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ARTICLE

Spatial and temporal variability of movements among sympatric salmonids in an unfragmented inland watershed

Michael J. Lance[1] | **T. David Ritter**[1] | **Alexander V. Zale**[2] | **Grant G. Grisak**[3] | **Jason A. Mullen**[3] | **Stephen J. Walsh**[4] | **Kurt C. Heim**[5] | **Robert Al-Chokhachy**[6]

[1]Montana Cooperative Fishery Research Unit, Department of Ecology, Montana State University, Bozeman, Montana, USA

[2]U.S. Geological Survey, Montana Cooperative Fishery Research Unit, Montana State University, Bozeman, Montana, USA

[3]Montana Fish, Wildlife, and Parks, Great Falls, Montana, USA

[4]Statistical Consulting and Research Services, Montana State University, Bozeman, Montana, USA

[5]Department of Ecology, Montana State University, Bozeman, Montana, USA

[6]U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, Montana, USA

Correspondence
Michael J. Lance
Email: michael.j.lance@gmail.com

Abstract

Objective: Our aim was to determine the movement patterns of three abundant salmonids—Brown Trout *Salmo trutta*, Mountain Whitefish *Prosopium williamsoni*, and Rainbow Trout *Oncorhynchus mykiss*—in the Smith River watershed of Montana.

Methods: We tagged 7172 fish with passive integrated transponder (PIT) tags, monitored their movements past 15 stationary PIT arrays over 4 years, and located tagged fish between arrays by conducting mobile surveys.

Result: Movement patterns varied seasonally, among species, and among locations. Movement was greatest in the middle portion of the watershed, which included a pristine main-stem canyon and lower reaches of major tributaries. Fish rarely left the canyon, but movement into the canyon from other regions was common. Mountain Whitefish were most likely to move, and Brown Trout were least likely to move. Most fish travelled less than 10 km, but some fish travelled over 100 km. Distinct movement patterns were not evident; rather, a continuous spectrum of movement behaviors was apparent. Movements by Mountain Whitefish and Rainbow Trout increased during their spawning periods. Movements peaked when mean daily water temperatures were between 11.3 and 17.1°C.

Conclusion: Movements were diverse and probably contributed to metapopulation dynamics, population resiliency, and species diversity. Fish movements along stream networks connect populations across diverse landscapes, and therefore, protecting and restoring stream connectivity along inland streams such as the Smith River is critical to maintaining productive fish assemblages.

KEYWORDS

Brown Trout, coldwater fishes, connectivity, fish movement, Montana, Mountain Whitefish, movement diversity, Rainbow Trout, Smith River, spatial patterns of movement, water temperature

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INTRODUCTION

Diverse movement and life history patterns can optimize resource availability, increase genetic exchange, and promote population resilience to environmental disturbances (Rieman et al. 1995; Greene et al. 2010; Schindler et al. 2010; Moore et al. 2014). Movement also facilitates increased gene flow, prevents inbreeding depression, and maintains genetic diversity (Neville et al. 2006; Hollander et al. 2014). Moreover, movements can result in recolonization of disturbed habitats and can help to expedite population recovery (Detenbeck et al. 1992). Populations connected by diverse movement patterns experience less severe declines and recover more quickly from localized environmental disturbances than do fragmented populations (Dunham and Rieman 1999; Campbell Grant et al. 2010).

Diverse movement patterns are the result of differences in how individual fish respond to biological and environmental drivers that influence the frequency, distance, and timing of movements (Chapman et al. 2011). Some differences in movement patterns are species specific. However, movements can differ within a species when individuals are confronted with stressors such as resource scarcity (Olsson et al. 2006; Berger and Gresswell 2009) or high predator density (He and Kitchell 1990; Brönmark et al. 2008). The propensity of an individual to move can change over time (Heim et al. 2019) and can be related to genetic lineage and individual personality traits (e.g., boldness), leading to a variety of intraspecific movement patterns (Klemetsen et al. 2003; Nilsson et al. 2014).

Seasonality and changes in landscape geomorphology influence the movements of fish (Lucas and Baras 2001). Changes in discharge influence fish movements by altering habitat suitability, food availability, and fluid dynamics (Schlosser 1995; Brooks et al. 2003; Uthe 2015). Extremes in temperature expose fish to conditions far from their species-specific thermal optima (Magoulick and Kobza 2003; Bear et al. 2007; Isaak et al. 2015). Habitat structure and food availability can vary along the length of a stream, as can the relative influence of local- versus watershed-scale disturbances (Vannote et al. 1980; Sedell et al. 1989; Sparks 1995). Movements across variable landscapes provide access to optimal habitats for different portions of the life cycle of stream fishes but can make species dependent upon connectivity among habitats for spawning, rearing, feeding, and holding.

Movements of stream-dwelling fishes can be obstructed or hindered by habitat alterations and instream barriers, and fragmentation of stream networks affects many taxa worldwide (Zwick 1992; Lindström et al. 2014). Human infrastructure (e.g., dams and irrigation diversions) alters channels and imposes instream barriers to fish movement (Poff et al. 2007; Schramm 2017), resulting in decreased life history and genetic diversity as well as localized extinctions (Dunham et al. 1997; Yamamoto et al. 2004; Homel et al. 2015). Descriptions of the movement behaviors of fish in unfragmented watersheds can help to contextualize the effects of barriers on fish movements in fragmented systems.

Impact statement

Fish movement was common and diverse. Movement patterns varied seasonally, among species, and among different locations in the watershed. Some fish travelled over large portions of the watershed, and many travelled further than typical daily movements.

We sought to evaluate some of the factors affecting fish movements (species, physical drivers, seasons, and landscapes) and to describe movement behaviors across an inland watershed while avoiding some common limitations of movement studies (e.g., limited spatial or temporal scopes, species, and sample sizes). Our goal was to consider how movement behaviors varied across group-specific (e.g., species and tagging location), spatial, and temporal scales. Accordingly, our specific objectives were to (1) determine whether movement varied among and within sympatric species, (2) describe how the amount of movement (movement volume, analogous to vehicular traffic volume on highways) varied spatially across a watershed, and (3) determine whether temporal changes in the frequency of movement were related to species-specific spawning periods, stream discharge, or water temperature. To meet our objectives, we documented the movement behaviors of 7172 tagged individuals belonging to three sympatric species over 4 years in the Smith River watershed of central Montana.

METHODS

Study area

The Smith River originates near White Sulphur Springs in central Montana and flows 195 km northwest to its confluence with the Missouri River near Great Falls, Montana, draining 5190 km^2 of privately and publicly owned lands (Figure 1; Figure S2.1 [available in Supplement S2 in the online version of this article]). Wetted channel width during base flows varies from about 10 m in the headwaters to over 30 m near the confluence with the Missouri River. Discharge peaks in late spring and is driven by snowmelt runoff and seasonal rains. Discharge subsequently diminishes gradually to base discharge in mid-summer, when

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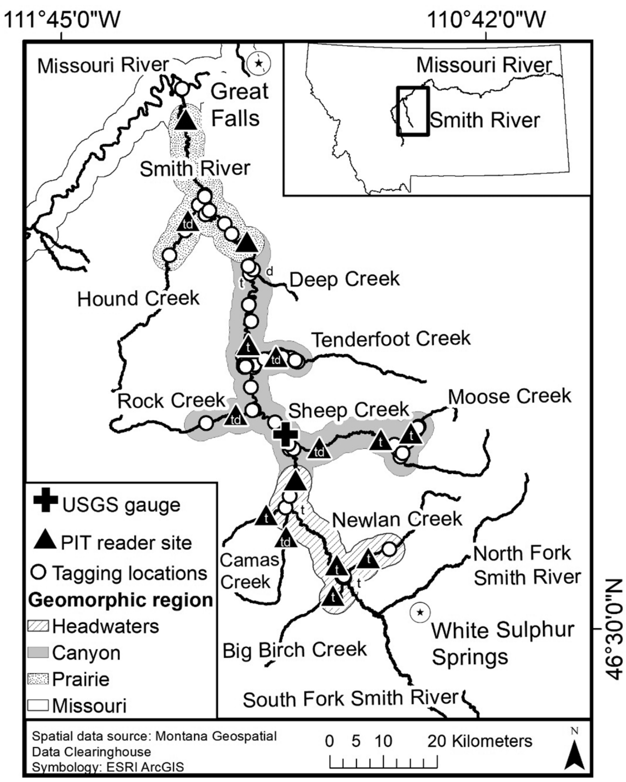

FIGURE 1 The Smith River watershed in central Montana. Shaded buffers depict areas where fish movements were monitored by stationary passive integrated transponder (PIT) arrays, mobile PIT array surveys, and physical recaptures. The shade of each buffer depicts the extent of each geomorphic region. Streams outside of the buffers are areas where movements of fish were not monitored because they were upstream of tagging locations, stationary PIT arrays, or mobile PIT tag survey reaches. Letters designate the locations of instream temperature loggers (t) and stream depth loggers (d). The plus symbol (+) denotes the location of U.S. Geological Survey (USGS) stream monitoring station 06077200.

water temperatures are warmest. Seasonal rains and the cessation of irrigation withdrawals in early autumn cause an increase in discharge. Winter discharge is low, and many tributaries freeze over.

The Smith River is naturally delineated into three geomorphic regions: the headwaters, the canyon, and the prairie (Figure 1; Table S2.1 and Figure S2.1 [available in Supplement S2 in the online version of the manuscript). The headwaters region includes all portions of the watershed upstream of the confluence with Sheep Creek, a section that is largely composed of a broad, unconstrained agricultural valley between the Castle Mountains and the Big Belt Mountains (Chase et al. 2014). Shrub–steppe is the predominant land cover, followed by forests and grasslands, and most of the land is privately owned (Lance 2019). The canyon region makes up the middle portion of the watershed, where the Smith River cuts through the Little Belt Mountains and frequently flows adjacent to cliffs higher than 50 m. Much of the region is forested, and public lands adjacent to the Smith River in the canyon geomorphic region are managed by the Smith River State Park in a semi-wilderness state to preserve the relatively unaltered condition of the landscape (Montana Department of Fish and Game 1973). The lowermost region is the prairie, which is less constrained than the canyon region, and the river often flows through agricultural lands.

The fish assemblage of the Smith River watershed consists of both native and nonnative species. Salmonids that are present include the Mountain Whitefish *Prosopium williamsoni*, Brown Trout *Salmo trutta*, Rainbow Trout *Oncorhynchus mykiss*, Westslope Cutthroat Trout *O. lewisi* (mainly isolated in small tributaries), Rainbow Trout × Westslope Cutthroat Trout hybrids, and Brook Trout *Salvelinus fontinalis*. Three sucker species are present: the White Sucker *Catostomus commersonii*, Longnose Sucker *Catostomus catostomus*, and Plains Sucker *Pantosteus jordani*. Other fishes include the Burbot *Lota lota*, Stonecat *Noturus flavus*, Rocky Mountain Sculpin *Cottus bondi*, and Longnose Dace *Rhinichthys cataractae*. Arctic Grayling *Thymallus arcticus* were native to the Smith River but were extirpated from the watershed in the mid-20th century (Montana Department of Fish and Game 1973). Brown, Rainbow, and Brook trout are not native to the Smith River and were intentionally introduced during the 20th century to create recreational angling opportunities (Montana Fish, Wildlife and Parks 2013).

