

SPATIAL AND TEMPORAL VARIABILITY IN MOVEMENTS AND
VITAL RATES OF SYMPATRIC SALMONIDS IN AN
UNFRAGMENTED, INLAND WATERSHED

by

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ABSTRACT

The life history patterns and vital rates of stream dwelling fish can differ across biological, spatial, and temporal scales. We determined the movement patterns and vital rates of three abundant salmonids—brown trout (*Salmo trutta*), mountain whitefish (*Prosopium williamsoni*), and rainbow trout (*Oncorhynchus mykiss*)—in the Smith River watershed of Montana, a system with three distinct geomorphic regions: the headwaters, semi-wilderness canyon, and prairie. We marked 7,172 fish with passive integrated transponder (PIT) tags, monitored their watershed-scale movements past 15 stationary PIT arrays over four years, and relocated fish between arrays by conducting mobile surveys along the Smith River and major tributaries. Fish movement patterns and survival probabilities varied seasonally, among species, and among locations within the watershed. Volume of movement and diversity of movers were both greatest in the canyon region and in lower portions of tributaries. Fish rarely left the canyon, but movement into the canyon from other regions was common among some groups of fish. Mountain whitefish were most likely to move and brown trout were least likely to move. The stream lengths traversed by fish followed a leptokurtic distribution with most fish travelling < 10 km and decreasing numbers of fish travelling farther. Distinct life history patterns were not evident as judged by the stream lengths traversed by tagged fish; rather, a continuous spectrum of distances traversed was apparent. Species-specific spawning periods were associated with increased frequency of movement by mountain whitefish and rainbow trout. Increases in the frequency of watershed-scale movements of all three species were associated mean daily water temperatures of 11.7–15.3°C, compared to periods when water temperatures were cooler or warmer. Annual probabilities of survival were highest among mountain whitefish (0.38–0.54) and lower among brown trout (0.16–0.38) and rainbow trout (0.08–0.39). Survival of rainbow trout and mountain whitefish was highest in the canyon. Survival of mountain whitefish was also high in the headwaters but was lowest in the prairie. Movements of fish in the Smith River watershed were diverse, allowed movement among habitats with different probabilities of survival, and probably contributed to meta-population function, population resiliency, and species diversity.

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). Fish that move can access food, favorable thermal conditions, and spawning substrates that may be unavailable or limited within local habitat patches (Schlosser and Angermeier 1995, Chapman et al. 2014). Increased gene flow associated with inter-population movements of fish prevents inbreeding depression and maintains genetic diversity (Neville et al. 2006, Hollander et al. 2014). Moreover, movements of fish can result in recolonization of disturbed habitats and help 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 such as wildfires and floods 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). Biological drivers that can shape movement patterns include species-specific internal cues to initiate spawning and emigration. Among migratory salmonids, individuals in a population often move between different ecosystems in distinct pulses of movement of which the timing, magnitude, and distances travelled can differ greatly by species (Dunham and Rieman 1999, Quinn 2005). However, not all differences in movement patterns are species-specific, and

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 increased predator density (He and Kitchell 1990, Brönmark et al. 2008). The propensity of an individual to move can be related to genetic lineage as well as individual personality traits (e.g., boldness) leading to a variety of intraspecific movement patterns (Klemetsen et al. 2003, Nilsson et al. 2014).

Seasonal changes in environmental conditions can influence the movements of fish (Lucas and Baras 2001). Water temperature can fluctuate in temperate streams from near freezing (0°C) during winter to almost 30°C during summer. These periodic extremes expose fish to temperatures far from their species-specific thermal optima (Magoulick and Kobza 2003, Bear et al. 2007, Isaak et al. 2015) resulting in declines in swimming and metabolic performance (Rand et al. 2006). Many fishes therefore migrate during periods of relatively moderate water temperatures (10 - 15°C; Lucas and Baras 2001), and some migratory fish that encounter extreme water temperatures will stop migrating and occupy thermal refuges until water temperatures are more suitable (Keefer et al. 2009). Seasonal changes in discharge also influence fish movements by altering habitat suitability, food availability, and fluid dynamics (Schlosser 1995, Brooks et al. 2003, Uthe 2015). Some fish move into seasonally wetted habitats during periods of elevated discharge where they can avoid strong currents and consume seasonally available food resources (Kwak 1988, Colvin et al. 2009). Then, as main-stem discharges decrease to base flows, fish leave drying or freezing habitats (Magoulick and Kobza 2003, Roberts and Angermeier 2007, Heim et al. 2015).

The movements and population dynamics of stream-dwelling fish are mediated spatially by landscape features that are the template for available habitats and migration corridors (Vannote et al. 1980, Fausch et al. 2002). Local geomorphologic characteristics including lithology, topography, and climate influence the hydrologic characteristics of streams and thereby can affect movement patterns and habitat selection behaviors of stream-dwelling fish (Jones et al. 1974, Montgomery et al. 1999, Power et al. 1999). Stream velocity is directly associated with watershed topography and can define the boundaries of movement if stream velocities and gradients exceed swimming capabilities (Lucas and Baras 2001, Quinn 2005). 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). Some fish move to spawn in geomorphic regions that have appropriate sediment sizes, groundwater inputs, and stream velocities for juvenile survival and incubation of eggs (Dunham and Rieman 1999, Baxter and Hauer 2000, Jaeger et al. 2005). Thermal landscapes of rivers vary spatially (Vatland et al. 2015), and fish can thermoregulate behaviorally by moving to habitats with water temperatures closest to species-specific optima (Torgersen et al. 1999). Sections of stream near tributary junctions or groundwater inputs can provide refuge habitats where fish can avoid seasonal temperature extremes (Power et al. 1999, Armstrong et al. 2013, Dugdale et al. 2016). Geomorphologic structure can further influence fish movements through complex interactions of land use, plant communities, climate, topography, and geology that influence sediment transport, hydrologic patterns, water chemistry, and channel morphology (Brooks et al. 2003).

Movements of stream-dwelling fishes can be obstructed or hindered by habitat alterations and in-stream barriers, and such fragmentation of habitats deleteriously affects many taxa worldwide (Zwick 1992, Lindström et al. 2014). Streams and rivers are socially and economically important, often serving as transportation corridors, water supply conduits, and power generators. However, the infrastructure associated with these uses (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). Thorough descriptions of the movement behaviors of fish in unfragmented watersheds can help contextualize the effects of barriers on fish movements in fragmented systems.

Quantification of the vital rates of fish within habitat patches is necessary to identify and protect meta-population processes. The abundance and stability of fish populations can be influenced by probabilities of survival (S) and site fidelity (F ; Pulliam 1988, Schlosser 1991). Population inputs (immigration and reproduction) must equal losses ($1 - S \cdot F$) for populations to be stable. Local population abundance will increase if inputs are greater than losses but will decrease if losses are greater than inputs and place the population at risk of extinction (Hanski and Gilpin 1991). Movement of individuals among populations and habitats can stabilize meta-populations and increase the geographic distributions of species (Schlosser and Angermeier 1995, Peery et al. 2006). Quantification of probabilities of site fidelity and survival can help identify

habitats with the highest probabilities of survival and delineate movement corridors that connect populations of fish across diverse landscapes.

