RESEARCH ARTICLE

Small giants: Tributaries rescue spatially structured populations from extirpation in a highly fragmented stream

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Abstract

1. Habitat fragmentation is a pervasive threat to biodiversity. Linearly arranged habitats such as stream networks are particularly vulnerable to fragmentation. As the landscape becomes increasingly human dominated, conservation values of fragmented habitat patches cannot be overlooked. It is critical to understand the demographic mechanisms of population persistence or extirpation in fragmented patches.

2. We studied dynamics of spatially structured populations of two Japanese landlocked salmonids persisting for >30 years in a headwater stream network that is highly fragmented due to low-head dams in the mainstem. We parameterised and analysed spatial matrix population models using 9-year mark–recapture data.

3. Tributaries supported higher survival rates in some life stages, and movement was asymmetrical from the tributaries to the mainstem. Accordingly, population growth rates were higher in the tributary patches than the mainstem in both species despite the tributaries occupying only 12% or 18% of the study stream network by surface area. The tributaries harboured more physically and hydraulically complex instream habitats (i.e. higher wood density and flow refugia), indicating that habitat patch quality was more important than habitat patch size in determining the dynamics of these spatially structured populations.

4. Tributary locations in the stream network were important in the trajectory of these populations. The upstream-dwelling charr persisted in the highly

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fragmented mainstem patch (i.e. six impassable infrastructures in a <500 m patch) due to immigration of fish from upstream including the tributary. However, the downstream-dwelling salmon has been gradually extirpated from the uppermost section of the fragmented mainstem patch because they could not maintain a positive population growth rate after loss of emigrants was accounted for and immigration was prevented due to fragmentation.

5. *Synthesis and applications.* We conclude that small tributaries have rescued the spatially structured populations from extirpation (charr) or at least slowed down extirpation (salmon). Legal protection of headwaters as aquatic habitats is weak globally. Our results suggest that stream management plans underestimating the demographic value of small tributaries will likely fail to conserve populations of headwater inhabitants and therefore endanger aquatic biodiversity. We discuss conservation implications of this study related to habitat connectivity and fisheries management.

1 | INTRODUCTION

Habitat fragmentation is a widespread threat to biodiversity in terrestrial and aquatic habitats (Grill et al., 2019). Fragmented habitat patches are unlikely to harbour species that require large patches (Bender et al., 1998) or dispersal (Ehlers Smith et al., 2018), and support fewer species than larger or connected patches (Connor et al., 2000). However, the conservation value of fragmented patches is growing in an increasingly human-dominated landscape (Wintle et al., 2019). Accordingly, there is an urgent need for understanding demographic mechanisms of population persistence or extirpation in fragmented patches.

Understanding the demographics of fragmented populations requires the identification of spatial population structure among habitat patches (Cooke et al., 2016). Vital rates such as survival and movement differ over space, which makes some habitat patches more important than others for the persistence of spatially structured populations (Furrer & Pasinelli, 2016). In some cases, population persistence in patches depends on immigration from other source patches (Furrer & Pasinelli, 2016). Identifying such a source–sink structure among patches is therefore paramount in predicting demographic trajectories of fragmented populations. However, characterising spatial population structure can be challenging without detailed knowledge on vital rates of individual patch populations (Heinrichs et al., 2018). Although patch size is often assumed to determine source–sink dynamics (Verboom et al., 2010), patch quality can outweigh patch size in some cases (Fleishman et al., 2002). Small high-quality patches can be easily overlooked in conservation planning, and it is important to identify these features for mobile organisms in the fragmented landscape.

Linearly arranged habitats (e.g. hedgerows, roadsides, streams) are particularly vulnerable to the detrimental effects of habitat fragmentation because animal movement is restricted along the linear ribbon of habitat and can be readily blocked by physical barriers (e.g. fences, dams; Gelling et al., 2007; Grant et al., 2007; Hubbell et al., 2020). Understanding how stream habitat fragmentation affects persistence of headwater species is critical in freshwater conservation. Headwaters (first- and second-order streams) comprise the majority of lotic habitats (70%–80% by total channel length; Wohl, 2017), and serve as key feeding, spawning and nursery habitats for aquatic species. However, fragmentation by small dams is pervasive in headwaters, and these have caused local extirpations of stream fishes globally (Charles et al., 2000; Morita & Yamamoto, 2002). For example, there are one million small instream barriers (<10 m high) in Europe (Belletti et al., 2020), which impede upstream passage by fish (Jones et al., 2020). The widespread fragmentation is partly because legal protection of headwaters is weak in many countries (Colvin et al., 2019; Doyle & Bernhardt, 2011). To inform freshwater conservation, a fuller understanding of spatial population dynamics in fragmented headwater streams is much needed.

Headwaters are typically characterised by spatial habitat heterogeneity that generates spatially dynamic populations. Although numerous, first-order streams (i.e. beginning of perennial streams) are short (Wohl, 2017). Because stream habitat characteristics may shift greatly at confluences (Benda et al., 2004), headwater stream networks are best characterised as linear habitat segments (i.e. patches) delineated by stream confluences and natural or artificial barriers (e.g. waterfalls, dams). Headwaters are composed of small tributaries feeding into the larger mainstem, and aquatic organisms

exploit this spatial heterogeneity to meet their habitat requirements which change through ontogeny (Ma et al., 2020). However, detailed demographic analysis of aquatic populations in the headwaters remains limited (e.g. Ebersole et al., 2006; Letcher et al., 2015) due to the labour- and time-intensive nature of such investigations.

In this study, we evaluated dynamics of spatially structured populations in a tributary–mainstem headwater network that is highly fragmented by five low-head small dams and a culvert in a <500 m mainstem segment. Populations of two native salmonids inhabiting these Japanese headwaters have persisted for >30 years after the dam construction. Analysis of a 9-year mark–recapture dataset showed that small tributary patches have made disproportionate contributions demographically and have likely rescued these spatially structured populations from extirpation in a highly fragmented stream.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in the Sabusawa Stream, a mountainous headwater stream (880–1,360 m in altitude) in the Fuji River system, central Japan (35°48′28″N, 138°34′13″E). The study area has two tributaries (T1 and T2) flowing into the mainstem, representing a

headwater network system with a total length of 1,050 m (Figure 1). The headwater network system harbours two landlocked salmonid species, white-spotted charr (*Salvelinus leucomaenis japonicus*, 'charr' hereafter) and red-spotted masu salmon (*Oncorhynchus masou ishikawae*, 'salmon' hereafter), with relative abundance of charr increasing upstream and that of salmon increasing downstream (Tsuboi et al., 2020). These headwater inhabitants spend their short lives (<5 years) in local stream reaches (10's–100's m; Nakano et al., 1990; Sato & Watanabe, 2004), exhibiting relatively limited movement even in the breeding season (Sakata et al., 2005).