Analyses of movement patterns were restricted to the three most abundant and recreationally valuable species in the watershed: Rainbow Trout, Mountain Whitefish, and Brown Trout (Table 1). Brown and Rainbow trout have formed abundant, self-sustaining populations in the Smith River. Mountain Whitefish are ecologically important, can make up large portions of fish biomass, and are frequently among the most abundant native fish in western U.S. rivers (Lance and Baxter 2011; Meyer et al. 2011). Westslope Cutthroat Trout occurred infrequently, and Brook Trout were found almost exclusively in tributaries, where they rarely moved (Ritter 2015); we therefore excluded these species. The number of tagged nonsalmonids was not sufficient for effective analysis (Table 1).

Discharge and water temperature

We characterized seasonal environmental conditions to understand relationships among discharge, water temperature, and fish movements. To characterize seasonal trends in discharge and water temperature, we used U.S. Geological Survey (USGS) data recorded every 15 min at

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TABLE 1 Numbers of individuals of each fish species tagged in the main-stem Smith River (Smith) and tributary (Trib) locations in each geomorphic region of the Smith River watershed, Montana.

Species	Headwaters		Canyon		Prairie		Total
	Smith	Trib	Smith	Trib	Smith	Trib	
Rainbow Trout	85	7	682	2465	54	24	3317
Mountain Whitefish	425	5	616	1077	212	11	2346
Brown Trout	275	71	401	323	72	367	1509
Brook Trout	15	44	0	133	0	0	192
White Sucker	30	48	18	13	10	48	167
Longnose Sucker	6	0	21	1	9	19	56
Burbot	5	8	19	0	0	0	32
Westslope Cutthroat Trout	2	0	2	0	1	0	5
Mountain Sucker	0	0	1	0	0	0	1

the Smith River gauging station that was located 3.4 km downstream of the confluence with Sheep Creek (station number 06077200; USGS 2018). We also monitored stream depth and water temperature at sites throughout the watershed, most of which were associated with stationary passive integrated transponder (PIT) arrays (Figure 1). We used our observations to model brief gaps in the USGS record; gaps were most common during late autumn and winter, when discharge and water temperature were stabilized by subfreezing air temperatures. Stream depth was recorded every 2 h with water depth loggers (TruTrack WT-HR Water Height Logger), and submerged temperature loggers recorded hourly water temperatures (Onset Hobo Pendant Logger). Water temperatures at 16 of 19 remote temperature monitoring sites were highly correlated with the water temperature at the USGS site (Pearson's product-moment correlation coefficient [Pearson's r] $\geq$0.95), and water depths at five of the seven remote water depth monitoring sites were correlated with discharge at the USGS site (Pearson's $r \geq 0.70$). Data from the remaining sites were also positively correlated with data from the USGS site but were influenced by groundwater or short periods of record (Lance 2019). Among sites, mean daily water temperatures varied from 1.6°C to 9.2°C (mean difference among sites = 5.2°C). The coolest sites were in tributaries, whereas the warmest sites were along the main-stem Smith River.

Monitoring fish movements

Movements of tagged fish were monitored at 15 stationary PIT arrays from July 1, 2014, to May 31, 2018 (Figure 1). Stationary arrays were located on all major tributaries near their confluences with the Smith River, along the Smith River near geomorphic region boundaries, and in the upper Sheep Creek watershed. The exact locations of stationary arrays were determined by land access; therefore, some array locations coincided with tagging locations. The median length of stream between adjacent stationary arrays in the Smith River watershed was 23 km (25th percentile = 9 km; 75th percentile = 30 km), and the maximum was 44 km. Montana Fish, Wildlife and Parks (MFWP) operated eight stationary arrays in the adjacent Missouri, Dearborn, and Sun River watersheds, which identified tagged fish that left the Smith River watershed. Few fish were observed leaving the Smith River watershed; therefore, information about fish that did so was used mainly to understand the proportion of fish that made movements out of the watershed and to describe those movement behaviors.

Each stationary PIT array consisted of a long-range half-duplex (HDX) reader (Oregon RFID) connected to instream antennas and powered by 12-V DC, supplied either by solar cells or by 120-V AC converters. Antennas spanned the stream channel across riffles or glides, and each consisted of a single loop of multi-strand, insulated copper wire anchored to the stream bottom in a “flat bed” orientation (Armstrong et al. 1996; Ritter 2015). Exact antenna construction varied by location, but, generally, small antennas placed where channel widths were less than 14 m were constructed with 8-gauge speaker wire (3.3-mm diameter); medium-sized antennas spanning channels with a width of 14–25 m were constructed with 4-gauge power supply cable (5.2-mm diameter); and large antennas spanning channels wider than 25 m were constructed with 2-gauge welding cable (6.5-mm diameter; Tranquilli 2007). Readers were placed in weatherproof boxes that were adjacent to the stream but out of the active flood channel. The location of each stationary array was used for georeferencing detections of fish. Data were retrieved from stationary arrays during regular site visits or through satellite communicators that were accessed

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through a website interface (Rockfish; https://www.ritterdesigns.com). Detections recorded at stationary arrays were filtered to remove multiple detections of the same fish less than 6 h apart at the same antenna.

We used mobile PIT arrays to locate tagged fish between and above stationary array sites. Mobile PIT arrays consisted of Oregon RFID long-range HDX readers powered by 12- or 18-V batteries with single antennas affixed to a raft, kayak, or handheld pole (Hill et al. 2006; McKinstry and Mackinnon 2011). Boat-mounted antennas consisted of two loops of 8- or 4-gauge wire placed in bailing channels of rafts or floated (in "pool noodles") outside of kayaks. Hand-held pole antennas consisted of five wraps of 12-gauge wire within a circular polyvinyl chloride (PVC) housing (~0.45 m in diameter) mounted to the end of a PVC pole (~1.5 m in length). A handheld Global Positioning System (GPS) unit ran a continuous track log during mobile surveys to provide a GPS location for detected tags. Mobile PIT tag surveys were completed along the Smith River from Big Birch Creek to Eden Bridge (139 km) and along tributaries where we had access (Big Birch, Camas, Sheep, Moose, and Rock creeks). Seventeen mobile surveys of the Smith River from Sheep Creek to Hound Creek were conducted from 2015 to 2017 during all seasons except winter. Mobile surveys were conducted once at all other sites during the summer of 2017. Attempts were made, when possible, to discern whether tags were still in live fish by actively disturbing the area where the tag was detected (Bowerman and Budy 2012). Observations of tags that were no longer in live fish were used in our analyses of movement behaviors as the final known location for a given fish.

Over the course of the study, we attempted to capture and mark 50–200 fish at 5–10-km intervals in all three geomorphic regions as well as in all major tributaries (Figure 1; Table 1). However, some of the intervals in the headwaters and the prairie exceeded 15 km because we were constrained to sites where we had access. The exact numbers of fish tagged were influenced by the densities and capture rates at each location. Most sites where fish were captured and tagged were visited only once. However, we visited a limited number of sites multiple times to increase sample sizes or to mark fish as part of an associated study of predation by American white pelicans *Pelecanus erythrorhynchos*. Most fish were tagged in 2014, but smaller numbers of fish were tagged from 2016 to 2017 (Table S2.2). From 2010 through 2014, some fish were tagged in Tenderfoot Creek (a tributary in the canyon geomorphic region; Figure 1; Ritter 2015; Ritter et al. 2020) and adjacent portions of the Smith River, and observations of those fish after 2014 were incorporated into our study.

Fish were collected with boat, barge, and backpack electrofishers; anesthetized with Aqui-S 20E (10–20 mg/L, titrated to efficacy; Aqui-S New Zealand Ltd); measured for total length (TL; mm); and tagged with HDX PIT tags. The date when a fish was captured and tagged was recorded as the first observation of each fish, and the time at large for each fish was calculated as the number of days between when a fish was tagged and when it was last observed alive. The PIT tags were implanted surgically or using an implanter syringe into the abdominal cavity of each captured fish at a location that was 5–20 mm anterior to the right pelvic fin (Ritter 2015; Uthe et al. 2016). Fish larger than 150 mm TL were tagged with either 23- or 32-mm HDX PIT tags, and fish smaller than 150 mm TL were tagged with 12-mm HDX PIT tags (Biomark MK7 implanter; Biomark 2015). Fish smaller than 55 mm were not tagged. The majority of fish captured were larger than 150 mm (Figure S2.2), corresponding to the size at which stream-dwelling Brown Trout, Mountain Whitefish, and Rainbow Trout are subadults or adults (Figure S2.2; Brown 1971).

General data analysis

The statistical program R was used for analyzing trends in fish movement, plotting relationships, and constructing tables of results (R Core Team 2017). Packages that were not part of the standard R download are listed with the corresponding analyses. We used Esri ArcMap version 10.4.1 for spatial analyses and construction of maps (Esri 2015).

Detection efficiency

We estimated detection efficiency and simulated movements of missed fish to correct for bias associated with variable detection efficiency of our stationary PIT arrays; details are provided in the supplemental materials (Supplement S1). We determined that tag size did not influence our conclusions about fish movements in the Smith River watershed because few fish were tagged with 12-mm tags (213 of 7172 tagged fish) and no difference existed in the detection efficiency of 23- and 32-mm tags. Therefore, we did not attempt to correct for bias associated with variable detection efficiency arising from different tag sizes implanted in fish. We estimated in situ detection efficiency at all of our stationary PIT arrays (Zydlewski et al. 2006; Connolly et al. 2008) and then expanded our estimates of fish movement past each array. We estimated array-specific detection efficiency during

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array operation by using our entire fish movement data set, including release locations, mobile detections, and stationary array detections (Zydlewski et al. 2006).

We simulated movements of fish that were not detected at each array by duplicating randomly selected detections. We assumed that the detected fish were representative of the fish that were not detected. The number of detections simulated was equal to the estimated number of tagged fish that were not detected when they passed the array during periods when the array was operational. We did not attempt to estimate detection efficiencies of mobile arrays, which were probably influenced by water depth, survey speed, battery voltage, and surveyor bias; therefore, estimates of individual movements based on mobile detections are likely conservative.

