

## Research

### Spatial covariation of fish population vital rates in a stream network

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Animal populations are spatially structured in heterogeneous landscapes, in which local patches with differing vital rates are connected by dispersal of individuals to varying degrees. Although there is evidence that vital rates differ among local populations, much less is understood about how vital rates covary among local patches in spatially heterogeneous landscapes. In this study, we conducted a nine-year annual mark–recapture survey to characterize spatial covariation of survival and growth for two Japanese native salmonids, white-spotted charr *Salvelinus leucomaenis japonicus* and red-spotted masu salmon *Oncorhynchus masou ishikawae*, in a headwater stream network composed of distinctly different tributary and mainstem habitats. Spatial structure of survival and growth differed by species and age class, but results provided support for negative covariation between vital rates, where survival was higher in the tributary habitat but growth was higher in the mainstem habitat. Thus, neither habitat was apparently more important than the other, and local habitats with complementary vital rates may make this spatially structured population less vulnerable to environmental change (i.e. portfolio effect). Despite the spatial structure of vital rates and possibilities that fish can exploit spatially distributed resources, movement of fish was limited due partly to a series of low-head dams that prevented upstream movement of fish in the study area. This study shows that spatial structure of vital rates can be complex and depend on species and age class, and this knowledge is likely paramount to elucidating dynamics of spatially structured populations.

Keywords: Bayesian analysis, Cormack–Jolly–Seber models, mark–recapture, meta-population, spatial heterogeneity, stream salmonids



## Introduction

Animal populations are spatially structured in heterogeneous landscapes, in which local patches differing in population dynamics are connected by dispersal of individuals (Hanski 1994, Thomas and Kunin 1999). The spatial structure is generated because vital rates differ among local patches, including survival (Ozgul et al. 2006, Saracco et al. 2010), growth (Indermaur et al. 2010, Letcher et al. 2015) and reproduction (Donovan et al. 1995, Kanno et al. 2014). For example, in the yellow-bellied marmot *Marmota flaviventris*, Ozgul et al. (2006) measured that annual survival rate varied among sites of different habitat size and quality, especially at younger ages. In the European common toad *Bufo bufo*, Indermaur et al. (2010) reported tadpole growth rates differed between riverbed and forest ponds with contrasting environmental conditions. Animal populations are also structured by age and life stage (e.g. maturity). These stages influence or are influenced by animal body size, on which vital rates depend (Coulson 2012). Accordingly, heterogeneous landscapes typically harbour age- or stage-structured populations of wildlife, with local patches linked by dispersal of individuals (Hunter and Caswell 2005).

Although there is evidence that vital rates differ among local populations, much less is understood about how vital rates covary among local patches in spatially heterogeneous landscapes. That is, is a set of vital rates always high or low in certain local patches ('positive covariation hypothesis', hereafter), or do local patches harbour spatial juxtaposition in vital rates ('negative covariation hypothesis', hereafter)? Spatial covariation in vital rates in the context of spatially linked populations is of great interest because it affects the types of metapopulation dynamics and spatial population structure (Hanski 1994, Koizumi 2011). The positive covariation hypothesis is likely to hold true when vital rates are linked synergistically. For example, individuals in some habitats grow better, which then leads to higher survival (Garvey et al. 1998, McNamara et al. 2016), whereas diminished growth in other habitats constrains survival. Under the positive covariation hypothesis, spatial heterogeneity in habitat quality would be pronounced (Thomas and Kunin 1999), making certain local patches disproportionately important to the persistence of metapopulations (i.e. source-sink dynamics). On the other hand, the negative covariation hypothesis is likely when different resources or events affect different vital rates. For example, when disturbances occur, individuals in refuge habitats may survive better, but other locations may provide critical resources for growth and reproduction (Schlosser 1995, Fausch et al. 2002). Under this circumstance, animals may exhibit symmetrical or bi-directional movement between local patches and local patches contribute to the metapopulation persistence differently but more evenly. Current understanding of spatial covariation in vital rates is based primarily on sets of local patches without connectivity or dispersed over long distances, and little is known for spatially structured populations in which individuals may move among local patches.

Stream networks provide an ideal system to investigate spatial covariation of vital rates, because habitat characteristics change distinctly over short geographic distances. Stream networks represent a series of connected habitats for aquatic species along linear pathways, where confluences greatly change habitat characteristics (e.g. stream flow, gradient and temperature) and delineate local patches in the riverscape (Charles et al. 2000, Fagan 2002, Koizumi 2011). Riverine organisms move to exploit spatial heterogeneity in resources, and the optimal local patch likely differs for survival, growth and reproduction (Schlosser 1995, Fausch et al. 2002, Fullerton et al. 2010). This conceptual underpinning suggests that the negative covariation hypothesis of vital rates may be common in stream networks, although empirical data are lacking. The degree to which the negative covariation hypothesis is prevalent is critical in assessing resistance and resiliency of spatially structured populations under climate change, where the frequency and magnitude of extreme weather events and disturbances are already increasing (Milly et al. 2008, McCluney et al. 2014). In addition, artificial structures such as dams and culverts contribute to spatial population structures of aquatic species by creating asymmetric patterns of dispersal (Tortorotot et al. 2014, Nathan et al. 2018). Many rivers in the world are anthropogenically fragmented (Nilsson et al. 2005), and their effects cannot be overlooked when managing and conserving riverine organisms and ecosystems.

In this study, spatial covariation between two key vital rates, survival and growth, was measured in stream-dwelling salmonids inhabiting a fragmented headwater stream channel network, using a nine-year mark-recapture data set. Support for the negative covariation hypothesis was evaluated by comparing survival and growth between mainstem and tributary habitats for two life stages of two species; juveniles (young-of-the-year, YOY) and adults (age 1+ and older) of landlocked white-spotted charr *Salvelinus leucomaenis japonicus* and red-spotted masu salmon *Oncorhynchus masou ishikawae*. We predicted that negative covariation of vital rates for the study species would be characterised with higher growth and lower survival in the mainstem versus lower growth and higher survival in the tributary habitats. Given its larger habitat volume (i.e. width and depth), the mainstem habitat would likely support higher growth and larger individuals relative to the tributary habitat (Letcher et al. 2015). However, survival would be higher in the tributary versus mainstem because habitat structures are more complex and diverse in the tributary (Ebersole et al. 2006), and the structural complexity would buffer individuals from predation and disturbances (e.g. floods).

## Material and methods

An unbiased study of vital rates must be conducted at a sufficiently broad spatial extent relative to the movement of aquatic organisms to minimise emigration of individuals from the study area, and it must be studied for a number of

years to quantify a set of vital rates subject to inter-annual variation. These challenges were overcome by annual intensive sampling of uniquely marked individuals in a well-defined stream system composed of markedly different tributary and mainstem habitats.

## Study area

This study was conducted in the Sabusawa Stream of the Fuji River system, central Japan ( $35^{\circ}48'28''\text{N}$ ,  $138^{\circ}34'13''\text{E}$ ). The study area encompassed a total stream network length of 1050 m with an altitude range of 880–1360 m (Fig. 1). Within the study area, there are two tributaries (T1 and T2) and seven mainstem sections (A–G) divided by erosion control dams.

