

A multistate mark–recapture approach to characterize stream fish movement at multiple spatial scales

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Abstract: We studied movement of a native salmonid, white-spotted char (*Salvelinus leucomaenis*), in a 1-km tributary in northern Hokkaido, Japan, in May–July 2018. Based on physical mark–recapture of 501 unique individuals and detection by mobile PIT antenna over monthly intervals, a majority of fish (70%–80%) stayed within 60 m of previously released locations, demonstrating what appeared to be restricted movement patterns. However, fixed PIT antenna data showed that as much as 17% of marked individuals emigrated from the study area during the 2-month study period. Probability of emigration did not depend on where in the 1-km segment individuals had been released, indicating that emigration likely represented long-distance movement. Once emigrants made a decision to emigrate, they left the tributary within 1–3 median days by moving downstream in a unidirectional manner, based on detections at a total of three antenna arrays deployed throughout the tributary. Our multiscale analysis provided strong support for co-existence of short- and long-distance movement patterns, and we conclude that movement data at multiple spatial scales complement each other to characterize population-scale movement.

Résumé : Nous avons étudié les déplacements d'un salmonidé indigène, l'omble à taches blanches (*Salvelinus leucomaenis*), dans un affluent de 1 km dans le nord d'Hokkaido (Japon), de mai à juillet 2018. À la lumière du marquage-recapture de 501 individus et de détections par des antennes mobiles pour transpondeurs intégrés sur des intervalles mensuels, une majorité de poissons (70 % – 80 %) demeuraient dans un rayon de 60 m des lieux d'où ils avaient été lâchés, semblant faire preuve de motifs de déplacement restreints. Les données d'antennes fixes pour transpondeurs intégrés montrent toutefois que jusqu'à 17 % des individus marqués ont émigré de la région d'étude durant les deux mois de la période d'étude. La probabilité d'émigration ne dépendait pas de l'endroit dans le tronçon de 1 km où un individu avait été relâché, ce qui indique que l'émigration représente vraisemblablement des déplacements sur de longues distances. Une fois que les émigrants avaient pris la décision d'émigrer, il leur fallait un nombre médian de 1 à 3 jours pour quitter l'affluent en se déplaçant vers l'aval de manière unidirectionnelle, à la lumière de détections à un total de trois batteries d'antennes déployées dans tout l'affluent. Notre analyse multiéchelle appuie fortement l'interprétation de la coexistence de motifs de déplacement de courtes et de longues distances, et nous concluons que des données sur les déplacements à différentes échelles spatiales fournissent des renseignements complémentaires pour la caractérisation des déplacements à l'échelle de la population. [Traduit par la Rédaction]

Introduction

Movement is a key demographic process that influences population dynamics, gene flow and host–parasite interactions in stream fishes (Koizumi 2011; Terui et al. 2017; Davis et al. 2018). Despite its importance in understanding population ecology, movement of stream fishes is challenging to study for at least two common reasons. First, movement differs greatly among individuals; some fish are sedentary, being located in the same location (<10s m) over time, but others disperse to different locations in the riverscape, sometimes for long distances (>1–10s km) (Fausch et al. 2002). Propensity for movement differs among individuals based on body size (Peterson and Fausch 2003), body condition (Clark et al. 2019), or personality (Rasmussen and Belk 2017). Variation in movement distances necessitates a large sample size of individuals to characterize population-scale movement.

Second, long-distance movement is inherently more difficult to detect than short-distance movement. Movement is traditionally studied by tracking marked individuals over time in a defined study area. However, this approach cannot detect individuals that move out of the study area and never return during the study period (i.e., long-distance movement or emigration). Thus, the study design results in failure to characterize long-distance movement, and accordingly data overrepresent short-distance movement (Gowan et al. 1994; Fausch et al. 2002). This methodological drawback, along with difficulties in predicting how far stream fish move once they make a decision to move, is partly responsible for the prevailing view that frequency distributions of movement distances are leptokurtic with a cluster of individuals exhibiting restricted movement (i.e., a higher peak near the mean than normal distributions) and the rest dispersing in the riverscape equally likely to any other location (i.e., longer tails in both up-

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stream and downstream directions than normal distributions; Skalski and Gilliam 2000; Rodríguez 2002).

These challenges to studying stream fish movement have been alleviated to a large extent with an application of passive integrated transponder (PIT) tags and antenna technology (Cooke et al. 2013). PIT tags are inexpensive relative to other tags (e.g., radio telemetry), and a large number of individuals can be tracked in a single study. Mobile antennas facilitate relocation of tagged individuals without the need for physical recapture. An array of PIT antennas deployed throughout a study stream provides richer information on fish movement (Raabe et al. 2014), and those placed at the boundary of study area monitor emigration from the study area continuously over time. Knowledge on stream fish movement has expanded in the last two decades aided by physical mark-recapture of PIT tagged fish (Albanese et al. 2004) and by mobile (Bliss et al. 2015) and fixed antennas (Horton et al. 2011; Kanno et al. 2014).

Still, inferences on population-scale movement remain elusive in stream fishes. We argue that a fuller understanding has been hampered partly because stream fish movement is studied at various spatial scales independently. Previous work focused not only on movement distances (Albanese et al. 2004) but also on tendency to leave local mesohabitats (Gowan and Fausch 2002), “patch-scale” movement in the metapopulation context (Koizumi 2011), or emigration from the study area, including diadromous species (Svendsen et al. 2007; Horton et al. 2011). Only few studies simultaneously incorporated movement at multiple spatial scales (Labbe and Fausch 2000; Rodríguez 2002), although multiscale investigations are not new to stream fish ecology, such as species occupancy and abundance models (Kanno et al. 2015; Midway and Peoples 2019). Integration of movement analysis across spatial scales has been attempted only partially; for example, patterns of movement within a defined study area have been extrapolated to infer emigration from the study area (i.e., long-distance movement) given the challenges of recording long-distance movement (Skalski and Gilliam 2000; Nathan et al. 2003). As a result, the prevalence of leptokurtic distributions of movement distances and their distributional shape are not well characterized for stream fishes.

