

ORIGINAL ARTICLE

Complex effects of body length and condition on within-tributary movement and emigration in stream salmonids

Yoichiro Kanno^{1,2}  | Audrey C. Harris¹  | Osamu Kishida³  | Shunsuke Utsumi⁴  | Hiromi Uno^{5,6} 

¹Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

²Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA

³Tomakomai Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Takaoka, Japan

⁴Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan

⁵Center for Ecological Research, Kyoto University, Otsu, Japan

⁶Faculty of Environmental Earth Science, Hokkaido University, Sapporo, Japan

Correspondence

Yoichiro Kanno, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523-1474, USA.

Email: yoichiro.kanno@colostate.edu

Funding information

Colorado State University; Japan Society for the Promotion of Science; The River Foundation, Japan; Colorado Water Center

Abstract

Movement patterns of stream fish vary individually, but little is known about how a set of individual characteristics affect movement at multiple spatial scales. We investigated the effect of body length and condition (i.e. weight relative to length) on emigration from a tributary and movement within the tributary during summer in Japanese salmonids (white-spotted charr *Salvelinus leucomaenis* and masu salmon *Oncorhynchus masou*) using mark-recapture and PIT antenna technology. Emigration from the tributary was influenced more strongly by body length than by body condition, whereas movement within the tributary (> 20 m) was influenced by body condition and their interaction with body length. Specifically, larger individuals in better body condition were more likely to stay locally (≤ 20 m), but smaller individuals in better condition were more likely to move in the tributary. We discuss benefits and costs of movement that vary with individual characteristics (i.e. body length and condition) and spatial scales. In one instance (charr between June and July), survival rates were lower in smaller individuals, which also were more likely to emigrate from the tributary, suggesting that emigration might have been facilitated by the mortality cost of staying in the tributary. This study indicates that stream fish movement is shaped by complex mechanisms that differ by spatial scale. Although complex, two study species often responded similarly, indicative of emerging regularities across species in determinants of multi-scale stream fish movement.

KEYWORDS

Bayesian analysis, dispersal, emigration, mark-recapture, riverscape ecology

1 | INTRODUCTION

Movement of stream fish is a key process that affects the structure and dynamics of populations, communities and ecosystems (Booth et al., 2020; Koizumi, 2011; Peterson & Fausch, 2003). Understanding why fish move is paramount not only to spatial ecology at multiple scales, but also for guiding management of stream fishes (Fausch et al., 2002). However, characterising stream fish movement and its determinants remains a challenging

endeavour because animal movement is a plastic behaviour (Shaw, 2020). Stream fish movement varies temporally (Albanese et al., 2004; Schlosser, 1995), spatially (Letcher et al., 2015) and individually due to body length (Young, 2011), condition (i.e. body weight relative to length) (Gowan & Fausch, 1996) and sex (Clark et al., 2019; Koizumi et al., 2006). In addition, we argue that our synthetic understanding of stream fish movement has been hampered because movement is not always defined and measured consistently across studies.

Movement is a broad concept that addresses fish locations over time at any spatial scale. Some studies investigated fine-scale movement of stream fish, such as movement within a meso-habitat (e.g. pool) and among adjacent meso-habitats (i.e. 10–100 m) (Clark et al., 2019; Gowan & Fausch, 2002; Pennock et al., 2018). Other studies measured movement distance to elucidate abiotic and biotic factors that explain why some individuals moved longer distances than others (Skalski & Gilliam, 2000; Terui et al., 2017; White & Wagner, 2021). In addition, movement into or from a defined study area has been a topic of concern in studies of spatially structured populations (Hooley-Underwood et al., 2019; Horton et al., 2007; White & Wagner, 2021). Previous studies evaluated how multiple individual characteristics (e.g. body length and condition) may affect movement at a single spatial scale (Gowan & Fausch, 1996; Heim et al., 2016; Young, 2011). However, little is known about whether consistent sets of individual characteristics affect movement at different spatial scales (but see Railsback et al., 1999; Rodriguez, 2002; Young, 2011). Filling this knowledge gap will advance our understanding of the factors that influence movement and its role in shaping processes from biotic interactions at fine spatial scales (Fausch et al., 2020) to riverscape-scale gene flow and connectivity (Koizumi, 2011).

Stream fish move to a different location when their fitness (e.g. survival) declines in their current local habitat (Railsback et al., 1999). Consequently, stream fish are more likely to depart from their local habitat when food resources become scarce or fish density increases (Clark et al., 2019; Olsson et al., 2006). Thresholds of when fish depart from their local habitat vary individually in size-structured populations, in which competitive outcomes are determined by body size (Werner & Gilliam 1984; Fausch et al., 2020).

Once fish leave their local habitat, stream fish move various distances including long-distance movement in the mainstem-tributary network (Skalski & Gilliam, 2000; White & Wagner, 2021). Stream habitat often shifts substantially at confluences when two streams merge (Benda et al., 2004). Fish movement also occurs at shorter distances linearly within the tributary or mainstem without passing through confluences. Movement behaviour allows fish to exploit spatial habitat heterogeneity in the stream network and meet their resource needs that change through ontogeny (Fausch et al., 2002). Importantly, mechanisms that affect whether fish depart from their local habitats and how far they move may not be always identical (Railsback et al., 1999; Rodriguez, 2002). In terrestrial animals, determinants differ among movement phases including departure from local habitats and settlement in new habitats (Bowler & Benton, 2005; Ducros et al., 2020). However, empirical data demonstrating similar scale-dependency of movement determinants are still scant in stream fishes.

Stream salmonids are a suitable group of fishes for evaluating how individual characteristics such as body length and condition affect multi-scale movement. Movement distances differ greatly among individuals in stream salmonid populations, ranging from individuals that are sedentary (move ≤ 20 m) to those that move various distances in the stream network (Gowan et al., 1994; Nakamura et al., 2002; White & Wagner, 2021). Stream salmonids compete for

drifting food and establish social dominance hierarchies in pools during spring and summer, and outcomes of competition depend on body size (Fausch et al., 2020; Nakano, 1995b). This suggests that the benefit of movement varies individually due to body length and condition, which may affect their ability to access territories and food in occupied locations versus elsewhere (Gowan & Fausch, 2002; O'Connor et al., 2000). Plus, movement incurs risk of predation and physiological costs (Bonte et al., 2012; Gilliam & Fraser, 2001), which also depend on body length and condition. If the trade-off between benefits and costs of movement depends on individual characteristics and varies with spatial scale, then body length and condition should affect movement differently at different spatial scales.

The aim of this study was to investigate the effect of body length and condition on stream salmonid movement at two spatial scales, namely, emigration from the tributary to the mainstem and within-tributary movement (>20 m given that individuals stayed in the tributary). To seek generality of patterns across species over time, we conducted a mark-recapture survey for two sympatric native Japanese salmonids in a small tributary segment (1 km long and 1.9 m wide) during two monthly intervals in May–July of 2018. Our study objectives were twofold. First, we evaluated whether movement at different spatial scales is affected similarly by body length and condition. Second, we characterised how body length and condition affected fish survival in the study tributary to evaluate whether emigration from the study tributary (long-range movement) was facilitated by the high cost of staying in the tributary (i.e. mortality). If so, we predicted that individuals with smaller body length or poor body condition would suffer higher mortality rates in the tributary, and they would more likely emigrate from the study tributary into the mainstem habitat.