The study area is located in the transitional zone of land-locked white-spotted charr ('charr' hereafter) and red-spotted masu salmon ('salmon' hereafter), with relative abundance of charr increasing upstream and a concurrent increase in salmon downstream (Endou et al. 2006, Fig. 1). Upstream movement of fish is impeded at the impassable dams, but fish can move freely between tributary and mainstem (i.e. T1-A and T2-F). The low-head dam (ca 1.4 m) between section F and G was the only artificial structure over which fish could ascend upstream in the study area, and both upstream and downstream movements were detected at this dam. In this

study, three spatial locations were defined for each species: tributary (section T1 for charr and section T2 for salmon), mainstem sections with unimpeded connectivity to tributaries ('mainstem connected' hereafter; section A for charr and section F and G for salmon), and mainstem sections without connectivity to tributaries ('mainstem fragmented' hereafter; downstream from section B for charr and upstream from section E for salmon) (Fig. 1). Our primary focus was to compare survival and growth between the mainstem and tributary locations, but the mainstem was divided into two types of reaches because we hypothesized that connectivity to the tributary could affect vital rates.

## Habitat measurement

Spatial heterogeneity in habitat characteristics is a prerequisite for generating spatial covariation between survival and growth. Thus, detailed habitat measurements were taken in the mainstem and tributaries. Stream width (wetted width) was measured every 5 m in the mainstem and 10 m in the tributaries (Table 1). Water temperatures in section T1, A, D, T2 and G were measured hourly with data loggers from April 2009 to October 2018.

To compare habitat complexities between tributary and mainstem connected sections, physical variables were measured in sections T1, A, T2, F and G in 2019 (Table 2).

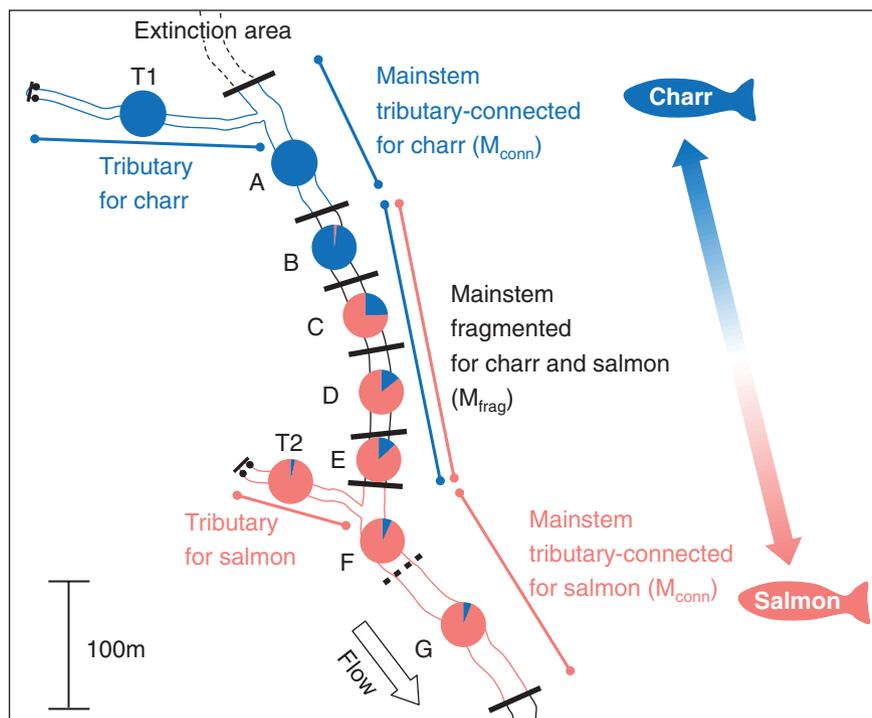


Figure 1. Map of the study area at Sabusawa Stream, Yamanashi Prefecture, located in central Japan. Pie charts show the proportion of charr (blue) and salmon (red) caught in each of the nine sections (A–G, T1 and T2) between 2009 and 2017. Dams and culverts (black lines) impede upstream movement of fish, except that two-way movement is possible between section F and G. Fish movement is unimpeded between T1 (tributary) and A (tributary-connected mainstem) for charr, and T2 (tributary) and F–G (tributary-connected mainstem) for salmon. Sections B through E are defined as the mainstem fragmented location. The upper end of T1 and T2 are bounded by cascades, which prevent upstream movement of fish.

Table 1. Environmental characteristics of the study sections in Sabusawa stream. Water temperature was measured at hourly intervals during 2009 and 2017 in five sections (T1, A, D, T2 and G).

Species	Spatial patch	Section	Length (m)	Width $\pm$ SD (m)	Water temp. $\pm$ SD min–max ( $^{\circ}$ C)
Charr	tributary	T1	279	1.7 $\pm$ 0.4	8.0 $\pm$ 4.7 0.2–17.2
Charr	mainstem connected	A	145	4.6 $\pm$ 2.0	8.0 $\pm$ 5.2 0–18.6
Charr/salmon	mainstem fragmented	B, C, D, E	284	5.3 $\pm$ 3.5	8.2 $\pm$ 4.9 0–18.1
Salmon	tributary	T2	144	2.1 $\pm$ 0.4	7.8 $\pm$ 5.0 0.1–17.5
Salmon	mainstem connected	F, G	148	5.0 $\pm$ 1.9	8.3 $\pm$ 4.9 0.2–17.9

Stream gradient was surveyed by an automatic level. Habitat units in each section were classified as a cascade, pool, riffle or rapid, according to Bisson et al. (2006) (Supplementary material Appendix 1 Table A1). The cascade is the most typical unit in steep channels, with gradient ranging from 4 to 25%, and contains small, turbulent pools (Bisson et al. 2006). In a total of 87 stream units, physical shelters for fish, such as undercut bank and coarse woody debris, were located, and we measured their length and width (nearest 0.1 m). Percent undercut bank and coarse woody debris were defined as their respective total area divided by wetted surface area of each stream unit (i.e. stream length  $\times$  width) (Table 2).

Water depth, current velocity, current orientation and substrate were measured in a cascade unit in each section (8.4–19.8 m in stream length), because this was the predominant unit inhabited by charr and salmon in both tributaries and mainstem (Supplementary material Appendix 1 Table A1). Longitudinal transects at 1.5-m intervals were established. Up to four equally spaced quadrats (0.5  $\times$  0.5 m), each composed of 25 grids (0.1  $\times$  0.1 m), were set along each transect for a total of 31 transects and 103 quadrats (2575 grids) in section T1, A, T2 and F. Water depth and current velocity were measured at the four corners and the centre points of the 0.5  $\times$  0.5 m quadrats (Inoue and Nunokawa 2002). Velocity was measured at 60% of the depth from the surface (mean water column velocity, Gatz et al. 1987) using a propeller-type current meter, and orientation was categorised

as one of 12 directions by 30 $^{\circ}$  increments (i.e. upstream, 0 $^{\circ}$  and downstream, 180 $^{\circ}$ ) with a colourful streamer (2 mm in width). The circular standard deviation of current orientation was measured according to Zar (2007). In addition, percent upstream current orientation was calculated (i.e. 0–90 $^{\circ}$  and 270–360 $^{\circ}$ ). Substrate type within each 0.1  $\times$  0.1 m grid was classified as bedrock (code=0), sand (dominant particle size < 2 mm, code=1), gravel (2–16 mm, code=2), pebble (17–64 mm, code=3), cobble (65–256 mm, code=4) or boulder (> 256 mm, code=5), according to Bain et al. (1985).