Here, we investigated movement of native white-spotted char (*Salvelinus leucomaenis*) in northern Japan at multiple spatial scales by conducting a mark-recapture study in a 1-km tributary segment. Specifically, our aim was to use physical recapture and mobile and fixed PIT antennas to study char movement at three spatial scales: among 20-m sections, among three longitudinal reaches with distinguishable habitat characteristics within the tributary, and emigration from the tributary to the main stem. Stream fish movement is most commonly studied during the summer baseflow conditions to facilitate physical capture of individuals (Riley et al. 1992; Rodríguez 2002; Pépino et al. 2012). However, our study encompassed a period of spring snowmelt, during which stream fish movement is under-studied. Physical recapture and mobile antennas were used to quantify 20-m scale movement, and Bayesian multistate Cormack–Jolly–Seber (CJS) models were used to infer movement among reaches and emigration from the study tributary. CJS models infer survival probability of marked individuals while accounting for imperfect capture of individuals based on detection histories of individuals (Lebreton et al. 1992). Multistate CJS models infer transitions among discrete “states” of individuals such as locations and age or body size groups (e.g., movement and growth; Horton et al. 2011; Raabe et al. 2014). Based on movement analysis at multiple spatial scales, we demonstrate that movement data within the study tributary were not indicative of patterns of emigration from the tributary (i.e.,

long-distance movement) and the multifaceted approach using physical recapture and PIT antennas were necessary to characterize population-scale movement.

Materials and methods

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 is predominated by mixed stands of conifer and broad-leaved trees. Mean annual air temperature is 4.2 °C, and mean annual precipitation is 1236 mm. Snow cover usually extends from late November to early May, with maximum depth of ~3 m (Aoyama et al. 2011). Snowmelt occurs typically from April to May (refer to online Supplementary material S1¹).

The study site was located in a 1-km segment of the unnamed perennial tributary and was bound downstream by the confluence with the Butokomabetsu River (Fig. 1). Fifty permanent sections (20-m long) were established from the confluence with the main stem (0 m) and extended upstream (1000 m). The tributary harbored three distinguishable longitudinal reaches composed of spatially continuous sections. In this study, we investigated movement of white-spotted char at section and reach scales, as well as emigration from the tributary.

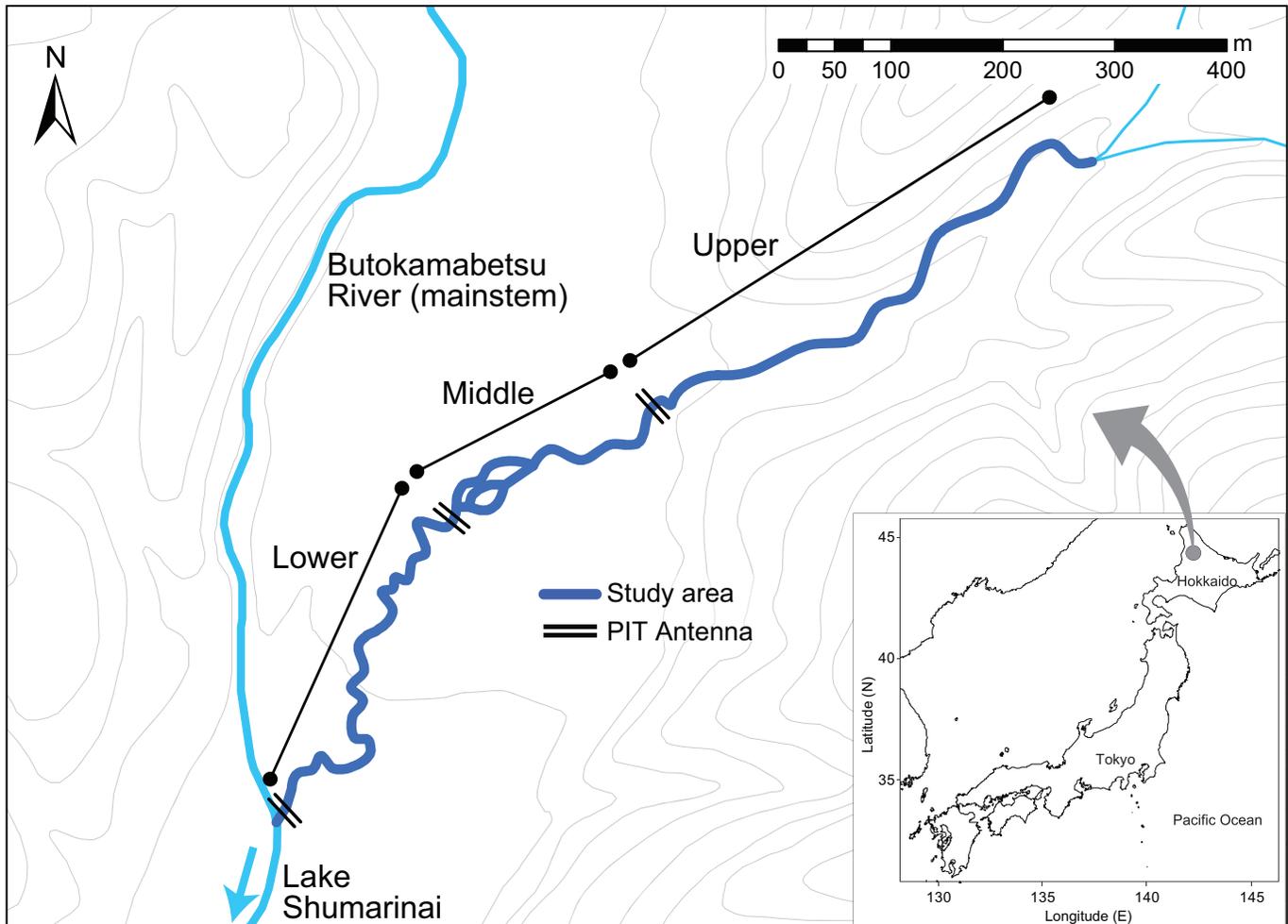
The three reaches were similar in mean wetted width (lower = 2.0 m; middle = 1.8 m; upper 1.9 m, based on measurements on 14 June 2018), but differed in mean depth (lower = 18 cm; middle = 14 cm; upper = 11 cm) and other habitat characteristics. The lower reach was 440 m in waterway distance from the confluence and was characterized with a deeper and meandering channel. The riparian zone was densely populated by 1–2 m high broad-leaf bamboo (*Sasa senanensis*), which hang over the stream channel. Traversing the lower reach on foot was much more challenging than the other two reaches, let alone sampling fish (see fish capture probability below). The middle reach (440–640 m upstream of the confluence) was similarly characterized with low-gradient channels, but differed greatly from the downstream reach due to the presence of side channels developed in the floodplain-like habitat (Fig. 1). The channel was dominated by fine substrate (i.e., silt and clay) and was inhabited by skunk cabbage (*Lysichiton camtschatcensis*). The upper reach (640–1000 m) was shallower and steeper (Fig. 1), containing cobble, pebble, and gravel substrate. The riparian zone of this riffle-dominated reach was composed mainly of alder trees (*Alnus japonica*). The study species, white-spotted char, was the predominant fish species in all reaches, followed by masu salmon (*Oncorhynchus masou*). Both species of salmonids are native to the study area, and a portion of their populations in the Butokamabetsu River displays an adfluvial life form (Tamate and Maekawa 2004) by moving to Lake Shumarinai, a man-made reservoir located 5 km downstream of the study tributary (Fig. 1). Public access to the study area is restricted, and harvest of white-spotted char (i.e., fishing mortality) did not occur.