Most studies of fish movements and vital rates have been limited in demographic, spatial, or temporal scope and focused on a single species of social, economic, or conservation importance. Many movement studies have been temporally restricted to seasons of interest (e.g., spawning) or to the battery life of transmitters and have not examined movements of fish over multiple years. Moreover, movement studies have often been based on relatively few individuals (< 100) despite a growing understanding that relatively small proportions of fish make long distance movements that are critical for dispersal, genetic exchange, and metapopulation dynamics (Radinger and Wolter 2014). However, fish occur across and move among a variety of complex stream habitats including small headwater streams and large rivers (Meyers et al. 1992, Baxter 2002, Starcevich et al. 2012), and the behaviors and population dynamics of stream fishes can vary across spatial and temporal scales (Berger and Gresswell 2009, Kanno et al. 2015). Therefore, movement behaviors and vital rates of small numbers of fish restricted over small spatial extents, or during isolated seasons of interest may not be indicative of the behaviors and vital rates of fish populations in larger, unfragmented systems over multiple years.

Considering the pervasive effect of movement, and the amount thereof, on individuals and populations, we sought to comprehensively determine the factors affecting unconstrained fish movements (species, physical drivers, seasons, and landscapes) and how movements and vital rates (survival, site fidelity) interrelate in a

large, inland watershed, while also avoiding some common limitations of movements studies (e.g., limited spatial or temporal scopes, species, and sample sizes). Our goal was to determine how unconstrained movement behaviors and population vital rates of fish varied across group-specific (e.g., species, tagging location), spatial, and temporal scales. Accordingly, our specific objectives were to (1) determine if movement varied among and within sympatric species, (2) determine if the amount (volume) of movement and diversity of movers (by species and location where fish were tagged) varied spatially across the Smith River watershed, (3) determine if movement patterns varied seasonally and if temporal changes in the frequency of movement were related to species-specific spawning periods, stream discharges, or water temperatures, and (4) determine if probabilities of site fidelity and survival varied among sympatric species, geomorphic regions, or seasons. We therefore documented the movement behaviors and vital rates of 7,172 marked individuals of three sympatric species over four years in the Smith River watershed in central Montana, USA, an unfragmented watershed that includes multiple, distinct geomorphic regions where long distance movements of fish can occur (> 100 km; Grisak et al. 2012). Quantification of fish movements and vital rates in an unfragmented setting can help inform conservation and management aimed at protecting and restoring life history diversity and recreational opportunities in fragmented inland watersheds.

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 5,190 km² of privately and publicly owned lands across three distinct geomorphic regions: the headwaters, the canyon, and the prairie (Figures 1 and 2). 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 (Figure 3). Discharge subsequently diminishes gradually to base discharge in mid-summer when water temperatures are greatest. During the summer, about half of the volume of the river ($1.7 \text{ m}^3\text{sec}^{-1}$ of the available $3.1 \text{ m}^3\text{sec}^{-1}$) is diverted to irrigate agricultural lands. The return of 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 headwaters of the watershed (2,193 km²) encompass a broad, unconstrained agricultural valley between the Castle and Big Belt mountains (Chase et al. 2014). The geology of the headwaters is dominated by sandstones and limestones, and the soils of the headwaters are predominantly alluvial cobbles, gravels, and clay (U.S. Geological Survey 2019b). Sinuosity (ratio of stream length to straight-line distance) of the Smith River in the headwaters varies between 1.6 and 2.2, and the river gradient is from 0.16 to 0.28%. Sinuosities of headwater tributaries vary from 1.1 to 3.3 and gradients vary from

0.5 to 2.9%. The elevations of the headwaters range from 1,332 to 2,893 m, and the median elevation is 1,686 m (Figure 4). The median ruggedness index (mean difference in elevation among adjacent cells) across the entire geomorphic region is 8.7 and is 4.2 within 500 m of the stream network. Shrub/steppe is the predominant land cover followed by forests and grasslands (Figure 5). Commercial grazing occurs at least seasonally on most areas of shrub/steppe and grassland. About 10% of the area of the headwaters has been altered for human use (primarily tilled crops). Most land in the headwaters is privately owned (72%); public lands are managed by the State of Montana or the U.S. Forest Service (Figure 4).

The canyon comprises the middle 1,855 km² of the watershed where the river flows through the Little Belt Mountains. Limestone and sandstone formations dominate the geology (U.S. Geological Survey 2019b). Multiple igneous intrusions form mineral deposits that have periodically been explored for gold, silver, and copper. Soils in the canyon are composed of colluvium and alluvial cobbles, gravels, and clays. The Smith River cuts a deep canyon through the sedimentary bedrock of the mountains and frequently flows adjacent to cliffs higher than 100 m. Sinuosity of the Smith River in the canyon varies from 1.3 to 2.0, and the gradient varies from 0.20 to 0.34%. Sinuosity of canyon tributaries is generally low (1.0 to 2.4), and gradients are high (0.95 to 6.8%). Elevation in the canyon geomorphic region ranges from 1,109 to 2,498 m (Figure 4); the median elevation is 1,748 m and is higher than that of the headwaters because mountains make up a large portion of the region. The median ruggedness index of the canyon geomorphic region is 14.4, and is 19.2 within 500 m of the stream network reflecting the

steep topography adjacent to the Smith River and its tributaries. Much of the canyon region is forested (47%) with lesser amounts of shrub/steppe (23%) and grasslands (18%, Figure 5). Only 1.6% of the land in the canyon region has been altered for human use although commercial grazing occurs on many of the grassland and shrub/steppe areas. Forty-seven percent of the area of the canyon region is public land managed by the U.S. Forest Service or the State of Montana (Figure 4). Public lands adjacent to the Smith River are managed by the Smith River State Park in a semi-wilderness state (Montana Department of Fish and Game 1973).

The lower, prairie reach is less constrained than the canyon and the river often flows through agricultural lands. The geology of the prairie is predominantly sandstones, shales, and limestones that are younger than the bedrock in the canyon (U.S. Geological Survey 2019a). The soils in the prairie are dominated by alluvial cobbles, gravels, and clay. Sinuosity of the Smith River in the prairie varies from 1.7 to 1.9, and sinuosity of Hound Creek, the main tributary in the prairie, is 1.4. Gradient of the Smith River in the prairie varies from 0.11 to 0.27%, and the gradient of Hound Creek is 0.81%. The elevation of the prairie geomorphic region ranges from 1,014 m to 2,405 m, and the median elevation is 1,395 m (Figure 4). The ruggedness index of the prairie region is 10.2, and 8.5 within 500 m of the stream network. The predominant land cover in the prairie is grassland (44%) followed by shrub/steppe (28%, Figure 5). Ten percent of the prairie has been converted for human use (tilled agriculture). Public lands make up only 10% of the land area in the prairie geomorphic region (Figure 4).

The fish assemblage of the Smith River watershed consists of both native and nonnative species. Salmonids present are mountain whitefish (*Prosopium williamsoni*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), westslope cutthroat trout (*O. clarkii lewisi*, mainly isolated in small tributaries), rainbow-cutthroat trout hybrids, and brook trout (*Salvelinus fontinalis*). Three sucker species are present: white sucker (*Catostomus commersonii*), longnose sucker (*C. catostomus*), and mountain sucker (*C. platyrhynchus*). Other fishes include burbot (*Lota lota*), stonecats (*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 twentieth century (Montana Department of Fish and Game 1973). Brown trout, rainbow trout, and brook trout are not native to the Smith River and were intentionally introduced during the twentieth century to create recreational fishing opportunities (Montana Fish, Wildlife and Parks 2013). Brown trout, mountain whitefish, and rainbow trout are the most abundant fishes in the Smith River watershed and are highly valued by recreation anglers who travel from across the United States and beyond to float the canyon section of the Smith River (Montana Fish, Wildlife and Parks 2013).

Analyses of movement patterns were restricted to the three most abundant species in the watershed: rainbow trout, mountain whitefish, and brown trout (Table 1). Brown trout 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. 2011a). 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. Non-salmonids were not tagged in sufficient numbers to analyze effectively (Table 1).