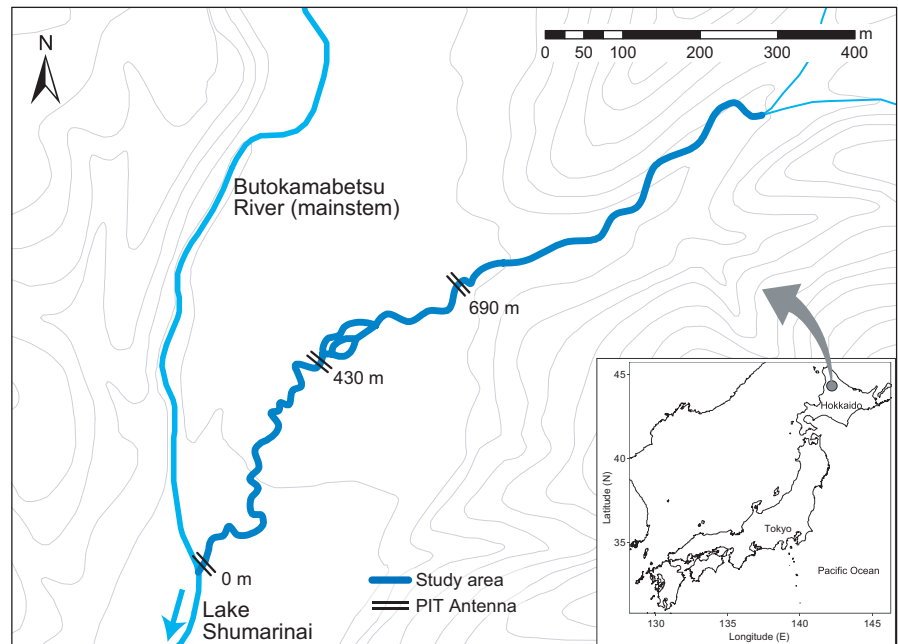
2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in an unnamed tributary to the Butokamabetsu River located in Hokkaido University Uryu Experimental Forest, northern Japan (25,000 ha; 44° 24' N, 142° 07' E). The forest was primarily mixed stands of conifer and broad-leaved trees. The study area was located in the coldest region of Japan (mean annual air temperature = 4.2°C), with mean annual precipitation of 1,236 mm. Snow cover usually extends from late November to early May and can reach approximately 3 m deep (Aoyama et al., 2011). This study was conducted from just after peak snowmelt through summer (May–July), concurrent with dynamic changes in streamflows over time (Appendix S1a). Daily mean water temperature in the tributary ranged 7–12°C during the fish survey period (May 24–July 25 in 2018) (Appendix S1b).

We designated a 1-km study segment of the unnamed perennial tributary, upstream from the confluence with the Butokamabetsu River mainstem (Figure 1). The tributary was small composed of riffles (fast, shallow) and pools (slow, deep) (mean wetted width = 1.9 m

FIGURE 1 Map of study tributary in Hokkaido University Uryu Experimental Forest, Japan, showing a 1-km segment in which mark-recapture surveys were conducted (thick blue) and the mainstem Butokamabetsu River (thick cyan). A pair of PIT antennas installed at the confluence (two black lines: 0 m) monitored emigration of marked individuals from the tributary to the mainstem, and two additional pairs of antennas were installed at 430 m and 690 m upstream. Contour lines (grey) were based on a topographic map made available by the Geospatial Information Authority of Japan, the Ministry of Land, Infrastructure, Transport and Tourism



based on measurements on June 14, 2018). Fish-bearing stream habitat extended approximately 300 m and 250 m in two headwater branches upstream of the study area (Figure 1), but fish larger than the minimum body size for tagging (i.e. 70 mm TL) were rare (see below). Fifty permanent sections (20-m long) were established from the confluence with the mainstem (0 m) and extended upstream (1,000 m). Habitat changed longitudinally including a meandering channel with dense broad-leaf bamboo (*Sasa senanensis*) in the riparian area (0–440 m), floodplain-like habitat with side channels (440–640 m) and steeper riffle-dominated habitat with alder trees (*Alnus japonica*) in the riparian (640–1,000 m). More detailed descriptions of the habitat characteristics in the tributary can be found in Kanno et al. (2020).

The study species, white-spotted charr (*Salvelinus leucomaenis*) and masu salmon (*Oncorhynchus masou*), are native to the study area and sympatric in the tributary, although white-spotted charr was more abundant than masu salmon. Drifting food resources influence habitat suitability and movement of stream salmonids in summer (Gowan & Fausch, 2002), and white-spotted charr and masu salmon compete for these resources within and between species (Fausch et al., 2020; Sato & Watanabe, 2014). Both species are landlocked in the study area and spend their entire life in the freshwater environment. Some individuals of both species in the Butokamabetsu River display an adfluvial life history (Tamate & Maekawa, 2004) by moving to Lake Shumarinai, a man-made reservoir located 5 km downstream of the study tributary (Figure 1). Tributary residents and adfluvial individuals could not be visually differentiated in our study tributary (Y. Kanno, *personal observation*), although adfluvial individuals show external signs of smoltification (i.e. silvery body colour and black edges along dorsal and caudal fins) prior to moving to lentic habitats elsewhere (Yamamoto et al., 1999). Public access to the study area is restricted, and there was no angling mortality of white-spotted charr and masu salmon. The two study species accounted for the majority of individuals captured (> 95%) in the tributary, and we also

recorded Sakhalin taimen (*Parahucho perryi*), fluvial sculpin (*Cottus nozawae*), Siberian stone loach (*Noemacheilus toni*) and Far Eastern brook lamprey (*Lethenteron reissneri*).

2.2 | Field sampling

A combination of physical recaptures and stationary PIT antennas were used to characterise fish movement at two spatial scales (i.e. emigration from the tributary and within-tributary movement). We tracked locations of individuals among 20-m sections within the study tributary including the side channels (Figure 1) by conducting a mark-recapture survey with PIT tags on May 24–29, June 17–20, and July 23–25 of 2018 and monitoring movement using three PIT antenna pairs deployed in the study area (Figure 1). High stream-flows due to snowmelt had just subsided by the May survey, entering base flow condition in June and July, although two significant precipitation events occurred in July due to storms (Appendix S1). An additional survey of less extensive scope was conducted on October 17–18 to estimate parameters of multi-state Cormack–Jolly–Seber (CJS) models up to July, because survival and recapture probabilities for the last interval cannot be independently estimated in the CJS framework (see 2.3 Data analysis below).

Fish were captured using a single backpack electrofishing unit (Model LR-24, Smith-Root Inc., Vancouver, WA) with pulsed direct current settings (300–400V, 30–45Hz and 25% duty cycle). A crew of three or four members sampled each 20 m section in an upstream direction. All sections including side channels were sampled with a two-pass removal method in June and July to maximise recaptures of marked individuals. In May, every third section of the main channel and side channels was sampled with a two-pass method, and the rest were sampled with a single-pass method. In October, 34 of 50 sections dispersed throughout the 1-km main channel and all of

the side channels were sampled with a single-pass method. Fish captured were held in a bucket and subsequently a live well separated by section and pass until processing.

In each survey, fish were anaesthetised with clove oil, measured for total length (TL in mm) and weight (g), and checked for the presence of PIT tags. Fish ≥ 70 mm TL without tags were marked with 12-mm half duplex PIT tags (Oregon RFID, Portland, OR). The PIT tag was inserted into the abdominal cavity through a ventral incision just large enough to insert the PIT tag made lateral to the midline and posterior of the pectoral fins. This tagging technique has been applied with negligible tag loss and mortality in our previous studies (Cary et al., 2017; Kanno et al., 2014). Body length of fish tagged (≥ 70 mm TL) was larger than the minimum length to which 12-mm PIT tags have been applied (55–60 mm TL) (Gries & Letcher, 2002; Richard et al., 2013), and the main study period (May through July) did not overlap with the spawning season of the two study species (autumn), when tag loss is most likely to occur (Cooke et al., 2013; Meyer et al., 2011). After processing, fish were allowed to recover in a live well and were returned alive to the section of capture.

We installed three pairs of PIT antennas in the tributary to monitor fish movement (Figure 1). One pair was deployed at the downstream boundary of the tributary (i.e. confluence with the mainstem) to detect emigration of fish from the tributary (Figure 1). Two additional antenna pairs were installed 430 m and 690 m upstream from the confluence to coincide approximately with longitudinal habitat shifts within the tributary (see 2.1 Study area). Each pair of antennas was operated by a multi-antenna reader (Oregon RFID). Antennas were placed across the entire stream width by looping 3.5-mm² wires twice, and tags were detected when they passed through anywhere inside the loop. Read range also extended < 20 cm outside the loop. Antennas operated continuously between May 24 and July 26, except that the antennas located at 430 m from the confluence began operating on June 5. This period covered the mark-recapture surveys conducted between May 24–29 and July 23–25, 2018.

Finally, we used a mobile antenna upstream in the tributary to assess emigration upstream from the study area. The mobile antenna consisted of a single antenna reader contained in a backpack, connected to a pole antenna (Oregon RFID). The read range of 12-mm PIT tags was < 30 cm and varied with the orientation of tags. On June 21 and July 21, 2018, we used the mobile antenna to detect marked fish 100 m beyond the upstream boundary in the tributary (Figure 1). We detected only two individuals on June 21 and three individuals on July 27 (one individual was detected on both days). The stream was < 1 –2 m wide upstream of the study area, harbouring mainly individuals below the minimum tagging size (< 70 mm TL) based on a preliminary electrofishing survey. Therefore, we considered upstream emigration negligible.