Analysis of group-specific patterns of fish movement

Fish were grouped by species, the geomorphic region where they were tagged, and whether they were tagged in the main-stem Smith River or a tributary of the Smith River. We compared the proportions of tagged fish in these groups that moved after they were released (yes or no), the proportions of fish that occupied multiple geomorphic regions, and the proportions of fish that occupied both the Smith River and at least one tributary. We defined a tagged fish as having moved if it was detected at two or more locations that were at least 0.5 km apart, including the initial capture location; daily home ranges of stream-dwelling salmonids often are less than 500 m (Young et al. 1997; Bunnell et al. 1998; Young 1999; Roni 2019). The proportions of tagged fish that moved were calculated by dividing the numbers of tagged fish that moved by the total numbers of tagged fish.

We determined the proportions of fish that moved among the Smith River and its tributaries and the proportions of fish that moved among major geomorphic regions to understand the ecological significance of movements among these regions of the watershed and to help inform management decisions. The proportions of fish that occupied multiple geomorphic regions were calculated by dividing the number of tagged fish that left, for any amount of time, the geomorphic region in which they were tagged by the total number of fish tagged in the same geomorphic region. The proportions of fish that occupied the Smith River and at least one tributary were calculated by dividing the number of tagged fish that occupied the Smith River and a tributary by the total number of tagged fish. The number of fish that occupied the Smith River and a tributary included fish from tributary tagging locations that later occupied the Smith River and fish tagged in the Smith River that later occupied tributaries. Differences in the proportions of fish that moved, occupied multiple geomorphic regions, or occupied the Smith River and a tributary were considered significant if 95% confidence intervals did not overlap. The 95% confidence intervals for proportions were calculated using the binom.confint function in the R package binom (Dorai-Raj 2014), which accounted for the nonparametric nature of binomial confidence intervals.

The effects of species and tagging location on the proportions of fish that moved at least 0.5 km were estimated with generalized linear models having a quasi-binomial distribution. Independent variables were species, geomorphic regions in which the fish were tagged, and whether fish were tagged in the main-stem Smith River or a tributary. The dependent variable was the proportion of fish within each group that moved at least 0.5 km. We fitted a full model that included every combination of two-way interactions among the independent variables. We then performed a reverse stepwise model selection process using the drop1 function in R and an *F*-test (Faraway 2016), which helped to identify predictors (or interaction terms among predictors) that were not useful for explaining variation in the data. The resulting model contained all three primary independent variables and an interaction term between the species variable and the variable representing whether fish were tagged in the main-stem Smith River or a tributary. Diagnostic plots were examined to ensure proper model fit. The effects of tagging location and species were considered significant if p-values of predicted coefficients were less than or equal to 0.05.

Analysis of spatial patterns of fish movement

We mapped travel routes of fish along the stream network using Network Analyst tools in ArcGIS to delineate the minimum portion of stream network traversed by each fish that was detected at one or more locations after it was initially captured (Esri 2015). The minimum length of stream network traversed (hereafter, referred to as "length of stream traversed") was calculated from the shape length of the travel route of each tagged fish, discounting multiple passes over the same sections of the stream network. The frequencies of the lengths of stream traversed by tagged fish were plotted by species and tagging location.

We overlaid travel routes of tagged fish to determine the volume of fish movement within and among species spatially along the stream network and to assess the relative importance of spatial connectivity for the fish. Each travel route was assigned a weighted individual value (WIV):

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$$\mathrm{WIV} = \left(\frac{1}{n_{\text{tag group}}} \right),$$

where $n_{\text{tag group}}$ is the number of fish of the same species tagged in the same 15-km section of the Smith River or a tributary.

Assigning a WIV to each travel route helped to account for bias associated with spatially uneven tag distribution. A tag group consisted of fish of the same species that were tagged at any time during the study within a specific tributary or main-stem section (e.g., all Rainbow Trout that were tagged in the Smith River in the section upstream of Rock Creek). Stream sections were created by dividing the Smith River and tributaries into 15-km segments using the ArcGIS Points Along Lines tool (Esri 2015), which produced equal-sized sections except for sections at the ends of stream features. The WIV of passing fish was summed to provide a metric of the volume of fish movement along the stream network. This process was repeated for each species and then again with all species collectively to determine the spatial patterns of movement volume within species and across the entire fish assemblage.

Analysis of temporal patterns of fish movement

Weekly counts of tagged fish detected as passing stationary PIT arrays were plotted to assess seasonal trends in movement. Plotted data were restricted to observations of tagged fish during 2015–2017 because movements were not monitored for the entire year in 2014 and 2018. We demarcated local species-specific spawning periods (Ritter 2015) and summer thermal stress periods (Ritter et al. 2020) to examine associated changes in the frequency of movements.

We evaluated the influence of water temperature, discharge, and species-specific spawn timing on temporal changes in the numbers of fish detected as moving past stationary array sites. Separate statistical models were created for Brown Trout, Mountain Whitefish, and Rainbow Trout; models included mean weekly water temperature, mean weekly discharge, species-specific spawn timing, and year as independent variables. The dependent variable was the weekly count of individual tagged fish detected at all stationary array sites in the Smith River watershed. Multiple detections of the same fish in the same week at any location across the watershed were removed so that no single fish was counted more than once per week. Both mean weekly water temperature and mean weekly discharge recorded at the USGS site on the Smith River downstream of Sheep Creek were calculated. Spawning periods were defined based on the timing of spawning movements in Tenderfoot Creek in 2012 and 2013 (Ritter 2015): October 1–November 10 for Brown Trout and Mountain Whitefish and April 1–May 31 for Rainbow Trout.

The tsglm function from the R package tscount, which fits generalized linear models with a negative binomial distribution and an autoregressive correlation structure, was used to model the timing of fish movements for each species (Liboschik et al. 2017). The strength of the autocorrelative structure of the data and the subsequent evaluation of appropriate model structure to accommodate observed autocorrelation were evaluated graphically with plots of the autocorrelative function of Pearson's residuals and periodogram plots of Pearson's residuals. Based on observed autocorrelative trends, time-specific predictors were added that incorporated conditional means of the counts of fish movement for the previous 2 weeks. Additionally, observed movements in the previous 1 week and the previous 2 weeks were included as part of the autocorrelative structure of the models. Because the movement patterns of Rainbow Trout had stronger serial autocorrelation among observations than the patterns of Brown Trout and Mountain Whitefish, observed movements in the previous 3 weeks and in the previous 12 months were included in Rainbow Trout models. Model selection was performed using quasi-likelihood Akaike's information criterion scores. Candidate models included linear and quadratic predictors of discharge and water temperature. Independent variables in the best supported models were considered significant predictors of fish movement if the 95% confidence intervals of their estimated coefficients did not overlap zero.

Effect sizes across observed values of discharge and temperature were calculated from the estimated coefficients for each and were plotted to ascertain their influence on the multiplicative change in the number of unique fish passing stationary arrays when water temperatures were near 0°C or when hypothetical discharge was 0 m^3/s. The value at which each predictor had the largest effect on movement was calculated using the optimize function in R. Model fit was checked with diagnostic plots (Figures S2.3–S2.5) and by plotting the square root of fitted values against the square root of observed values (Figures S2.6–S2.8).

RESULTS

General patterns in fish movement without simulated movements

About 52% of fish tagged in the Smith River watershed (3718 of 7172 fish) were detected again after they were released; 40% (2838 of 7172 fish) were detected at stationary PIT arrays. The median number of unique detections of

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individual fish at arrays was 3 (25th percentile = 2; 75th percentile = 7), with some fish detected over 50 times. We found 1607 PIT tags (22.4% of tags deployed) during mobile surveys, of which 332 tags were recovered at pelican nesting colonies (4.6% of all tags deployed; 88 Brown Trout, 176 Mountain Whitefish, and 68 Rainbow Trout). Tagged fish were detected up to 12 times during mobile surveys, but the median number of mobile detections was 1 detection/fish (25th percentile = 1; 75th percentile = 2).

The median time at large was 351 days (Table 2), with little variation among species. The maximum time at large was 2358 days (6.5 years; observed for a Mountain Whitefish); however, most fish were at large between 90 and 500 days. The maximum time between successive relocations (excluding relocations during mobile surveys) varied from less than 1 day to over 3.5 years but was commonly about 6, 12, or 18 months (Lance 2019); of the periods between successive relocations, 58–79% were 6 months or longer and 14–34% were greater than 1 year.

Group-specific patterns of fish movement

Of the 7172 fish tagged in the Smith River watershed, 3505 (49%) moved 0.5 km or more after they were released (2701 observed movements; 804 simulated movements). Most (66%; 1864) of the 2822 fish tagged in the main-stem Smith River moved after they were released. Depending on the geomorphic region in which they were tagged, about 50–75% of Mountain Whitefish and Rainbow Trout moved (Figure 2, left panel), whereas smaller proportions of Brown Trout moved (38–55%). Fish that were tagged in Smith River tributaries moved less than fish that were tagged in the main stem (1641 [38%] of 4350 fish tagged in tributaries moved ≥0.5 km) regardless of the geomorphic region where they were tagged (Figure 2, right panel; Table 3); the difference was greatest among Brown and Rainbow trout. Mountain Whitefish that were tagged in tributaries also moved less than those that were tagged in the Smith River, but the difference was less pronounced than among trout.

The proportions of tagged fish that moved between the Smith River and at least one tributary varied by species and tagging location (Figure 3, top panel). Among fish that were tagged in tributaries, a majority of Mountain Whitefish that were tagged in the canyon region and almost half of Brown Trout that were tagged in the headwaters region moved into the Smith River. Less than 25% of all other groups tagged in tributaries out-migrated to the Smith River. Among fish that were tagged in the

TABLE 2 Percentiles of the number of days at large between successive handling or detection events for fish that were tagged in the Smith River watershed.

Percentile of observation	All fish	Brown Trout	Mountain Whitefish	Rainbow Trout
25th	180	90	108	198
50th	351	322	349	364
75th	633	570	739	592

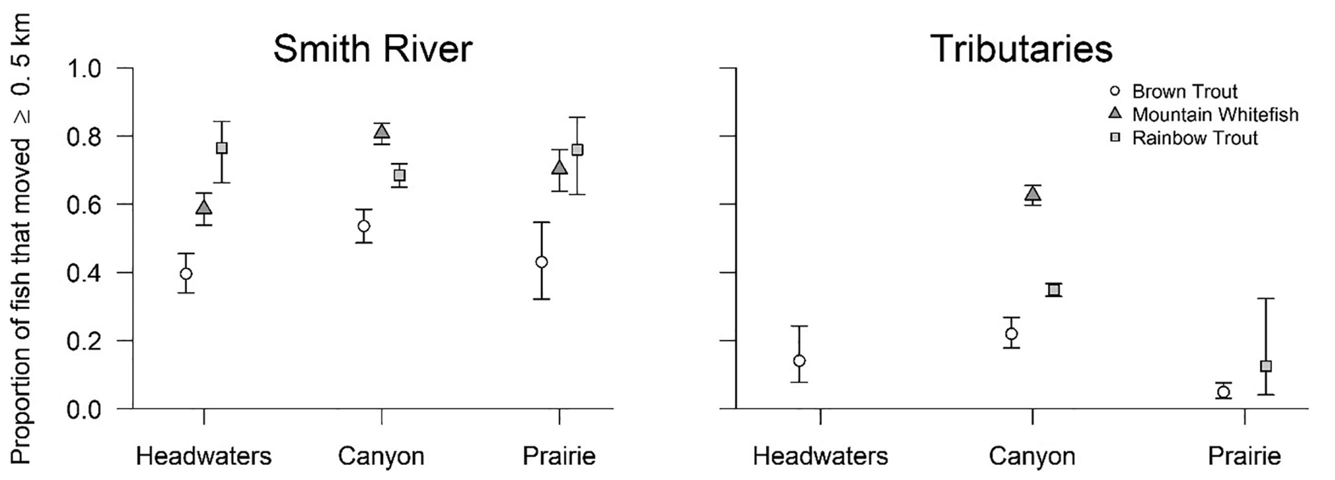

FIGURE 2 Proportions of Brown Trout, Mountain Whitefish, and Rainbow Trout that moved at least 0.5 km after tagging and release. The left panel represents fish that were tagged in the main-stem Smith River, and the right panel represents fish that were tagged in tributaries of the Smith River. Both panels are grouped by the geomorphic regions in which fish were tagged. Values for groups represented by fewer than 20 fish are omitted (Table 1). Error bars represent 95% confidence intervals.