Discharge and Water Temperature Measurement

We characterized seasonal trends in environmental conditions to understand relationships between changes in discharge, water temperature, and fish movements. We used U.S. Geological Survey (USGS) data recorded every 15 minutes at the Smith River gaging station 3.4 km downstream of the confluence of Sheep Creek (station number 06077200) to characterize seasonal trends in discharge and water temperature. 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 sub-freezing air temperatures. Stream depth was recorded every two hours with water depth loggers (TruTrack WT-HR Water Height Logger, New Zealand), and submerged temperature loggers recorded water temperature hourly (Onset Hobo Pendant Logger). Water temperatures at 16 of 19 remote temperature-monitoring sites were highly correlated to the water temperature at the USGS site ($r \geq 0.95$). The remaining sites were also positively correlated to the USGS site but were influenced by groundwater or short periods of record (Benton Creek, groundwater influenced, $r = 0.89$; Deep Creek, groundwater influenced, $r = 0.74$; Smith River at Truly Bridge, 24-day period of record, r

= 0.88). Mean daily water temperatures varied from 1.6 to 9.2°C among sites (mean = 5.2°C). The coolest sites were in tributaries whereas the warmest sites were along the main-stem Smith River. Water depths at five of the seven remote water depth-monitoring sites were correlated to discharges at the USGS site ($r \geq 0.7$); the exceptions were Deep Creek ($r = 0.38$), which is a short stream originating at a spring about 400 m from the Smith River, and Rock Creek ($r = 0.20$), at which damage to the data logger from ice flows created large data gaps.

Monitoring Fish Movements

Movements of tagged fish were passively and continuously monitored at 15 stationary PIT arrays from July 1, 2014, to May 31, 2018 (Figure 1) to understand the movement behaviors of fish across the watershed over multiple years. 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, and some therefore 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 operated eight stationary arrays in the adjacent Missouri, Dearborn, and Sun River watersheds that identified tagged fish that left the Smith River watershed.

Each stationary PIT array consisted of an Oregon RFID long-range half-duplex (HDX) reader (Oregon RFID, Portland, Oregon) connected to a single instream antenna

with Category-6 Ethernet cable and powered by 12-V DC supplied by either solar cells or 120-V AC converters. Antennas spanned the stream channel across shallow riffles 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). 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 14-25 m wide were constructed with 4-gauge power supply cable (5.2-mm diameter), and large antennas spanning channels greater than 25 m were constructed with 2-gauge welding cable (6.5-mm diameter, Tranquilli 2007). Readers were placed in weatherproof boxes 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. However, some stationary arrays could only be accessed after multiple days travel by raft. Data were retrieved from these sites using remote satellite communicators accessed 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 relocate 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-gauge or 4-gauge wire placed in raft bailing channels or floated in foam pipe insulation (“pool noodles”) outside of kayaks. Hand-held pole antennas consisted of five

wraps of 12-gauge wire within a circular PVC housing about 0.45 m in diameter mounted to the end of a PVC pole about 1.5 m in length. A handheld global positioning system (GPS) unit ran a continuous track log while conducting mobile surveys. Detected fish were georeferenced by matching the detection time stamp with the corresponding GPS location from the track log. 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 if relocated 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, and they were entered into survival models as dead recoveries.

Our goal was to mark fish in a variety of habitats representative of what is available to fish in the Smith River watershed (Figure 1). Over the course of the study, we attempted to capture and mark 50 to 200 fish at 5 to 10 km intervals in all three geomorphic regions as well as in all major tributaries (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 on privately owned lands. Exact numbers of fish tagged were influenced by densities and capture rates at each location. Fish were collected and marked once at most sites. However, we collected fish more than once at a limited

number of sites where we needed to increase sample sizes or mark fish to study predation by American white pelicans (*Pelecanus erythrorhynchos*). Most fish were marked in 2014, but smaller numbers of fish were tagged from 2016 to 2017 (Table 2). Some fish were tagged in the canyon geomorphic region between 2010 and 2014 as part of the Tenderfoot Creek study (Ritter 2015, Ritter and Zale 2015), and the movements of fish that were still alive after 2014 were incorporated into our study.

Fish were collected with boat, barge, and backpack electrofishers, anesthetized with Aqui-S 20E (Aqui-S New Zealand Ltd.; 10 to 20 mg/L titrated to efficacy), measured (total length TL, mm), and marked with HDX PIT tags. The date when a fish was captured and marked 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 marked and when it was last observed alive. PIT tags were surgically implanted into the abdominal cavities of captured fish through small (< 4 mm) incisions made 5 to 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 less than 150 mm TL were tagged with 12-mm HDX PIT tags (Biomark 2015, Biomark MK7 implanter). Fish shorter than 55 mm were not tagged. The majority of fish captured were larger than 150 mm and therefore most of our marked fish were sub-adults or adults (Figure 6; Brown 1971). Total length at the time a fish was tagged was recorded for each fish but was not used in any data analyses because we recaptured insufficient numbers of tagged fish to produce accurate growth models and could not accurately estimate total lengths of fish in subsequent years after release. Therefore, our results are not specific to life stage (e.g.,

juvenile, sub-adult, adult), but describe collective movements by fish across all life stages and include dispersal movements by sub-adults, feeding movements, and spawning movements.

We restricted our analyses to fish tagged in the Smith River watershed because movement among the Smith River watershed and adjacent watersheds was rare. Only five fish tagged in the Smith River watershed were observed at arrays outside of the Smith River watershed, and only two tagged fish entered the Smith River watershed from elsewhere. These movements proved that fish populations in the Smith, Missouri, Sun, and Dearborn Rivers are connected through emigration, but movement among the watersheds occurs infrequently.

General Data Analysis

The statistical computer program R was used for analyzing trends in fish movement, plotting relationships, and constructing tables of results (R Core Team 2017). Packages used within the program R that are not part of the standard R download are listed with each analysis. Mark-recapture analyses were performed using the program MARK (White and Burnham 1999), through the package RMark in R (Laake 2013). ESRI ArcMap 10.4.1 was used for spatial analyses and construction of maps (ESRI 2015).

Detection Efficiency

Imperfect detection efficiency can result in biased estimates of fish movement. Therefore, we estimated detection efficiency and simulated movements of missed fish to correct for bias associated with variable detection efficiency of our stationary PIT arrays. Our general approach and findings are presented here; methods are detailed in subsequent paragraphs. Detection efficiencies of PIT arrays are influenced by tag size, antenna shape, water depth, and periods when arrays are damaged or non-functional (Zydlewski et al. 2006, Horton et al. 2007, Homel and Budy 2008). We determined that tag size did not influence our conclusions about fish movements in the Smith River watershed because we tagged few fish with 12-mm tags (213 of 7,172 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 ($E_{in situ}$) 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 array operation using our entire fish movement dataset including release locations, mobile detections, and stationary array detections (Zydlewski et al. 2006). Array-specific detection efficiencies varied from 0.66 to 1.0 (Table 3) with the lowest detection efficiencies associated with main-stem arrays along the lower half of the Smith River and the highest detection efficiencies associated with arrays at tributary mouths and the upper half of the Smith River. We assumed that fish detected were representative of fish that passed an operational reader but were not detected. We

simulated movement of fish not detected at each array by duplicating randomly selected detections. The number of detections selected 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. Failure to account for variability in array-specific detection efficiencies would have inflated estimates of the proportion of fish that moved past arrays with high detection efficiencies and underestimated the proportions of fish that moved past arrays with low detection efficiencies. We did not attempt to estimate detection efficiency of mobile arrays, which were probably influenced by many factors such as water depth, survey speed, battery voltage, and surveyor bias.