Environmental characteristics differ between the tributaries and the mainstem, with the former having slower water velocity and more abundant physical shelters for fish created by undercut banks and coarse woody debris than the mainstem (Figure 1, details are described in Tsuboi et al., 2020). The mainstem is divided into seven sections (A–G) by barriers including low-head erosion control dams and a culvert, which were installed between 1987 and 1992. Although fish can move freely between the tributaries and the mainstem (i.e. T1-A and T2-F), upstream movement of fish is blocked by the structures in the mainstem except for the small low-head dam (*c.* 1.4 m high) between Section F and G. We defined three spatial patches for demographic analysis of 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 a set of
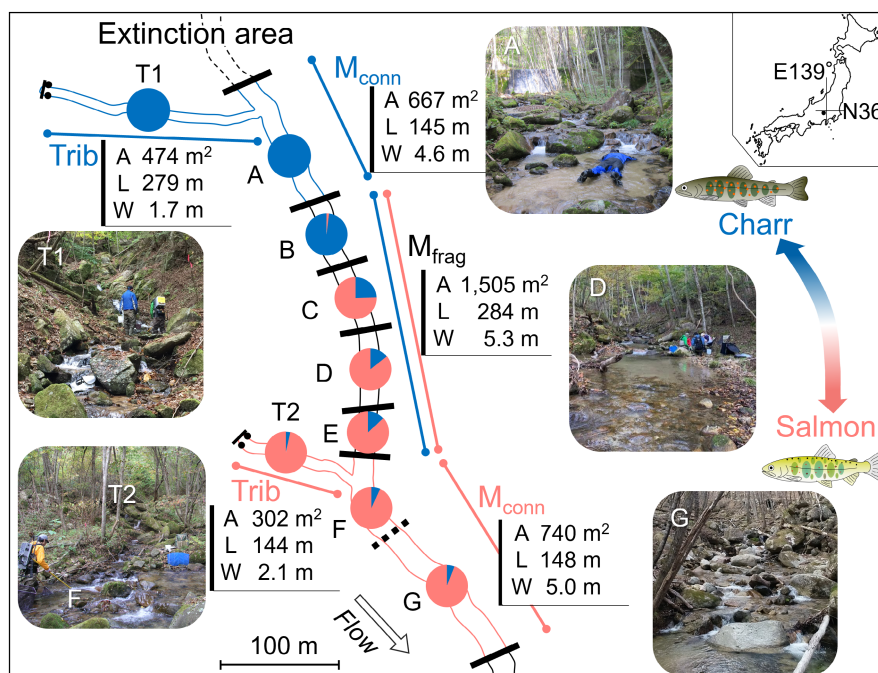

FIGURE 1 Map of the study area in Sabusawa Stream, Yamanashi Prefecture, located in central Japan (see map at top right). Pie charts show the proportion of charr (blue) and salmon (red) count in each of the nine sections (A–G, T1 and T2) averaged between 2009 and 2017. Dams and culverts (solid lines) impede upstream movement of fish, except that two-way movement is possible between Section F and G (dotted line). 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 comprise the mainstem fragmented patch. The upper ends of T1 and T2 are bounded by high-gradient cascades, which prevent upstream movement of fish. Surface area (A), stream length (L) and stream width (W) are shown for each patch. This figure was modified from Tsuboi et al. (2020)

mainstem sections without connectivity to tributaries ('*mainstem fragmented*' hereafter; Section B through Section E for both species; Figure 1). Stream width was approximately 2 m in the tributaries versus 5 m in the mainstem, and the tributary patches were shorter than the mainstem patches. Consequently, the tributary patches occupied only 18% (charr) and 12% (salmon) of the total habitat by surface area (Figure 1).

2.2 | Field sampling

The population survey of the two species was conducted annually during the third weekend of October in 2009–2017. Sampling occurred immediately before the spawning season, which overlaps between the two species. The details of the survey are described in Tsuboi et al. (2020). Briefly, fish were captured using a backpack electrofishing unit (300–400 VDC, model 12B or LR20, Smith-Root, Inc.) and 3-mm mesh dip nets. All captured fish with fork length >43 mm, the smallest fish captured by electrofishing, were individually marked with a unique combination of four elastomer colours injected subcutaneously on the forehead (Visible Implant Elastomer Tags, Northwest Marine Technology, Inc.). The colour marks combined with data of species, sex, fork length, and section of capture and release allowed us to uniquely identify all recaptured individuals. The timing of survey allowed us to confidently determine maturity status of individuals by the presence of eggs and milt and other external characteristics. We recorded maturity status of individuals as 0-year old (young-of-the-year; YOY), immature, and mature. A total of 1,372 charr and 1,335 salmon were captured and marked uniquely during 2009–2017. Field sampling was conducted in accordance with a permit issued by the Governor of Yamanashi Prefecture. An approval for ethical animal care was not needed to conduct this research in Japan.

2.3 | Statistical analyses

2.3.1 | Population density and body size distribution

Annual population density of YOY, immature and mature fish of each species in each patch (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). Specifically, individuals captured in the first electrofishing pass were kept in a live well, while the second pass was conducted subsequently in the same area. The depletion data were used to infer capture probability and fish abundance. Annual density estimates and body size (fork length) were compared among the patches using one-way ANOVA. When population density and body size differed significantly, a Tukey's Honest Significant Difference test was conducted to determine which patches were different. Statistical significance was assessed at $\alpha = 0.05$.

2.3.2 | Construction of metapopulation projection models

We constructed metapopulation matrix models for charr and salmon representing dynamics of three habitat patches and three life stages. Following Tsuboi et al. (2020), three habitat patches (i.e. tributary, mainstem connected and mainstem fragmented) were defined differently for each species because of their different longitudinal distributions (Figure 1). The few charr captured farther downstream in section F, G and T2 were included in the mainstem fragmented patch.

Metapopulation matrix models were constructed using pre-breeding census representation. The three life stages defined for each species were YOY, immature and mature fish (Figure 2). In both species, a proportion of YOY reach sexual maturity in the following year, and transition probabilities to next stages were denoted by Ω (maturation), given survival (Φ). Fecundity (F), or number of eggs, was based on body size of mature females (see *Parameter estimation*). Vital rates were modelled to differ by patch, and movement among patches was modelled for the three life stages in charr but not in salmon.