Field sampling

We conducted a mark-recapture study with PIT tags on 24–29 May, 17–20 June, 23–25 July, and 17–18 October 2018 to characterize char movement within the tributary and emigration from the tributary. Fish were captured using a backpack electrofishing unit (Model LR-24, Smith-Root Inc., Vancouver, Washington, USA) with direct current settings (300–400 V, 30–45 Hz, and 25% duty cycle). A crew of three or four members sampled in an upstream direction by 20-m section. All sections including side channels in the middle reach were sampled with a two-pass removal method in June and July for estimating section-scale abundance longitu-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0329>.

Fig. 1. Map of study area in Uryu Experimental Forest, Hokkaido, Japan, showing a 1-km segment in which mark–recapture surveys were conducted (thick blue) and the main stem (thick cyan) to which permanent emigration was monitored. A pair of two antennas were placed at each antenna location. Contour lines (gray) were based on a topographic map made available by the Geospatial Information Authority of Japan, the Ministry of Land, Infrastructure, Transport and Tourism. [Colour online.]



dinally using the Carle–Strub method (Carle and Strub 1978). In May, every third section of the main channel and side channels in the middle reach were sampled with a two-pass method, with the rest sampled with a single-pass method. In October, only 34 out of 50 sections in the main channel and all of the side channels in the middle reach were sampled with a single-pass method, and the October survey was conducted to estimate parameters of multi-state CJS models monthly up to July because survival and recapture probabilities for the last interval cannot be independently estimated in the CJS framework (see below). Once captured, fish were held in a bucket and live well separated by section and pass until processing.

Fish were measured for total length (TL in mm), scanned for a tag, and fish ≥ 70 mm TL without a tag were anesthetized with a dose of clove oil and marked with 12-mm half duplex PIT tags (Oregon RFID, Portland, Oregon). The PIT tag was inserted into the abdominal cavity through a ventral incision made lateral to the midline and posterior of the pectoral fins. The size of the incisions was just large enough to insert the PIT tag, and incisions were made by scalpels with a No. 11 blade. We considered tag loss and mortality negligible because this tagging technique was applied successfully in our previous studies involving multiple taxa including salmonids (Kanno et al. 2014; Cary et al. 2017). In addition, 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 and Letcher 2002; Richard et al. 2013), and the main study period (May through July) did not overlap with white-spotted char's spawning period (autumn), when tag loss may be of the greatest concern (Meyer et al. 2011; Cooke et al. 2013). After processing, fish were allowed to recover in a live well and were returned alive to the 20-m section of capture.

We used mobile and fixed PIT antennas to monitor movement of white-spotted char at multiple spatial scales. Mobile antenna supplemented the mark–recapture method to quantify 20-m scale movement within the 1-km tributary. 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 by the orientation of tags. The 1-km tributary including side channels was travelled on foot in an upstream direction to locate PIT-tagged char on 21 June and 27 July 2018. This occurred just after mark–recapture surveys were completed in each month. One person operated the mobile antenna, and a second person recorded the section (20 m) in which tags were detected. We assumed tags had been expelled from fish when they were detected in microhabitats unlikely occupied by char (e.g., edge of water, shallow pool with good visibility) and tags were still present after disturbing the area by kicking. Expelled or “ghost” tags should not be a major concern in this study, given the short study period (May–July) and high true survival of char (see Results). On both sampling days with mobile antenna,

we surveyed 100 m beyond the upstream boundary of the 1-km study area for char that may have emigrated from the study area. We detected only two individuals on 21 June and three individuals on 27 July (a single individual was detected on both days), and the stream was <1–2 m wide upstream of the study area, harboring mainly individuals below the minimum tagging size (<70 mm TL). Furthermore, the stream upstream of the study area was only ~650 m in length, including intermittent sections. Therefore, we considered upstream emigration negligible.