### Fish sampling

Field surveys were conducted annually (the third weekend of October) in 2009–2017. Fish were captured using a backpack electrofishing unit (300–400 V DC) and 3-mm mesh dip nets. Two passes of electrofishing were conducted for fish density estimates of each section with a depletion method (Zippen 1958). Captured fish were anaesthetised with phenoxyethanol (ca 0.5 ml l $^{-1}$  water), measured for fork length (FL: nearest 1 mm), and were marked individually with visible implant elastomer tags or their individual code was recorded if recaptured. A unique combination of four elastomer colours were subcutaneously administered to the forehead of each individual. All captured fish with FL > 43 mm were marked. During each year of the study, juveniles (young-of-the-year, YOY) and adults (age 1+ and older) were

Table 2. Physical characteristics in section T1 and A for charr and section T2, F and G for masu salmon. Stream gradient, undercut banks and coarse woody debris were measured throughout sections. Depth, velocity, circular standard deviation of current orientation, frequency of upstream current, and substrate size were measured in the predominant habitat (i.e. cascade unit) across sections.

Section	Stream gradient (%)	Total cover (%)		Depth $\pm$ SD (cm)	Velocity $\pm$ SD (cm s $^{-1}$ )	Circular SD ( $^{\circ}$ )	Upstream current (%)	Substrate $\pm$ SD
		Undercut banks (%)	Coarse woody debris (%)					
T1	17.5	8.9		17.2 $\pm$ 10.7	20.6 $\pm$ 21.7	76.6	35.1	3.2 $\pm$ 1.6
		4.1	4.8					
A	8.9	5.2		14.2 $\pm$ 7.9	49.0 $\pm$ 38.0	39.2	9.6	4.1 $\pm$ 1.0
		4.8	0.4					
T2	15.9	9.4		14.8 $\pm$ 8.9	25.0 $\pm$ 24.6	58.2	21.1	3.5 $\pm$ 1.1
		5.1	4.3					
F,G	9.7	3.8		14.0 $\pm$ 11.3	40.9 $\pm$ 34.6	44.9	10.1	3.6 $\pm$ 1.2
		3.6	0.2					

distinguished based on length–frequency histograms. For individuals which cannot be assigned to an age class due to their intermediate body size, a few scales were taken using a scalpel and the annuli were counted. All fish were returned alive to the capture site (< 20 m for mainstem, < 40 m for tributaries) after recovering from anaesthesia. All captured individuals retained at least two of the four elastomer colours, and were marked again with the lost colour(s). We identified all individuals uniquely based on species, sex, body size and study section at mark (i.e. asymmetrical movement at dams).

## Statistical analyses

### Habitat characteristics

Habitat characteristics were compared between tributary and mainstem connected sections (i.e. section T1 and A for charr, and section T2, F and G for salmon). To analyse the physical shelters for fish, percent total cover (i.e. sum of percent undercut bank and coarse woody debris) in each stream unit was compared between tributaries and mainstem using a Mann–Whitney U test (Table 2, Supplementary material Appendix 1 Table A1). To evaluate the current complexity, percent upstream current orientation was compared between tributaries and mainstem using a G test. Other environmental characteristics such as stream width, water temperature, water depth, current velocity, substrate size were compared using Mann–Whitney U tests.

### Population density estimation

Population density of juvenile and adult fish of each species in each location (i.e. tributary, mainstem connected and mainstem fragmented) was estimated by the two-pass depletion method using the model M(b) in program CAPTURE (White et al. 1982; available at <www.mbr-pwrc.usgs.gov/software/capture.html>). Annual density estimates were compared among the locations using one-way ANOVA. When population density differed significantly, a Tukey's honest significant difference test was conducted to determine which locations were different. Statistical significance was assessed at  $\alpha = 0.05$ .

### Survival and movement

A multi-state Cormack–Jolly–Seber (CJS) model was developed to infer state-specific annual survival, capture and transition probabilities for charr and salmon. States were defined based on age (juveniles and adults) and location (tributary, mainstem connected and mainstem fragmented). Because locations were considered states, the state-transition probability referred to the movement probability among locations, which varied by age. To account for imperfect recapture of individuals, a state–space model was developed, composed of an ecological model following the state transitions over time and an observation model linking the true states to observed data.

Data were formatted in a two-dimensional array ( $y_{i,t}$ ), where rows indicated individuals ( $i$ ) and columns indicated annual sampling occasions ( $t$ ). Elements of the array were

observed states defined by age and location. A unique combination of ages (juvenile and adult) and locations (tributary, mainstem connected and mainstem fragmented) resulted in six states (1 = juveniles in tributary; 2 = juveniles in mainstem connected; 3 = juveniles in mainstem fragmented; 4 = adults in tributary; 5 = adults in mainstem connected; and 6 = adults in mainstem fragmented). In addition, sampling occasions on which individuals were not detected were coded as 7. Prior to fitting multi-state CJS models to data, we used the R2ucare package (Gimenez et al. 2018) to confirm that there was no evidence for trap-dependence ( $p > 0.27$ ), transience ( $p = 1.00$ ) and memory of past states ( $p > 0.35$ ) in either charr or salmon.

The multi-state CJS model was developed following an approach by Kéry and Schaub (2012). The ecological model characterized state transitions from the first capture of each individual over an annual time step. The true state of individual  $i$  on occasion  $t$  was denoted by a two-dimensional matrix  $z_{i,t}$ . In addition, a four-dimensional state-transition matrix,  $\Omega$ , defined the state of departure in the first dimension, the state of the arrival in the second, individual  $i$  in the third and occasion  $t$  in the fourth. Annual state transitions were modelled to follow a categorical distribution:

$$z_{i,t+1} | z_{i,t} \sim \text{categorical}(\Omega_{z_{[i,t],1} \dots S,i,t})$$

The argument of the categorical distribution is a vector of length equal to seven ( $S$ , or number of states), representing state transition probabilities for given values of the first ( $z_{i,t}$ ), third ( $i$ ) and fourth ( $t$ ) dimension. The first two dimensions of  $\Omega$  (i.e. states of departure at occasion  $t$  and arrival at occasion  $t+1$ ) were defined in a  $7 \times 7$  matrix, assuming that all juvenile individuals transitioned to adult over an annual time step, adult individuals could not transition back to juvenile, and bi-directional movement between two locations was possible only between tributaries and mainstem connected sections due to the presence of low-head dams (Table 3). Annual survival was modelled to vary by age (juvenile versus adult) and location (tributary, mainstem connected and mainstem fragmented), and was denoted by  $\phi_{1,6}$ ; mortality was assumed to occur with a probability of  $1 - \phi$  for each state. Survival referred to apparent survival, that is, the probability that an individual survived and remained in the study area. Additionally, movement probability was denoted by  $\psi$ , and the matrix was populated differently between two species because the constraint of movement was different for an upstream-occupying charr and a downstream-occupying salmon (Table 3). For example, juvenile charr in the tributary (section T1) that survived over a year could either move to the mainstem connected location (section A) with a probability of  $\psi_2$ , move farther downstream to the mainstem fragmented location with a probability of  $\psi_3$  (section B through E), or stay in the tributary with a probability of  $1 - \psi_2 - \psi_3$  (denoted as  $\psi_1$ ; Fig. 1, Table 3). However, juvenile charr in the mainstem fragmented location could not move upstream to the tributary or the mainstem connected location, and

Table 3. State transition matrix corresponding to the first two dimensions of  $\Omega$  for charr (a) and salmon (b). For charr, Trib refers to section T1 and  $M_{\text{conn}}$  (Mainstem connected location) is section A. For salmon, Trib refers to section T2 and  $M_{\text{conn}}$  refers to section F and G.  $M_{\text{frag}}$  (Mainstem fragmented location) is section B through E for both species.