We determined whether tag size (12, 23, or 32 mm) influenced detection efficiency by passing fish models (fishing lures guided by angling gear) affixed with PIT tags over stationary array antennas and recording the number of successful detections (Zydlewski et al. 2006). Fish models with each tag size were passed about 10 to 15 cm above antennas in both upstream and downstream directions and at both slow and fast speeds; 10 passes of each combination were conducted for each tag size at each antenna. Slow retrieval simulated fish slowly passing the antenna at an average speed of 33 cm/s (95% confidence limits 31 and 35 cm/s). Fast retrieval simulated fish moving quickly at an average speed of 93 cm/s (95% confidence limits 84 and 102 cm/s). The effect of tag size on detection efficiency was evaluated using a generalized linear model and a quasi-binomial distribution to account for overdispersion (Faraway 2016). An F-test was used to evaluate the strength of evidence for independent variables, which were antenna width (m), speed of retrieval (fast or slow), direction of retrieval (upstream or downstream), and

tag size. Independent variables were considered strong predictors of detection efficiency if P values were ≤ 0.05 and the predicted detection efficiencies did not have overlapping confidence limits (95%). Tag size was the strongest predictor of detection efficiency in models that included all tag sizes ($F_{2,193} = 106.0$, $P < 0.001$). However, in models that excluded 12-mm tags, weak evidence existed for a difference in detection efficiency between 23 and 32-mm tags ($F_{1,131} = 3.7$, $P = 0.058$), and antenna width replaced tag size as the strongest predictor of detection efficiency ($F_{1,134} = 97.1$, $P < 0.001$). Predicted detection efficiencies were estimated with the “effect” function in the effects package in R (Fox 2003). Predicted detection efficiency was similar for both 23 and 32-mm tags (0.88 for 23-mm; 0.93 for 32-mm) and confidence limits for both tag sizes overlapped (23-mm confidence limit 0.81 and 0.92; 32-mm confidence limit 0.88 and 0.95). We therefore assumed that tag size (23 versus 32 mm) did not bias our estimates of movement. Detection efficiency of 12-mm tags (0.22, confidence limit 0.16 and 0.29) was lower than that of larger tags. However, only 2.8% (217 of 7,172) of fish tagged in our study were tagged with 12-mm tags and only 75 of these were relocated after they were released. Because these relocations made up an insignificant fraction ($< 1\%$) of the total number of relocations, we did not separately estimate detection efficiency of fish tagged with 12-mm tags.

We estimated in-situ detection efficiency ($E_{in situ}$) of each stationary array when it was operational by dividing the probability that a fish was detected given that it passed a reader (p_{total}) by the proportion of time that the array was operational ($p_{operational}$).

$$E_{in situ} = \frac{p_{total}}{p_{operational}}$$

The probability that a fish was detected given it passed an array (p_{total}) was calculated as the proportion of fish with confirmed locations both upstream and downstream of the array (n_{passed}) that were detected ($n_{detected}$) by the array.

$$p_{total} = \frac{n_{detected}}{n_{passed}}$$

Confirmed locations were the result of physical capture, detection at other stationary arrays, or detection during mobile surveys. Some fish were tagged prior to the construction of some array sites, and some array sites were not present for the entire study period. Movements of tagged fish past an array site when the array was not present were excluded from detection efficiency calculations. We assumed that estimated detection efficiencies at sites where ≥ 30 tagged fish passed were reasonable approximations of true detection efficiency. Detection efficiencies at sites where fewer than 30 tagged fish passed ($n_{passed} < 30$) were calculated by pooling estimates across sites with antennas that spanned similar channel widths (small, < 10 m; medium, 10 to 20 m; large, ≥ 20 m) to prevent bias associated with small numbers of binomial trials.

We estimated the proportion of time an array was operational ($p_{operational}$) as the time the array was on and functional divided by the time the array site was present (Homel and Budy 2008). Periods when arrays were non-operational were identified from maintenance records and startup messages in array logs. The proportions of time that arrays were operational varied by season because of changing solar inputs affecting

power supplies and peaks in stream discharge that damaged antennas. Therefore, the probability that a passing fish encountered the array when the array was operational varied seasonally as well. To account for seasonal changes in the probability that an array was operational, we weighted our estimates of the proportion of time an array was operational by the proportion of fish movements observed in each season (p_{moved}). The proportion of fish moving during each season was estimated from sites that were operational more than 80% of the time across all seasons (Table 3).

$$p_{moved\ in\ season\ i} = \frac{n_{moved\ in\ season\ i}}{n_{moved\ total}}$$

$$p_{operational} = \sum_{i = spring}^{winter} (p_{moved\ in\ season\ i} \times p_{operational\ in\ season\ i})$$

$p_{moved\ in\ season\ i}$ = The proportion of movements occurring during a given season

$n_{moved\ in\ season\ i}$ = The number of detections of fish moving past an array in a given season

$n_{moved\ total}$ = The number of detections of fish moving past an array during all seasons

$p_{operational}$ = The proportion of time a reader was on and operational during a given period

Detections missed when an array was operational were simulated by duplicating information from randomly selected detections (Table 3). The number of observations to duplicate (n_{sample}) was calculated with the following equation in which $n_{detected}$ was

the number of detections of passing fish at a given array and $E_{in situ}$ was the estimated detection efficiency of the array.

$$n_{sample} = \frac{n_{detected}}{E_{in situ}} - n_{detected}$$

n_{sample} = Number of observations to replicate

$n_{detected}$ = Number of detections of tagged fish

$E_{in situ}$ = The estimated detection efficiency

Simulated detections were added to the detection record, and an extra character was appended to the tag code of the simulated detection to distinguish simulated observations from actual observations. Each simulated observation was assigned by species, location where the detected fish was initially tagged, total length when initially tagged, and date when initially tagged (within 90 days) to a corresponding fish that was never detected after being tagged and released. If a simulated detection could not be assigned to an unobserved fish (i.e., all matching fish were detected at least once after they were tagged), the simulated detection was not added to the tag record. Missed detections caused by arrays not being present or operational were not simulated because we lacked data representative of fish movements during those periods; all analyses thereby produced conservative estimates of fish movement.

Analysis of Group-Specific Patterns of Fish Movement

Fish were grouped by species, geomorphic region where they were tagged, and whether they were tagged in the Smith River or a tributary of the Smith River to

determine if differences existed in movement behaviors among different species of fish or among fish occupying different regions of the watershed. Among these groups, we compared the proportions of tagged fish that moved after they were released, 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 located at two or more locations that were ≥ 0.5 km apart; daily home ranges of stream dwelling salmonids 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. Fisheries management often varies between tributaries and main-stem rivers and among major geomorphic regions of watersheds (Montana Fish, Wildlife and Parks 2013). Therefore, we wanted to determine what proportions of fish move among the Smith River and its tributaries as well as what proportions of fish move 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 numbers of tagged fish that left, for any amount of time, the geomorphic regions where they were tagged by the total numbers 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 numbers of tagged fish that occupied the Smith River and a tributary by the total numbers of tagged fish. The numbers 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. Confidence intervals (95%) for proportions were calculated using the “binom.confint” function in the binom package in R (Dorai-Raj 2014), which accounted for the non-parametric nature of binomial confidence intervals.

The effects of species and tagging location on the proportions of fish that moved ≥ 0.5 km were estimated with generalized linear models having a quasi-binomial distribution. Independent variables were species, geomorphic regions where 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 ≥ 0.5 km. We fit a full model that included every combination of two-way interactions and then performed a reverse stepwise model selection process using the “drop1” function in R and an F-test (Faraway 2016). The resulting model contained all three primary independent variables and an interaction term between the species variable and the variable for 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 ≤ 0.05 .