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TABLE 3 Coefficient estimates, standard errors (SEs), and goodness-of-fit statistics for the most supported binomial model evaluating differences in the proportions of fish that moved at least 0.5 km after tagging and release. Coefficient estimates and SEs are on the logit scale. The baseline group against which all comparisons were made was Brown Trout in the Smith River (dispersion parameter = 5.174; deviance = 55.948; null deviance = 1195.770; difference between deviance and null deviance = 1139.823).

Model term	Estimate	SE	*t*-value	*p*-value
(Intercept)	0.203	0.188	1.078	0.307
Mountain Whitefish	0.983	0.222	4.438	0.001
Rainbow Trout	0.591	0.245	2.418	0.036
Tributary	−1.812	0.311	−5.822	<0.001
Headwaters	−0.699	0.207	−3.376	0.007
Prairie	−0.588	0.243	−2.424	0.036
Mountain Whitefish: tributary	1.116	0.381	2.928	0.015
Rainbow Trout: tributary	0.354	0.368	0.962	0.359

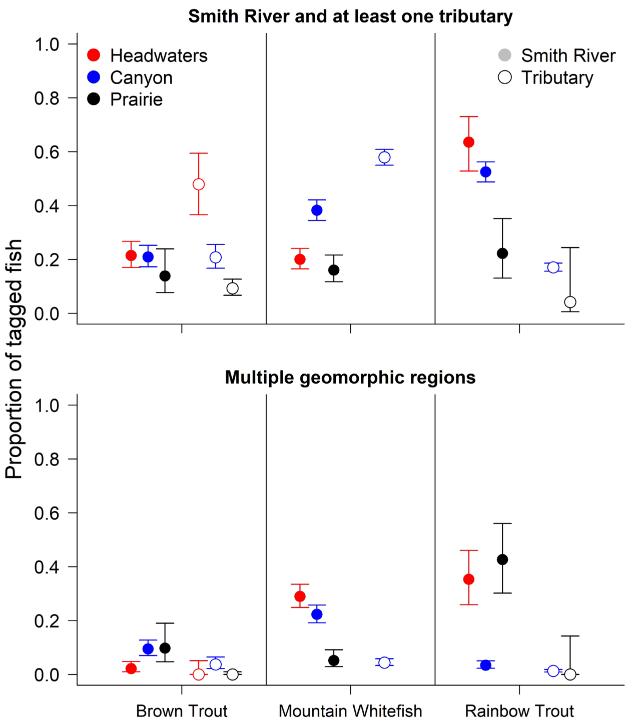

FIGURE 3 Proportions of tagged fish that occupied the Smith River and at least one tributary (top panel) and the proportions of fish that occupied multiple geomorphic regions (bottom panel). Symbol colors depict the geomorphic region in which fish were tagged. Solid symbols represent fish that were tagged in the Smith River, and hollow symbols represent fish that were tagged in tributaries. Values for groups represented by fewer than 20 fish are omitted. Error bars are 95% confidence limits.

Smith River, movement into tributaries was common for Rainbow Trout that were tagged in the headwaters and canyon regions and for Mountain Whitefish that were tagged in the canyon region. Interchange among the Smith River and tributary habitats was most common among Rainbow Trout tagged in the Smith River as they moved into tributaries, presumably to spawn. Mountain Whitefish frequently moved into tributaries during the autumn, but many Mountain Whitefish also moved into the lower reaches of tributaries in late spring.

The proportions of fish that occupied multiple geomorphic regions also varied by species and tagging location (Figure 3, bottom panel). Across all three geomorphic regions, fewer than 10% of fish that were tagged in tributaries occupied multiple geomorphic regions. Among fish that were tagged in the canyon region, 22% of Mountain Whitefish moved among multiple geomorphic regions, whereas less than 10% of Brown Trout or Rainbow Trout did. Among individuals that were tagged in the main stem within the headwaters or prairie geomorphic region, 35–43% of Rainbow Trout, 5–29% of Mountain Whitefish, and 10% or fewer Brown Trout occupied multiple geomorphic regions.

Spatial patterns of fish movement

Movements by fish linked distant parts of the watershed. Tagged fish moved across 426 km of stream network, including the upper regions of tributaries and into the adjacent Missouri, Dearborn, and Sun River watersheds. The minimum length of stream traversed by tagged individuals varied by species and based on whether fish were tagged in the Smith River or in a tributary (Figure 4). Most fish moved over relatively short distances, and decreasing numbers of fish traveled farther. Bimodal movement patterns (e.g., mobile versus stationary or migratory versus resident) were not evident for any species in the Smith River watershed. Depending on the species, 28–52% of fish tagged in the Smith River traversed 5 km or more of the stream network and 6–15% traversed 30 km or more. Smaller proportions of fish tagged in tributaries traversed 5 km or more of the stream network (7–30%) compared to

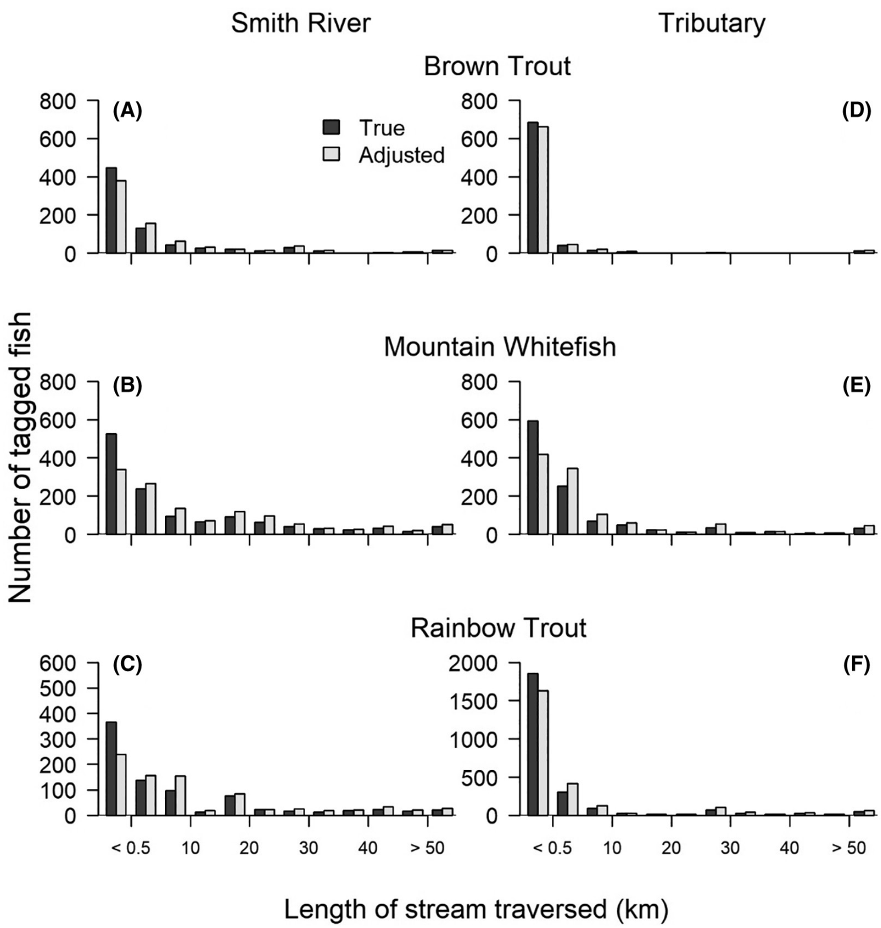

FIGURE 4 Frequency distributions of the numbers of fish that traversed minimum specified lengths of stream network (km) for fish that were (A)–(C) tagged in the main-stem Smith River and (D)–(F) tagged in tributaries of the Smith River. Dark-gray bars are the true frequencies of fish traversing specified lengths of stream, and light-gray bars are the frequencies adjusted to account for imperfect detection efficiencies of stationary passive integrated transponder arrays. Bars are grouped into 5-km bins except for two groups with separate bins on the ends of the *x*-axis: fish that traveled less than 0.5 km and fish that traveled more than 50 km.

fish tagged in the Smith River. Although rare, some individuals of all three species traversed over 100 km of stream network (Lance 2019). A Mountain Whitefish tagged in the Smith River near Tenderfoot Creek traversed the greatest stream length (182 km); this individual left the Smith River in 2015, traveled through the Missouri River to the Sun River, and then returned to the Smith River in 2016. This Mountain Whitefish made similar movements again the next year, suggesting that it traveled about 300 km annually.

The volume of movements was greatest along the main-stem Smith River in the canyon geomorphic region and in the lower reaches of Sheep and Tenderfoot creeks (Figure 5). The volume of Brown Trout movement was relatively uniform across the watershed and generally less than the volume of movement by Mountain Whitefish and Rainbow Trout. The greatest volume of movement by Mountain Whitefish occurred in the Smith River from Deep Creek in the canyon to Camas Creek in the headwaters, whereas the greatest volume of Rainbow Trout movement was within the canyon from Deep Creek to Tenderfoot Creek.