We installed a pair of fixed antennas at the confluence with the main stem to monitor emigration from the tributary (Fig. 1). Two additional pairs of fixed antennas were installed at the boundary of downstream and middle reaches (440 m from the confluence) and middle and upstream reaches (640 m) to record intervals (i.e., number of days) at which individuals were detected at multiple antennas. Paired antennas (<5 m apart) were constructed for each multi-antenna reader (Oregon RFID) to identify the direction of movement. 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 were installed and operational prior to the first mark–recapture occasion (24 May), except for the antennas between downstream and middle reaches, which were installed on 5 June. All antennas were operated until 26 July (i.e., ≤63 days).

Analysis of section-scale (20 m) movement

Movement within the tributary was quantified based on the sections of capture and physical recapture or mobile antenna detections (20-m resolution) over two intervals (May–June and June–July). Movement distance was the waterway distance for individuals captured and recaptured–detected inside the tributary and its side channels. For those located in the side channels of the middle reach (Fig. 1), the shortest waterway distance to the main channel was calculated based on coordinates, and the waterway distance between the confluence and fish location in the main channel was added to calculate movement distance. Propensity to move upstream versus downstream was tested using a sign test, and this analysis was conducted by removing individuals that stayed in the same section (movement distance = 0 m) and those whose movement direction could not be identified (e.g., a fish in the side channel moved downstream to enter the main channel and moved upstream to be recaptured).

Analysis of reach-scale movement and emigration

We investigated movement among reaches in the tributary and emigration from the tributary to the mainstem Butokamabetsu River. Reach-scale movement complements section-scale analysis, given that both measure movement within the tributary. We also quantified the frequency of emigration and the reach from which fish emigrated to characterize long-distance movement. If movement from the tributary to the main stem epitomizes long-distance movement (>1 km), the reach in which fish were captured and marked should not influence the probability of emigration. However, if movement to the main stem is a form of short-distance movement, fish captured in the downstream reach should be more likely move to the main stem relative to those in the middle and upstream reaches. To address these questions, we analyzed mark–recapture data and fixed antenna data jointly using the multistate CJS analysis (Lebreton et al. 1992). Our multistate CJS model infers monthly movement among reaches and from each reach to the main stem, along with true survival, transition from small (≤100 mm TL) to large (>100 mm TL) size classes, and recapture probability. States were defined based on body size (small and large) and reach (upper, middle, and lower). Therefore, state transitions represented size-specific movement among

reaches, and the pair of fixed antennas at the mainstem confluence was used to account for emigration from the tributary (i.e., another state).

Data were formatted in a two-dimensional array ($y_{i,t}$), where rows indicated individuals (i) and columns indicated sampling occasions (t). Elements of the array were observed states defined by body size, reach, and emigration. The body size threshold (100 mm TL) was chosen based on length frequency distributions (Supplementary material S2¹), sample size distributions, and more frequent section-scale movement of fish below this threshold (see Results). A unique combination of size classes (small and large) and locations (upper, middle, and lower) resulted in six states (1 = small fish in upper reach; 2 = small fish in middle reach; 3 = small fish in lower reach; 4 = large fish in upper reach; 5 = large fish in middle reach; and 6 = large fish in lower reach). One additional state was defined to incorporate emigration; individuals that were detected at the confluence PIT antennas between survey t and survey $t + 1$ and never captured or detected again were given a value of 7 for survey $t + 1$. Lastly, individuals that were not detected were coded as 8 for survey t . Prior to fitting multistate CJS models to data, we used the R2ucare package (Gimenez et al. 2018) to evaluate potential violations of model assumptions and confirmed that there was no evidence for trap dependence ($P = 0.67$), transience ($P = 0.99$), and memory of past states ($P = 0.97$). That is, recapture probability on the next occasion did not differ between captured individuals and undetected live individuals (trap dependence), previously marked individuals had the same recapture probability as newly marked individuals (transience), and state transition probability depended only on the current state but not on the history of previous states (memory of past states).

The multistate CJS model was developed using the state-space modeling approach of Kéry and Schaub (2012). It is a hierarchical model composed of an ecological process following the state transitions over time and an observation process linking the latent states to observations (i.e., data) while accounting for imperfect detection of char during mark–recapture electrofishing surveys. The ecological process described state transitions from survey t to survey $t + 1$, starting with the first survey occasion in 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 (Table 1) were populated with conditional probabilities of emigration, true survival, movement among reaches, and growth from the small to large size (Table 1). Specifically, the transition matrix considered ecological processes in the following manner: (i) an individual may remain in the 1-km tributary between sampling intervals with a probability equaling f (fidelity) and emigrate from the tributary with a probability of $1 - f$; (ii) given an individual stayed in the tributary, the individual may survive with a probability of s (mortality = $1 - s$); (iii) given survival, the individual may move to one of the other two reaches (denoted by ψ) or stay in the same reach; and (iv) an individual in the small size group may grow to the large size group with a probability of ω , and individuals in the large size group do not shrink. Survival (s) refers to true survival, not apparent survival, because emigration has been accounted for (i.e., apparent survival = $s \times f$). Reach-scale movement probabilities were constrained to sum to 1. For example, a small char in the upper reach may move to the middle reach with a probability of ψ_1 , move to the lower reach with a probability of ψ_2 , and stay in the upper reach with a probability of $1 - \psi_1 - \psi_2$ (Table 1). The transition probability from the small to large size group (ω) was set to be spatially constant because growth did not vary among reaches during the study period (Y. Kanno, unpublished data). Fidelity, survival, movement, and body size transition were modeled to vary monthly to examine temporal patterns in these parameters between the first (May to June) and second (June to July) sampling intervals.

Table 2. Observation matrix linking latent state to observations (data) in the multistate CJS model.