We followed the vec-permutation matrix approach (Hunter & Caswell, 2005) to construct metapopulation matrix models. During annual census steps, movement between patches was modelled to occur first, followed by the demographic processes of survival and transition to the next stages. To model movement of YOY, immature and mature fish between patches, a block diagonal matrix $\mathbb{M}_j$ for species j was constructed, in which diagonal element $M_{h,j}$ represents movement of stage h (1 = YOY, 2 = immature and 3 = mature) of species j among the three patches;

$$\mathbb{M}_j = \begin{pmatrix} M_{1,j} & 0 & 0 \\ 0 & M_{2,j} & 0 \\ 0 & 0 & M_{3,j} \end{pmatrix}.$$
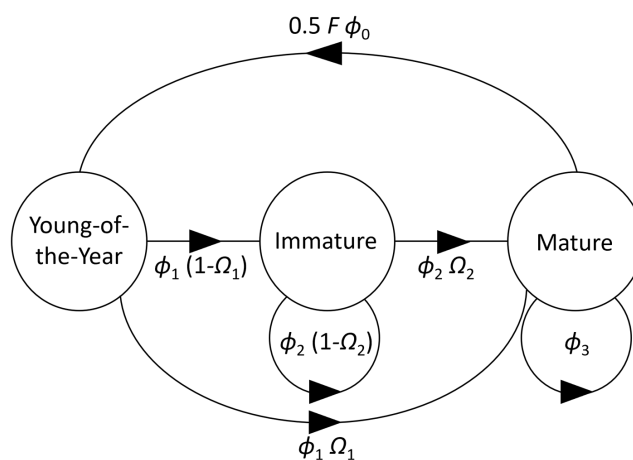

FIGURE 2 Life cycle graph of charr and salmon that represent stage-structured demographic parameters in a local habitat patch. Symbols indicate: F = fecundity, ϕ_0 = survival probability of eggs, ϕ_1 = survival probability of young-of-the-year fish, ϕ_2 = survival probability of immature fish, ϕ_3 = survival probability of mature fish, Ω_1 = maturation probability of young-of-the-year fish and Ω_2 = maturation probability of immature fish

For each stage (h = 1, 2, 3) of charr in $M_{h,1}$, their elements $\Psi_{h,j,p,q}$ represented the probability that an individual in stage h moves from patch p to patch q (1 = tributary, 2 = mainstem connected and 3 = mainstem fragmented; Figure 1). For example, $\Psi_{1,1,1,2}$ represented the movement probability of charr (j = 1) in the YOY stage (h = 1) moving from the tributary (p = 1) to the mainstem connected patch (q = 2). No movement occurred and individuals stayed in the same patch when $p = q$. For charr ($M_{h,1}$), this was represented by:

$$M_{h,1} = \begin{pmatrix} \Psi_{h,1,1,1} & \Psi_{h,1,2,1} & 0 \\ \Psi_{h,1,1,2} & \Psi_{h,1,2,2} & 0 \\ \Psi_{h,1,1,3} & \Psi_{h,1,2,3} & 1 \end{pmatrix}.$$

Charr in the fragmented mainstem could not move upstream due to habitat fragmentation (Figure 1). Therefore, all individuals were locked in this patch (i.e. $\Psi_{h,1,3,3} = 1$).

For salmon ($M_{h,2}$), elements $\Psi_{h,j,p,q}$ represented the probability that an individual in stage h of salmon ($j = 2$) moved from patch p to patch q;

$$M_{h,2} = \begin{pmatrix} \Psi_{h,2,1,1} & \Psi_{h,2,2,1} & \Psi_{h,2,3,1} \\ \Psi_{h,2,1,2} & \Psi_{h,2,2,2} & \Psi_{h,2,3,2} \\ 0 & 0 & \Psi_{h,2,3,3} \end{pmatrix}.$$

Immigration into the mainstem fragmented patch could not happen in salmon (Figure 1) so that $\Psi_{h,2,1,3} = \Psi_{h,2,2,3} = 0$. In salmon, movement was modelled to be constant across life stages such that $M_{1,2} = M_{2,2} = M_{3,2}$, due to a small sample size which caused the model not to converge. This approach was justified because movement probability was nearly identical between YOY and their older stages (immature and mature fish combined) in this study area (Tsuboi et al., 2020).

Demography was represented by a block diagonal matrix $\mathbb{B}_j$ for species j, which included 3×3 local patch demographic matrices diagonally and 0 elsewhere. Let $\mathbf{B}_{i,j}$ be a 3×3 demographic projection matrix for patch i (1 = tributary, 2 = mainstem connected and 3 = mainstem fragmented) and species j (1 = charr and 2 = salmon):

$$\mathbb{B}_j = \begin{pmatrix} \mathbf{B}_{1,j} & 0 & 0 \\ 0 & \mathbf{B}_{2,j} & 0 \\ 0 & 0 & \mathbf{B}_{3,j} \end{pmatrix}.$$

Furthermore, each patch demographic projection matrix $\mathbf{B}_{i,j}$ was represented by patch-specific vital rates, where $F_{i,j}$ is fecundity, or number of eggs that a mature female of average size will produce in patch i for species j, $\Phi_{h,i,j}$ is the probability of annual survival of stage h of species j in patch i, and $\Omega_{h,i,j}$ is the probability of maturation (i.e. transition to mature fish) of stage h of species j in patch i. The sex ratio approximates 1:1 in landlocked charr (Yamamoto et al., 1999) and salmon (Morita et al., 2018) so that

fecundity was multiplied by 0.5. Because our projection matrices are represented by pre-breeding census formulation, fecundity was multiplied by egg-to-YOY survival probability, $\phi_{0,j}$, for each species j (Kendall et al., 2019);

$$B_{i,j} = \begin{pmatrix} 0 & 0 & 0.5 F_{i,j}\Phi_{0,j} \\ \Phi_{1,i,j}(1-\Omega_{1,i,j}) & \Phi_{2,i,j}(1-\Omega_{2,i,j}) & 0 \\ \Phi_{1,i,j}\Omega_{1,i,j} & \Phi_{2,i,j}\Omega_{2,i,j} & \Phi_{3,i,j} \end{pmatrix}.$$