Analysis of Spatial Patterns of Fish Movement

We mapped travel routes of fish along the stream network to delineate the portion of stream network traversed by each fish. Analyses based on travel routes were only representative of fish that were detected after initial capture because travel routes could only be mapped for individuals that were located at least twice (including the initial capture event). Each travel route represented the minimum portion of the stream network through which a tagged fish moved. Travel routes of individual tagged fish were mapped using Network Analyst tools in ArcGIS (ESRI 2015). 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. For example, the distance traversed by a fish that travelled from Rock Creek to Tenderfoot Creek and back to Rock Creek would be the distance from Rock Creek to Tenderfoot Creek but not the round trip distance travelled between the creeks. The frequency of the lengths of stream traversed by tagged fish was plotted to determine trends in the length of stream traversed relative to species and whether fish were tagged in the main-stem Smith River or a tributary.

We determined volume of movement (analogous to vehicular traffic volume) throughout the Smith River watershed to assess the relative importance of spatial connectivity to fish. We overlaid travel routes of tagged fish to determine the volume of fish movement within and among species spatially along the stream network. Each travel route was assigned a weighted individual value (WIV) that was equal to one divided by the total number of individuals ($n_{tag\ group}$) in the tag group of the fish whose movements

were depicted by the travel route. Assigning a WIV to each travel route helped account for bias associated with spatially uneven tag distribution.

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

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

WIV = Weighted value associated with each travel route

A tag group consisted of fish of the same species tagged at any time during the study in a specific tributary or main-stem section (e.g., all of the rainbow trout tagged in the Smith River in the section upstream of Rock Creek or all of the mountain whitefish tagged in Sheep Creek in the section downstream of Moose Creek). Stream sections were created by dividing the Smith River and tributaries into 15-km segments using the ArcGIS “points along a line” tool (ESRI 2015), which produced equal-sized sections except for sections at the ends of stream features where less than 15 km of stream remained. To visualize patterns in the volume of fish movement along the stream network, a spatial overlay of all travel routes was created and joined to a data table that included tag codes, species, tag group designation, and WIV. The WIV of passing fish was summed to provide a metric of volume of fish movement along the stream network. This process was repeated for each species and then again with all species collectively to determine spatial patterns of movement volume within species and across the entire fish assemblage.

We identified portions of the stream network with the greatest diversity of movers to understand where along the stream network connectivity was most important for maintaining life history diversity of fish in the Smith River watershed. Mover diversity along the stream network was calculated by modifying Hurlbert's probability of interspecific encounter (1971), which calculates the probability that two individuals in a sample will be different species. We modified the original equation to calculate the probability that two individuals moving past a section of the stream network originated from different tag groups ($p_{multi\ tag\ group}$). Hurlbert's calculations for probability of interspecific encounter were based on integer counts of individuals, but WIVs were a continuous metric with some decimal values less than 0.01. Therefore, the WIVs of passing fish were multiplied by 10,000 and rounded to the nearest integer value to eliminate the potential to produce negative or undefined values. The probability that passing individuals came from multiple tag groups was calculated for the entire stream network and plotted to highlight spatial variability in mover diversity.

$$p_{multi\ tag\ group} = \left(\frac{10,000 \times \sum WIV}{(10,000 \times \sum WIV) - 1} \right) \times \left(1 - \sum_{i=1}^{n_{tag\ groups}} \left(\frac{10,000 \times WIV_i}{10,000 \times \sum WIV} \right)^2 \right)$$

$p_{multi\ tag\ group}$ = the probability that two movers were from different tag groups

$n_{tag\ groups}$ = the number of unique tag groups associated with fish that passed through a given section of stream network

WIV = Weighted value associated with each travel route

Analysis of Temporal Patterns of Fish Movement

We mapped the volume of movement during individual seasons to identify temporal patterns of movement across the watershed. Movements during a season were mapped using network analysis tools in ArcGIS. The volume of movement was calculated as the sum of weighted individual values (WIV) passing through a given segment of the stream network. All observations within a given season were included. Observations immediately prior to the season of interest were included as the starting point for movements that occurred during the season of interest (e.g., for a given tagged fish the last observation in summer would be included as the starting point for movements in the autumn). Seasons were delineated by changes in hydrology and water temperature. Spring occurred from March 14, when ice dams begin to break up, to May 31 and included the spawning period of rainbow trout. Summer lasted from June 1 to September 30 and covered months with the warmest water temperatures and decreasing discharges. Autumn lasted from October 1 to November 30 and covered a period of cooling water temperatures as well as the spawning periods of both brown trout and mountain whitefish. The winter period extended from December 1 to March 13 when much of the river is frozen over and water temperatures stabilize around freezing.

The timing of fish movements can be influenced by changing environmental conditions (Lucas and Baras 2001). Therefore, we evaluated the influence of water temperature, discharge, and species-specific spawning timing on temporal changes in the numbers of fish detected moving past stationary array sites; these three factors can influence the timing of fish movements (Gowan and Fausch 1996, Homel and Budy

2008, Benjamin et al. 2014). Separate statistical models were created for brown trout, mountain whitefish, and rainbow trout, all of which included mean weekly water temperature, mean weekly discharge, species-specific spawning timing, and year as independent variables. The dependent variable was weekly counts 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 in a given week. Both mean weekly water temperature and mean weekly discharge were calculated from data recorded at the USGS site on the Smith River downstream of Sheep Creek. Spawning periods were defined by the timing of spawning movements in Tenderfoot Creek in 2012 and 2013 (Ritter 2015). Spawning periods of brown trout and mountain whitefish were October 1 to November 10, and the spawning period of rainbow trout was April 1 to May 31. Time specific predictors were added that incorporated values of predictor variables for the two previous weeks. Observed movements in the two previous weeks were included as part of the autocorrelative structure of the models. We used the “tsglm” function from the tscount package in R, which fits generalized linear models with a negative binomial distribution and an autoregressive correlation structure, to model the timing of fish movements for each species (Liboschik et al. 2017). Model selection was performed using Quasi-Likelihood Information Criterion (QAIC) scores and was used to remove independent variables that were not supported by the data. Candidate models included linear, exponential, or quadratic predictors of discharge and water temperature to evaluate for non-linear relationships. 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 predictor and plotted to ascertain the influence of each predictor on the multiplicative change in the number of unique fish passing stationary arrays relative to periods when water temperatures were near 0°C or a hypothetical discharge of 0 m³sec⁻¹. For example, if 8 fish per week were observed in the winter when water temperatures were near 0°C, and the effect of temperature was associated with a multiplicative change of two at 10°C, we would expect to observe 16 fish during a week when the water temperature was 10°C given all other conditions were the same. 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 and by plotting the square root of fitted values against the square root of observed values.

We evaluated all independent variables in the time series model to identify any confounded relationships. Water temperature and discharge were plotted against each other and revealed no obvious trend (Figure 7). We assumed that our inferences were robust to confounding between timing of spawning and discharge or water temperature because each model included counts of fish movement during and outside of spawning periods and because the ranges of discharges and water temperatures observed during spawning seasons overlapped with conditions observed outside of spawning periods (Figure 8). An exception was the relationship between spawning timing of rainbow trout

and discharge, which was confounded because rainbow trout spawning occurred concurrently with the highest observed levels of discharge.