2.3 | Data analysis

We evaluated, by species and survey interval, how body length and condition affected movement at two spatial scales, including

emigration from the study tributary and movement within the tributary. Emigration was informed by the PIT antenna pair located at the confluence with the mainstem Butokamabetsu River. Although movement distances of emigrants cannot be known, emigration was considered long-range movement from the tributary to the mainstem habitat or the lentic habitat farther downstream (i.e. Lake Shumarinai) (Figure 1) for three reasons (Kanno et al., 2020). First, across species and seasons, emigrants were detected at the farthest upstream of the two antennas (430 m and 690 m from the confluence) with a median of 1–3 days before their antenna detection at the confluence. Thus, they moved downstream in a quick, unidirectional manner. Second, both species combined, only two of the 97 individuals detected by the PIT antenna at the confluence were subsequently recaptured in the tributary by electrofishing, suggesting that almost no emigrants returned to the tributary during the study period. Third, the probability of emigration did not depend on where in the 1-km tributary fish were last captured prior to emigration. If emigration had been owing to shorter-range movement, fish near the confluence should have more likely emigrated from the tributary.

Of the fish that did not emigrate, within-tributary movement was defined as relocations of individuals > 20 m, and individuals that stayed ≤ 20 m between mark-recapture survey intervals were considered not to have moved (i.e. sedentary). Relocations of fish were informed by physical recaptures of marked individuals and two additional antenna pairs within the tributary (Figure 1). Movement distance was measured as the absolute waterway distance between the section of release and that of physical recapture or antenna detection. For individuals collected in side channels, the shortest waterway distance to the confluence with the main channel was calculated based on coordinates recorded in the field, and the waterway distance between this confluence and the fish location in the main channel was added to calculate movement distance. When individuals were both physically recaptured and detected by antennas during a sampling interval, the longer distance of the two was used as movement distance. Fish marked with PIT tags (≥ 70 mm TL) were most commonly captured in the pool habitat, and 0–2 pools occurred per 20 m section. Therefore, within-tributary movement was the departure of individuals from a cluster of few adjacent pools to other locations in the tributary (i.e. home range) (reviewed by Gowan et al., 1994).

To facilitate comparisons across the two scales, effects of body length and condition on each movement scale were analysed based on the logistic regression approach using a Markov chain Monte Carlo (MCMC) method in Program JAGS (Plummer, 2017) called from R Program (R Core Team, 2019) with the *jagsUI* package. We used uninformative priors in this Bayesian approach (JAGS code in Appendix S2). Posterior distributions of model parameters were characterised by taking every 10th sample from 15,000 iterations of three chains after a burn-in period of 5000 iterations. Model convergence was assumed by visually examining plots of the MCMC chains for good mixture and confirming that the R-hat statistic was less than 1.1 for all model parameters (Gelman & Hill, 2007). Effect size (i.e. regression slope) of body length (β_1) and condition (β_2) on

movement probability at the two scales, as well as survival and recapture probability (multi-state CJS model for the long-range movement analysis), were used to assess the strength of these predictors of movement by considering posterior samples as a measure of uncertainty (Gelman et al., 2003). Specifically, we considered effects of body length or condition and their interactions to be strong when >95% of posterior samples (PS) of effect size were either positive or negative, and moderate when >85% of PS were either positive or negative. We calculated odds ratios by exponentiating posterior mean effect sizes (i.e. $\exp(\beta_1)$ or $\exp(\beta_2)$) and interpreted them as a change in odds of movement associated with a 1 SD change in body length or condition because they were standardised prior to analysis (below).

Emigration from tributary

The body length, condition and their interactive effects on emigration from the tributary were quantified using a multi-state Cormack-Jolly-Seber (CJS) model. The traditional (single-state) CJS model infers survival of marked individuals, while accounting for imperfect recaptures (Lebreton et al., 1992). By considering emigration as another state, the multi-state CJS model makes it possible to infer the probability of emigration, survival and recapture as a function of covariates (e.g. body length, condition and their interaction). This approach was necessary because some individuals marked on the first survey occasion (May) emigrated by the second survey (June) whereas others emigrated between the second (June) and third (July) surveys. Therefore, the survival probability between the first and second surveys needed to be considered to infer the probability of emigration between the second and third surveys accurately. In addition, survival was used as a measure of cost of staying in the tributary (i.e. mortality), and we evaluated whether emigration from the tributary and mortality were both body-length- or condition-dependent.

Data were formatted in a two-dimensional array ($y_{i,t}$), where rows indicated individuals (i) and columns indicated survey occasions (t). Elements of the array were observed states; 1 = physically recaptured in the tributary on survey t , 2 = detected as emigrating downstream past the confluence antennas between survey $t-1$ and survey t , and 3 = neither physically recaptured nor detected at the confluence antennas. The true states of individuals coded as 1 and 2 are known without error. Individuals coded as 3 may either have died or were alive but evaded recaptures. Furthermore, we assumed that emigration was recorded without error because one antenna at the confluence missed only one out of the 85 emigrating charr and none of the 11 salmon during the study period (see Results).

Data were analysed using the state-space approach, which decomposes multi-state CJS models hierarchically into ecological and observation processes (Kéry & Schaub, 2012). The ecological process tracks the state transitions of individuals over time, and the observation process links the latent states to observed data while accounting for imperfect detections of fish. The ecological process

described state transitions from survey t to survey $t+1$, starting with the first survey occasion on which an individual was captured. State-transition probabilities were defined by a categorical distribution that included all possible fates of individuals at survey $t+1$, given their states at survey t . Entries of the transition matrix were populated with conditional probabilities of emigration and true survival (Appendix S2). Specifically, we considered that (1) an individual may emigrate from the 1-km tributary between survey intervals with a probability equal to e (emigration) and remain in the tributary with a probability of $1-e$, and (2) given an individual stayed in the tributary, the individual may survive with a probability of s (mortality = $1-s$). Here, survival refers to true survival, not apparent survival, because emigration has been accounted for (i.e. apparent survival = $s \times (1-e)$). Emigration and survival were modelled to vary by species j and survey interval t as a function of body length (TL) and condition of individual i and their interactive effect on the logit scale:

$$\text{logit}(e_{i,t}) = \beta_0 e_{j|i,t} + \beta_1 e_{j|i,t} \times TL_{i,t} + \beta_2 e_{j|i,t} \times \text{condition}_{i,t} + \beta_3 e_{j|i,t} \times \text{interaction}_{i,t}$$

$$\text{logit}(s_{i,t}) = \beta_0 s_{j|i,t} + \beta_1 s_{j|i,t} \times TL_{i,t} + \beta_2 s_{j|i,t} \times \text{condition}_{i,t}$$

Body condition was estimated by comparing the weight of fish to the predicted weight of fish at the same body length in this study. This approach characterises body condition of individuals while accounting for body length, thus body condition does not depend on body length (Al-Chokhachy et al., 2019). Pooling weight (g) data across May and June sampling occasions, we developed a length-weight relationship for each species:

$$\log_{10}(\text{Charr weight}) = -4.66 + 2.82 * \log_{10}(\text{Charr TL}) (r^2 = 0.95)$$

$$\log_{10}(\text{Salmon weight}) = -5.33 + 3.17 * \log_{10}(\text{Salmon TL}) (r^2 = 0.97)$$

Body condition was calculated as $\frac{\text{measured weight}}{\text{predicted weight}} - 1$, so that fish at the average body condition would have a value of 0, with negative values indicative of poor body condition and positive values indicative of good body condition.

Our model required TL and body condition values be imputed on the June survey occasion for individuals that were not recaptured in June. Missing TL (mm) values were predicted by developing simple linear regression for each survey species:

$$(\text{Charr TL in June}) = 10.06 + 0.99 * (\text{Charr TL in May}) (r^2 = 0.93)$$

$$(\text{Salmon TL in June}) = 24.59 + 0.84 * (\text{Salmon TL in May}) (r^2 = 0.94)$$

Missing body condition was imputed with a value of 0 because the previous body condition did not predict the current body condition in either sampling interval for either species ($p = 0.08-0.77$). Prior to analysis, TL was standardised by subtracting the mean value across May and June sampling occasions and then divided by SD, and condition was standardised by dividing by SD. Mean TL was 94 mm (SD = 18) in charr and 115 mm (SD = 26) in salmon, and mean

body condition was 0 in both species (SD = 0.09 in charr and 0.10 in salmon) (Appendix S3).