Metapopulation projection matrix $\mathbb{A}_j$ for species j is then $\mathbb{A}_j = \mathbb{B}_j\, \mathbf{P}^T\, \mathbb{M}_j\, \mathbf{P}$, where $\mathbf{P}$ is the vec-permutation matrix (Hunter & Caswell, 2005). For a metapopulation composed of s life stages and t patches, $\mathbf{P}$ has a $st \times st$ dimension and is derived by;

$$P(s,t) = \sum_{i=1}^{s} \sum_{j=1}^{t} E_{ij} \otimes E_{ij}^T,$$

where $\mathbf{E}_{ij}$ is an $s \times t$ matrix with 1's in the (i,j) positions and 0's elsewhere, and $\otimes$ denotes the Kronecker matrix product. The resulting $\mathbb{A}_j$ for species j is a 9×9 matrix representing diagonally demography of patch i ($\mathbf{A}_{i,j}$; a 3×3 matrix) after emigration from the patch was accounted for, and a combination of demography and movement dynamics off-diagonally:

$$\mathbb{A}_j = \begin{pmatrix} \mathbf{A}_{1,j} & \mathbf{a}_{2,1,j} & \mathbf{a}_{3,1,j} \\ \mathbf{a}_{1,2,j} & \mathbf{A}_{2,j} & \mathbf{a}_{3,2,j} \\ \mathbf{a}_{1,3,j} & \mathbf{a}_{2,3,j} & \mathbf{A}_{3,j} \end{pmatrix},$$

where $\mathbf{a}_{p,q,j}$ denotes demography and emigration of individuals in species j from patch p to patch q (1 = tributary, 2 = mainstem connected and 3 = mainstem fragmented).

2.3.3 | Parameter estimation

Metapopulation projection matrices were parameterised based on multi-state Cormack–Jolly–Seber (CJS) analysis of mark–recapture data (Kéry & Schaub, 2012), except for fecundity (F) and annual survival probability of eggs (ϕ_0; Figure 2) because it was not possible to mark eggs. Fecundity ($F_{i,j}$) was estimated based on the mean fork length of mature females in patch i and species j following Tsuboi et al. (2013). The estimated fecundity of charr was 197 in the tributary patch, 226 in the mainstem connected patch and 223 in the mainstem fragmented patch. The estimated fecundity of salmon was 190 in the tributary patch, 201 in the mainstem connected patch and 228 in the mainstem fragmented patch. Egg-to-YOY survival probability was inferred by estimating YOY abundance using the two-pass removal method and dividing it by the number of eggs based on adult abundance estimates in the previous year in the entire study area (i.e. patches were combined). The estimated annual egg-to-YOY survival was 0.0329 in charr and 0.0429 in salmon, based on the geometric mean.

Other parameters were estimated using multi-state CJS models, as described in Tsuboi et al. (2020). For each species, a unique combination of three patches (tributary, mainstem connected and mainstem fragmented) and three life stages that could be physically marked (YOY, immature and mature) resulted in nine states, plus a 10th state for individuals which were not captured. The models were analysed with a Bayesian approach using a Markov chain Monte Carlo (MCMC) method in Program JAGS (Plummer, 2018) called from Program R (R Core Team, 2021) with the JAGSUI package. Posterior distributions of model parameters were characterised by taking every fifth sample from 10,000 iterations of four chains after a burn-in period of 5,000 iterations. A total of 8,000 posterior samples were used in demographic analysis of metapopulation projection models to account for parameter uncertainties. Model convergence was checked by ensuring that the R-hat statistic was <1.1 for all parameters (Gelman & Hill, 2007). Details of the multi-state CJS models and JAGS code are provided in Appendices.

2.3.4 | Demographic analysis of metapopulation projection models

Eigen analyses were used to characterise metapopulation dynamics of charr and salmon based on projection matrices. Metapopulation growth rate (λ_M) was inferred for species j based on metapopulation projection matrix $\mathbb{A}_j$. Additionally, population growth rate was inferred for patch i for species j before loss of emigrants was accounted ('pre-emigration' lambda, λ_{Pre}) based on matrix $\boldsymbol{B}_{i,j}$ and after loss of emigrants was accounted for, that is, subtracting contributions to other patches ('post-emigration' lambda, λ_{Post}) based on matrix $\boldsymbol{A}_{i,j}$. We interpreted the difference in patch growth rates between the two ($\Delta\lambda = \lambda_{Pre} - \lambda_{Post}$) as a measure of demographic contribution of the patch to the metapopulation growth rate because emigrants from a patch ended up elsewhere in our isolated study area. Analysis of population growth rates was based on posterior samples of movement and demography in the multi-state CJS models, so uncertainties about population growth rates were quantified using 95% credible intervals (CI). We interpreted population growth to be positive if the 95% CI of λ_{Pre} or λ_{Post} was >1 and negative if it was <1. Finally, we conducted an elasticity analysis of posterior mean vital rates in patch i and species j based on patch matrix $\boldsymbol{B}_{i,j}$ to evaluate the degree to which patch population growth rates were affected by proportional changes in vital rates. The elasticity analysis quantified relative importance of life stage transitions with the dominant eigenvalue using the 'elas' function in the POPDEMO package (Stott et al., 2012) in Program R. Details of the metapopulation projection models and R code are provided in Appendices.

3 | RESULTS

Throughout the 9 years of mark–recapture sampling, fish density was higher and body size was smaller in the two tributaries compared to the mainstem patches, and this pattern was more pronounced in charr (Figure S1). Importantly, the uppermost distribution of salmon shifted downstream during the study period (2009–2017), although charr distribution did not change (Figure S2). Initially, salmon occurred as far upstream as Section B, but they were extirpated from Section B in 2010 and Section C in 2020.
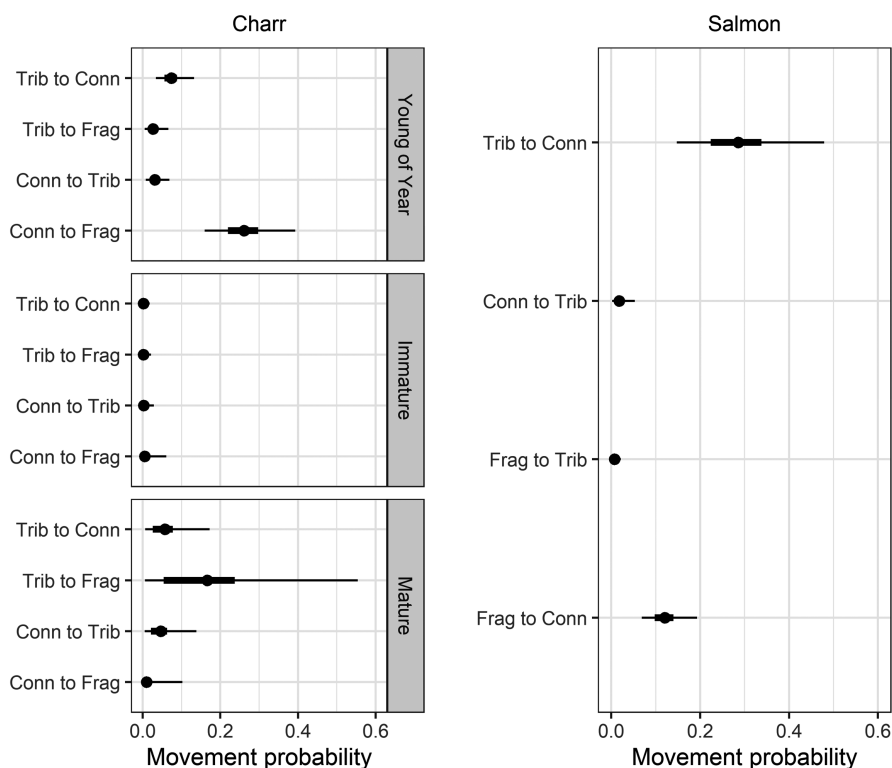

