and 12.2 km from the river mouth (reach A: solid black line) is the primary habitat of masu salmon (i.e., habitat of residents and prospective migrants), where the *study 2* (i.e., resident-survey) was conducted. River habitat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

located in an urbanized landscape and is highly altered with concrete revetment, which harbors few salmonids and function only as a migration corridor.

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

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

We captured migrants at the onset of their seaward migration by installing a fyke-net type trap (hereafter called the migrant trap) placed where the river narrows (50 cm wide) just below a cascade (70 cm high) at the uppermost boundary of the

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

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

Study 2: size-selective mortality of residents

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

Statistical analysis of study 1

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

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

$$\text{logit}(q_i) = \gamma_0 + \gamma_1 \times \text{recap}_i + \gamma_2 \times \text{date}_i + \gamma_3 \times \text{FL}_i$$

The response variable was the detection at the lowermost antenna, where $y_i=1$ if individual i was detected and 0 otherwise. Fork length was measured when individuals were captured and released at the migrant trap. Timing of migration was the number of

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

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

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

$$\text{logit}(p_{ai}) = \beta_{a0} + \beta_{a1} \times \text{date}_i + \beta_{a2} \times \text{FL}_i + \beta_{a3} \times \text{recap}_i$$

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

As a second confounding mechanism, we considered the possible size-dependent detectability by the PIT antenna. Detectability of PIT tags might have been higher in the larger migrants than smaller ones.

To examine the alternative mechanism, we used data of the complete and incomplete detections by the PIT antenna. Specifically, we investigated whether timing of migration (date), fork length (FL), and tagging (recap) affected the detection of the PIT antenna using logistic regression:

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

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

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

Statistical analysis of study 2

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

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

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

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

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

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

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

Model fitting

The logistic regression (study 1) and CJS analyses (study 2) were conducted in the Bayesian framework using a Markov Chain Monte Carlo (MCMC) method in Program JAGS (Plummer 2017) called from R (R Core Team 2020) with the *jagsUI* package. Uninformative priors were used for all parameter estimates (JAGS code in supplementary information 3). Posterior samples of the parameters were obtained by taking every 5th sample from 5,000 iterations of three chains after discarding 3,000 iterations as a burn-in period. Model convergence was checked by confirming that the R-hat statistic was less than 1.1 for all the parameters (Gelman and Hill 2006). Effects of predictors on survival during the seaward migration and in river residency were considered statistically significant when their 95% credible intervals (CI) did not overlap zero. We calculated odds ratios by exponentiating posterior mean effect sizes of continuous predictors and interpreted them as a change in odds of survival and capture with a 1 SD change in the predictors due to the mean standardization of the continuous predictors.

Results

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

In the migrant trap at the uppermost boundary of the migrant-survey section in reach B, we captured a total of 578 fish, among which 179 had PIT tags already (1%, 19%, and 11% individuals were tagged in spring 2019, autumn 2019, and spring 2020, respectively), 399 were tagged anew, and 77 died in the handling

processes (71% of fish that died were newly tagged). Thus, 501 fish were used for survival analysis of migrants during the seaward migration. All of these fish expressed external morphological characteristics of migrants (i.e., smolts). The PIT antenna system at the lowermost boundary of the migrant-survey section detected 261 (see summary in Fig. S1).

Survival probability of migrants depended on body size during the seaward migration (Fig. 2a) (Table 1). The mean effect of body size on survival (γ_3) was 0.37 (95% CI: 0.18–0.57) and the odds ratio was 1.45, indicating that fish were 1.45 times more likely to survive as fork length increased by 10 mm (1 SD). The tagging also affected the survival of the migrants. The mean tagging effect on survival (γ_1) was 0.55 (95% CI: 0.16–0.95). This

result indicated that survival of the migrants previously tagged during a mark-recapture survey was higher than migrants newly tagged at the migrant trap. Date of migration also affected the survival. The mean date effect on survival (γ_2) was -0.21 (95% CI: -0.4 and -0.02), indicating that the survival of the earlier migrants was higher. The posterior mean survival probability was 0.48 (95% CI: 0.43–0.53).