The observation process was represented by another categorical distribution, which accounted for imperfect capture of individuals despite their presence in the tributary (Appendix S2). The model assumed that individuals and states were recorded without error (i.e. no false positives) but individuals could escape captures (i.e. false negatives). Similar to emigration and survival, we let recapture probability of individuals with two electrofishing passes, denoted by p , vary by species j and survey interval t . Recapture probability was regressed against TL (measured or predicted) of individual i , but not on body condition, on the logit scale:

$$\text{logit}(p_{i,t}) = \beta 0 p_{j[t],t} + \beta 1 p_{j[t],t} \times TL_{i,t}$$

Prior to fitting the multi-state CJS model to data, we used the R2ucare package (Gimenez et al., 2018) to evaluate potential violations of model assumptions. There was no evidence for trap dependence ($p = 0.93$ in white-spotted charr and $p = 0.19$ in masu salmon) or transience ($p = 1.00$ in white-spotted charr and $p = 0.74$ in masu salmon). That is, recapture probability on the next sampling occasion did not differ between captured individuals and undetected but live individuals (trap-dependence) and previously marked individuals had the same recapture probability as newly marked individuals (transience).

Within-tributary movement

Logistic regression was used to evaluate whether body length, condition and their interaction influenced the probability of within-tributary movement. Of individuals captured on a sampling occasion and recaptured physically on or antenna-detected by the next sampling occasion, those that moved >20 m were coded 1's, and 0's otherwise, to indicate whether fish moved within the tributary. Absolute movement distance was used because fish movement was equally likely in upstream and downstream directions (Kanno et al., 2020). For each species j and sampling interval t , probability of within-tributary movement (denoted m) was modelled in relation to body length and condition of individual i and their interaction as:

$$\text{logit}(m_{i,t}) = \beta 0 m_{j[t],t} + \beta 1 m_{j[t],t} \times TL_{i,t} + \beta 2 m_{j[t],t} \times \text{condition}_{i,t} + \beta 3 m_{j[t],t} \times \text{interaction}_{i,t}$$

Emigrants were removed from the within-tributary movement analysis because probabilities of mutually exclusive and exhaustive events sum to one, and otherwise, movement probabilities at different spatial scales would not be independent. That is, unless conditional probabilities are sequentially considered (i.e. given that fish stayed in the tributary), an increasing movement probability at one scale would inherently result in decreasing movement probability at the other scale due to the constraint that the probabilities must sum to one.

3 | RESULTS

A total of 501 unique individuals of charr and 89 unique individuals of salmon were marked with PIT tags on the two sampling occasions (May and June) to monitor their emigration from the study tributary and movement within the tributary. Movement data from physical recaptures or PIT antenna detections were available for 104 individuals (50 physical recaptures and 54 antenna detections; mean TL = 89.0 mm) over the May–June interval and 196 individuals (107 recaptures; mean TL = 101.1 mm) for the June–July interval for charr, and 33 individuals (19 recaptures; mean TL = 108.0 mm) in May–June and 44 individuals (34 recaptures; mean TL = 114.0 mm) in June–July for salmon (Table 1; Appendix S4). Fish tagged were <200 mm TL in May and June, and age classes could not be readily distinguished beyond young-of-the-year fish based on length-frequency distributions (Appendix S5). Across sampling intervals and species, within-tributary movement (27–38%) was more common than emigration (9–29%) (Table 1), despite the imperfect physical recapture of live individuals by electrofishing in the tributary. Large proportions of individuals (37–64%) were relocated within 0–20 m from the section of release (i.e. no movement) (Table 1; Appendix S6).

3.1 | Emigration from tributary

Body length and condition influenced emigration from the tributary, but their interaction did not influence emigration in any instance (Table 2; Figure 2). In charr, smaller individuals were more likely to emigrate, and the effect of body length was nearly moderate in May–June (effect size or $\beta 1e = -0.29$, PS = 84%) and moderate in June–July ($\beta 1e = -0.27$, PS = 94%). In salmon, smaller individuals were

	No movement (0–20 m)	Within-tributary movement	Emigration from tributary
Charr			
May-June	38	39	27
June-July	81	58	57
Salmon			
May-June	15	11	7
June-July	28	12	4

TABLE 1 Sample size (number of individuals) by movement pattern

TABLE 2 Summary of body length and condition effects on emigration from tributary and within-tributary movement in white-spotted charr and masu salmon in each sampling interval

	Effects on movement probability	
	Emigration from tributary	Within-tributary movement
Body length		
Charr		
May-June	- (84%)	- (60%)
June-July	<i>Negative (94%)</i>	- (68%)
Salmon		
May-June	Negative (99%)	- (56%)
June-July	- (76%)	- (82%)
Body condition		
Charr		
May-June	- (70%)	- (81%)
June-July	- (52%)	- (52%)
Salmon		
May-June	Negative (97%)	Negative (95%)
June-July	- (67%)	<i>Negative (92%)</i>
Interaction		
Charr		
May-June	- (71%)	- (55%)
June-July	- (73%)	Negative (96%)
Salmon		
May-June	- (73%)	<i>Negative (90%)</i>
June-July	- (84%)	- (56%)

Note: Effects for slope coefficients in regression analyses: Bold letters refer to strong effects ($\geq 95\%$ of posterior samples are negative or positive), italicized letters refer to moderate effects (85–94% of posterior samples), and hyphens (-) denote no effects.

again more likely to emigrate from the tributary in May–June, and this body length effect was strong ($\beta_{1e} = -1.34$, PS = 99%). Based on odds ratios, salmon in May–June were 3.82 times less likely to emigrate with a unit SD increase in length (26 mm). We did not find evidence that body length influenced salmon emigration in June–July ($\beta_{1e} = -0.55$, PS = 76%).

Body condition influenced emigration only of salmon in May–June ($\beta_{2e} = -0.87$, PS = 97%) (Table 2). Odds ratios indicated that, with a unit increase in SD of body condition (10%), salmon were 2.39 times less likely to emigrate from the tributary in May–June. In charr, body condition did not affect emigration either in May–June ($\beta_{2e} = -0.13$, PS = 70%) or June–July ($\beta_{2e} = 0.01$, PS = 52%). Overall, emigration from the tributary was influenced more strongly by body length than by condition, with no evidence for their interactive effects (PS = 71–84%) (Table 2; Figure 2).

Survival (s) was not significantly affected by body length or condition, except moderate effects in two instances (Figure 3). Larger charr were more likely to survive during the June–July interval ($\beta_{1s} = 0.76$, PS = 87%; Figure 3a), and individuals of salmon in better

body condition were more likely to survive during the June–July interval ($\beta_{2s} = 0.40$, PS = 87%; Figure 3b). The mean survival rate of salmon in June–July (0.77: 95% credible interval [CRI] = 0.60–0.96) was lower than that of salmon in May–June (0.93: 95% CRI = 0.77–1.00), charr in May–June (0.96: 0.87–1.00) and charr in June–July (0.93: 95% CRI = 0.71–1.00).

Recapture probability (p) of marked individuals varied among species and sampling intervals (Appendix S7). The mean recapture probability of fish at the average size (charr = 94 mm and salmon = 115 mm) was 0.33 (95% CRI = 0.26–0.41) in June and 0.39 (95% CRI = 0.31–0.51) in July for charr, and 0.53 (0.36–0.69) in June and 0.81 (95% CRI = 0.61–0.96) in July for salmon. Recapture probability of larger individuals of salmon was strongly lower in June ($\beta_{1p} = -0.61$, PS = 96%), but larger charr were more readily recaptured in July ($\beta_{1p} = 0.24$, PS = 99%). Body length did not affect recapture probability of charr in June ($\beta_{1p} = 0.06$; PS = 62%) or salmon in July ($\beta_{1p} = 0.76$, PS = 81%).

3.2 | Within-tributary movement

Within-tributary movement (>20 m movement, given that fish stayed in the tributary) was primarily influenced by body condition and its interaction with length, but not by body length in any instance (PS = 56–82%) (Table 2; Figure 4). Body condition had a strong negative effect on the within-tributary movement probability for salmon in May–June ($\beta_{1m} = -0.71$, PS = 95%) and a moderately negative effect for salmon in June–July ($\beta_{1m} = -0.51$, PS = 92%). For example, salmon of the average body length were 1.67 times less likely to move within the tributary in June–July as body condition increased by 10% (1 SD).

In addition, body length and condition had a strong interactive effect on within-tributary movement of charr in June–July (PS = 96%) and a moderate interactive effect on salmon in May–June (PS = 90%) (Table 2; Figure 4). In both instances, larger individuals in poorer body condition were more likely to move within the tributary, but smaller individuals with better body condition were more likely to move (Figure 4). In general, larger individuals with better body condition were sedentary (i.e. did not move >20 m) across species and sampling intervals, but effects of body condition on within-tributary movement varied by species and sampling interval (Figure 4).