Temporal patterns of fish movement

Periods of increased fish movements occurred from spring through autumn (Figure 6). Movements of all three species were strongly associated with the mean weekly water temperatures of the Smith River, and the best supported models for all three species included a positive linear term and a negative quadratic term (Tables 4 and 5). Absent the influence of spawn timing and including both the linear and quadratic predictor terms, the movements of Brown Trout, Mountain Whitefish, and Rainbow Trout were greatest when the mean weekly water temperatures of the Smith River at the USGS gauge downstream of Sheep Creek were 17.1, 14.6, and 11.3°C, respectively (Figure 7). Discharge was not a predictor in the best supported models for any

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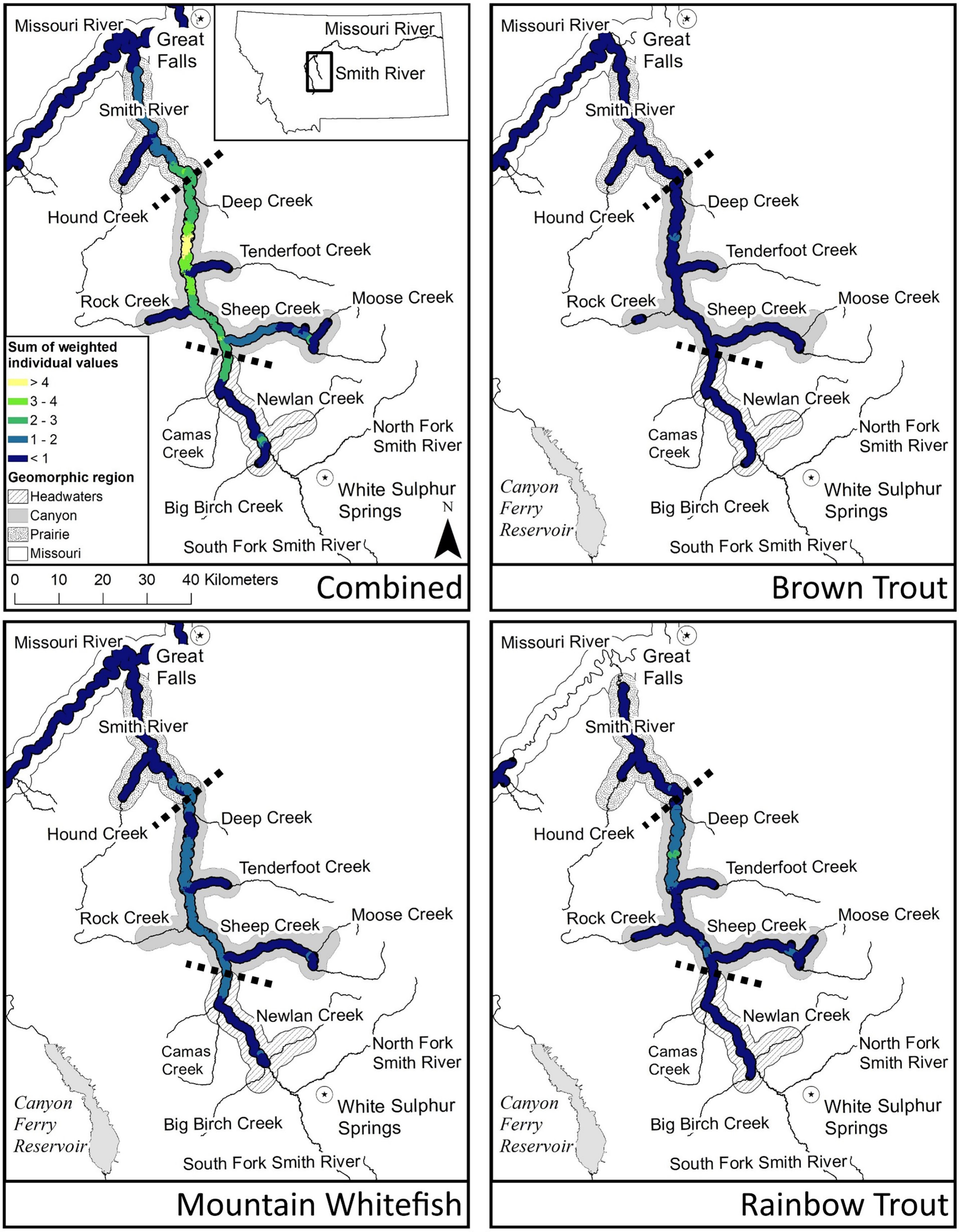

FIGURE 5 Movement volumes for tagged Brown Trout, Mountain Whitefish, and Rainbow Trout in the Smith River watershed. Each panel depicts the volume of movement as the sum of weighted individual values for fish that passed along the stream network. The top left panel depicts the movement volume for all three species combined, and the other three panels depict the volumes of movement for each species individually. Thick dashed lines across the Smith River represent the locations of the breakpoints between the three major geomorphic regions. Thin black lines denote stream segments where movement was not observed, and thin black lines outside of the geomorphic region buffers indicate areas above passive integrated transponder arrays or tagging locations, where observations of tagged fish could not be made.

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of the three species (Table 5). Species-specific spawn timing was associated with increases in movements of Mountain Whitefish but was less strongly associated with movements of Brown Trout or Rainbow Trout.

Confounding between water temperature and discharge was not present (Figure S2.9). We assumed that our inferences were robust to confounding between the timing of spawning and discharge or water temperature because (1) each model included counts of fish movement during and outside of spawning periods and (2) the ranges of discharge levels and water temperatures observed during the spawning seasons overlapped with conditions observed outside of the spawning periods. An exception was the relationship between the spawn timing of Rainbow Trout and discharge, as spawning occurred at the highest levels of discharge (Figure S2.10).

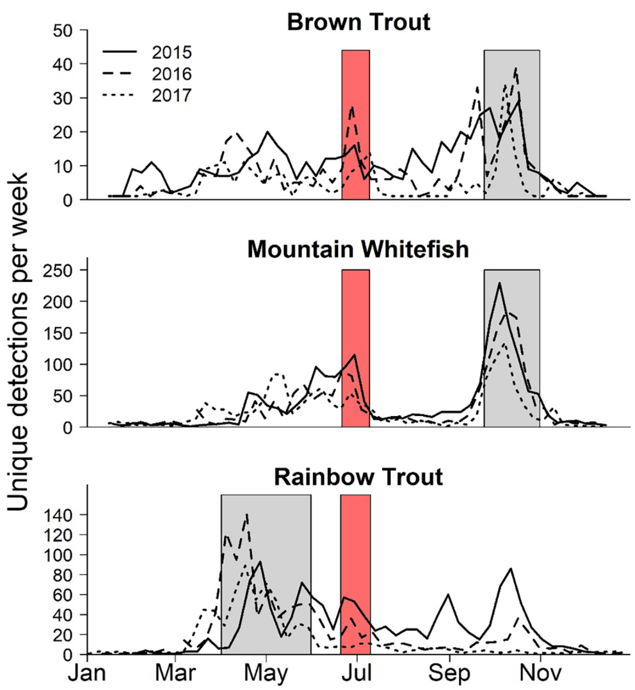

FIGURE 6 Observed weekly counts of unique tagged fish detected by stationary passive integrated transponder arrays in the Smith River watershed, 2015–2017. Gray shaded boxes indicate species-specific spawning periods. Red shaded boxes indicate periods when Smith River discharge decreased to base levels and water temperatures increased to peaks.

TABLE 5 Model structure and associated quasi-likelihood Akaike's information criterion (QAIC) values for the five best supported models for each species (ΔQAIC = difference in QAIC between the given model and the best performing model for a species).

Species	Model	QAIC	ΔQAIC
Brown Trout	Temperature + temperature^2 + spawn timing	−1037.18	0.00
	Temperature + temperature^2 + discharge + spawn timing + year	863.38	1900.56
	Temperature + discharge	1861.81	2898.99
	Temperature	1879.58	2916.77
	Temperature + discharge^2	1924.81	2961.99
Mountain Whitefish	Temperature + temperature^2 + spawn timing	3840.74	0.00
	Temperature + temperature^2 + discharge^2 + spawn timing	3873.18	32.44
	Temperature + temperature^2 + discharge + spawn timing	3878.73	37.99
	Temperature + temperature^2 + discharge + discharge^2 + spawn timing	3897.82	57.08
	Temperature + discharge + discharge^2 + spawn timing	3935.82	95.09
Rainbow Trout	Temperature + temperature^2	2525.47	0.00
	Temperature + temperature^2 + spawn timing	2536.16	10.69
	Temperature + temperature^2 + discharge^2 + spawn timing	2555.38	29.91
	Temperature + temperature^2 + year	2594.52	69.05
	Temperature + temperature^2 + discharge + spawn timing	2638.23	112.76

TABLE 4 Estimated coefficients and standard errors (SEs) of the predictors of weekly counts of movements by passive integrated transponder-tagged fish in the Smith River. Cells containing an en dash (–) are predictors that were not supported by model selection and therefore were not included in the final models. Predictors that were not supported for any species were omitted from the table. Estimated coefficients are on the natural log scale, with 95% confidence limits listed in parentheses. Predictors with confidence limits that did not overlap zero were considered strongly supported.

	Brown Trout		Mountain Whitefish		Rainbow Trout	
Predictor	Estimate	SE	Estimate	SE	Estimate	SE
Temperature	0.1250 (0.0487, 0.2013)	0.0389	0.1561 (0.0471, 0.2651)	0.0556	0.0938 (0.0321, 0.1554)	0.0315
Temperature^2	−0.0036 (−0.0075, 0.0002)	0.0019	−0.0053 (−0.0101, −0.0006)	0.0024	−0.0042 (−0.0071, −0.0012)	0.0015
Spawn timing	0.2753 (−0.2302, 0.7808)	0.2579	0.9173 (0.2619, 1.5727)	0.3344	–	–

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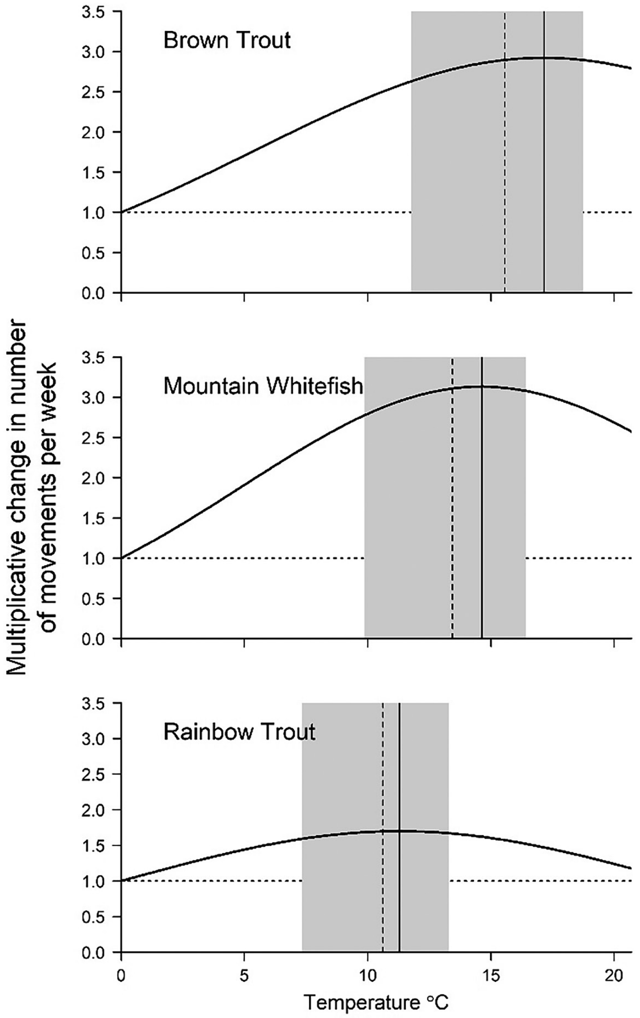

FIGURE 7 Predicted effects of mean weekly temperatures on the magnitude of fish movement in the Smith River. The *y*-axis represents the estimated multiplicative change in the number of tagged fish that were detected as moving past stationary array sites relative to when the water temperature was near 0°C. The *x*-axis represents the weekly mean water temperature of the Smith River at the U.S. Geological Survey (USGS) stream monitoring station downstream of Sheep Creek. Solid vertical black lines represent the USGS station water temperatures at which the effect of temperature on movement was greatest for each species. The vertical dashed lines denote the calculated mean water temperatures of the entire watershed, and the gray shaded areas are the ranges of water temperatures across the watershed when USGS station water temperatures were equal to the temperatures depicted by the solid black lines. The dashed horizontal line is equal to the magnitude of fish movement at 0°C.