		True state at time $t + 1$						
		Juvenile Trib	Juvenile $M_{\text{conn}}$	Juvenile $M_{\text{frag}}$	Adult Trib	Adult $M_{\text{conn}}$	Adult $M_{\text{frag}}$	Dead
(a) Charr								
True state at time $t$	Juvenile in Trib	0	0	0	$\phi_1 \psi_1^a$	$\phi_1 \psi_2$	$\phi_1 \psi_3$	$1 - \phi_1$
	Juvenile in $M_{\text{conn}}$	0	0	0	$\phi_2 \psi_4$	$\phi_2 \psi_5^b$	$\phi_2 \psi_6$	$1 - \phi_2$
	Juvenile in $M_{\text{frag}}$	0	0	0	0	0	$\phi_3$	$1 - \phi_3$
	Adult in Trib	0	0	0	$\phi_4 \psi_7^c$	$\phi_4 \psi_8$	$\phi_4 \psi_9$	$1 - \phi_4$
	Adult in $M_{\text{conn}}$	0	0	0	$\phi_5 \psi_{10}$	$\phi_5 \psi_{11}^d$	$\phi_5 \psi_{12}$	$1 - \phi_5$
	Adult in $M_{\text{frag}}$	0	0	0	0	0	$\phi_6$	$1 - \phi_6$
	Dead	0	0	0	0	0	0	1
(b) Salmon								
True state at time $t$	Juvenile in Trib	0	0	0	$\phi_1 \psi_1^e$	$\phi_1 \psi_2$	0	$1 - \phi_1$
	Juvenile in $M_{\text{conn}}$	0	0	0	$\phi_2 \psi_3$	$\phi_2 \psi_4^f$	0	$1 - \phi_2$
	Juvenile in $M_{\text{frag}}$	0	0	0	$\phi_3 \psi_5$	$\phi_3 \psi_6$	$\phi_3 \psi_7^g$	$1 - \phi_3$
	Adult in Trib	0	0	0	$\phi_4 \psi_8^h$	$\phi_4 \psi_9$	0	$1 - \phi_4$
	Adult in $M_{\text{conn}}$	0	0	0	$\phi_5 \psi_{10}$	$\phi_5 \psi_{11}^i$	0	$1 - \phi_5$
	Adult in $M_{\text{frag}}$	0	0	0	$\phi_6 \psi_{12}$	$\phi_6 \psi_{13}$	$\phi_6 \psi_{14}^j$	$1 - \phi_6$
	Dead	0	0	0	0	0	0	1

<sup>a</sup>  $\psi_1 = 1 - \psi_2 - \psi_3$ , <sup>b</sup>  $\psi_5 = 1 - \psi_4 - \psi_6$ , <sup>c</sup>  $\psi_7 = 1 - \psi_8 - \psi_9$ , <sup>d</sup>  $\psi_{11} = 1 - \psi_{10} - \psi_{12}$ , <sup>e</sup>  $\psi_1 = 1 - \psi_2$ , <sup>f</sup>  $\psi_4 = 1 - \psi_3$ , <sup>g</sup>  $\psi_7 = 1 - \psi_5 - \psi_6$ , <sup>h</sup>  $\psi_8 = 1 - \psi_9$ , <sup>i</sup>  $\psi_{11} = 1 - \psi_{10}$ , <sup>j</sup>  $\psi_{14} = 1 - \psi_{12} - \psi_{13}$

they either survived and stayed in the same section with a probability of  $\phi_3$ , or died or emigrated with a probability of  $1 - \phi_3$ . Probabilistic elements in each row of the matrix summed to one (Table 3).

The observation model characterized the generation of the data ( $y_{i,t}$ ) given the true latent state ( $z_{i,t}$ ) by accounting for imperfect recapture of individuals. The observation model was represented by another categorical distribution parameterized by a four-dimensional matrix ( $\Theta$ ), with true state in the first dimension, observed state in the second, individual  $i$  in the third and occasion  $t$  in the fourth:

$$y_{i,t} | z_{i,t} \sim \text{categorical}(\Theta_{z[i,t],1 \dots w,i,t})$$

The length of each of the first two dimensions of  $\Theta$  was seven (Supplementary material Appendix 1 Table A2), and the number of observed states was denoted by a vector  $w$  (length = 7). This vector represented capture probabilities for given values of the first ( $z_{i,t}$ ), third ( $i$ ) and fourth ( $t$ ) dimension. Capture probability of individuals with two electrofishing passes was denoted by  $p_1$  for juvenile and  $p_2$  for adult fish (Supplementary material Appendix 1 Table A2). The model assumed that individuals and states were recorded without error. We fit a preliminary model in which capture probability of each age was set to vary by location, but 95% credible intervals (CRIs) of capture probability overlapped among locations for both species. Therefore, capture probability was set to be constant across locations. It should be noted that  $p_1$  (juvenile capture probability) could not be identified in our models because juveniles were never captured as such (i.e. juvenile always transitioned to adult over an annual time step). Thus, we report only adult capture probability ( $p_2$ ).

Models were analysed with a Bayesian approach using a Markov chain Monte Carlo (MCMC) method in Program STAN (Carpenter et al. 2017) called from program R (<www.r-project.org>) with the rstan package (Stan Development Team 2018). Uninformative priors were used throughout, such that  $\phi_{1:6} \sim \text{uniform}(0, 1)$ ,  $\psi_{1:8} \sim \text{uniform}(0, 1)$  and  $p_{1:2} \sim \text{uniform}(0, 1)$ . Posterior distributions of model parameters were estimated by taking every sample from 500 iterations of four chains after a warm-up period of 500 iterations. Model convergence was checked by visually examining plots of the MCMC chains for good mixture as well as ensuring that the R-hat statistic was less than 1.1 for all model parameters (Gelman and Hill 2007). Statistical significance was evaluated based on an overlap of 95% CRI between parameters of interest (e.g. survival probabilities between two locations).