4 | DISCUSSION

This study demonstrated that salmonid movement at different spatial scales was influenced by different individual characteristics. Emigration from the tributary was affected more strongly by body length than by body condition, and their interactive effect was neither strong nor moderate. Within-tributary movement was influenced by body condition but not by body length, and their interactive effect was strong or moderate in two instances. These

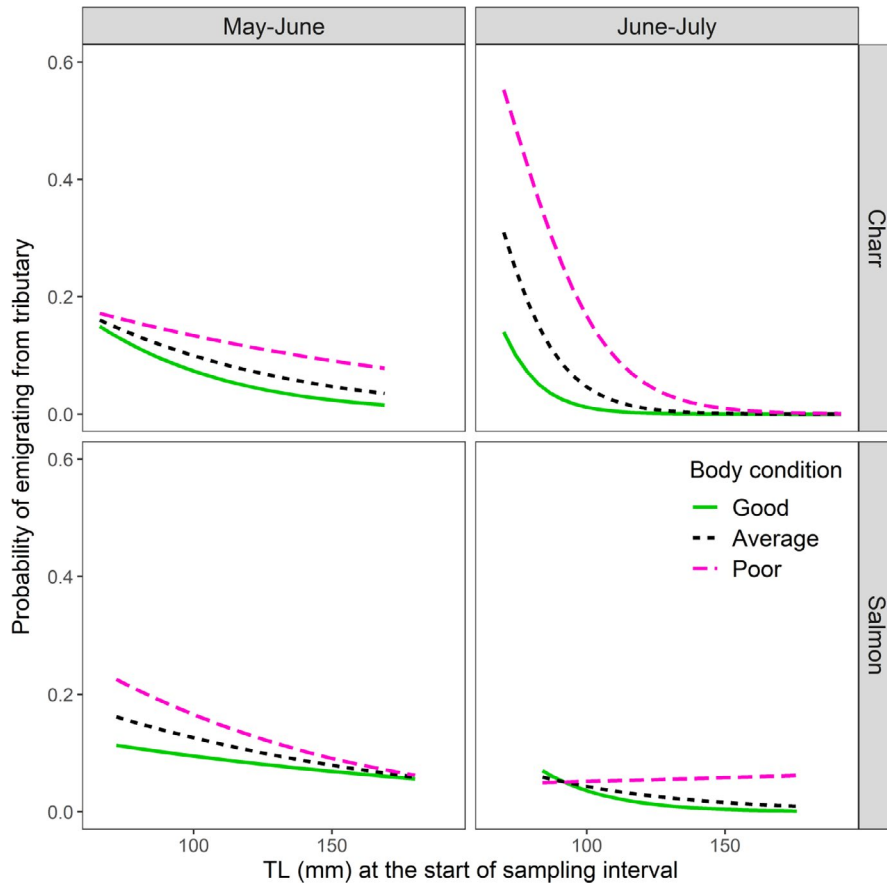


FIGURE 2 Mean posterior probability of emigrating from the tributary in relation to body length. The relationships are shown for three different values of body condition; fish in average condition (short-dashed black), fish in good condition (mean + 1SD: solid green) and fish in poor condition (mean - 1SD: long-dashed pink). Mean and SD of body condition were based on measurements across May and June. Mean was 0 in both species, and SD was 0.09 in charr and 0.10 in salmon

results indicated complex mechanisms of stream fish movement, which was uncovered by an intensive mark-recapture survey coupled with an array of PIT antennas. Although complex, charr and salmon often responded similarly across sampling intervals, indicative of emerging regularities in determinants of multi-scale stream fish movement.

Smaller individuals of charr and salmon were more likely to emigrate from the study tributary (i.e. long-range movement). It is uncertain whether emigrants from the tributary stayed in the mainstem Butokamabetsu River or moved farther downstream to Lake Shumarinai (Figure 1). We tagged individuals ≥ 70 mm TL, and smaller individuals in this study typically were age 1+ fish that had hatched in spring of the previous year (2017) based on the length-frequency distributions (Appendix S5). Smaller individuals in our study were immature and emigration from the tributary was not related to reproduction. Instead, smaller and immature fish may have moved to the larger mainstem habitat for higher growth benefits (Tsuboi et al., 2020; White & Wagner, 2021). Charr and salmon in the mainstem were much larger in body length than those in the tributary. During the study period, we commonly captured individuals of each species >300 mm TL in the mainstem (Y. Kanno, *unpublished data*), which were never collected in the tributary and were approximately three times the mean TL of charr (94 mm) and salmon (115 mm) marked in the tributary. Small tributaries such as our study stream (mean wetted width = 1.9 m) may provide key spawning and rearing habitats that sustain spatially structured fish populations in stream channel

networks (Kanno et al., 2014; Tsuboi et al., 2020). At the same time, some individuals likely complete their entire life without leaving the study tributary. We surmise that the propensity of larger individuals to remain in the study tributary may be explained due in part to the study period (May–July) that preceded the onset of spawning (September–October).

A potential mechanistic explanation of body-length-dependent emigration is fish survival in the tributary, which also depended on body length in one instance (i.e. charr between June and July). As predicted, smaller individuals suffered higher mortality rates than larger individuals. Intriguingly, smaller charr were more likely to emigrate from the tributary in this interval. It indicates that the mortality cost of staying in the tributary was higher for smaller charr, and they may have emigrated from the tributary given the perceived and potential benefits of moving to the mainstem, such as higher growth rates and larger body size (see above). However, this hypothesis is incomplete because long-range movement per se comes with costs (Bonte et al., 2012). In our study area, predation risk is one such cost when moving to the mainstem occupied by much larger conspecifics and other large-bodied predators such as Sakhalin taimen. In fact, survival of salmonids is often lower in the mainstem than tributaries in the stream network (Letcher et al., 2015; Tsuboi et al., 2020; but see White & Wagner, 2021). Long-range movement may also incur a physiological cost (Bonte et al., 2012; Brodersen et al., 2008).

In stark contrast to emigration from the tributary, within-tributary movement was affected by body condition and its