Thermoregulatory movements associated with extreme warm water temperatures

Fish from the Smith River moved into Sheep Creek in 2017, apparently in response to the single instance when water temperatures in the main stem exceeded 26.0°C for over 4h (maximum=27.4°C, duration=4.75h; Figure S2.11). No tagged fish had been observed at the lower Sheep Creek array for 4days prior to the period of elevated water temperatures, but 24 tagged Brown Trout, Mountain Whitefish, and Rainbow Trout passed the lower Sheep Creek array in the 2days after temperatures exceeded 26.0°C in the main stem and were up to 2.1°C warmer than the temperatures in lower Sheep Creek. This was the only instance in which we observed a pulse of fish movement into a tributary concurrent with an acute increase in water temperature of the main stem.

DISCUSSION

Some fish in the Smith River watershed moved substantial distances, and movement behaviors varied among species, seasons, and landscapes. Mountain Whitefish moved the most, whereas Brown Trout moved the least. The proportion of fish that moved after being tagged varied relative to where the fish were originally captured, suggesting that some areas of the watershed had more appropriate habitats than others for certain portions of their life cycles. Species-specific spawning periods and periods with moderate water temperatures were associated with increased movements of fish and indicated times of year in which connectivity is probably most critical for maintaining life history diversity. The volume of fish movement was greatest in the canyon as well as near major creek mouth junctions, indicating that fragmentation in these areas could potentially have negative effects on populations.

Group-specific patterns of fish movement

Tributary use varied by species and life stage. Brown and Rainbow trout that were tagged in tributaries generally moved less often and over shorter distances than fish that were tagged in the Smith River, perhaps because spawning substrates and rearing habitats in tributaries are typically more common than and superior to those in river main stems (Dunham and Rieman 1999; Quinn 2005). Despite the observed continuum of fish movement behaviors, many Brown and Rainbow trout in tributaries expressed what traditionally have been referred to as stationary or resident life history patterns. Conversely, Mountain Whitefish appeared to be more dependent on main-stem habitats, which perhaps provide access to food and habitat conditions that are limited in tributary streams (Schlosser 1995; Chapman et al. 2014). Most Mountain Whitefish that were tagged in tributaries used the Smith River during at least some portion of their lives, and many Mountain Whitefish never left main-stem habitats; others

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temporarily moved into tributaries, presumably to access feeding, refuge, or spawning habitats (Ritter 2015).

Temporal patterns of fish movement

Spawning periods and habitats were associated with movements of all three species. Rainbow Trout moved into Tenderfoot and Sheep creeks from throughout the watershed during their known spawning period in the spring (Ritter 2015), suggesting that a substantial portion of the population may depend on these creeks for spawning and rearing. Mountain Whitefish appeared to spawn in the lower portions of these and other tributaries as well as in the canyon and headwaters regions of the main-stem Smith River. Mountain Whitefish lack specific spawning substrate requirements (Pierce et al. 2012; Boyer et al. 2017), which may have afforded them choices among a wide variety of spawning sites throughout the watershed. Movements of Brown Trout during their spawning period were generally short and occurred within or to tributaries (Ritter 2015) or along the main-stem Smith River. Spawning season movements into Rock and Big Birch creeks were more frequent than to other portions of the watershed. Although most Brown Trout appeared to move short distances, some moved up to 80 km during the autumn.

Connectivity is particularly important for stream fishes during periods when they move. Movements of Mountain Whitefish and Rainbow Trout were associated with moderate water temperatures that probably coincided with physiological optima at which swimming ability, metabolic performance, and digestion were maximized (Elliott 1976; Lee et al. 2003; Armstrong et al. 2013; Verhille et al. 2016). Movements of Brown Trout were also greatest during periods of moderate temperatures, but the relationship was less pronounced than those in the other two species. Generally, movements during species-specific spawning periods occurred at temperatures that were cooler than species-specific physiological optima. Movements into spawning tributaries are associated with changes in discharge among some fishes (Gresswell et al. 1997; Quinn 2005), but this pattern was not clearly apparent among Smith River fishes. The cause of peak movements of Rainbow Trout during the spring could not be distinguished because their spawning period and peak discharges coincided.

Periods of decreased movement identify conditions (e.g., extreme water temperatures) that may constitute partial barriers to movements by fish. Fish moved infrequently during periods of stressful water temperatures in winter and summer, when mean daily water temperatures were near freezing or greater than 20°C. At such times, fish may have remained within thermal refuge habitats, decreased their activity, or both; fish occupied thermal refuges in the Smith River when mean daily water temperatures exceeded 20°C (Ritter et al. 2020). However, fish did move appreciably (into Sheep Creek) during one brief period when water temperatures in the Smith River remained above 26°C for an extended time. Sustained water temperatures of 26°C or greater may be a threshold at which fish in the Smith River watershed can no longer compensate by decreased activity or local movements. Climate predictions for central Montana (Whitlock et al. 2017) suggest that elevated water temperatures will occur more frequently; connectivity to thermal refuges such as Sheep Creek may be important for reducing the effects of such extreme temperature events. Moreover, the highest water temperatures occurred during early to mid-summer and coincided with peak demand by irrigators (Essaid and Caldwell 2017). Many irrigation structures do not afford fish passage (Silva et al. 2018), and such structures could inhibit movement into upstream thermal refuge habitats during periods of elevated water temperatures. Installation of fishways (Triano et al. 2022) or temporary opening of diversion structures when water temperatures are elevated could enhance access to thermal refugia.

Spatial patterns of fish movement

Movement patterns revealed both critical movement corridors and partial barriers to movement. Identification of movement corridors where the volumes of movement are greatest promotes the conservation and protection of mobile species (Ziv et al. 2012) because these corridors facilitate dispersal among populations and allow fish to travel among habitats for feeding, refuge, and spawning (Fausch et al. 2002). Movement volume was greatest in the main stem and in the lower reaches of major tributaries of the canyon geomorphic region. Habitat degradation can impede movements among suitable habitats (Hansson and Åkesson 2014), whereas pristine habitats like those found in the canyon maintain natural hydrological processes that sustain complex habitats and connectivity (Elosegi et al. 2010), allowing fish to move to habitats that are optimal for different seasons, environmental conditions, and individual life stages (Fausch et al. 2002). Therefore, few fish left the canyon, but large numbers immigrated into it from the headwaters or prairie. Habitat alterations associated with land use practices probably contributed to the low volumes of movement in the headwaters and prairie, implying that these areas were partial barriers to movement. Reduced riparian cover and associated streambank destabilization were common in these sections. Land use

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activities that destabilize stream channels can decrease habitat suitability for coldwater fishes (Brooks et al. 2003). Although the Smith River watershed is generally free of barriers that are traditionally thought to cause fragmentation (e.g., dams, impassable culverts, and irrigation diversions), fish appeared to be less willing to traverse habitats that were simplified or altered. Fragmentation of streams is therefore probably more pervasive than inferred from absolute barriers, as habitat alterations can create partial barriers to migration.

Stream lengths traversed by fish in the Smith River watershed were comparable to those traversed in larger unfragmented river systems (Starcevich et al. 2012; Benjamin et al. 2014) and were much longer than those in smaller headwater streams and in streams with barriers to movement (Young 1996, 1999; Bunnell et al. 1998). The average length of stream between obstacles on mid-sized rivers in North America is 45 km (Poff et al. 2007), but fish in the Smith River watershed and adjacent Missouri River watershed used a stream network almost 10 times larger.

Management implications

Fisheries management policies and regulations that incorporate an understanding of the extensive spatial extent of stream fish movements and that manage populations over corresponding spatial scales will increase the likelihood of desired outcomes in connected watersheds such as the Smith River. For example, harvest regulations that apply to the entire spatial and temporal distributions of a population will ensure that all individuals of the population are subjected to the regulations consistently, thereby enhancing their effectiveness.

Opportunities for unrestricted movements probably enhance population stability. Recovery efforts directed at improving or re-establishing populations of imperiled fishes may be most successful if target populations have access to sufficiently long reaches where they can express a variety of movement behaviors like those seen among fish in the Smith River watershed (Rosenfeld and Hatfield 2006). However, many imperiled fish species are restricted to small habitats (Schaefer et al. 2003; Uthe et al. 2016), where the risks of extinction and loss of genetic diversity are high (Dunham et al. 1997; Yamamoto et al. 2004). Maintaining or re-establishing movement corridors among isolated groups of fish may afford imperiled populations the ability to maintain mobile life history patterns that are necessary for metapopulation function and population resilience. Reintroduction efforts will have the highest probability of success in systems with adequate connectivity and if diverse source populations are used (Andrews et al. 2013), thereby promoting the establishment of populations that express diverse movement behaviors. Removal or modification of barriers to fish movement, where such measures are socially acceptable, will allow expression of the full range of movement behaviors present in a population and thereby maximize population abundance, productivity, and persistence (Yamamoto et al. 2004; Hitt et al. 2012).

CONCLUSIONS

Movements by fish in the Smith River that were greater than typical daily movement distances were common and overlapped, thus connecting distant groups of fish. For each species, the movement volumes peaked at specific locations and during specific seasons. Studies that are restricted in scope to single species or seasons of interest therefore risk mischaracterizing the diversity of movements expressed by a fish assemblage. By accounting for the temporal diversity and spatial extent of movement patterns expressed by all species in a fish assemblage, management actions can promote life history and species diversity while helping to ensure the persistence of robust fish populations. Managers may perhaps best protect life history diversity of inland fishes by emulating the management of highly migratory anadromous fishes, which seeks to facilitate unhindered movements.