True state at sample t	Observation at sample t							Not seen
	Small fish in upper	Small fish in middle	Small fish in lower	Large fish in upper	Large fish in middle	Large fish in lower	Emigrated	
Small fish in upper	p_1	0	0	0	0	0	0	$1 - p_1$
Small fish in middle	0	p_1	0	0	0	0	0	$1 - p_1$
Small fish in lower	0	0	p_2	0	0	0	0	$1 - p_2$
Large fish in upper	0	0	0	p_3	0	0	0	$1 - p_3$
Large fish in middle	0	0	0	0	p_3	0	0	$1 - p_3$
Large fish in lower	0	0	0	0	0	p_3	0	$1 - p_3$
Emigrated	0	0	0	0	0	0	1	0
Dead	0	0	0	0	0	0	0	1

Table 3. Number of individuals marked for the first time and recaptured with a PIT tag by state (body size and reach) and sampling occasion.

Body size	Reach	PIT tag	May	June	July
Small	Upper	Marked	73	64	—
		Recaptured	—	17	21
	Middle	Marked	58	66	—
		Recaptured	—	10	12
	Lower	Marked	32	55	—
		Recaptured	—	6	10
Large	Upper	Marked	12	21	—
		Recaptured	—	9	34
	Middle	Marked	13	27	—
		Recaptured	—	6	26
	Lower	Marked	18	62	—
		Recaptured	—	9	52

Note: No individuals were recaptured in May, and no individuals were marked in July. Mark-recapture sampling occurred on 24–29 May, 17–20 June, and 23–25 July 2018.

TL), but individuals of this size group comprised 28% of the recaptured fish in July (Table 3). The mobile PIT antenna detected 102 individuals in June out of 206 marked in May, and 169 individuals in July out of 352 marked or recaptured in June. Mobile PIT antenna recorded eight additional “ghost” tags in June and an additional four in July.

A total of 85 emigrants were identified to leave from the tributary to the main stem based on their detections at the PIT antennas at the confluence with the main stem. Of those, 28 individuals emigrated between May and June surveys, and 57 individuals emigrated between June and July surveys. Antenna detections at the confluence indicated signs of emigration (i.e., one-way movement from the tributary to the main stem) because (i) 76 of the 85 individuals (89%) were detected at the confluence antenna within 48-hour windows encompassing their first and last detections and exited the tributary, (ii) only a single individual was recaptured by electrofishing after it was detected by the confluence antenna, and (iii) only four individuals were detected in the tributary by the mobile antenna after they had been detected at the fixed antenna pair at the confluence.

Based on the Carle–Strub removal method, char abundance increased upstream, particularly for the small size group (70–100 mm TL; Fig. 3). In addition, the longitudinal pattern was particularly striking for individuals < 70 mm TL, below the minimum threshold for PIT tagging. These individuals represented young-of-the-year fish, based on the length–frequency histogram (Supplementary material S2¹). The upper reach is clearly a key spawning and rearing habitat for white-spotted char in this tributary, and an increase of young-of-the-year fish abundance from June and July was likely because they grew large enough to be captured more efficiently by electrofishing (Fig. 2).

Section-scale (20 m) movement

Section-scale movement was limited based on mark–recapture and mobile PIT antenna data. Most individuals were physically recaptured (79% from May to June and 80% from June to July) or detected by the mobile antenna (70% from May to June and 72% from June to July) within 60 m of original physical capture (Fig. 3). There were no statistically significant differences in the frequency of upstream versus downstream movement in any combination of method and month (sign tests: $P = 0.07$ – 0.84 ; Fig. 4). Large fish (≥ 100 mm TL) were more sedentary than small fish (70–99 mm TL) during both sampling intervals. Movement distances > 300 m were not commonly detected, and the vast majority of them (86%) were displayed by small fish (Fig. 3).

Reach-scale movement and permanent emigration

Multistate CJS analysis suggested that, given char stayed in the tributary (and survived), the majority of individuals (60%–96%) remained in the reach where they had been present 1 month earlier (Fig. 4). This result corroborated with restricted movement patterns observed at the 20-m section-scale analysis. Movement of small char (≤ 100 mm TL) from the middle reach was the most common, with 60% remaining in the middle reach between May and June and 70% between June and July (Fig. 4). Between May and June, a higher proportion of small char moved from the middle reach to the lower reach (30%) versus the upper reach (10%), but movement directionality was not present between June and July. Importantly, movement between adjacent reaches (upper and middle, and middle and lower) was more common (range: 0.01–0.30) than that between nonadjacent upper and lower reaches (range: 0–0.07; Fig. 4). Therefore, both section- (Fig. 3) and reach-scale (Fig. 4) data suggested that movement to a more distant section or reach was less likely to occur within the tributary.

However, a total of 85 out of 501 individuals (17%) were identified as emigrants from the tributary to the main stem. Intriguingly, probability of emigration ($1 - f$) did not depend on the reach in which char had been present (Fig. 5). Differences in probabilities of emigration from the three reaches were not statistically significant (i.e., overlapping 95% CrI) for each combination of sampling interval and size class (Supplementary material S5¹). Depending on the sampling interval and body size class, 5%–20% of individuals emigrated from the tributary reaches to the main stem (Fig. 5). Once they made a decision to emigrate, fish typically traversed through the tributary within days. Based on detections at the fixed antennas at reach boundaries, a group of 19 emigrants moved from the middle reach to the main stem in a median of 1 day (range: 0–11 days), and a different group of 25 emigrants moved from the upstream reach to the main stem in a median of 3 days (range: 0–37 days) during the 63-day period in which fixed antennas were operational.