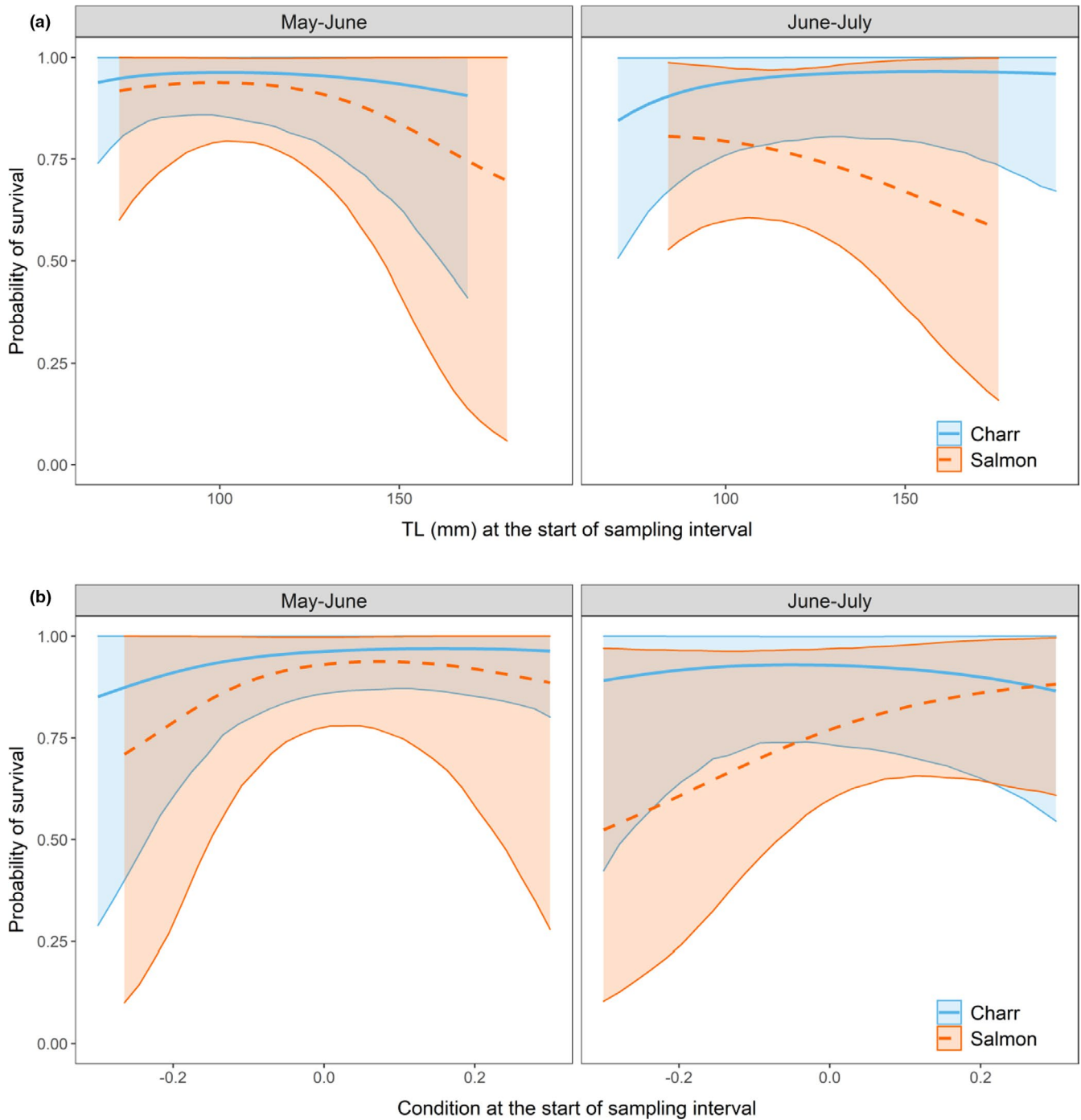


FIGURE 3 Probability of true survival against (a) body length and (b) condition. Effects of body length are shown for individuals at mean body condition, and effects of body condition are for individuals at mean body length. Posterior mean responses (lines) are shown with 95% credible intervals (shades)

interaction with body length. In general, fish in poorer body condition were more likely to move >20 m in the tributary. This finding aligns with the theoretical prediction that stream fish leave their local habitat when individuals cannot sufficiently access food and gain weight (Railsback et al., 1999). In spring and summer, individuals of charr and salmon compete for foraging positions to capture drifting invertebrates and develop social dominance hierarchies in pools (Fausch et al., 2020; Nakano, 1995a). During our post-snowmelt

study period, decreasing streamflows and increasing water temperature created a dynamic environment in which availability of food resources shifted over space and time (U. Hiromi, *unpublished data*). It is plausible that charr and salmon responded to the spatiotemporal shift via movement (Gowan & Fausch, 2002). Our finding that individuals in better body condition were sedentary (0–20 m movement distance) suggests that they did not move because they were able to access sufficient food resources within their local sections (i.e. home

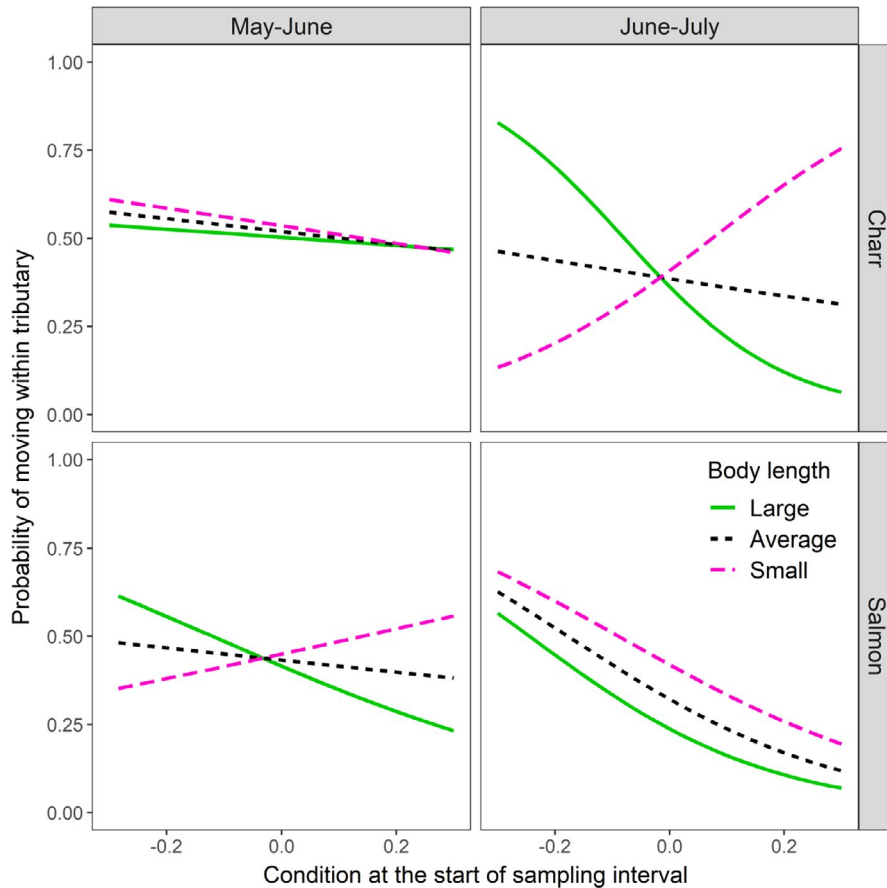


FIGURE 4 Mean posterior probability of moving within the tributary (i.e. departing from the local habitat >20 m) in relation to body condition. The relationships are shown for three different values of body length; fish of average length (short-dashed black), large fish (mean + 1SD: solid green) and small fish (mean - 1SD: long-dashed pink). Mean and SD of total length (TL in mm) were based on measurements across May and June. Mean was 94 mm, and SD was 18 in charr, and mean was 115 mm, and SD was 26 mm in salmon

range) to maintain body condition (i.e. weight) and consequently fitness (Railsback et al., 1999).

Interestingly, larger individuals in better body condition were more likely to stay locally (≤ 20 m), but smaller individuals in better condition were more likely to move in the tributary (i.e. interaction between body length and condition). This pattern was detected for charr in the June–July interval and salmon in the May–June interval, suggesting that the strength of the interactive effect varied temporally. We speculate that the interactive effect was perhaps due to benefits and costs of movement that vary with body size. Because dominance hierarchies are determined by body length in stream salmonids (Fausch et al., 2020; Nakano, 1995b), larger fish access and defend the most profitable foraging locations in pools. Larger fish typically occupy deeper pools, but deep pools were not abundant in our small tributary (1.9 m wide). In addition, competition for foraging location between similar-sized salmonids depends on which fish has already established territory in dominance hierarchies (i.e. prior residency) (Huntigford & Garica de Leaniz, 1997; Kvingedal & Einum, 2011). Consequently, benefits of staying locally (≤ 20 m) should have outweighed benefits of moving in larger individuals. On the other hand, smaller fish would have more readily located suitable pools elsewhere because shallow pools were more common in the tributary for them to settle. This indicates that exploratory behaviour in the tributary could have been more beneficial for smaller individuals, and smaller individuals in better body condition were more willing to leave the local habitat in search of other foraging

locations elsewhere in the tributary. Collectively, our data show that body condition affected whether or not fish left their local habitat, whereas body length influenced whether fish moved long distances and emigrated from the tributary to the mainstem.

Our study shows complexities associated with identifying drivers of stream fish movement and may explain why effects of body length and condition on movement differed among previous studies conducted at different spatial scales (Albanese et al., 2004; Gowan & Fausch, 1996; Heim et al., 2016). Movement can be characterised at multiple spatial scales in stream fish (Rodriguez, 2002), and our data demonstrate that determinants of movement may depend on scale. We also show that determinants of movement may shift over time (e.g. the interactive effect of body length and condition in the two sampling intervals). Elucidating spatiotemporal variation in factors influencing movement will require additional investigations to understand context-dependent movement. In this regard, we conclude by providing three specific recommendations for future studies of stream fish movement. First, determinants of movement should be evaluated at multiple spatial scales. Given their linear and dendritic habitat, streams provide a suitable system to track multi-scale movement (e.g. movement among and within stream segments, and emigration from the study area). Multi-scale control of movement is not limited to stream fish (Bowler & Benton, 2005; Ducros et al., 2020), and additional research on stream fish movement will likely offer key insights on animal movement ecology in general. Second, fish movement should be studied across seasons to evaluate whether

drivers of movement interact with time. Fish movement can vary greatly over time (Schlosser, 1995), and a temporally continuous view of drivers of movement can now be obtained by using technology such as PIT antennas (Kanno et al., 2014). Finally, factors influencing movement should be studied among species because movement of sympatric species may not be controlled by the same drivers (Albanese et al., 2004; Bryant et al., 2009; Pennock et al., 2018; Terui et al., 2021). Simultaneous evaluations of multiple species at multiple spatial scales will advance our knowledge of meta-community assembly (Brown et al., 2011; Falke & Fausch, 2010) and allow us to understand better the role of movement in predicting fish population and community responses to environmental change and anthropogenic disturbances.