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Smith River Advisory Council, U.S. Forest Service, U.S. Fish and Wildlife Service, or National Institutes of Health. The Montana Cooperative Fishery Research Unit is jointly sponsored by the USGS, MFWP, MSU, and U.S. Fish and Wildlife Service.

CONFLICT OF INTEREST STATEMENT

T. David Ritter and Michael J. Lance worked on developing the satellite communication units referenced in the manuscript. Neither individual received compensation for this work. Ritter still works for Ritter Designs. Reference to the satellite communication unit or Ritter Designs is for descriptive purposes only and is not an endorsement or advertisement for Ritter Designs or associated products. All other authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Project data are not housed in a publically accessible data repository. Inquiries regarding source data can be made to the corresponding author or to Montana Fish, Wildlife and Parks, 4600 Giant Springs Road, Great Falls, Montana 59405.

ETHICS STATEMENT

All standards and regulations regarding the ethical treatment of animals were followed. Fish handling and marking followed American Fisheries Society guidelines. The project was overseen by the Montana State University Institutional Animal Care and Use Committee under protocols 2009-09, 2013-50, and 2014-50.

ORCID

Michael J. Lance https://orcid.org/0000-0001-7035-2990
Kurt C. Heim https://orcid.org/0000-0002-6257-8284
Robert Al-Chokhachy https://orcid.org/0000-0002-2136-5098

REFERENCES

Andrews, T. M., Shepard, B. B., Litt, A. R., Kruse, C. G., Zale, A. V., & Kalinowski, S. T. (2013). Juvenile movement among different populations of cutthroat trout introduced as embryos to vacant habitat. *North American Journal of Fisheries Management*, *33*(4), 795–805. https://doi.org/10.1080/02755947.2013.812582

Armstrong, J., Braithwaite, V., & Rycroft, P. (1996). A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic Salmon parr and other fish. *Journal of Fish Biology*, *48*(3), 539–541. https://doi.org/10.1111/j.1095-8649.1996.tb01446.x

Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E., & Torgersen, C. E. (2013). Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, *94*(9), 2066–2075. https://doi.org/10.1890/12-1200.1

Bear, E. A., McMahon, T. E., & Zale, A. V. (2007). Comparative thermal requirements of Westslope Cutthroat Trout and Rainbow Trout: Implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society*, *136*(4), 1113–1121. https://doi.org/10.1577/T06-072.1

Benjamin, J. R., Wetzel, L. A., Martens, K. D., Larsen, K., & Connolly, P. J. (2014). Spatio-temporal variability in movement, age, and growth of Mountain Whitefish (*Prosopium williamsoni*) in a river network based upon PIT tagging and otolith chemistry. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(1), 131–140. https://doi.org/10.1139/cjfas-2013-0279

Berger, A. M., & Gresswell, R. E. (2009). Factors influencing Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) seasonal survival rates: A spatially continuous approach within stream networks. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(4), 613–632. https://doi.org/10.1139/F09-029

Biomark. (2015). *Fish tagging methods*. Biomark.

Bowerman, T., & Budy, P. (2012). Incorporating movement patterns to improve survival estimates for juvenile Bull Trout. *North American Journal of Fisheries Management*, *32*(6), 1123–1136. https://doi.org/10.1080/02755947.2012.720644

Boyer, J. K., Guy, C. S., Webb, M. A. H., Horton, T. B., & McMahon, T. E. (2017). Reproductive ecology, spawning behavior, and juvenile distribution of Mountain Whitefish in the Madison River, Montana. *Transactions of the American Fisheries Society*, *146*(5), 939–954. https://doi.org/10.1080/00028487.2017.1313778

Brönmark, C., Skov, C., Brodersen, J., Nilsson, P. A., & Hansson, L. A. (2008). Seasonal migration determined by a trade-off between predator avoidance and growth. *PLOS ONE*, *3*(4), Article e1957. https://doi.org/10.1371/journal.pone.0001957

Brooks, K. N., Ffolliott, P. F., Gregersen, H. M., & DeBano, L. F. (2003). *Hydrology and the management of watersheds* (3rd ed.). Iowa State University Press.

Brown, C. J. D. (1971). *Fishes of Montana*. Big Sky Books, Montana State University.

Bunnell, D. B., Jr., Isely, J. J., Burrell, K. H., & Van Lear, D. H. (1998). Diel movement of Brown Trout in a southern Appalachian river. *Transactions of the American Fisheries Society*, *127*(4), 630–636. https://doi.org/10.1577/1548-8659(1998)127<0630:DMOBTI>2.0.CO;2

Campbell Grant, E. H., Nichols, J. D., Lowe, W. H., & Fagan, W. F. (2010). Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(15), 6936–6940. https://doi.org/10.1073/pnas.1000266107

Chapman, B. B., Brönmark, C., Nilsson, J.-Å., & Hansson, L.-A. (2011). The ecology and evolution of partial migration. *Oikos*, *120*(12), 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Chapman, B. B., Hulthén, K., Wellenreuther, M., Hansson, L. A., Nilsson, J. Å., & Brönmark, C. (2014). Patterns of animal migration. In L. A. Hansson & S. Åkesson (Eds.), *Animal movement across scales* (pp. 11–35). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199677184.003.0002

Chase, K. J., Caldwell, R. R., & Stanley, A. K. (2014). *A precipitation-runoff model for simulating natural streamflow conditions in the*

15488659, 2024, 5, Downloaded from https://afspubs.onlinelibrary.wiley.com/doi/10.1002/tafs.10485 by Montana State University Library, Wiley Online Library on [09/12/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Smith River watershed, Montana, water years 1996–2008. U.S. Geological Survey.

Connolly, P. J., Jezorek, I. G., Martens, K. D., & Prentice, E. F. (2008). Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. *North American Journal of Fisheries Management*, *28*(2), 402–417. https://doi.org/10.1577/M07-008.1

Detenbeck, N. E., DeVore, P. W., Niemi, G. J., & Lima, A. (1992). Recovery of temperate-stream fish communities from disturbance: A review of case studies and synthesis of theory. *Environmental Management*, *16*(1), 33–53. https://doi.org/10.1007/BF02393907

Dorai-Raj, S. (2014). *binom: Binomial confidence intervals for several parameterizations*. R package version 1.1-1.1. https://cran.r-project.org/package=binom

Dunham, J., & Rieman, B. (1999). Metapopulation structure of Bull Trout: Influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications*, *9*(2), 642–655. https://doi.org/10.1890/1051-0761(1999)009[0642:MSOBTI]2.0.CO;2

Dunham, J. B., Vinyard, G. L., & Rieman, B. E. (1997). Habitat fragmentation and extinction risk of Lahontan Cutthroat Trout. *North American Journal of Fisheries Management*, *17*(4), 1126–1133. https://doi.org/10.1577/1548-8675(1997)017<1126:HFAERO>2.3.CO;2

Elliott, J. (1976). The energetics of feeding, metabolism and growth of Brown Trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *The Journal of Animal Ecology*, *45*, 923–948. https://doi.org/10.2307/3590

Elosegi, A., Díez, J., & Mutz, M. (2010). Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. *Hydrobiologia*, *657*(1), 199–215. https://doi.org/10.1007/s10750-009-0083-4

Esri. (2015). *ArcGIS 10.4.1 for desktop*. Esri.

Essaid, H. I., & Caldwell, R. R. (2017). Evaluating the impact of irrigation on surface water–groundwater interaction and stream temperature in an agricultural watershed. *Science of the Total Environment*, *599*, 581–596. https://doi.org/10.1016/j.scitotenv.2017.04.205

Faraway, J. J. (2016). *Extending the linear model with R: Generalized linear, mixed effects and nonparametric regression models* (2nd ed.). CRC Press. https://doi.org/10.1201/9781315382722

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience*, *52*(6), 483–498. https://doi.org/10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2

Greene, C. M., Hall, J. E., Guilbault, K. R., & Quinn, T. P. (2010). Improved viability of populations with diverse life-history portfolios. *Biology Letters*, *6*(3), 382–386. https://doi.org/10.1098/rsbl.2009.0780

Gresswell, R. E., Liss, W. J., Larson, G. L., & Bartlein, P. J. (1997). Influence of basin-scale physical variables on life history characteristics of Cutthroat Trout in Yellowstone Lake. *North American Journal of Fisheries Management*, *17*(4), 1046–1064. https://doi.org/10.1577/1548-8675(1997)017<1046:IOBSPV>2.3.CO;2

Hansson, L. A., & Åkesson, S. (2014). A synthesis of animal movement across scales. In L. A. Hansson & S. Åkesson (Eds.), *Animal movement across scales* (pp. 259–267). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199677184.003.0014

He, X., & Kitchell, J. F. (1990). Direct and indirect effects of predation on a fish community: A whole-lake experiment. *Transactions of the American Fisheries Society*, *119*(5), 825–835. https://doi.org/10.1577/1548-8659(1990)119<0825:DAIEOP>2.3.CO;2

Heim, K. C., Arp, C. D., Whitman, M. S., & Wipfli, M. S. (2019). The complementary role of lentic and lotic habitats for Arctic Grayling in a complex stream-lake network in Arctic Alaska. *Ecology of Freshwater Fish*, *28*(2), 209–221. https://doi.org/10.1111/eff.12444

Hill, M. S., Zydlewski, G. B., Zydlewski, J. D., & Gasvoda, J. M. (2006). Development and evaluation of portable PIT tag detection units: PITpacks. *Fisheries Research*, *77*(1), 102–109. https://doi.org/10.1016/j.fishres.2005.08.001

Hitt, N. P., Eyler, S., & Wofford, J. E. (2012). Dam removal increases American Eel abundance in distant headwater streams. *Transactions of the American Fisheries Society*, *141*(5), 1171–1179. https://doi.org/10.1080/00028487.2012.675918

Hollander, J., Verzijden, M., Svensson, E., & Brönmark, C. (2014). Dispersal and phenotypic plasticity. In L. A. Hansson & S. Åkesson (Eds.), *Animal movement across scales* (pp. 110–125). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199677184.003.0007

Homel, K. M., Gresswell, R. E., & Kershner, J. L. (2015). Life history diversity of Snake River Finespotted Cutthroat Trout: Managing for persistence in a rapidly changing environment. *North American Journal of Fisheries Management*, *35*(4), 789–801. https://doi.org/10.1080/02755947.2015.1044625

Isaak, D. J., Young, M. K., Nagel, D. E., Horan, D. L., & Groce, M. C. (2015). The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*, *21*(7), 2540–2553. https://doi.org/10.1111/gcb.12879

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic Salmon *Salmo salar* L., Brown Trout *Salmo trutta* L. and Arctic Charr *Salvelinus alpinus* (L.): A review of aspects of their life histories. *Ecology of Freshwater Fish*, *12*(1), 1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x

Lance, M. J. (2019). *Spatial and temporal variability in movements and vital rates of sympatric salmonids in an unfragmented, inland watershed* [Master's thesis, Montana State University]. MSU ScholarWorks. https://scholarworks.montana.edu/handle/1/15575

Lance, M. J., & Baxter, C. V. (2011). Abundance, production, and tissue composition of Mountain Whitefish (*Prosopium williamsoni*) in a central Idaho wilderness stream. *Northwest Science*, *85*(3), 445–454. https://doi.org/10.3955/046.085.0303

Lee, C. G., Farrell, A. P., Lotto, A., MacNutt, M. J., Hinch, S. G., & Healey, M. C. (2003). The effect of temperature on swimming performance and oxygen consumption in adult Sockeye (*Oncorhynchus nerka*) and Coho (*O. kisutch*) Salmon stocks. *Journal of Experimental Biology*, *206*(18), 3239–3251. https://doi.org/10.1242/jeb.00547

Liboschik, T., Fokianos, K., & Fried, R. (2017). Tscount: An R package for analysis of count time series following generalized linear models. *Journal of Statistical Software*, *82*, 1–51. https://doi.org/10.18637/jss.v082.i05

Lindström, Å., Chapman, B. B., Jonzén, N., & Klaassen, M. (2014). Movement and migration in a changing world. In L. A.