Estimates of other parameters can be found in the online Supplementary material S5¹. Briefly, posterior mean true survival (s) was high, ranging 56%–92% depending on the body size and month (Fig. 5). Two-pass electrofishing recaptured 41% of small

Fig. 2. Longitudinal abundance of white-spotted char by 20-m section in the tributary on the second (17–20 June) and third (23–25 July) mark–recapture sampling occasions. Estimates are based on the two-pass Carle–Strub removal method for three size classes (<70 mm; 70–99 mm (small size group in Cormack–Jolly–Seber (CJS) analysis); and ≥100 mm (large size group)). [Colour online.]

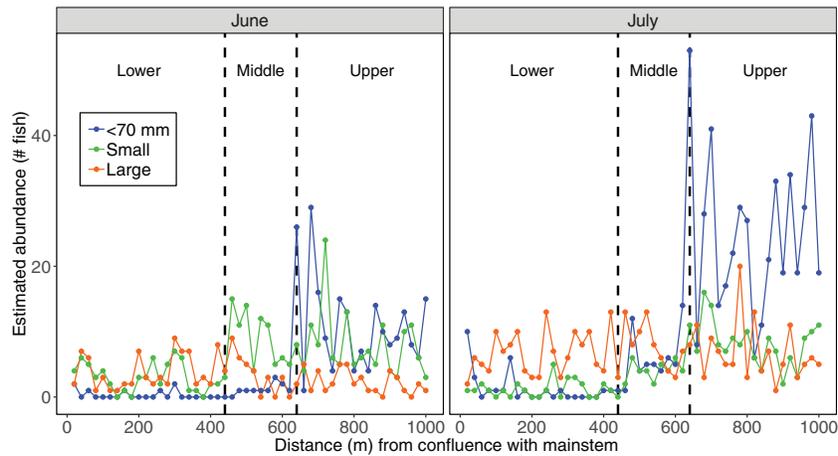
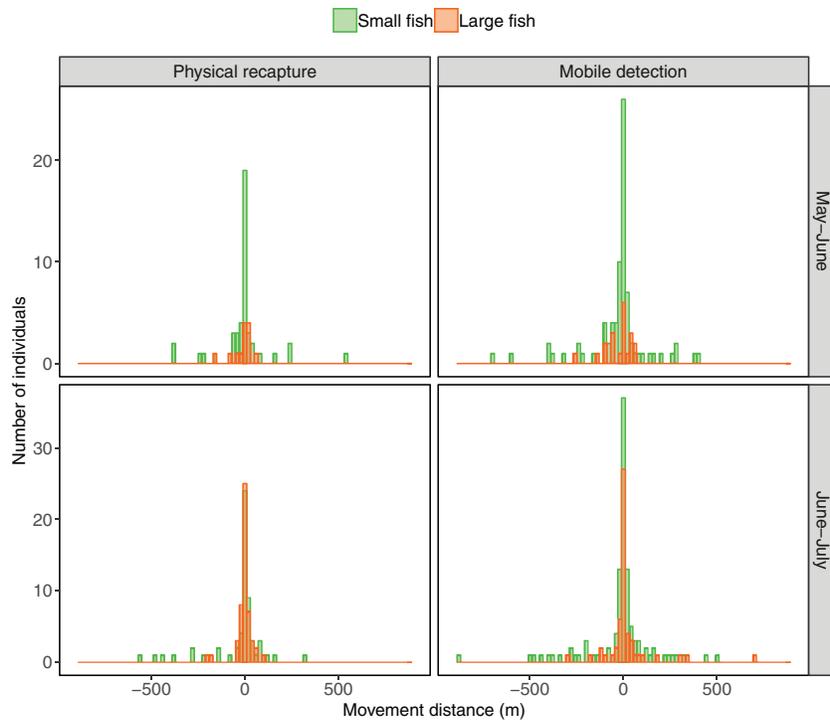


Fig. 3. Frequency distributions of movement distances for small (70–99 mm TL) and large (≥100 mm TL) fish during two intervals based on mark–recapture sampling (physical recapture) and mobile PIT antenna (mobile detection). Positive distances indicate upstream movement and negative distances indicate downstream movement. Movement between May and June is based on capture by electrofishing and marking on 24–29 May and physical recapture on 17–20 June or mobile detection on 21 June 2018. Movement between June and July is based on capture on 17–20 June and physical recapture on 23–25 July or mobile detection on 27 July 2018. [Colour online.]