FIGURE 3 Posterior distributions of movement probabilities between three habitat patches. Movement was modelled to differ by young-of-the-year, immature and mature fish for white-spotted charr, and was constant among stages for red-spotted salmon due to low sample size. Posterior mean values are shown by dots with 50% (thick lines) and 95% (thin lines) credible intervals. Three habitat patches of charr are tributary (T1), mainstem sections with unimpeded connectivity to tributaries ('mainstem connected': Section A) and mainstem sections without connectivity to tributaries ('mainstem fragmented': Sections B through E). Three habitat patches of salmon are tributary (T2), mainstem connected (Section F and G), and mainstem fragmented (Sections B through E)

3.1 | Movement

Fish movement among habitat patches was limited overall. When movement occurred, it was asymmetrical from upstream to downstream patches even when physical barriers were absent (Figure 3). In charr, movement was most common from the mainstem connected (Section A) to the mainstem fragmented patch (Section B-G) at the YOY stage (mean probability = 0.26; 95% CI = 0.16–0.39; Table S3 in Appendix 1). Movement of mature fish from the tributary (Section T1) to the mainstem fragmented patch was the next most frequent (mean probability = 0.17; 95% CI = 0.01–0.55). These movement patterns indicated that individuals of different life stages in the tributary and mainstem connected patches immigrated to the mainstem fragmented patch, located at the lowermost end of the charr metapopulation (Figure 1). Movement between remaining pairs of patches was limited (mean probability <0.10).

Salmon similarly emigrated to the lowermost, mainstem connected patch (Section F and G) from upstream (Figure 3). The most common movement occurred from the tributary (Section T2) to the mainstem connected patch (mean probability = 0.29; 95% CI = 0.15–0.48), followed by movement from the mainstem fragmented (Section B-E) to the connected patch (0.12; 95% CI = 0.07–0.19). In both species, immigration into the tributary patch was infrequent.

3.2 | Demography

In general, tributaries supported higher annual survival rates than mainstem patches (Figure 4). In charr, survival of mature fish was higher in the tributary patch (mean probability = 0.47; 95% CI = 0.32–0.86) than in the mainstem connected (0.18; 95% CI = 0.11–0.27) and fragmented (0.06; 95% CI = 0.02–0.12) patches. Survival of YOY and immature fish did not differ by patch, as indicated by overlapping 95% CI for each life stage. In salmon, the tributary supported higher survival rates of YOY (0.47; 95% CI = 0.32–0.69) and immature stage (0.37; 95% CI = 0.13–0.71), compared to the mainstem connected and fragmented patches. Survival of mature salmon depended less on patch, with 95% CI of survival overlapping among the three patches.

Maturation probability was similar among habitat patches, except that a smaller proportion of YOY charr matured in the tributary patch (mean = 0.69; 95% CI = 0.61–0.79), compared to the mainstem connected (0.83; 95% CI = 0.74–0.90) and fragmented patch (0.90; 0.83–0.95; Figure S2 in Appendix 1). Across patches, the mean maturation probability ranged 0.86–0.97 in immature charr, 0.62–0.73 in YOY salmon and 0.64–0.73 in immature salmon.

3.3 | Metapopulation structure

Mean metapopulation growth rate (λ_M) was positive in both species, reaching 1.05 (95% CI = 0.95–1.15) in charr and 1.03 (95% CI = 0.89–1.21) in salmon. The tributary patches had the highest pre-emigration

population growth rate in both species, with a mean λ_{Pre} of 1.22 (95% CI = 1.10–1.48) in charr and mean λ_{Pre} of 1.30 (95% CI = 1.06–1.60) in salmon (Figure 5). The lower bound of the 95% CI was >1 in both cases, indicating that population growth rates were positive in the tributaries, before emigration was accounted for. The posterior samples of λ_{Pre} were mostly >1 for the mainstem connected patch for charr (mean = 1.07; 95% CI = 0.94–1.23) but were about equally positive and negative with a mean population growth rate that approximated 1 in the mainstem fragmented patch for charr, and the mainstem connected and fragmented patches for salmon.

Once emigration was accounted for, population growth rates decreased most in the tributary patches for both species (Figure 5). The mean λ_{Post} of the tributary patch was 1.00 (95% CI: 0.78–1.13) for charr and 0.92 (95% CI: 0.74–1.12) for salmon. The mean difference between pre- and post-emigration population growth rates ($\Delta\lambda$) was 0.22 in charr and 0.38 in salmon, and $\Delta\lambda$ of the tributary patch was larger than those of the mainstem connected and fragmented patches in both species, demonstrating that the tributaries made disproportionate demographic contributions to metapopulation
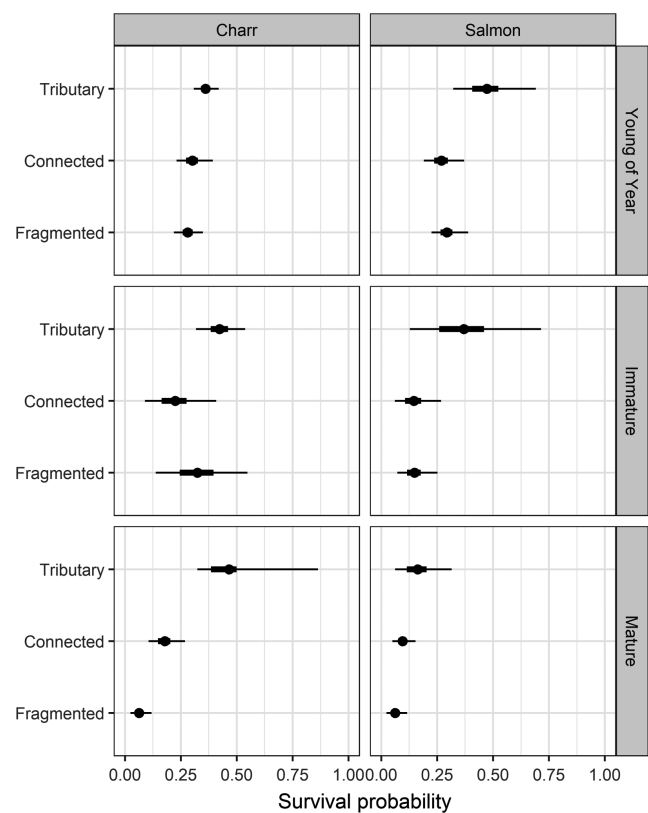