15488659, 2024, 5, Downloaded from https://afspubs.onlinelibrary.wiley.com/doi/10.1002/nafm.10485 by Montana State University Library, Wiley Online Library on [09/12/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hansson & S. Åkesson (Eds.), *Animal movement across scales* (pp. 36–50). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199677184.003.0003

Lucas, M., & Baras, E. (2001). *Migration of freshwater fishes*. Blackwell Science. https://doi.org/10.1002/9780470999653

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology*, *48*(7), 1186–1198. https://doi.org/10.1046/j.1365-2427.2003.01089.x

McKinstry, M., & Mackinnon, P. (2011). *Floating PIT tag detection system* (Western Water and Power Solution Bulletin 71). Bureau of Reclamation.

Meyer, K. A., Elle, F. S., & Lamansky, J. A. (2011). Environmental factors related to the distribution, abundance, and life history characteristics of Mountain Whitefish in Idaho. *North American Journal of Fisheries Management*, *29*(3), 753–767. https://doi.org/10.1577/M08-015.1

Montana Department of Fish and Game. (1973). *Smith River drainage inventory and planning investigation*. Montana Department of Fish and Game, Environmental and Information Division.

Montana Fish, Wildlife and Parks. (2013). *Statewide fisheries management plan 2013–2018*. Montana Fish, Wildlife and Parks.

Moore, J. W., Yeakel, J. D., Peard, D., Lough, J., & Beere, M. (2014). Life-history diversity and its importance to population stability and persistence of a migratory fish: Steelhead in two large North American watersheds. *Journal of Animal Ecology*, *83*(5), 1035–1046. https://doi.org/10.1111/1365-2656.12212

Neville, H. M., Dunham, J. B., & Peacock, M. M. (2006). Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecology*, *21*(6), 901–916. https://doi.org/10.1007/s10980-005-5221-4

Nilsson, J.-Å., Brönmark, C., Hansson, L.-A., & Chapman, B. B. (2014). Individuality in movement: The role of animal personality. In L. A. Hansson & S. Åkesson (Eds.), *Animal movement across scales* (pp. 90–109). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199677184.003.0006

Olsson, I. C., Greenberg, L. A., Bergman, E., & Wysujack, K. (2006). Environmentally induced migration: The importance of food. *Ecology Letters*, *9*(6), 645–651. https://doi.org/10.1111/j.1461-0248.2006.00909.x

Pierce, R., Davidson, M., & Podner, C. (2012). Spawning behavior of Mountain Whitefish and co-occurrence of *Myxobolus cerebralis* in the Blackfoot River basin, Montana. *Transactions of the American Fisheries Society*, *141*(3), 720–730. https://doi.org/10.1080/00028487.2012.675900

Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(14), 5732–5737. https://doi.org/10.1073/pnas.0609812104

Quinn, T. P. (2005). *The behavior and ecology of Pacific salmon and trout*. 1st ed. University of Washington Press.

R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rieman, B. E., Lee, D. C., Chandler, G., & Myers, D. (1995). Does wildfire threaten extinction for salmonids? Responses of redband trout and Bull Trout following recent large fires on the Boise National Forest. In J. M. Greenlee (Ed.), *Proceedings—Fire effects on rare and endangered species and habitats conference, Coeur d'Alene, Idaho, USA* (pp. 47–57). International Association of Wildland Fire.

Ritter, T. D. (2015). *Connectivity in a montane river basin: Salmonid use of a major tributary in the Smith River system* [Master's thesis, Montana State University]. MSU ScholarWorks. https://scholarworks.montana.edu/handle/1/9154

Ritter, T. D., Zale, A. V., Grisak, G., & Lance, M. J. (2020). Groundwater upwelling regulates thermal hydrodynamics and salmonid movements during high-temperature events at a montane tributary confluence. *Transactions of the American Fisheries Society*, *149*(5), 600–619. https://doi.org/10.1002/tafs.10259

Roni, P. (2019). Does river restoration increase fish abundance and survival or concentrate fish? The effects of project scale, location, and fish life history. *Fisheries*, *44*(1), 7–19. https://doi.org/10.1002/fsh.10180

Rosenfeld, J. S., & Hatfield, T. (2006). Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(3), 683–698. https://doi.org/10.1139/f05-242

Schaefer, J. F., Marsh-Matthews, E., Spooner, D. E., Gido, K. B., & Matthews, W. J. (2003). Effects of barriers and thermal refugia on local movement of the threatened Leopard Darter, *Percina pantherina*. *Environmental Biology of Fishes*, *66*(4), 391–400. https://doi.org/10.1023/A:1023906424075

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*(7298), 609–612. https://doi.org/10.1038/nature09060

Schlosser, I. J. (1995). Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia*, *303*(1–3), 71–81. https://doi.org/10.1007/BF00034045

Schramm, H. L., Jr. (2017). The fishery resources of the Mississippi River: A model for conservation and management. *Fisheries*, *42*(11), 574–585. https://doi.org/10.1080/03632415.2017.1377554

Sedell, J. R., Richey, J. E., & Swanson, F. J. (1989). The river continuum concept: A basis for the expected ecosystem behavior of very large rivers? In *Proceedings of the international large river symposium* (Canadian Special Publication of Fisheries and Aquatic Sciences, pp. 49–44). Fisheries and Oceans Canada.

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C., Braun, D. C., & Burnett, N. J. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, *19*(2), 340–362. https://doi.org/10.1111/faf.12258

Sparks, R. E. (1995). Need for ecosystem management of large rivers and their floodplains. *Bioscience*, *45*(3), 168–182. https://doi.org/10.2307/1312556

Starcevich, S. J., Howell, P. J., Jacobs, S. E., & Sankovich, P. M. (2012). Seasonal movement and distribution of fluvial adult Bull Trout in selected watersheds in the mid-Columbia River and Snake River basins. *PLOS ONE*, *7*(5), Article e37257. https://doi.org/10.1371/journal.pone.0037257

Tranquilli, V. (2007). Guide to half-duplex RFID: Lessons learned tracking Bull Trout in the upper Willamette basin since 2001. In *Proceedings of the inter-agency PIT tag detection workshop, Vancouver, Washington* (pp. 143–188).

Triano, B., Kappenman, K. M., McMahon, T. E., Blank, M., Heim, K. C., Parker, A. E., Zale, A. V., Platt, N., & Plymesser, K. (2022). Attraction, entrance, and passage efficiency of Arctic Grayling, trout, and suckers at Denil fishways in the Big Hole River

15488659, 2024, 5, Downloaded from https://afspubs.onlinelibrary.wiley.com/doi/10.1002/tafs.10485 by Montana State University Library, Wiley Online Library on [09/12/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

basin, Montana. *Transactions of the American Fisheries Society*, *151*(4), 453–473. https://doi.org/10.1002/tafs.10362

U.S. Geological Survey. (2018). *Water data for the nation* [Online database]. U.S. Geological Survey. https://doi.org/10.5066/F7P55KJN

Uthe, P., Al-Chokhachy, R., Zale, A. V., Shepard, B. B., McMahon, T. E., & Stephens, T. (2016). Life history characteristics and vital rates of Yellowstone Cutthroat Trout in two headwater basins. *North American Journal of Fisheries Management*, *36*(6), 1240–1253. https://doi.org/10.1080/02755947.2016.1206643

Uthe, P. R. (2015). *Life history characteristics and the effects of climate on growth of Yellowstone Cutthroat Trout in headwater basins* [Master's thesis, Montana State University]. MSU ScholarWorks.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Verhille, C. E., English, K. K., Cocherell, D. E., Farrell, A. P., & Fangue, N. A. (2016). High thermal tolerance of a Rainbow Trout population near its southern range limit suggests local thermal adjustment. *Conservation Physiology*, *4*(1), Article cow057. https://doi.org/10.1093/conphys/cow057

Whitlock, C., Cross, W., Maxwell, B., Silverman, N., & Wade, A. (2017). *2017 Montana climate assessment*. Montana State University; University of Montana, Montana Institute on Ecosystems. https://doi.org/10.15788/m2ww8w

Yamamoto, S., Morita, K., Koizumi, I., & Maekawa, K. (2004). Genetic differentiation of White-spotted Charr (*Salvelinus leucomaenis*) populations after habitat fragmentation: Spatial–temporal changes in gene frequencies. *Conservation Genetics*, *5*(4), 529–538. https://doi.org/10.1023/B:COGE.0000041029.38961.a0

Young, M. (1999). Summer diel activity and movement of adult Brown Trout in high-elevation streams in Wyoming, USA. *Journal of Fish Biology*, *54*(1), 181–189. https://doi.org/10.1111/j.1095-8649.1999.tb00621.x

Young, M. K. (1996). Summer movements and habitat use by Colorado River Cutthroat Trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(6), 1403–1408. https://doi.org/10.1139/f96-054

Young, M. K., Wilkison, R. A., Phelps, J., III, & Griffith, J. (1997). Contrasting movement and activity of large Brown Trout and Rainbow Trout in Silver Creek, Idaho. *The Great Basin Naturalist*, *57*(3), 238–244.

Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I., & Levin, S. A. (2012). Trading-off fish biodiversity, food security, and hydropower in the Mekong River basin. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 5609–5614. https://doi.org/10.1073/pnas.1201423109

Zwick, P. (1992). Stream habitat fragmentation—A threat to biodiversity. *Biodiversity and Conservation*, *1*(2), 80–97. https://doi.org/10.1007/BF00731036

Zydlewski, G. B., Horton, G., Dubreuil, T., Letcher, B., Casey, S., & Zydlewski, J. (2006). Remote monitoring of fish in small streams: A unified approach using PIT tags. *Fisheries*, *31*(10), 492–502. https://doi.org/10.1577/1548-8446(2006)31[492:RMOFIS]2.0.CO;2

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