Analysis of Spatial and Temporal Patterns of Survival

We applied a robust-design mark-recapture model with Barker resight parameters to create estimates of survival and associated confidence intervals (Kendall et al. 2013). We used passive recaptures of fish detected at stationary PIT arrays, confirmed live observations of fish during mobile PIT surveys, and live recaptures of tagged fish to build individual encounter histories for fish in each geomorphic region. We did not include simulated observations of fish movements at stationary arrays because the mark-recapture modeling techniques we used included parameters for collective detection probability at all sites within each geomorphic region.

To understand patterns of emigration and their influence on vital rates, probabilities of site fidelity (F , hereafter referred to as geomorphic region fidelity) were calculated for each combination of geomorphic region and species as the proportion of fish observed in a given geomorphic region that were in the same geomorphic region at the time of their final observation. Confidence intervals (95%) were calculated using the “binom.confint” function in the binom package in R (Dorai-Raj 2014), and estimates of geomorphic region fidelity were considered different if their confidence intervals did not overlap. Estimates and confidence intervals were transformed to annual estimates of geomorphic region fidelity using the following equation.

$$F_{annual} = F^{\left(\frac{\text{periods per year}}{\text{total study periods}}\right)}$$

Estimated probabilities of geomorphic region fidelity did not represent true probabilities of site fidelity because we did not monitor fish movements over the entire lives of tagged fish, and we could not confirm natal habitat locations.

We estimated survival of tagged fish with a robust design model that included Barker resight parameters (Kendall et al. 2013) because traditional mark-recapture models such as Cormack-Jolly-Seber models can produce biased estimates when applied to continuous data such as relocations at stationary PIT arrays (Bowerman and Budy 2012, Conner et al. 2015). Robust design models are useful for studies with continuous observations because they derive their estimates from both closed and open population estimation methods (Williams et al. 2002, Pine et al. 2012). The population is assumed stable during closed periods (primary survey occasions) with no immigration, emigration, births, or deaths. Closed periods consist of a series of shorter survey periods (secondary survey occasions) that are assumed instantaneous and independent. Secondary survey occasions need to be sufficiently brief with continuous observations such as relocations of fish marked with PIT tags so that each secondary survey occasion reasonably meets these assumptions. Robust design models estimate detection probability within primary survey occasions. Probabilities of survival and emigration are estimated between primary survey occasions. The inclusion of a resight parameter modifies estimates of survival and detection probability for each primary survey occasion based on observations of marked individuals between primary survey occasions (Conner et al. 2015).

We identified three, 14-day primary survey occasions per year (12 total) that each corresponded to periods when movement by fish was common such that tagged fish

would be most likely to be available for detection at stationary PIT arrays. Each day of a 14-day primary period was considered a secondary survey occasion. The spring primary period was March 14 through March 27 before rainbow trout spawning began. The summer primary period was from May 31 to June 13 after rainbow trout spawning but before the onset of base discharge. The autumn primary period was October 1 to October 14 concurrent with the beginning of brown trout and mountain whitefish spawning. Each primary survey occasion was associated with a resight period that included all observations that occurred between the last day of the primary survey occasion of interest and the first day of the next primary survey occasion.

Individual encounter histories were constructed from tagging events and relocations that occurred from March 15, 2014, to May 30, 2018. All relocations of tagged fish were assigned to one of the three geomorphic regions of the Smith River watershed by performing a spatial join between relocations and stream layers. Encounter histories of individual fish were constructed separately for each geomorphic region the fish occupied and indicated whether a given tagged fish was observed during secondary or resight period. The first observation of some tagged fish occurred during resight periods. The encounter histories of these fish were modified by adding an observation to the last secondary period of the primary survey period immediately prior to the resight period when each fish was initially observed. Ensuring that all encounter histories started with an observation during a primary period was necessary for model structure and assumed that tagged fish that were first observed during a resight period were alive in the same geomorphic region during the primary period immediately prior. We assumed that

adding an observation to the encounter history when the first observation was during a resight period did not bias our estimates because of the short time involved (less than three months). Mobile relocations and recaptures of fish during electrofishing surveys were included as resight observations. Mobile relocations of fish were only included as live observations if the associated fish later passed a stationary reader site or were relocated ≥ 5 km away in subsequent mobile surveys. Relocations of tags that were not in live fish were entered into encounter histories as dead recoveries (Bowerman and Budy 2012).

We used the package RMark in R (Laake 2013) to estimate survival probabilities. We ran separate models for each species in each of the three geomorphic regions. Candidate model structure (Table 4) for the nuisance parameters detection probability (p and c), availability for recapture (a' and a''), and probability of resight (r , R , and R') were based on a priori knowledge of sampling efficiency and fish behavior (Bowerman and Budy 2012). Seasonal model structures included separate parameter estimates for spring, summer, and autumn-winter. Separate parameters for winter were not estimated because too few tagged fish were detected during winter months. Candidate model structures of nuisance parameters were compared using model selection techniques with S fixed to a seasonal parameter structure and F fixed to estimated probabilities of site fidelity. The best supported nuisance model structure was determined separately for each species and geomorphic region and was used as the starting model for comparing different parameterizations of S (season, year, and constant). Estimates of survival were retrieved from the output of the model with the lowest Akaike Information Criterion (AIC) score

(Table 5). We selected the model with the greatest degree of time variation, in the event that the difference in AIC score between the two best supported models was < 2 (e.g., the season model of S would be selected over the constant model of S). We calculated annual survival as the product of the estimates for spring, summer, and autumn-winter survival. Annual survival was estimated as the constant rate of survival to the third power (S^3) in models where constant probabilities of survival were the best supported parameter structure. Standard errors and 95% confidence intervals of estimates of survival were calculated using the “deltamethod.special” function in the RMark package in R (Laake 2013).

Handling mortality and early tag loss can bias survival estimates (Raabe et al. 2014), but both are rare ($< 5\%$) within the first two to three months when fish are marked with PIT tags implanted into abdominal cavities (Gries and Letcher 2002, Skov et al. 2010, Uthe 2015). We therefore assumed that bias associated with handling mortality and early tag loss was minor, and we did not attempt to correct for it. Annual probabilities of tag loss can be substantial (0.20 to 0.31 per year; Bateman et al. 2009), especially among adult fish that probably expel tags during spawning (Meyer et al. 2011b). We assumed that probabilities of annual tag loss did not vary among species and that tag loss did not influence comparative differences in probabilities of survival because brown trout, mountain whitefish, and rainbow trout share a similar body shape and physiology. However, all of our estimates of survival are probably underestimates of true probabilities because tag loss was unaccounted for in our analyses.

RESULTS

General Patterns in Fish Movement Excluding Simulated Movements

We detected 2,838 of the 7,172 fish tagged in the Smith River watershed when they passed stationary PIT arrays. Fish that were not detected did not move past a stationary array, were not detected when they did (because of imperfect detection efficiency of our stationary arrays), or died before moving. The median number of unique detections of fish relocated at stationary arrays was three detections (25th percentile = 2, 75th percentile = 7) with some fish detected over 50 times (Figure 9). The median number of detections of brown trout and rainbow trout was two (25th percentile = 1, 75th percentile = 4), and the median number of detections of mountain whitefish was 4 (25th percentile = 2, 75th percentile = 10). We relocated 1,607 PIT tags during mobile surveys including 818 live fish (148 brown trout, 444 mountain whitefish, 226 rainbow trout). We confirmed that 737 tags were no longer in live fish (173 brown trout, 288 mountain whitefish, 276 rainbow trout), of which 332 tags (88 brown trout, 176 mountain whitefish, 68 rainbow trout) were recovered during mobile surveys of pelican nesting colonies. We could not determine if 52 tagged fish relocated during mobile surveys were dead or alive. Tagged fish were detected up to 12 times during mobile surveys, but the median number of mobile detections was one per fish (25th percentile = 1, 75th percentile = 2). The number of mobile detections per fish did not vary among species with the median and 25th percentiles being one detection per fish, but the 75th percentile of the

number of mobile detections was higher for brown trout and mountain whitefish (two) than for rainbow trout (one).