### Growth

To compare spatial variation in body growth, annual growth in fork length (FL) of recaptured individuals between occasion  $t$  and  $t + 1$  was regressed against their FL on occasion  $t$ . For each age and species, linear models (ANCOVA models) were fit in Program R using annual growth as a response variable and including FL on occasion  $t$  (continuous covariate), location/movement patterns (categorical covariate) and their interaction as predictors. The interaction was included to let intercept and slope of regression models vary by location/movement pattern. Annual growth did not differ between the mainstem connected and fragmented locations, and recaptures of fish that moved from mainstem to the tributaries were not common (i.e. we recorded 4 juvenile charr, 2 adult charr, 3 juvenile salmon and 0 adult salmon). Thus, three patterns

of location and movement were defined for each species; (1) captured in the mainstem on occasion  $t$  and recaptured again in the mainstem on occasion  $t+1$ , (2) captured in the tributary on occasion  $t$  and recaptured again in the tributary on occasion  $t+1$ , and (3) captured in the tributary on occasion  $t$  and recaptured in the mainstem on occasion  $t+1$ . When growth differed significantly, a Tukey's honest significant difference test was conducted to determine which location/movement pattern was different.

#### **Spatial covariation between survival and growth**

Spatial covariation in survival and growth was summarized on an interaction plot for each species and age class. Mean annual survival probability estimated from the multi-state CJS model ( $\pm$  95% credible interval) and annual growth increment of recaptured fish ( $\pm$  95% confidence interval) were plotted on the y-axis for the tributary and mainstem connected locations (x-axis), and mean values were connected by a line plot for each vital rate. Crossed line plots with opposite directions of slopes were considered evidence supporting the negative covariation hypothesis of survival and growth. Support was judged strong if both survival and growth differed significantly between the tributary and mainstem connected locations, and moderate otherwise.

## **Results**

### **Spatial heterogeneity in habitat characteristics**

Tributary and mainstem sections differed greatly in habitat characteristics. Tributaries were narrower than the mainstem connected sections (Table 1, Mann–Whitney U test, section T1 versus A;  $p < 0.001$ , T2 versus F, G;  $p < 0.001$ ), and were steeper (Table 2). A total of 594 undercut banks ( $82.3 \text{ m}^2$ ) and 110 coarse woody debris ( $34.9 \text{ m}^2$ ) were identified in the sections surveyed. The physical shelters for fish created by undercut banks and coarse woody debris were more common in tributaries versus the mainstem (section T1 versus A;  $p = 0.03$ , T2 versus F, G;  $p < 0.001$ ) (Table 2). The physical complexities created local pockets of eddies with irregular current patterns. That is, current velocity was slower and more frequently oriented upstream in tributaries than in mainstem (velocity, section T1 versus A;  $p < 0.001$ , T2 versus F, G;  $p < 0.001$ , upstream current, T1 versus A;  $p < 0.001$ , T2 versus F, G;  $p = 0.04$ ). Current orientation varied widely in tributaries and the circular standard deviations increased with stream gradient. Water temperature did not vary by habitat type; section T1 was  $0.01^\circ\text{C}$  higher than section A ( $p = 0.01$ ) while section T2 was  $0.5^\circ\text{C}$  lower than section G ( $p < 0.001$ ). No apparent trend was observed by habitat type in substrate size; T1 was dominated by finer substrates than section A ( $p < 0.001$ ), while section T2 and F showed similar substrate sizes ( $p = 0.15$ ). Water depth did not differ between tributaries and mainstem ( $p > 0.07$ ).

### **Population surveys and densities**

A total of 1373 unique individuals of charr and 1335 unique individuals of salmon were captured and marked during 2009–2017. A majority of individuals were initially encountered and marked as juveniles of charr (1166 fish) and salmon (1131 fish), whereas fewer individuals were initially captured as adults (207 charr and 204 salmon). Sample size varied annually, including up to 294 juvenile charr (2015), 183 adult charr (2016), 356 juvenile salmon (2014) and 116 adult salmon (2015) (Supplementary material Appendix 1 Table A3). Posterior mean capture probability of adult individuals inferred from multi-state CJS models was higher for charr (0.87; 95% CRI: 0.80–0.92) than salmon (0.73; 95% CRI: 0.55–0.88). Despite high capture probabilities, of the 1373 individual charr marked, 1000 were never recaptured and 293 recaptured once, 69 twice, 9 three times, and one individual four and five times each. Of the 1335 individual salmon marked, 1071 individuals were never recaptured, and 240 were recaptured once, 22 twice, and 2 individuals three times. The relatively low incidence of multiple recaptures suggested that these headwater inhabitants have short life spans. Estimated population density of adult charr in the tributary was higher than that in the mainstem locations (Tukey's post hoc test,  $p = 0.020$ ). Densities of juvenile charr and both juvenile and adult salmon were similar between tributary and mainstem connected (Fig. 2).

### **Survival**

Survival of juvenile charr did not differ greatly among locations. The posterior mean annual survival was 0.35 ( $\phi_1$ ) in the tributary, 0.30 ( $\phi_2$ ) in the mainstem connected and 0.28 ( $\phi_3$ ) in the mainstem fragmented location (Fig. 3, Supplementary material Appendix 1 Table A4). However, in adult charr, survival differed significantly among locations. The posterior mean survival in the tributary ( $\phi_4$ ; mean = 0.38) was more than twice as high as those in the mainstem connected ( $\phi_5$ ; mean = 0.18) and fragmented locations ( $\phi_6$ ; mean = 0.10), and the 95% CRIs for the two groups did not overlap (Supplementary material Appendix 1 Table A4).

Annual survival of salmon did not differ significantly among locations in either juvenile or adult individuals, reflecting wide 95% CRIs of the posterior probability estimates (Fig. 3, Supplementary material Appendix 1 Table A4). However, in both ages, the mean annual survival in the tributary was over 1.4 times higher than that in the mainstem connected and fragmented locations.

### **Movement**

Overall, the posterior mean estimates of annual movement probability ranged from 0 to 0.25 (Fig. 3, Supplementary material Appendix 1 Table A4). In charr, the mean annual movement probability estimates were typically less than 0.10, except that juvenile movement probability from the mainstem connected location downstream to the mainstem

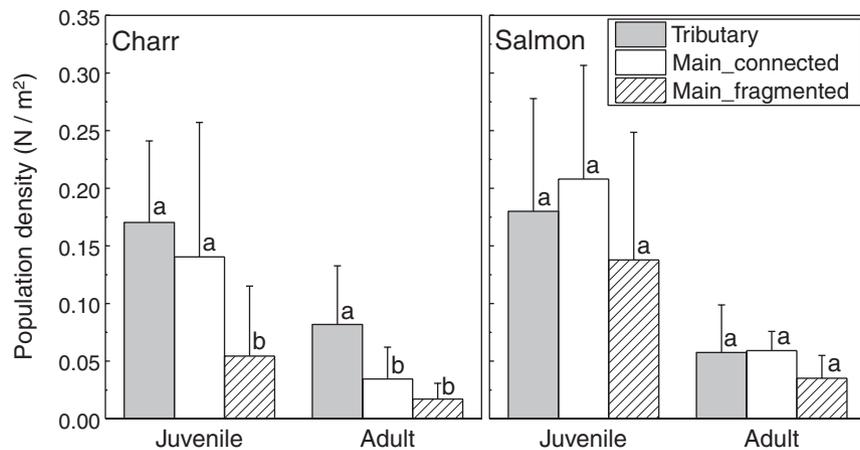


Figure 2. Population density estimates of juvenile and adult charr and salmon in the three spatial locations, based on the survey in late October between 2009 and 2017. Tributary refers to section T1 for charr, and section T2 for salmon. Mainstem tributary-connected refers to section A for charr, and section F and G for salmon. Mainstem fragmented refers to section B through E for both species. The error bars represent standard deviations. Different letters signify significant differences ( $p < 0.05$ ).

fragmented location was high ( $\psi_6$ ; mean = 0.25). In salmon, movement probabilities from the tributary and mainstem fragmented locations downstream to the mainstem connected location were relatively high, with the mean estimates of juveniles,  $\psi_2$  and  $\psi_6$ , equaling 0.19 and 0.11, respectively, and the mean estimates of adults,  $\psi_9$  and  $\psi_{13}$ , equaling 0.16 and 0.16, respectively.