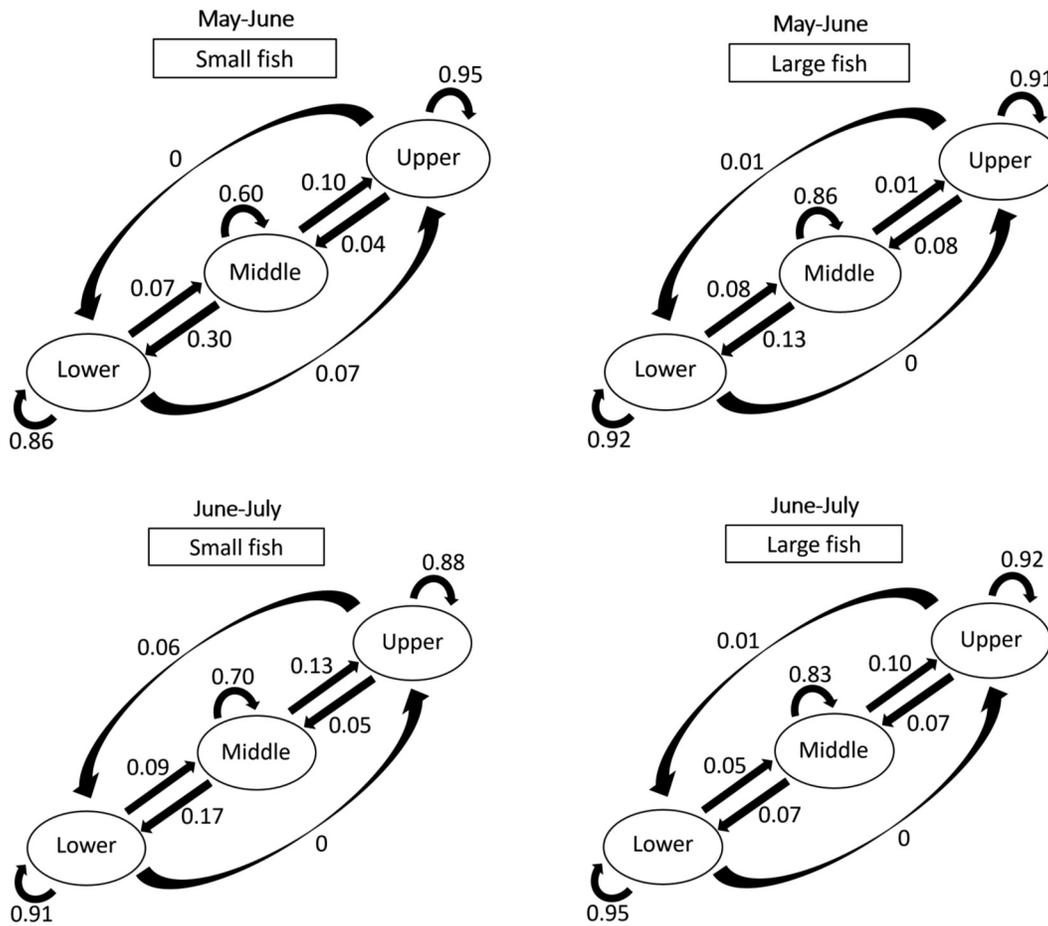
individuals that were alive and present in the upper and middle reaches and 28% in the lower reach. Recapture probability of large individuals was 47% (spatially constant *p*; Table 2). Finally, 23% of small fish transitioned to the large size group from May to June, and 43% transitioned from June and July.

Discussion

This study demonstrates that conclusions on stream fish movement depend on the ability of the study design to characterize long-distance movement, an idea proposed originally by Gowan et al. (1994) based on a critical review of stream fish movement studies. When movement was inferred based on the physical

mark–recapture and mobile PIT antenna surveys within the study tributary, fish appeared sedentary, with most fish (70%–80%) moving <60 m over 1 month (particularly large fish). Reach-scale data similarly indicated that movement between nonadjacent reaches (i.e., movement between upper and lower reaches) was less frequent than that between adjacent reaches (i.e., movement from middle to upper or lower reach, and vice versa). However, fixed antenna arrays at the mainstem confluence played a critical role in characterizing emigration from the tributary to the main stem (i.e., long-distance movement). As much as 17% of marked fish emigrated from the tributary and did not return over the course of the 2-month study period. More importantly, emigration was

Fig. 4. Mean posterior probability of movement among reaches, given that individuals remained in the tributary and survived, estimated by a multistate CJS model.



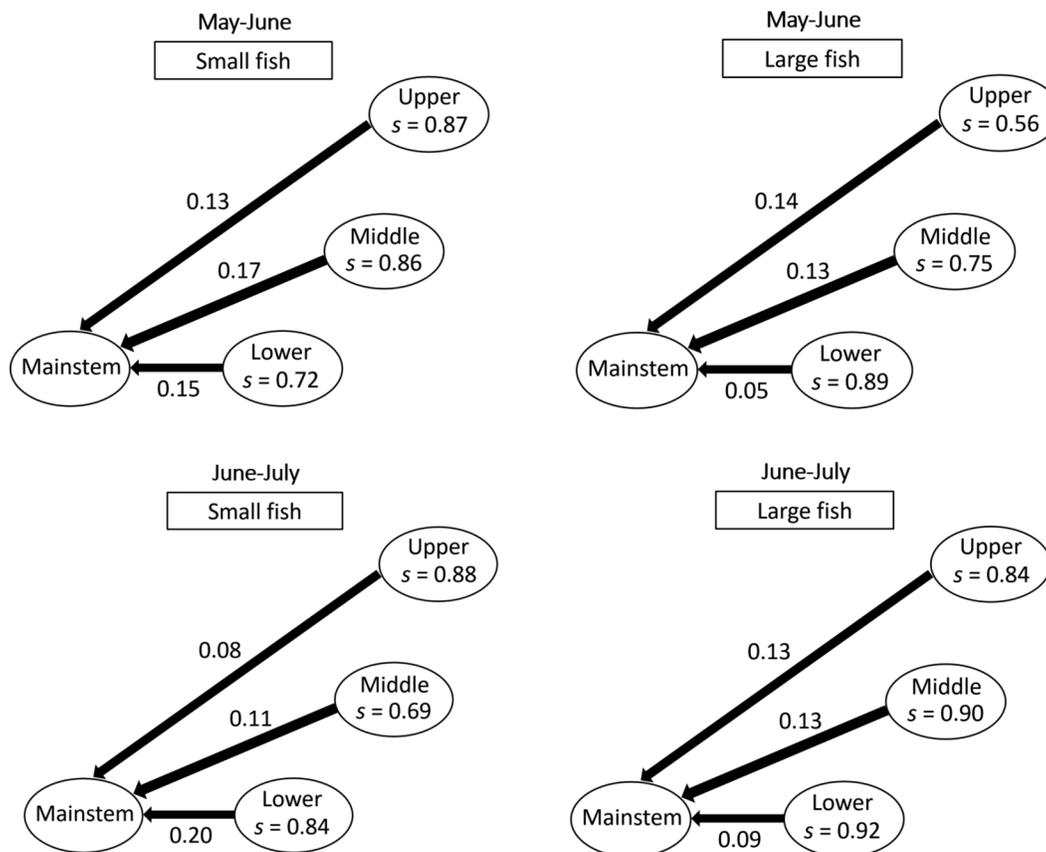
equally likely to occur from any of the three reaches located at different distances from the confluence. Antenna data still could not inform how much farther emigrants moved after they had left the tributary (i.e., total movement distance). However, the finding that emigration was equally likely to occur, regardless of in which reach fish were present, combined with restricted movement patterns based on mark-recapture data within the tributary, provides indirect but convincing evidence that population-scale movement was characterized with long tails and high peaks typical of leptokurtic distributions of movement distance frequency (Skalski and Gilliam 2000). Our analysis of movement at multiple spatial scales provided strong support for co-existence of short- and long-distance movement (Skalski and Gilliam 2000; Rodríguez 2002) during a period in which fish movement has been rarely studied (i.e., during and after snowmelt).