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

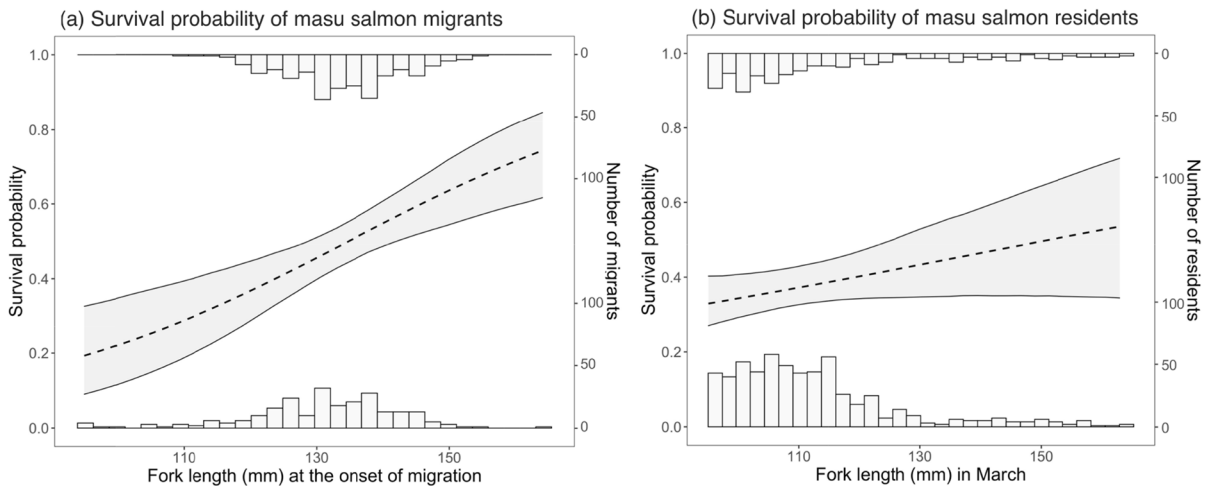


Fig. 2 Survival probability of masu salmon migrants and residents across the range of fork length. **a** Survival probability of masu salmon migrants in the passage through the migrant-survey section. The histograms show the number of individuals released below the migrant trap: the migrants successfully passed the PIT antenna ($y=1$) and otherwise ($y=0$). Dotted lines indicate posterior mean responses and solid lines

bound 95% credible intervals. **b** Survival probability of masu salmon residents from March to June across the range of fork lengths of migrants in March. Dotted lines indicate posterior mean responses and solid lines bound 95% credible intervals. The histograms show the number of individuals that were alive after the migration season ($y=1$) and otherwise ($y=0$)

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

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

providing yet another evidence of size-selective mortality.

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

Study 2: do size-selective mortality operate for residents

In the first survey, we captured (newly tagged or recaptured) 1512 fish and released 1498 fish (i.e., 14 individuals died in the measurement [handling mortality rate was 1%]). Among the released 1498 fish with PIT tags, 143 were trapped by the migrant trap in the first study and, hence, they were identified as migrants descending the river in the seaward migration period. Furthermore, we excluded 509 fish from the analyses because they were outside the body size range of migrants (FL: 95–164 mm) (i.e., larger or smaller than migrants in the first survey). Among the remaining 846 fish, 201 were recaptured in the second capture survey. These 201 fish were identified as residents because they remained in the river after the migration period. Consequently, the remaining 645 fish belonged to one of the following three groups: (1) residents that died in the interval between the

first and second occasions; (2) residents that were not recaptured but alive; (3) the prospective migrants that died in the interval between the first and second surveys (i.e., the prospective migrants failed to reach the migrant trap placed at the downstream area). Because the 645 unrecaptured fish included residents that died in the survey interval (i.e., category (1)), we can test the size-selective mortality of residents by examining whether survival rate in the migration period (i.e., period between first and second survey) depends on size at the first survey. The detailed information of the categorization of fish is summarized in Fig. S2.

In contrast to migrants, survival probability of residents in resident-survey section (i.e., reach A) did not depend on body size between March and July (Fig. 2b) (Table 2). The mean effect of body size on survival ($\beta_{\phi 1}$) was 0.14 , but its 95% CI ranged -0.02 and 0.30 , and overlapped zero. The posterior mean survival probability ($\alpha_{\phi 1}$) was 0.37 (95% CI: 0.32 – 0.42).

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

Discussion

We investigated whether masu salmon migrants suffered size-selective mortality in the seaward migration period. In the first study, we found that smaller migrants experienced higher mortality rates than larger migrants en route to the sea (Fig. 2a). The size-dependent mortality was unlikely to be caused by the handling effects such as anesthesia, measurement,

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

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

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

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

large individuals (> 40 cm in fork length) are commonly present in the slow-flowing reach (Futamura and Furusawa, *personal communication*). Actually, we found a consumed masu salmon migrant from the gut contents of a brown trout individual with typical size (FL: 297 mm) in the seaward migration period (Fig. 3).

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

An alternative mechanism of masu salmon migrants to survive the size-selective mortality in the seaward migration has been hypothesized. For example, masu salmon migrants are known to descend rivers in schools (Munakata 2012). In salmonids, this schooling is known as an adaptive behavior to



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

increase survival under strong predation pressure in the risky seaward migration (Furey et al. 2016). In fact, in the seaward migration period, we sometimes observed fish schools formed by several masu salmon migrants in the downstream area of the Horonai River where piscivores such as brown trout dominated (Futamura *personal observation*). If the piscivores are major factors of the size-selective mortality, the masu salmon migrants may exhibit size-dependent schooling behavior in their seaward migration. That is, smaller migrants are expected to form larger school sizes. Such a behavioral hypothesis warrants further investigations.