ACKNOWLEDGEMENTS

This study was made possible by financial support from the River Fund of The River Foundation, Japan, the Colorado Water Center, the Colorado State University Office of International Programs, and the Grants-in-Aid for Scientific Research Program of the Japan Society for the Promotion of Science (17H03725). Y. Kanno was supported as a Visiting Fellow by the Kyoto University Center for Ecological Research to conduct the fieldwork of this study. We are grateful for logistical assistance provided by the Hokkaido University Uryu Experimental Forest, and thank its staff members including Wataru Mamiya, Rei Sakai, Yuri Yabuhara, Tohru Miyazaki, Toshiya Yoshida, Chikara Kozuka, Michio Ishihara, Masaaki Ohmori, Toshiyuki Sasahara, Yoshiaki Takahashi, Takashi Hara, Toshio Morita, Masahiro Wakui and Masayuki Watarai. Field sampling was assisted by Naoki Yui, Fabian Droppelmann, Ryo Futamura, Kseniya Lyalina, Takehito Muto, Ryohei Sugime, Kunio Takatsu, Aya Yamaguchi and Seoghyun Kim. We thank Kurt Fausch and three anonymous reviewers for providing constructive criticisms that improved this manuscript.

CONFLICT OF INTEREST

There is no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Y.K., and H.U. designed the study. Y.K., O.K., S.U. and H.U. collected data in the field. Y.K. and A.C.H. analysed the data. Y.K. wrote the manuscript with input from A.C.H., and all authors approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Yoichiro Kanno  <https://orcid.org/0000-0001-8452-5100>

Audrey C. Harris  <https://orcid.org/0000-0001-9367-5119>

Osamu Kishida  <https://orcid.org/0000-0002-2663-8155>

Shunsuke Utsumi  <https://orcid.org/0000-0003-1558-8073>

Hiroimi Uno  <https://orcid.org/0000-0002-9343-3061>

REFERENCES

- Albanese, B., Angermeier, P. L., & Dorai-Raj, S. (2004). Ecological correlates of fish movement in a network of Virginia streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(6), 857–869. <https://doi.org/10.1139/f04-096>
- Al-Chokhachy, R., Kovach, R. P., Sepulveda, A., Strait, J., Shepard, B. B., & Muhlfeld, C. C. (2019). Compensatory growth offsets poor condition in native trout populations. *Freshwater Biology*, 64(12), 2120–2130. <https://doi.org/10.1111/fwb.13400>
- Aoyama, K., Yoshida, T., Harada, A., Noguchi, M., Miya, H., & Shibata, H. (2011). Changes in carbon stock following soil scarification of non-wooded stands in Hokkaido, northern Japan. *Journal of Forest Research*, 16(1), 35–45. <https://doi.org/10.1007/s10310-010-0204-y>
- Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The network dynamics hypothesis: How channel networks structure riverine habitats. *BioScience*, 54(5), 413–427.
- Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., ... Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, 87(2), 290–312. <https://doi.org/10.1111/j.1469-185X.2011.00201.x>
- Booth, M. T., Hairston, N. G., & Flecker, A. S. (2020). Consumer movement dynamics as hidden drivers of stream habitat structure: Suckers as ecosystem engineers on the night shift. *Oikos*, 129(2), 194–208. <https://doi.org/10.1111/oik.06396>
- Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: Relating individuals behaviour to spatial dynamics. *Biological Reviews*, 80(2), 205–225. <https://doi.org/10.1017/S1464793104006645>
- Brodersen, J., Nilsson, P. A., Hansson, L.-A., Skov, C., & Brönmark, C. (2008). Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology*, 89(5), 1195–1200. <https://doi.org/10.1890/07-1318.1>
- Brown, B. L., Swan, C. M., Auerbach, D. A., Campbell Grant, E. H., Hitt, N. P., Maloney, K. O., & Patrick, C. (2011). Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society*, 30(1), 310–327. <https://doi.org/10.1899/10-129.1>
- Bryant, M. D., Lukey, M. D., McDonnell, J. P., Gubernick, R. A., & Aho, R. S. (2009). Seasonal movement of Dolly Varden and cutthroat trout with respect to stream discharge in a second-order stream in south-east Alaska. *North American Journal of Fisheries Management*, 29(6), 1728–1742. <https://doi.org/10.1577/M09-022.1>
- Cary, J. B., Holbrook, J. L., Reed, M. E., Austin, T. B., Steffensen, M. S., Kim, S., Pregler, K. C., & Kanno, Y. (2017). Survival of upper Piedmont stream fishes implanted with 8-mm passive integrated transponder tags. *Transactions of the American Fisheries Society*, 146(6), 1223–1232. <https://doi.org/10.1080/00028487.2017.1370015>
- Clark, S. R., Kreiser, B. R., Schaefer, J. F., & Stewart, L. K. (2019). Scale dependence of sex-specific movement in a small-bodied stream fish. *Freshwater Biology*, 64(7), 1342–1353. <https://doi.org/10.1111/fwb.13309>
- Cooke, S. J., Midwood, J. D., Thiem, J. D., Klimley, P., Lucas, M. C., Thorstad, E. B., Eiler, J., Holbrook, C., & Ebner, B. C. (2013). Tracking animals in freshwater with electronic tags: Past, present and future. *Animal Biotelemetry*, 1, 1–19. <https://doi.org/10.1186/2050-3385-1-5>
- Ducros, D., Morellet, N., Patin, R., Atmeh, K., Debeffe, L., Cargnelutti, B., Chaval, Y., Lourtet, B., Coulon, A., & Hewison, A. J. M. (2020). Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. *Oikos*, 129(1), 81–92. <https://doi.org/10.1111/oik.06793>