## Growth

Growth differed between the mainstem and tributary locations in charr (Fig. 4). Annual growth increment of charr that were captured and subsequently recaptured in the tributary (T\_to\_T) was significantly lower than that of fish captured and recaptured in the mainstem (M\_to\_M) in juveniles and adults (Tukey's post hoc test,  $p < 0.001$ ). Over one year, a juvenile charr at 80 mm FL in either the tributary or mainstem grew, on average, to 161.2 mm (81.2 mm increment) if they were recaptured again in the mainstem and 142.0 mm (62.0 mm increment) if they were recaptured again in the tributary (Fig. 4). In addition, growth increment of juveniles that moved from the tributary to the mainstem (T\_to\_M) was higher than those that stayed in the tributary (T\_to\_T) (Tukey's post hoc test,  $p < 0.001$ ). The interaction of FL at occasion  $t$  and location/movement pattern was not significant for juvenile ( $p = 0.90$ ) but was significant for adult ( $p = 0.001$ ) charr, indicating that the slope of FL differed among location/movement patterns in adult charr. This was because smaller adult individuals grew more in the mainstem than in the tributary, but the growth increment of larger adults was similar between the two locations (Fig. 4).

In salmon, spatial variation in growth was less evident than charr (Fig. 4). Growth did not differ between juvenile individuals that stayed in the mainstem and those that stayed in the tributary, but juvenile salmon that moved from the tributary to the mainstem (T\_to\_M) grew faster than those that stayed in the mainstem ( $p = 0.004$ ) or the tributary

( $p = 0.02$ ). On average, an 80-mm juvenile salmon captured in the tributary (section T2) grew to 161.3 mm (81.3 mm increment) over one year if they moved to the mainstem versus 143.9 mm (63.9 mm increment) if they were recaptured again in the tributary (Fig. 4). Annual growth of adult salmon did not differ by location or movement pattern. Interaction between FL and location/movement pattern was not significant in either age group ( $p > 0.21$ ).

## Spatial covariation between survival and growth

Three out of four interaction plots (except adult salmon) of survival and growth provided support for the spatial negative covariation hypothesis between survival and growth, as evidenced by crossed line plots with opposite directions of slopes connecting mean values of each vital rate (Fig. 5). Evidence of the negative covariation hypothesis was strong for adult charr, and moderate for juvenile charr and salmon. In all three cases supporting the negative covariation hypothesis, mean annual growth was higher and mean annual survival was lower in the mainstem connected versus tributary locations. It should also be noted that the interaction plot for juvenile salmon, in which the annual growth is similar between the mainstem and tributary locations, does not take into account the finding that juvenile salmon captured in the tributary and moved to the mainstem grew more than those individuals that stayed in the tributary (Fig. 4), thus underestimating the strength of the negative covariation hypothesis.

## Discussion

### Spatial covariation between survival and growth

Data support our prediction that spatial covariation between survival and growth was negative in two salmonid species. Our results indicate that negative covariation of vital rates

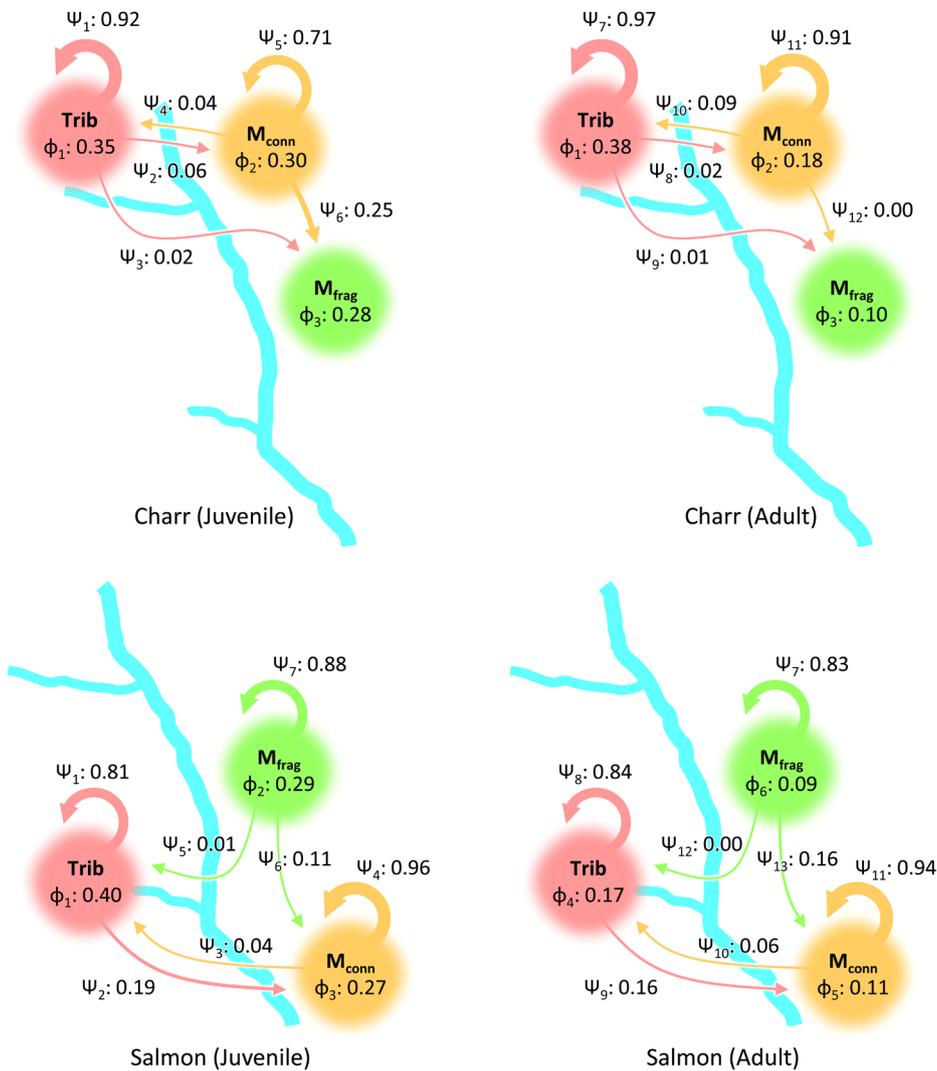


Figure 3. Annual survival ( $\phi$ ) and movement ( $\psi$ ) probabilities of charr and salmon. Posterior mean is shown for each probability. Trib: section T1 and  $M_{conn}$ : Mainstem connected (section A) for charr. Trib: section T2 and  $M_{conn}$ : Mainstem connected (section F and G) for salmon.  $M_{frag}$  is Mainstem fragmented (section B through E) for both species.