The median time at large was 351 days (25th percentile = 180 days, 75th percentile = 633 days; Figure 10), and the maximum time at large was 2,358 days (6.5 years; a mountain whitefish). The median time at large of brown trout (median = 322 days, 25th percentile = 90 days, 75th percentile = 570 days) was less than the median time at large of mountain whitefish (median = 349 days, 25th percentile = 108 days, 75th percentile = 739 days) and rainbow trout (median = 364 days, 25th percentile = 198 days, 75th percentile = 592 days). The maximum time between successive relocations of tagged fish (excluding relocations during mobile surveys) varied from less than a day to over 3.5 years but was commonly about 6, 12, or 18 months (Figure 11). Most fish had gaps between successive detections that were six months or longer (range 58 to 79%), and many fish had gaps greater than a year in duration (range 15 to 36%).

Group-Specific Patterns of Fish Movement

The proportions of fish that moved after release varied among species and tagging locations indicating that choice of species and release locations can influence results of movement studies of stream fishes. Of the 7,172 fish tagged in the Smith River watershed, 3,505 (49%) moved 0.5 km or more after they were released (2,701 observed movements, 804 simulated movements). Of the 2,822 fish tagged in the main-stem Smith River, most (1,864; 66%) moved after they were released (Figure 12, left panel). The proportions of mountain whitefish and rainbow trout that moved were similar (minimum

= 58%, maximum = 77%); smaller proportions of brown trout moved (minimum = 38%, maximum = 55%). Fish tagged in tributaries of the Smith River moved proportionately less than did fish tagged in the main stem (1,641 of 4,350 fish tagged in tributaries moved ≥ 0.5 km, 38%) regardless of which geomorphic region they were tagged in (Figure 12, right panel; Table 6); the difference was greatest among brown trout and rainbow trout. Mountain whitefish tagged in tributaries also moved less than those tagged in the Smith River, but the difference was less pronounced than among brown trout and rainbow trout. Among brown trout and mountain whitefish, fish tagged in the canyon geomorphic region moved more than fish tagged in the headwaters or prairie geomorphic regions regardless of whether they were tagged in the main-stem Smith River or a tributary. However, the proportions of rainbow trout that moved were similar across all three geomorphic regions.

The proportions of fish that occupied multiple geomorphic regions varied by species and tagging location (Figure 13, panels A, B, and C). Across all three geomorphic regions, fewer than 10% of fish tagged in tributaries occupied multiple geomorphic regions. Among fish tagged in the Smith River in the canyon, 22% of mountain whitefish moved among multiple geomorphic regions, but less than 10% of brown trout or rainbow moved among multiple geomorphic regions (Figure 13, panel B). Thirty-five to 43% of rainbow trout and 5 to 29% of mountain whitefish tagged in the headwaters or prairie geomorphic regions of the main-stem Smith River occupied multiple geomorphic regions. Of brown trout tagged in the Smith River in the headwaters and the prairie, 10% or less occupied multiple geomorphic regions.

The proportions of tagged fish that moved between the Smith River and at least one tributary also varied by species and tagging location (Figure 13, panels D, E, and F). Among fish tagged in tributaries, 55% of mountain whitefish tagged in the canyon region and 45% of brown trout tagged in the headwaters region moved into the Smith River. Less than 25% of all other groups of fish tagged in tributaries out-migrated to the Smith River. Among fish tagged in the Smith River, 48% of rainbow trout tagged in the headwaters, 43% of rainbow trout tagged in the canyon, and 31% of mountain whitefish tagged in the canyon moved into tributaries; smaller proportions of all other groups of fish tagged in the Smith River moved into tributaries. Interchange among the Smith River and tributary habitats was most common among rainbow trout tagged in the Smith River as they moved into tributaries to spawn. Mountain whitefish also frequently moved into tributaries to spawn, but many mountain whitefish also moved into the lower reaches of tributaries in late spring and remained there until early autumn, probably to avoid stressful thermal conditions in the main-stem Smith River.

Spatial Patterns of Fish Movement

Movements by fish linked distant parts of the watershed. Tagged fish moved across 426 km of unfragmented stream network including the upper regions of tributaries and into the adjacent Missouri, Dearborn, and Sun River watersheds. The length of stream traversed varied by species and by whether fish were tagged in the Smith River or in a tributary (Figure 14). The distributions of lengths of stream travelled by tagged fish were leptokurtic; most fish moved over relatively short distances and decreasing numbers of fish travelled farther. Bimodal movement patterns (e.g., mobile versus stationary) were

not evident among any species in the Smith River watershed. Depending on species, 28 to 52% of fish tagged in the Smith River traversed 5 km or more of the stream network, and 6 to 15% traversed 30 km or more. Smaller proportions of fish tagged in tributaries traversed 5 km or more of the stream network (7 to 30%) compared to fish tagged in the Smith River. Although rare, some individuals of all three species traversed > 100 km of stream network. Eighteen rainbow trout traversed more than 100 km of the stream network including multiple rainbow trout from the upper reaches of the Sheep Creek watershed that moved up to 150 km into the lower canyon and the prairie. A rainbow trout tagged in the Missouri River downstream of the confluence of the Smith River moved 111 km upstream into the Smith River watershed to spawn in Tenderfoot Creek. Only four brown trout traversed more than 100 km of stream network; three of these were tagged in Hound Creek, later moved into the Missouri River, and were then detected in the Dearborn River or Sheep Creek in the Missouri River watershed (located between Cascade and Craig, Montana—a different stream from Sheep Creek in the Smith River watershed). Twenty-two mountain whitefish traversed more than 100 km of the stream network. A mountain whitefish tagged in the Smith River near Tenderfoot Creek traversed the greatest length of stream of any fish tagged in our study (182 km). This fish left the Smith River in 2015, travelled through the Missouri River to the Sun River, and then returned to the Smith River the following year. This fish made similar movements again the next year suggesting that it travelled about 300 km annually.

The volume of movements varied across the watershed and was greatest along the main-stem Smith River in the Canyon geomorphic region and the lower reaches of Sheep

and Tenderfoot creeks (Figure 15). Volume of brown trout movement was 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. The volume of brown trout movement was relatively uniform across the watershed.

Mover diversity was greatest in the Smith River and lowest in the upper reaches of tributaries (Figure 16). The probability that two fish passing through a given stream segment were from different tag groups was greater than 0.9 along much of the length of the Smith River and Sheep Creek. Mover diversity was high in many areas of the Smith River watershed where the volume of movement was relatively low. Mover diversity was greatest among mountain whitefish and least among brown trout. Mountain whitefish mover diversity was elevated along the Smith River from Hound Creek in the prairie upstream through the canyon to Sheep Creek. Rainbow trout mover diversity was greatest along the Smith River within the canyon from Rock Creek to Sheep Creek and up Sheep Creek to Moose Creek. Brown trout mover diversity was greatest in the Smith River within the canyon downstream of Rock Creek.