FIGURE 4 Posterior distributions of annual survival probabilities of young-of-the-year, immature and mature fish in three habitat patches. Posterior mean values are shown by dots with 50% (thick lines) and 95% (thin lines) credible intervals. Three habitat patches differ between white-spotted charr and red-spotted salmon; tributary (Section T1 for charr and T2 for salmon), mainstem sections with unimpeded connectivity to tributaries ('mainstem connected': Section A for charr and Section F and G for salmon) and mainstem sections without connectivity to tributaries ('mainstem fragmented': Section B through E for both species)
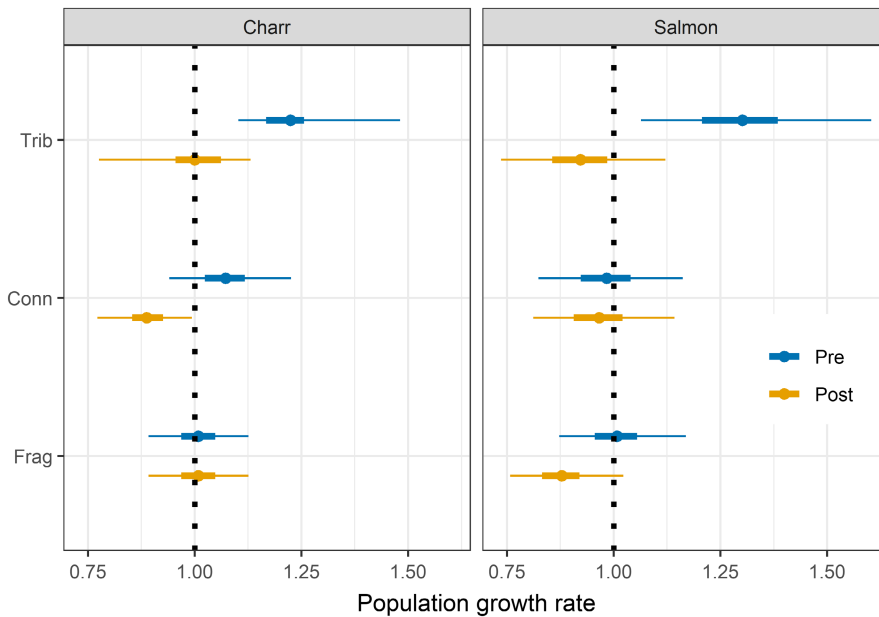
FIGURE 5 Posterior distributions of population growth rates before (λ_{Pre}) and after (λ_{Post}) loss of emigrants was accounted for in each habitat patch for white-spotted charr and red-spotted masu salmon. Posterior mean values are shown by dots with 50% (thick lines) and 95% (thin lines) credible intervals. The differences between λ_{Pre} and λ_{Post} ($\Delta\lambda$) represent demographic contributions of the patch to other patches in this isolated metapopulation. Vertical dotted lines indicate where population growth rates are 1 (i.e. populations are neither increasing nor decreasing)

persistence. The mean λ_{Post} of the mainstem connected patch decreased to 0.89 in charr; its 95% CI ranged below 1 (0.77–0.99), whereas 95% CI of λ_{Pre} was mostly above 1 when emigration was not accounted for (Figure 5). This indicated that the mainstem connected patch of charr relied on immigration from the tributary for population persistence because immigration could not happen from the mainstem fragmented patch due to dams. In salmon, the mean λ_{Post} of the fragmented mainstem patch was 0.88, and 95% of the posterior λ_{Post} samples barely overlapped 1 (0.76–1.02). This indicated that the salmon population in the fragmented mainstem patch could not maintain a positive population growth, which is corroborated by the empirical pattern of gradual loss of salmon in this patch during the study period (Figure S2).

Finally, population growth rates were most sensitive to proportional changes in fecundity (including egg survival) and transition of YOY to the adult stage across patches in both species (Figure 6). Across the three patches, elasticity values of fecundity ranged 0.36–0.48 in charr and 0.45–0.47 in salmon, and those of the YOY-to-adult transition ranged 0.32–0.46 in charr and 0.42–0.45 in salmon.

4 | DISCUSSION

The small tributaries were important for the metapopulation persistence of native salmonids in this highly fragmented tributary–mainstem network. Tributaries supported higher survival rates in certain life stages, and movement was asymmetrical from the tributaries to the mainstem when it occurred. Pre-emigration population growth rates (λ_{Pre}) were the highest in the tributaries in both species, but after accounting for emigration, population growth rates (λ_{Post}) were similar among the habitat patches. These demographic results showed that the spatially structured populations in our study system were characterised by source–sink dynamics in which tributaries were critically important in sustaining the metapopulations

that occupy the mainstem fragmented by a series of dams. Notably, the tributaries (c. 2 m wide) were less than half as wide as the mainstem (c. 5 m), and occupied only 18% (charr) and 12% of the study system by surface area. Thus, habitat size did not determine the identity of source and sink habitats in this study, even though larger patches are often assumed to make larger demographic contributions than smaller patches to the persistence of spatially structured populations in terrestrial (Ehlers Smith et al., 2018), marine (Kritzer & Sale, 2004) and freshwater systems (Williams et al., 2011). This unique and counterintuitive spatial population structure, in which smaller patches served as the demographic sources, was revealed by analysis of the 9-year mark–recapture data.