- Falke, J. A., & Fausch, K. D. (2010). From metapopulations to metacommunities: Linking theory with empirical observations of the spatial population dynamics of stream fishes. In K. B. Gido, & D. A. Jackson (Eds.), *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques* (pp. 207–233). American Fisheries Society.
- Fausch, K. D., Nakano, S., Kitano, S., Kanno, Y., & Kim, S. (2020). Interspecific social dominance networks reveal mechanisms promoting coexistence in sympatric charr in Hokkaido, Japan. *Journal of Animal Ecology*, *90*(2), 515–527. <https://doi.org/10.1111/1365-2656.13384>
- Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience*, *52*(6), 483–498.
- Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2003). *Bayesian Data Analysis* (2nd ed). Chapman and Hall/CRC Press.
- Gelman, A., & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models* (1st ed). Cambridge University Press.
- Gilliam, J. F., & Fraser, D. F. (2001). Movement in corridors: Enhancement by predation threat, disturbance, and habitat structure. *Ecology*, *82*(1), 258–273.
- Gimenez, O., Lebreton, J., Choquet, R., & Pradel, R. (2018). R2ucare: An R package to perform goodness-of-fit tests for capture–recapture models. *Methods in Ecology and Evolution*, *9*(7), 1749–1754. <https://doi.org/10.1111/2041-210X.13014>
- Gowan, C., & Fausch, K. D. (1996). Mobile brook trout in two high-elevation Colorado streams: Re-evaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(6), 1370–1381. <https://doi.org/10.1139/cjfas-53-6-1370>
- Gowan, C., & Fausch, K. D. (2002). Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes*, *64*, 139–153. <https://doi.org/10.1023/A:1016010723609>
- Gowan, C., Young, M. K., Fausch, K. D., & Riley, S. C. (1994). Restricted movement in resident stream salmonids: A paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(11), 2626–2637. <https://doi.org/10.1139/f94-262>
- Gries, G., & Letcher, B. H. (2002). Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. *North American Journal of Fisheries Management*, *22*(1), 219–222.
- Heim, K. C., Wipfli, M. S., Whitman, M. S., & Seitz, A. C. (2016). Body size and condition influence migration timing of juvenile Arctic grayling. *Ecology of Freshwater Fish*, *25*(1), 156–166. <https://doi.org/10.1111/eff.12199>
- Hooley-Underwood, Z. E., Stevens, S. B., Salinas, N. R., & Thompson, K. G. (2019). An intermittent stream supports extensive spawning of large-river native fishes. *Transactions of the American Fisheries Society*, *148*(2), 426–441. <https://doi.org/10.1002/tafs.10141>
- Horton, G. E., Dubreuil, T. L., & Letcher, B. H. (2007). A model for estimating passive integrated transponder (PIT) tag antenna efficiencies for interval-specific emigration rates. *Transactions of the American Fisheries Society*, *136*(5), 1165–1176. <https://doi.org/10.1577/T06-053.1>
- Huntigford, F. A., & Garica de Leaniz, C. (1997). Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. *Journal of Fish Biology*, *51*(5), 1009–1014. <https://doi.org/10.1111/j.1095-8649.1997.tb01539.x>
- Kanno, Y., Letcher, B. H., Coombs, J. A., Nislow, K. H., & Whiteley, A. R. (2014). Linking movement and reproductive history of brook trout to assess habitat connectivity in a heterogeneous stream network. *Freshwater Biology*, *59*(1), 142–154. <https://doi.org/10.1111/fwb.12254>
- Kanno, Y., Yui, N., Mamiya, W., Sakai, R., Yabuhara, Y., Miyazaki, T., Utsumi, S., Kishida, O., & Uno, H. (2020). A multistate mark-recapture approach to characterize stream fish movement at multiple spatial scales. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(6), 1090–1100. <https://doi.org/10.1139/cjfas-2019-0329>
- Kéry, M., & Schaub, M. (2012). *Bayesian Population Analysis using WinBUGS: A Hierarchical Perspective* (1st ed). Academic Press.
- Koizumi, I. (2011). Integration of ecology, demography and genetics to reveal population structure and persistence: A mini review and case study of stream-dwelling Dolly Varden. *Ecology of Freshwater Fish*, *20*(3), 352–363. <https://doi.org/10.1111/j.1600-0633.2010.00480.x>
- Koizumi, I., Yamamoto, S., & Maekawa, K. (2006). Decomposed pairwise regression analysis of genetic and geographic distances reveals a metapopulation structure of stream-dwelling Dolly Varden charr. *Molecular Ecology*, *15*(11), 3175–3189. <https://doi.org/10.1111/j.1365-294X.2006.03019.x>
- Kvingedal, E., & Einum, S. (2011). Prior residency advantage for Atlantic salmon in the wild: Effects of habitat quality. *Behavioral Ecology and Sociobiology*, *65*(6), 1295–1303. <https://doi.org/10.1007/s00265-011-1143-0>
- Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, *62*(1), 67–118. <https://doi.org/10.2307/2937171>
- Letcher, B. H., Schueller, P., Bassar, R. D., Nislow, K. H., Coombs, J. A., Sakrejda, K., Morrissey, M., Sigourney, D. B., Whiteley, A. R., O'Donnell, M. J., & Dubreuil, T. L. (2015). Robust estimates of environmental effects on population vital rates: An integrated capture-recapture model of seasonal brook trout growth, survival and movement in a stream network. *Journal of Animal Ecology*, *84*(2), 337–352. <https://doi.org/10.1111/1365-2656.12308>
- Meyer, K. A., High, B., Gastelecutto, N., Mamer, E. R. J., & Elle, F. S. (2011). Retention of passive integrated transponder tags in stream-dwelling rainbow trout. *North American Journal of Fisheries Management*, *31*(2), 236–239. <https://doi.org/10.1080/02755947.2011.572799>
- Nakamura, T., Maruyama, T., & Watanabe, S. (2002). Residency and movement of stream-dwelling Japanese charr, *Salvelinus leucomaenis*, in a central Japanese mountain stream. *Ecology of Freshwater Fish*, *11*(3), 150–157. <https://doi.org/10.1034/j.1600-0633.2002.00014.x>
- Nakano, S. (1995a). Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. *Canadian Journal of Zoology*, *73*(10), 1845–1854. <https://doi.org/10.1139/z95-217>
- Nakano, S. (1995b). Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *Journal of Animal Ecology*, *64*(1), 75–84. <https://doi.org/10.2307/5828>
- O'Connor, K. I., Metcalfe, N. B., & Taylor, A. C. (2000). The effects of prior residence on behavior and growth rates in juvenile Atlantic salmon (*Salmo salar*). *Behavioral Ecology*, *11*(1), 13–18. <https://doi.org/10.1093/beheco/11.1.13>
- Olsson, I. C., Greenberg, L. A., Bergman, E., & Wysujack, K. (2006). Environmentally induced migration: The importance of food. *Ecology Letters*, *9*(6), 645–651. <https://doi.org/10.1111/j.1461-0248.2006.00909.x>
- Pennock, C. A., Cathcart, C. N., Hedden, S. C., Weber, R. E., & Gido, K. B. (2018). Fine-scale movement and habitat use of a prairie stream fish assemblage. *Oecologia*, *186*(3), 831–842. <https://doi.org/10.1007/s00442-018-4073-y>
- Peterson, D. P., & Fausch, K. D. (2003). Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(12), 1502–1516. <https://doi.org/10.1139/f03-128>
- Plummer, M. (2017). *JAGS version 4.3.0 user manual*. <http://mcmc-jags.sourceforge.net/>
- R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>

- Railsback, S. F., Lamberson, R. H., Harvey, B. C., & Duffy, W. E. (1999). Movement rules for individual-based models of stream fish. *Ecological Modelling*, 123(2–3), 73–89. [https://doi.org/10.1016/S0304-3800\(99\)00124-6](https://doi.org/10.1016/S0304-3800(99)00124-6)
- Richard, A., O'Rourke, J., Caudron, A., & Cattaneo, F. (2013). Effects of passive integrated transponder tagging methods on survival, tag retention and growth of age-0 brown trout. *Fisheries Research*, 145, 37–42. <https://doi.org/10.1016/j.fishres.2013.03.001>
- Rodriguez, M. A. (2002). Restricted movement in stream fish: The paradigm is incomplete, not lost. *Ecology*, 83(1), 1–13. <https://doi.org/10.2307/2680115>
- Sato, T., & Watanabe, K. (2014). Do stage-specific functional responses of consumers dampen the effects of subsidies on trophic cascades in streams? *Journal of Animal Ecology*, 83(4), 907–915. <https://doi.org/10.1111/1365-2656.12192>
- Schlosser, I. J. (1995). Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia*, 303(1–3), 71–81. <https://doi.org/10.1007/BF00034045>
- Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement Ecology*, 8(1), 1–12. <https://doi.org/10.1186/s40462-020-0197-x>
- Skalski, G. T., & Gilliam, J. F. (2000). Modeling diffusive spread in a heterogeneous population: A movement study with stream fish. *Ecology*, 81(6), 1685–1700.
- Tamate, T., & Maekawa, K. (2004). Female-biased mortality rate and sexual size dimorphism of migratory masu salmon *Oncorhynchus Masou*. *Ecology of Freshwater Fish*, 13(2), 96–103. <https://doi.org/10.1111/j.1600-0633.2004.00043.x>
- Terui, A., Kim, S., Pregler, K. C., Kanno, Y. (2021). Non-random dispersal in sympatric stream fishes: Influences of natural disturbance and body size. *Freshwater Biology*. <https://doi.org/10.1111/fwb.13796>
- Terui, A., Ooue, K., Urabe, H., & Nakamura, F. (2017). Parasite infection induces size-dependent host dispersal: Consequences for parasite persistence. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171491. <https://doi.org/10.1098/rspb.2017.1491>
- Tsuboi, J.-I., Morita, K., Koseki, Y., Endo, S., Sahashi, G., Kishi, D., Kikko, T., Ishizaki, D., Nunokawa, M., & Kanno, Y. (2020). Spatial covariation of fish population vital rates in a stream network. *Oikos*, 129(6), 924–937. <https://doi.org/10.1111/oik.07169>
- Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, 15, 393–425. <https://doi.org/10.1146/annurev.es.15.110184.002141>
- White, S. L., & Wagner, T. (2021). Behaviour at short temporal scales drives dispersal dynamics and survival in a metapopulation of brook trout (*Salvelinus fontinalis*). *Freshwater Biology*, 66(2), 278–285. <https://doi.org/10.1111/fwb.13637>
- Yamamoto, S., Morita, K., & Goto, A. (1999). Geographic variations in life-history characteristics of white-spotted charr (*Salvelinus leucomaenis*). *Canadian Journal of Zoology*, 77(6), 871–878. <https://doi.org/10.1139/z99-055>
- Young, M. K. (2011). Generation-scale movement patterns of cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in a stream network. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(5), 941–951. <https://doi.org/10.1139/f2011-023>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Kanno, Y., Harris, A. C., Kishida, O., Utsumi, S., & Uno, H. (2022). Complex effects of body length and condition on within-tributary movement and emigration in stream salmonids. *Ecology of Freshwater Fish*, 31, 317–329. <https://doi.org/10.1111/eff.12632>