is not limited to spatially segregated habitats among which individuals cannot move (Hutchings 1993, Hesse et al. 2008, Lemaitre et al. 2018), but can be found even in spatially adjacent, permeable habitat patches. It was further intriguing that negative covariation between survival and growth was documented at such a fine-spatial scale (ca 1 km), highlighting the role of confluences in creating habitat heterogeneity within stream networks (Benda et al. 2004). Patterns of negative covariation occurred because individuals experienced higher growth but lower survival in the mainstem, and their survival was higher and growth was lower in the tributaries. Negative covariation of vital rates in landlocked salmonids is much more cryptic than that in migratory salmonids, in which juveniles show higher survival and lower growth in freshwater whereas adults show lower survival and higher growth in the ocean (Thorpe 1987, Morita et al. 2014). Animals often shift their habitat locations and requirements through ontogeny

(Law and Dickman 1998, Dahlgren and Eggleston 2000). Stage-specific habitat classifications such as 'nursery habitat' and 'adult habitat' (Beck et al. 2001) implicitly assume that each life stage might survive and grow better in a particular location relative to alternative habitats (i.e. positive covariation). Support for such positive covariation between survival and growth would have been shown by paralleled lines on the interaction plot (Fig. 5), but this was not the case in our study.

Available data do not fully explain why survival and growth could not be simultaneously maximised in a single habitat type (i.e. tributary or mainstem). We offer that the negative spatial covariation between survival and growth resulted from an interplay of density-independent and density-dependent processes. Stream salmonid survival depends greatly on habitat complexities that are typically characterised by localised pockets of deep habitats with physical cover (i.e. pool created

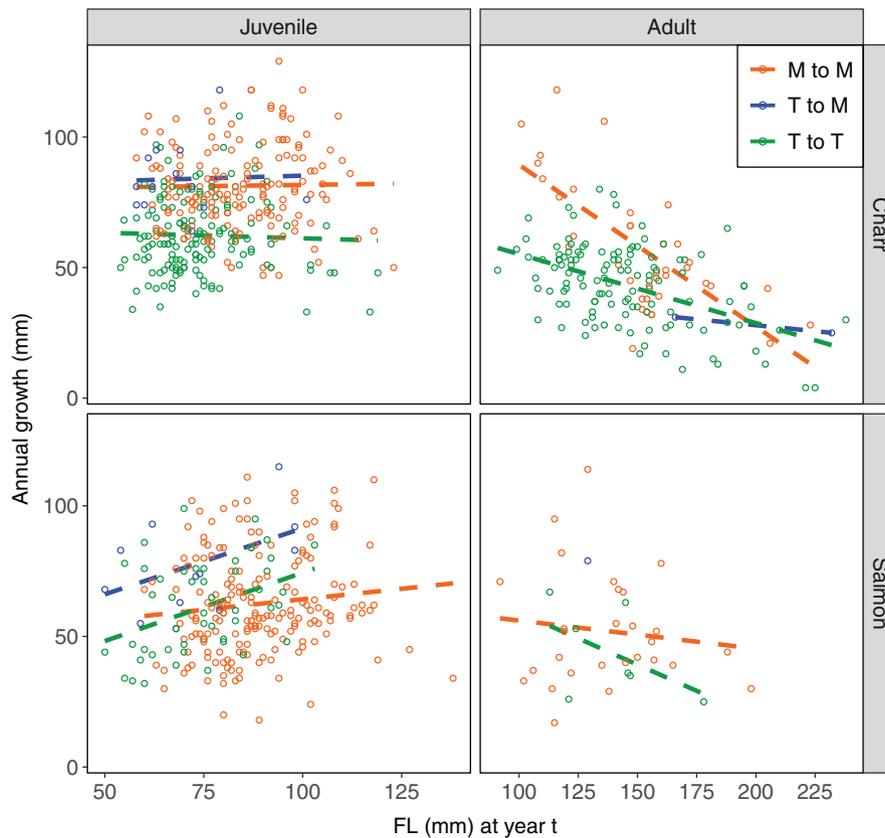


Figure 4. Annual growth patterns of charr and salmon in tributary versus mainstem. M\_to\_M: Mainstem to Mainstem (individuals remained in the mainstem), T\_to\_M: movement from Tributary to Mainstem, and T\_to\_T: Tributary to Tributary (individuals remained in the tributary).

by undercut banks and wood, Gowan and Fausch 1996a, Neumann and Wildman 2002). Indeed, physical cover created by undercut banks and coarse woody debris occurred more frequently in the study tributaries than mainstem. Water depth was also marginally deeper in tributaries versus mainstem, even though stream width was narrower. Moreover, the tributaries harboured slower and more complex current. High environmental complexities in the tributaries may have led to higher survival (i.e. safer habitat), which likely resulted in lower growth through negative density-dependence (Imre et al. 2005, Lobón-Cerviá 2007, Grossman et al. 2012), a pattern most evident for adult charr in our study. Stream temperature influences somatic growth of ectotherms, but this factor can be excluded as a driver of spatial variation in growth in this study because thermal regimes were similar between the tributaries and mainstem (Table 1). Overall, we consider that density-independent (i.e. abiotic) heterogeneity between the tributaries and mainstem habitats played a primary role in spatial juxtaposition in survival and growth, and density-dependent factors played a secondary role, particularly resulting in higher growth in the lower-density mainstem. More studies with a spatially and temporally rich dataset are needed to understand the abiotic and biotic context in which our findings (i.e. negative spatial covariation in vital rates) hold true among local habitat patches.

### Movement patterns in a heterogeneous landscape

Ecological theory predicts that animal movement is common in a spatially heterogeneous landscape (Labbe and Fausch 2000, Friedenberg 2003, Lowe 2009). However, observed movement of two salmonids was limited in this study despite spatial structure of survival and growth, which individuals could exploit by moving among locations. High local-scale residency is commonly reported in stream salmonids in headwaters (but see Gowan et al. 1994, Gowan and Fausch 1996b, Rodríguez 2002), including white-spotted charr (but see Nakamura et al. 2002, Sato and Watanabe 2004) and masu salmon (Nakano et al. 1990). Furthermore, Sakata et al. (2005) reported that fluvial masu salmon showed high residency even during the breeding period. For territorial animals such as charr and salmon (Nakano 1995), benefits of movement may be outweighed by various costs, including potential loss of established occupancy (Alerstam et al. 2003). Thus, restricted movement might develop as an adaptive strategy in stream salmonids.