We reason that the tributaries made large demographic contributions due to patch quality, not patch size. In particular, the tributaries harboured more physically complex instream habitats characterised by higher densities of large wood and more heterogeneous hydraulic patterns that created slower moving eddies (Tsuboi et al., 2020). Stream salmonids prefer these habitat characteristics (Ebersole et al., 2006), which were less common in the mainstem due presumably to the series of dams altering hydrological and sediment transport regimes. Habitat complexity coincided with higher survival rates of some life stages in each species in the tributaries, which led to higher population growth rates in the tributaries relative to the mainstem patches before loss of emigrants was accounted for. For short-lived and early-maturing fishes such as these landlocked salmonids, population growth rates are most sensitive to variation in vital rates associated with early life stages (Vélez-Espino et al., 2006). Our result conforms to this pattern because elasticity analysis showed that population growth rates were most sensitive to fecundity (including egg survival) and maturation of YOY. Smaller-bodied individuals in early stages require less physical space than larger individuals, which may explain why tributaries were critical for the charr and salmon metapopulations in the study area. Overall, our study adds to the growing literature that habitat size and quality

FIGURE 6 Elasticity of population growth rates due to changes in vital rates in each habitat patch for white-spotted charr and red-spotted masu salmon. Elasticity analysis was conducted using posterior distributions of vital rates and bars represent the mean across the posterior samples. Vital rates are arranged vertically by elasticity values: Fecundity (number of eggs per mature female × egg survival), YOY to mature transition (YOY to MAT), survival of mature fish (MAT to MAT), YOY to immature transition (YOY to IMM), immature to mature transition (IMM to MAT) and survival of immature fish without maturation (IMM to IMM)
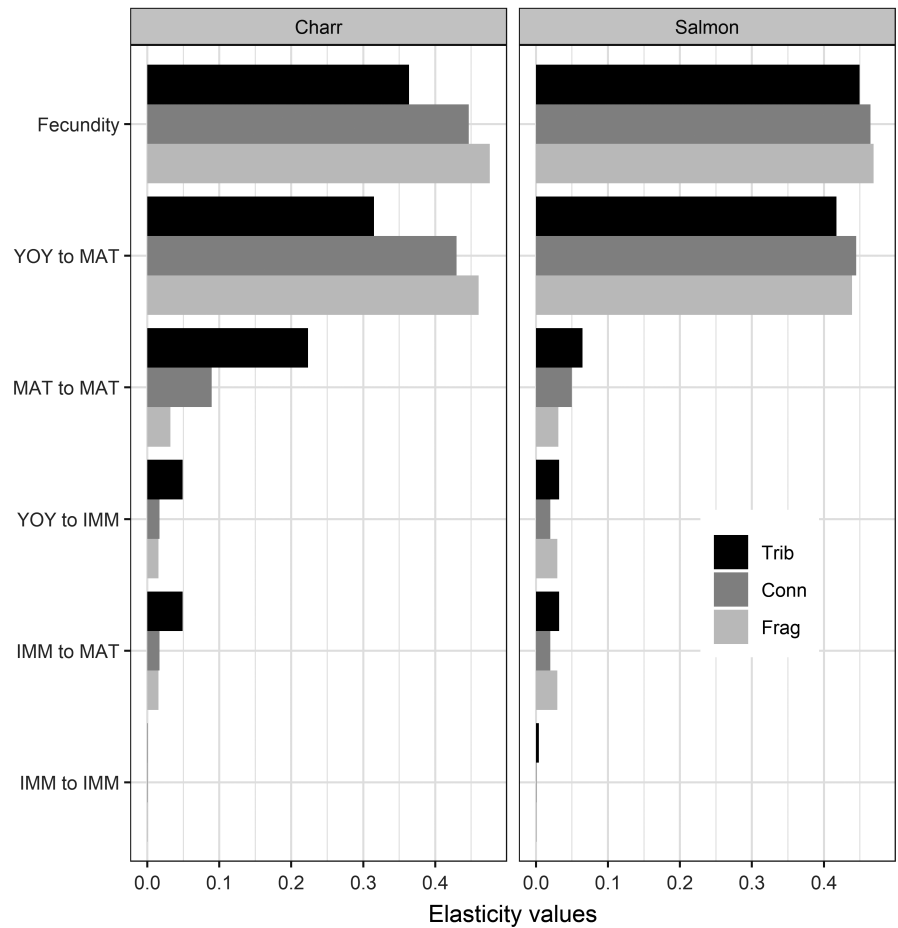
are not always positively correlated, and both determine the dynamics of spatially structured populations (Robles & Ciudad, 2012; Thornton et al., 2013).

Demographic importance of the tributaries was not immediately evident based on spatial patterns of vital rates and was revealed only by analysis of the metapopulation projection models. Although the tributaries supported higher survival rates of some stages in both species, the mean body size and fecundity were lower in the tributaries compared to the mainstem in both species. Tsuboi et al. (2020) showed that body growth rates of both species were slower in the tributaries than in the mainstem, which explains why fish are smaller in the tributaries. Slower growth rates in the tributaries could be attributed to restricted habitat size, increased fish density or both (Tsuboi et al., 2020). Thus, trade-offs of vital rates were spatially structured, where the tributaries supported higher survival and lower growth rates, and the mainstem supported lower survival and higher growth rates in the Sabusawa Stream. Similar spatial trade-offs of vital rates have been reported in other stream salmonid populations, which are the most common inhabitants of the headwater streams in the northern hemisphere (Boughton et al., 2009; Letcher et al., 2015). Accordingly, the demographic importance of the tributaries is likely not limited to the Sabusawa Stream, although its importance clearly depends on the magnitude of the spatial trade-offs.

It is likely that the demographic importance of the tributaries was not fully represented in our current analysis. Larval fish could

not be marked due to their small body size and timing of annual surveys relative to their spawning season; thus, larval movement was not accounted for in this study. Larvae of stream salmonids disperse predominantly downstream (Srivastava & Kratina, 2013). If such a pattern exists, it would reinforce the asymmetrical movement from the tributaries to the mainstem across more life stages, and consequently the source–sink dynamics. Tributaries can also serve as refugia from high flows (Koizumi et al., 2013), which is likely the case in Sabusawa Stream given the increased habitat complexity in the tributaries that provide hydraulic heterogeneity (Tsuboi et al., 2020). In contrast, tributaries are most vulnerable to drying due to droughts given their low flow volumes (Lake, 2003) and fish populations in tributaries may become locally extirpated if they are completely isolated from the downstream habitat (Morita & Yamamoto, 2002). As global climate change accelerates and extreme events increase in magnitude and frequency, understanding the demographic role and vulnerability of small, high-quality habitat patches (e.g. tributaries) is much needed.