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

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

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Data Availability Raw data are available by request from the corresponding author.

Code availability All codes are available by request from the corresponding author.

Declarations

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 (ID 2–6).

Consent to participate Not applicable.

Consent for publication The authors consent to publication of the manuscript.

Conflict of interest The authors declare no competing interests.

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>
- Brönmark C, Hulthén K, Nilsson PA et al (2014) There and back again: migration in freshwater fishes. *Can J Zool* 92:467–479. <https://doi.org/10.1139/cjz-2012-0277>
- Brown RS, Oldenburg EW, Seaburg AG et al (2013) Survival of seaward-migrating PIT and acoustic-tagged juvenile Chinook salmon in the Snake and Columbia Rivers: an evaluation of length-specific tagging effects. *Anim Biotelemetry* 1:1–13. <https://doi.org/10.1186/2050-3385-1-8>
- Brodersen J, Nilsson PA, Hansson LA, Skov C, Brönmark C (2008) Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology* 89:1195–1200. <https://doi.org/10.1890/07-1318.1>
- Chaput G, Carr J, Daniels J et al (2019) Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic. *ICES J Mar Sci* 76:1107–1121. <https://doi.org/10.1093/icesjms/fsy156>
- Chittenden CM, Melnychuk MC, Welch DW, McKinley RS (2010) An investigation into the poor survival of an endangered coho salmon population. *PLoS One* 5:3–12. <https://doi.org/10.1371/journal.pone.0010869>
- Davidson JG, Rikardsen AH, Halttunen E et al (2009) Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. *J Fish Biol* 75:1700–1718. <https://doi.org/10.1111/j.1095-8649.2009.02423.x>
- Flaten AC, Davidson JG, Thorstad EB et al (2016) The first months at sea: marine migration and habitat use of sea trout *Salmo trutta* post-smolts. *J Fish Biol* 89:1624–1640. <https://doi.org/10.1111/jfb.13065>
- Flávio H, Caballero P, Jepsen N, Aarestrup K (2021) Atlantic salmon living on the edge: smolt behaviour and survival during seaward migration in River Minho. *Ecol Freshw Fish* 30:61–72. <https://doi.org/10.1111/eff.12564>
- Flávio H, Kennedy R, Ensing D et al (2020) Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. *Fish Manag Ecol* 27:92–101. <https://doi.org/10.1111/fme.12405>
- Furey NB, Hinch SG, Bass AL et al (2016) Predator swamping reduces predation risk during nocturnal migration of