However, it was interesting that downstream movement was associated with higher growth (i.e. perceived benefit) in juvenile salmon. A relatively high proportion (19%) of juvenile salmon in the tributary moved to the mainstem connected location, and they showed approximately 1.3 times

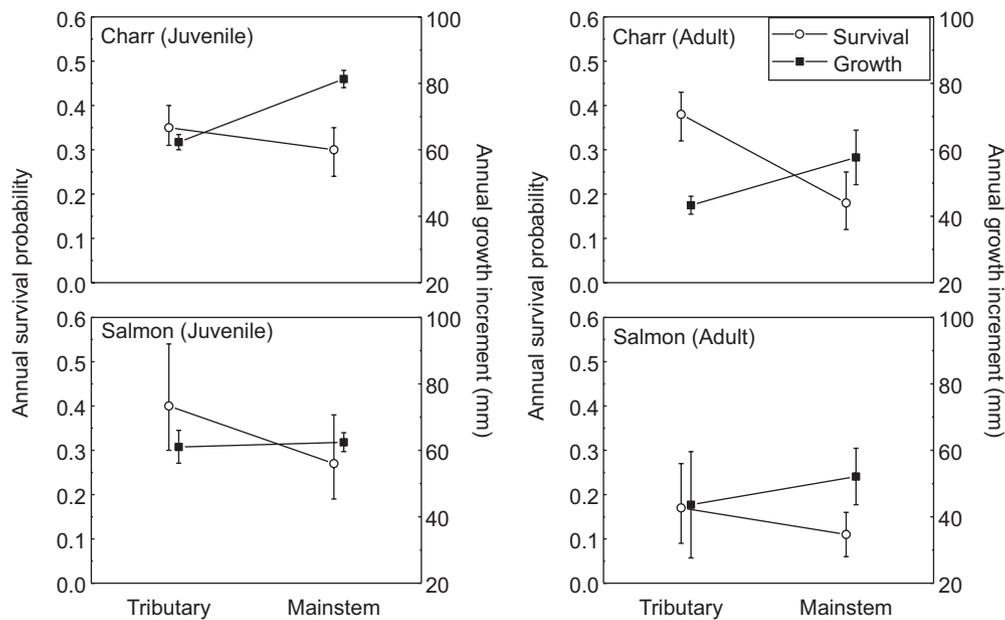


Figure 5. Summary of spatial covariation between survival (left y-axis and open circle plots) and growth (right y-axis and solid square plots) by life stage of charr and salmon in the tributary (T1 for charr and T2 for salmon) and the mainstem connected location (section A for charr and section F and G for salmon). Mean annual apparent survival probability with 95% credible interval was estimated from the multi-state Cormack–Jolly–Seber analysis. Mean annual growth increment with 95% confidence interval was calculated from recaptured fish. Growth values were based on individuals that were captured and recaptured in the same location over two consecutive years.

higher growth compared to those that were recaptured again in the tributary. Because sampling was conducted only annually and timing of movement was unknown, we cannot conclude whether individuals moved from the tributary to the mainstem to grow more or those that grew more in the tributary moved downstream to the mainstem. Despite an uncertainty in underlying mechanisms, this finding supports the importance of movement and abilities of aquatic organisms to exploit heterogeneous habitats in stream networks (Schlosser 1995, Fausch et al. 2002), and such benefits may be maximised when movement is unimpeded in both upstream and downstream directions.

We acknowledge that limited movement partly reflected our methodological approach. We could not mark individuals that were < 43 mm FL, and dispersal prior to reaching this body size could not be studied. In addition, permanent emigration from the study area was not quantified and our apparent survival estimates are a product of true survival times site fidelity (i.e. 1 – permanent emigration). However, this potential bias in survival estimates should not greatly affect our major conclusion on the negative covariation between survival and growth. Fish could not move upstream of the study area due to a dam (Fig. 1). Downstream movement was possible, but habitat downstream of the study area was much less hospitable to stream salmonids, due to increasing water temperature and competition with native and invasive fish species (Tsuboi et al. 2013). In addition, colonisation to another stream cannot happen due to dams common in this watershed. Because downstream dispersers are unlikely to survive over annual sampling intervals, we suspect that

apparent survival in this study should closely resemble true (unbiased) survival.

### Negative spatial covariation of vital rates and meta-populations

Spatial heterogeneity in vital rates implies that local population dynamics and size exhibit asynchronous patterns over time in response to broad-scale drivers such as climatic variation and disturbances. Such phenomena may be particularly idiosyncratic in stream network systems, where tributary confluences act as distinct boundaries to augment habitat heterogeneity (Benda et al. 2004, Yeakel et al. 2014). Spatial heterogeneity in vital rates among local patches may affect system-wide dynamics. Metapopulations may be more susceptible to extinctions when local patches are more similar to each other in terms of population dynamics and responses to environmental variation (Harrison and Quinn 1989, Sutcliffe et al. 1997). Terui et al. (2018) showed that increased branching complexities of stream networks stabilised temporal metapopulation sizes of several fish species. Negative covariation in local vital rates likely enhances a portfolio effect (Schindler et al. 2010, Brennan et al. 2019) in spatially structured populations. In fact, such an effect may be amplified by habitat heterogeneity among habitat patches. For example, it is conceivable that physical complexities of the tributaries may mitigate the effects of floods by readily providing refugia from high flows, and responses to disturbances may vary by habitat patch. Such mechanisms would be increasingly important for the persistence of riverine

organisms under extreme weather and frequent disturbances (McCluney et al. 2014).

## Conclusions and future directions

Higher growth in the mainstem and higher survival in the tributary were identified based collectively on analysis across two species and age classes in this study. Conducting mark-recapture surveys at the stream network scale for nearly a decade necessitates much field effort, and comparative studies are only few (Letcher et al. 2015). However, we predict that our finding may be common in headwater stream networks, especially for salmonids. Differences in habitat characteristics between tributaries and mainstem were the key driver of negative spatial covariation in survival and growth, and this longitudinal habitat pattern repeats across basins in Japan and elsewhere. In general, tributaries provide more complex habitats than mainstem because of steeper gradient and larger substrate size which increase physical and hydraulic heterogeneity (Hack 1973). Our prediction needs to be tested in stream network systems in other regions, and the global distribution of salmonids presents an ideal opportunity.

Further research is warranted to elucidate the relative importance of the mainstem versus tributary habitats in maintaining the metapopulations in the stream network. Tributaries within a stream network are frequently the key driver of metapopulation persistence for a resident salmonid because of their role as spawning and nursery habitats (Koizumi and Maekawa 2004, Letcher et al. 2007, Kanno et al. 2014). However, the importance of tributaries might be counterbalanced by higher growth in the mainstem because even relatively small increases in growth (20–30 mm FL) results in large differences in fecundity (1.5–2 fold) between females in the mainstem versus tributary habitats (Tsuboi et al. 2013). Moreover, larger females may produce eggs of a better quality (Barneche et al. 2018). Therefore, relative importance of the two habitats depends on the magnitude of spatial differences in survival and growth, as well as reproduction, which can also vary spatially (Kanno et al. 2014) but was not a focus in this study. An integrative study of vital rates in the stream network would clarify the dynamics of this spatially structured population (Merow et al. 2014, Letcher et al. 2015).

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.jm63xsj6t>> (Tsuboi et al. 2020).

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*Permits* – Field sampling was conducted in accordance with a permit issued by the Governor of Yamanashi Prefecture.

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Supplementary material (available online as Appendix oik-07169 at <[www.oikosjournal.org/appendix/oik-07169](http://www.oikosjournal.org/appendix/oik-07169)>). Appendix 1.