Our long-term study provides unique insights on how spatial configurations of patches may mediate the effects of habitat fragmentation. For more than 30 years after the installation of dams, the upstream-dwelling charr has persisted in the mainstem fragmented patch. The mean λ_{Pre} and λ_{Post} of the fragmented mainstem patch was 1.01 for charr, indicating that this patch can maintain only a slightly positive population growth rate. It is likely that the persistence of

charr was facilitated by immigration of fish from upstream patches, and the movement of YOY from the mainstem connected to fragmented patches was the most common in charr. In addition, we postulate that immigration of charr from the tributary was essential to the population persistence in the mainstem connected patch because its 95% CI of λ_{Post} was entirely below 1 (0.77–0.99) when emigration was accounted for and the tributary was the only source of immigrants for the mainstem connected patch. In contrast, the downstream-dwelling salmon has been gradually disappearing from the mainstem fragmented patch, and at present has been extirpated from Sections B and C. In salmon, the mean λ_{Post} of the fragmented mainstem patch was 0.88 (95% of the posterior samples <1), showing that local extirpation would be highly likely without immigration of fish from other patches. This species-specific pattern demonstrates that the location and connectivity of source patches (i.e. tributaries) in a habitat network determine the trajectories of other patches.

Although the salmon population may still continue to decline in the study area, the persistence of charr and salmon for over 30 years after dam construction is noteworthy and is likely linked to the presence of tributaries. The total stream length of the three habitat patches is <1 km for each species and includes five impassable dams. The basin size was only 0.41 km^2 for T1 and 0.64 km^2 for T2 in this study. Despite the small overall habitat size, tributary–mainstem networks possess increased habitat heterogeneity due to the habitat branching, in which habitat characteristics may shift greatly at stream confluences (Ma et al., 2020; Terui et al., 2018). Collectively, our analysis shows that the tributaries have prevented the metapopulation extirpation of charr and salmon in this small stream habitat network.

5 | CONCLUSIONS

This study highlights the importance of conserving small headwaters. Evidence for the ecological importance of tributaries, even intermittent ones, has been accumulated in previous studies (Benstead & Leigh, 2012; Colvin et al., 2019; Finn et al., 2011; Gauthier et al., 2020; Larsen et al., 2021; Wohl, 2017). However, headwaters are often overlooked in aquatic conservation planning. In Japan's River Act, headwaters are not considered an aquatic habitat, which has resulted in widespread constructions of dams in Sabusawa Stream and nationwide (Endou et al., 2006). Attempts are being made to install and improve fishways on small dams in headwater streams (Machida et al., 2019; Sato et al., 2021). However, a fundamental shift to recognise the importance of headwaters as aquatic habitat is needed to remediate the damage. Under the Clean Water Act of the U.S.A., waterways are afforded with legal protection only when they are deemed to have 'significant nexus' with seemingly larger, more productive habitats downstream (Colvin et al., 2019). Whether headwaters and wetlands possess such significant nexus and connectivity with downstream habitat is under frequent debate (Alexander, 2015; Doyle & Bernhardt, 2011). Our study shows that headwaters serve as fish habitat per se, not to mention

ecological connectivity to downstream (Hubbell et al., 2020; Larsen et al., 2021; Ma et al., 2020), and provides scientific support for the ecological importance of headwater habitats based on a long-term, mark–recapture demographic study.

Our findings offer some specific guidance on the conservation of headwater species. Restoring habitat connectivity in the stream network is a common conservation strategy given the ubiquity of stream habitat fragmentation globally (Kemp & O'Hanley, 2010; Warren & Pardew, 1998). Because these potential barriers are so many in the riverscape, managers need to prioritise barriers for removal and repair to improve aquatic organism passage (O'Hanley & Tomberlin, 2005). Whereas removing barriers located in the mainstem increases overall habitat connectivity at the watershed scale (Kraft et al., 2019), barriers that isolate small tributaries may not seem readily important from the overall connectivity perspective because they occur near the terminus of the stream network system. However, our study indicates that removing barriers that isolate small tributaries may warrant high priorities if tributaries are critically important for sustaining spatially structured populations of aquatic organisms.

This study also provides insights on fisheries management. Salmonids are popular recreational fishes globally and are managed by a set of regulations such as size and bag limit, and area closure (Lewin et al., 2006). Spatial population structures in this study argue for a spatially heterogeneous implementation of fisheries regulations. There have been many attempts to designate some sections of the stream network as no-take zones, including small tributaries (Carosi et al., 2022; Nakamura et al., 1994; Yamamoto et al., 2013), but empirical support for such zoning regulations has been surprisingly limited. A successful management case of native salmonids is found in Zako River located approximately 150 km north of Sabusawa Stream. There, a high level of catch has been sustained in the mainstem by protecting a group of small tributaries from fish harvest without any stocking (Yamamoto et al., 2013). Our finding of disproportionately large contributions of small tributaries to the metapopulation viability provides scientific basis for why spatially arranged fisheries regulations can be highly successful, and therefore encourages fisheries managers to consider their implementation as a management option.

In conclusion, this study showed that demographic contributions of small tributaries were critical in maintaining metapopulations of native stream fishes in a highly fragmented stream network. Freshwater conservation tends to focus on larger rivers downstream because they typically harbour higher species richness (Bailly et al., 2021), larger individuals (Minns, 1995) and increased genetic diversity (Thomaz et al., 2016). Although larger rivers should continue to receive conservation attention they deserve, headwaters should be given due recognition for ecosystem services including aquatic habitat. Globally, headwater streams are often the last strongholds for native salmonids in the northern hemisphere due to habitat loss and fragmentation, invasive species and climate change (Fausch et al., 2009; Isaak et al., 2015). Additional investigations of spatial population dynamics of

headwater native inhabitants are warranted to inform aquatic conservation policy.

AUTHORS' CONTRIBUTIONS

J.T. and K.M. conceived the ideas and designed the methodology; J.T., K.M., Y.Ko., S.E., G.S., D.K., T.K., D.I. and M.N. collected the data; Y.Ka. analysed the data; J.T. and Y.Ka. led the writing of the manuscript; J.T., K.M. and Y.Ka. provided the funding and material support. All authors contributed critically to the draft and gave final approval for publication.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

The authors declare that there are no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.fn2z34tx3 (Tsuboi et al., 2022).

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How to cite this article: Tsuboi, J, Morita, K., Koseki, Y., Endo, S., Sahashi, G., Kishi, D., Kikko, T., Ishizaki, D., Nunokawa, M., & Kanno, Y. (2022). Small giants: Tributaries rescue spatially structured populations from extirpation in a highly fragmented stream. *Journal of Applied Ecology*, 59, 1997–2009. https://doi.org/10.1111/1365-2664.14200