- juvenile salmon in a high-mortality landscape. *J Anim Ecol* 85:948–959. <https://doi.org/10.1111/1365-2656.12528>
- Garvey JE, Ostrand KG, Wahl DH (2004) Energetics, predation, and ration affect size-dependent growth and mortality of fish during winter. *Ecology* 85:2860–2871. <https://doi.org/10.1890/03-0329>
- Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge university press
- Goatley CHR, Bellwood DR (2016) Body size and mortality rates in coral reef fishes: a three-phase relationship. *Proc Royal Soc B: Biol Sci* 283:20161858. <https://doi.org/10.1098/rspb.2013.2066>
- Good SP, Dodson JJ, Meekan MG, Ryan DAJ (2001) Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. *Can J Fish Aquat Sci* 58:1187–1195. <https://doi.org/10.1139/cjfas-58-6-1187>
- Gregory SD, Armstrong JD, Britton JR (2018) Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo salar* smolt size affects marine survival. *J Fish Biol* 92:579–592. <https://doi.org/10.1111/jfb.13550>
- Hasegawa K, Honda K, Yoshiyama T et al (2021) Small biased body size of salmon fry preyed upon by piscivorous fish in riverine and marine habitats. *Can J Fish Aquat Sci* 8:1–8. <https://doi.org/10.1139/cjfas-2020-0339>
- Holtby LB, Andersen BC, Kadowaki RK (1990) Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). *Can J Fish Aquat Sci* 47:2181–2194. <https://doi.org/10.1139/f90-243>
- Hurst TP (2007) Causes and consequences of winter mortality in fishes. *J Fish Biol* 71:315–345. <https://doi.org/10.1111/j.1095-8649.2007.01596.x>
- Jensen H, Kahilainen KK, Amundsen PA et al (2008) Predation by brown trout (*Salmo trutta*) along a diversifying prey community gradient. *Can J Fish Aquat Sci* 65:1831–1841. <https://doi.org/10.1139/F08-096>
- Jonsson B, Jonsson N (1993) Partial migration: niche shift versus sexual maturation in fishes. *Rev Fish Biol Fish* 3:348–365. <https://doi.org/10.1007/BF00043384>
- Jonsson B, Jonsson M, Jonsson N (2016) Optimal size at seaward migration in an anadromous salmonid. *Mar Ecol Prog Ser* 559:193–200. <https://doi.org/10.3354/meps11891>
- Jonsson B, Jonsson M, Jonsson N (2017) Influences of migration phenology on survival are size-dependent in juvenile Atlantic salmon (*Salmo salar*). *Can J Zool* 95:581–587. <https://doi.org/10.1139/cjz-2016-0136>
- Kato F (1991) Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*). *Pacific Salmon Life Hist* 446–520
- Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS. Elsevier
- Kishida O, Trussell GC, Ohno A et al (2011) Predation risk suppresses the positive feedback between size structure and cannibalism. *J Anim Ecol* 80:1278–1287. <https://doi.org/10.1111/j.1365-2656.2011.01871.x>
- Koenings JP, Geiger HJ, Hasbrouck JJ (1993) Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. *Can J Fish Aquat Sci* 50:600–611. <https://doi.org/10.1139/f93-069>
- Melnychuk MC, Korman J, Hausch S et al (2014) Marine survival difference between wild and hatchery-reared steelhead trout determined during early downstream migration. *Can J Fish Aquat Sci* 71:831–846. <https://doi.org/10.1139/cjfas-2013-0165>
- Miyakoshi Y, Hayano H, Fujiwara M et al (2003) Size-dependent smolt yield and overwinter survival of hatchery-reared masu salmon released in fall. *North Am J Fish Manag* 23:264–269. [https://doi.org/10.1577/1548-8675\(2003\)023%3c0264:sdsyao%3e2.0.co;2](https://doi.org/10.1577/1548-8675(2003)023%3c0264:sdsyao%3e2.0.co;2)
- Morita K (2018) Ocean ecology of masu (cherry) salmon 1. Masu salmon group. In: Beamish R (ed) The ocean ecology of Pacific salmon and trout. American Fisheries Society, pp 697–730
- Munakata A (2012) Migratory behaviors in masu salmon (*Oncorhynchus masou*) and the influence of endocrinological factors. *Aqua-BioScience Monogr* 5:29–65. <https://doi.org/10.5047/absm.2012.00502.0029>
- Nagae M, Fuda H, Hara A et al (1994) Changes in serum concentrations of Immunoglobulin M (IgM), Cortisol and Thyroxine (T₄) during smoltification in the masu salmon *Oncorhynchus masou*. *Fish Sci* 60:241–242. <https://doi.org/10.2331/fishsci.60.241>
- Plummer M (2017) JAGS version 4.3.0 user manual [Computer software manual]. Retrieved from sourceforge net/projects/mcmc-jags/files/Manuals/4 x 2:
- Quinn TP (2018) The behavior and ecology of pacific salmon and trout. University of Washington press
- R Core Team (2020) R: a language and environment for statistical computing.
- Shimoda K, Naito K, Nakajima M, et al (2003) Marine survival and growth of masu salmon *Oncorhynchus masou*, in relation to smolt size. *Nippon Suisan Gakkaishi (Japanese Ed)* 69:926–932. <https://doi.org/10.2331/suisan.69.926>
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60:1129–1157
- 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>
- Tucker S, Mark HJ, Trudel M (2016) Size- and condition-dependent predation: a seabird disproportionately targets substandard individual juvenile salmon. *Ecology* 97:461–471. <https://doi.org/10.1890/15-0564.1>
- Thompson JN, Beauchamp DA (2014) Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. *Trans Am Fish Soc* 143:910–925. <https://doi.org/10.1080/00028487.2014.901253>
- Ward BR, Slaney PA (1988) Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Can J Fish Aquat Sci* 45:1110–1122. <https://doi.org/10.1139/f88-135>
- Welch DW, Melnychuk MC, Payne JC et al (2011) In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc Natl Acad Sci* 108:8708–8713. <https://doi.org/10.1073/pnas.1014044108>
- Werner EE, Gilliam JF (1984) The Ontogenetic niche and species interactions in size-structured populations. *Annu Rev*

Ecol Syst 15:393–425. <https://doi.org/10.1146/annurev.es.15.110184.002141>

Xu CL, Letcher BH, Nislow KH (2010) Size-dependent survival of brook trout *Salvelinus fontinalis* in summer: effects of water temperature and stream flow. J Fish Biol 76:2342–2369. <https://doi.org/10.1111/j.1095-8649.2010.02619.x>

Zabel RW, Wagner T, Congleton JL et al (2005) Survival and selection of migrating salmon from capture-recapture

models with individual traits. Ecol Appl 15:1427–1439. <https://doi.org/10.1890/04-0940>

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