Our data also shed light on a mechanism that partly explains why long-distance movement is so difficult to detect using a traditional approach (i.e., physical mark-recapture surveys inside a study area). Emigrants, once they decided to emigrate, exited the tributary typically within a few days. Mark-recapture studies for stream fish movement are conducted at intervals of >1 week (Skalski and Gilliam 2000; Albanese et al. 2004; Pépino et al. 2012). In our case, such weekly mark-recapture (or re-sight) surveys, which would require a major time and labor commitment, would not have been effective at recapturing or re-sighting these transient emigrants even if recapture or re-sight probability had been perfect. As a result, mark-recapture surveys within a defined study area alone underestimate long-distance movement because

data are biased towards representing movement of individuals that have stayed in the study area (Gowan et al. 1994).

Movement data of white-spotted char in this study need to be interpreted by considering local context and our methodological approach. Movement of nonanadromous white-spotted char has been investigated in other Japanese streams (Morita and Yamamoto 2001; Nakamura et al. 2002; Tsuboi et al. 2020); all of these studies were conducted in streams fragmented by dams. This is in stark contrast with our study system harboring a partially adfluvial population with access to a lentic habitat downstream. In addition, none of these previous studies focused on movement in relation to snowmelt and used fixed PIT antenna arrays to monitor movement continuously. These differences make comparisons of studies not straightforward, but our study has one thing in common with most others (Gowan et al. 1994; Nakamura et al. 2002; Rodríguez 2002); a majority of individuals move only locally, but the rest of the population moves over long distances. The leptokurtic distribution of movement distances may be prevalent irrespective of life history forms. In fact, the leptokurtic distribution may arise in a heterogeneous population composed of sedentary and mobile individuals (Skalski and Gilliam 2000). A key knowledge gap in stream fish ecology appears to lie in characterizing what environmental conditions (i.e., external factors) and which individuals (i.e., internal factors) are responsible for driving long-distance movement. Animal movement is plastic and context-dependent (Fronhofer et al. 2015; Terui et al. 2017) and is subject to personality and ontogeny (Riley et al. 1992; Cote et al. 2010). Synthetic understanding of long-distance movement is war-

Fig. 5. Mean posterior probability of true survival (s : inside circles) and permanent emigration to the main stem from three locations of the tributary (arrows), estimated by a multistate CJS model.



ranted because it is a fundamental mechanism that affects gene flow, recolonization, and population persistence in the riverscape (Fausch et al. 2002; Comte and Olden 2018).

Emigration from tributaries to the main stem may constitute a key demographic process that sustains the partially adfluvial population of white-spotted char in the study watershed. The study tributary was one of several tributaries in the watershed, and concentrations of young-of-the-year individuals in the upper reach (Fig. 2) suggested that the tributary provides a spawning and nursery habitat for white-spotted char. This pattern has been observed in other fishes of the genus *Salvelinus* (Starcevic et al. 2012; Kanno et al. 2014). Less spatially clustered distributions of fish large enough to be marked with PIT tags indicated that char dispersed downstream through ontogeny, and a portion of the population did leave the tributary. The finding that 17% of char emigrated from the tributary during just 2 months signifies a key source of dispersers that consequently affects dynamics of spatially structured populations. Understanding broader-scale, population-level patterns and processes requires a complementary approach (e.g., genetic analysis), and this knowledge is paramount to protecting and restoring connectivity in river ecosystems. In addition, our understanding of tributary-mainstem dynamics is incomplete because we could not study movement of char from the main stem to the tributary. Finally, our data could not inform whether emigrants from the tributary stayed in the main stem or moved farther downstream to Lake Shumarinai (Fig. 1). Adfluvial white-spotted char that move to lentic habitats display external characteristics of smoltification with silvery body color and black edges along dorsal and caudal fins in spring (Yamamoto et al. 1999). While we did not observe individuals with apparent external signs of smoltification in this study (Y. Kanno, personal observation), we cannot exclude the possibility that some phenotypically

cryptic individuals move between lotic and lentic habitat types in this and other waterbodies. A carefully designed antenna array system at the riverscape scale could provide novel information on life history variation in salmonids related to movement.

Mark-recapture data are increasingly analyzed jointly with other types of data (Dudgeon et al. 2015; Weegman et al. 2016), including fixed PIT antenna data (Horton et al. 2011; Connette and Semlitsch 2015). The integrated approach often allows for inferences of additional parameters (e.g., emigration and true survival) and more precise inferences of other parameters due to extra information available (Kéry and Schaub 2012). Our multiscale analysis using mark-recapture and mobile and fixed antennas led to robust characterization of char movement, and this study demonstrated that movement patterns at some spatial scales (i.e., within-tributary movement) cannot be extrapolated to infer patterns at other scales (i.e., emigration from the tributary). In this sense, different data complement with each other, and they may be combined further with other approaches (e.g., genetics, otolith microchemistry) to generate a fuller understanding of stream fish movement (Cooke et al. 2013; Comte and Olden 2018). Movement is a fundamental question in behavioral ecology, life history, and population ecology, but this knowledge is also critical in informing fisheries management actions such as the design of fish passage structures (Kondratieff and Myrick 2006; Pépino et al. 2012) and invasive species control (Peterson and Fausch 2003).

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