Temporal Patterns of Fish Movement

Brown trout and mountain whitefish moved throughout the Smith River watershed during the spring, but the volume of movements was relatively low (Figures 17 and 18). However, rainbow trout moved more during the spring than during any other season (Figure 19), with the greatest volume of movement in the canyon where fish from

throughout the watershed moved into tributaries to spawn, especially Tenderfoot Creek and Sheep Creek; many moved into the upper reaches of Sheep Creek near Moose Creek. Volume of movement by brown trout remained relatively low throughout the summer except for a small increase in portions of the canyon. Volume of movements of mountain whitefish increased in the summer between Rock Creek and Tenderfoot Creek as they moved into the lower portions of tributaries with the onset of warm water temperatures and base discharge levels. Movements of brown trout during the autumn suggested fish spawned throughout the watershed, but the slight increase in volume downstream of Rock Creek and Big Birch Creek suggested that those creeks were used for spawning disproportionately. Mountain whitefish moved throughout the canyon and into the lower portions of tributaries during the autumn and appeared to spawn both in tributaries and in the main-stem Smith River. Volume of movement by rainbow trout was generally low during the autumn. All three species were sedentary during the winter.

Periods of increased fish movements occurred from spring through autumn (Figure 20) and were associated with species-specific spawning periods, moderate water temperatures, or both (Table 8). Mean weekly water temperature of the Smith River was strongly associated with movements of mountain whitefish and rainbow trout. Model selection indicated that water temperature was also related to movements of brown trout (Table 7), but confidence limits of coefficient estimates slightly overlapped zero (Table 8). Absent the influence of spawning timing, movements of brown trout, mountain whitefish, and rainbow trout were greatest when the mean daily water temperatures of the Smith River at the USGS gauge downstream of Sheep Creek were 11.7, 15.3, and 13.5

°C, respectively (Figure 21). These temperatures corresponded to mean temperatures across the watershed of 11.0 (range 7.6–13.7 °C), 14.0 (range 10.4–17.0 °C), and 12.5 °C (range 9.0–15.4 °C) and were associated with weekly counts of fish moving past stationary arrays that were 2 to 3 times the weekly counts of fish moving past stationary arrays when water temperatures were near 0°C. Movement at the warmest temperatures was greater than near 0°C but less than at moderate water temperatures. Despite inclusion in the most supported models (Table 7), we found no significant relationship between discharge and movements of brown trout and rainbow trout (Table 8). Species-specific spawning timing was associated with increases in movements of mountain whitefish and rainbow trout, but not brown trout. Water temperature, discharge, and species-specific spawning periods collectively explained much of the observed timing and magnitude of fish movements (coefficient of correlation between fitted and observed values: brown trout = 0.81, mountain whitefish = 0.91, rainbow trout = 0.88).

Fish from the Smith River moved into Sheep Creek in 2017 in response to water temperatures that exceeded 26.0 °C for over 4 hours (maximum = 27.4 °C, duration = 4.75 hours, Figure 22). No fish had been observed at the lower Sheep Creek array for four days 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 2 days after temperatures exceeded 26.0 °C. Water temperature at the lower Sheep Creek array varied from 0.1 °C warmer to 2.1 °C cooler than the water temperature of the Smith River at the USGS gauge downstream of Sheep Creek during this period, which was the only time we observed sustained water temperatures greater than 26.0°C at the USGS

gauge and was the only time we observed a pulse of movement into a tributary concurrent with an increase in water temperature of the Smith River.

Spatial and Temporal Patterns of Survival

Annual geomorphic region fidelity was never less than 0.903 (Figure 23) and was highest in the canyon geomorphic region (0.958 to 0.987). Regional fidelity differed only among rainbow trout and was lower in the headwaters and prairie than in the canyon. Geomorphic region fidelity of mountain whitefish was higher in the canyon than in the headwaters, but overlapped with the prairie estimate. Brown trout geomorphic region fidelity was high across all three geomorphic regions. Twenty-five to 36% of some groups left the geomorphic region in which they were first observed over the course of the 4-year study despite high annual probabilities of geomorphic region fidelity.

Annual survival probabilities varied among geomorphic regions and species (Figure 24), but were highest among mountain whitefish in the canyon (0.54) and headwaters (0.51, Table 9). Survival probabilities of brown trout and mountain whitefish were highest in the canyon and the headwaters; survival of rainbow trout was highest in the canyon and lower in the headwaters. Survival of all three species was lowest in the prairie. Survival probabilities varied seasonally among all three species and were generally highest in the autumn (Figure 25, Table 10). Survival of rainbow trout in the prairie and canyon was lower in the spring and summer than in autumn indicating that adverse environmental conditions present during the late spring and the summer contributed to increased mortality. Stress associated with spawning was probably

unrelated to decreases in survival of rainbow trout in the prairie during the spring because almost all spawning by rainbow trout occurred in tributaries in the canyon. Survival of mountain whitefish during summer in the headwaters and prairie was lower than in the canyon, where seasonal differences in survival were not apparent. Survival of brown trout was relatively consistent across seasons except in the headwaters where survival was highest in autumn.

DISCUSSION

Spawning, feeding, and refuge drove movements of fish in the Smith River watershed to access spatially heterogeneous resources (Schlosser and Angermeier 1995), albeit differentially among species. All three species moved to spawn. Rainbow trout from throughout the watershed moved to spawn in Tenderfoot and Sheep creeks, where almost all spawning by rainbow trout occurred. The Tenderfoot Creek watershed is remote, undeveloped, has experienced relatively little anthropogenic disturbance compared to the rest of the Smith River watershed (Ritter 2015), and is therefore largely unaffected by levels of sedimentation that could affect the survival of salmonid embryos and juveniles (Chapman 1988, Kaufmann and Hughes 2006); only a few road crossings induce sediment delivery. Groundwater and hyporheic discharge are also unaltered; areas of upwelling that provide thermally moderated water to embryos in redds are abundant. Tenderfoot Creek therefore provides excellent spawning and nursery habitat (Ritter 2015). The rainbow trout population of the Smith River watershed is almost certainly dependent on Tenderfoot and Sheep Creeks, and maintenance of their habitat, water quality, and connectivity with the Smith River system are therefore critical. Mountain whitefish spawned in the lower portions of these and other tributaries, as well as in the main-stem Smith River in the canyon and headwaters. 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. Brown trout rarely made watershed-scale movements to spawn, generally making short movements within or to tributaries (Ritter 2015) or within the main-stem Smith River.

However, movements of brown trout into Rock and Big Birch creeks suggested that those two creeks were used for spawning more frequently than other portions of the watershed; some brown trout tagged in the upper Sheep Creek watershed moved 80 km to spawn in Big Birch Creek.

Some movements > 10 km may have been fish exploiting prey that were seasonally more available in different portions of the watershed, but the distances moved to access potential food sources appeared to vary by species. Similar to whitefish in other watersheds, whitefish in the Smith River moved into tributaries during the spring when discharges were elevated (Baxter 2002). Elevated discharge has been associated with increased food availability (Colvin et al. 2009, Uthe 2015), and movements of fish into tributaries during the spring may be to access seasonal pulses of food resources. Rainbow trout tagged in Sheep Creek and Tenderfoot Creek moved throughout the watershed, with the probable intent to find habitats with higher food availability. Movement to food rich habitats can result in higher growth rates and increased reproductive potential (Brönmark et al. 2014). Brown trout did not move frequently to access food resources. However, some brown trout tagged in upper Sheep Creek appeared, based on subsequent spawning movements, to be from as far away as Big Birch Creek. These individuals may have moved into and remained in upper Sheep Creek after finding suitable habitat and abundant food there. Juvenile Atlantic salmon moved about 20 km among different food patches, but benthic species in the same stream moved less (Rasmussen et al. 2009). Species-specific differences in feeding movements are most likely associated with differences in metabolic optima, size at maturity, and diet preferences.

Movements into refuge habitats were apparent among all three species during early summer and again in late autumn. Increases in the volume and frequency of movement of all three species occurred in late June and early July in all years before the onset of base discharge levels and high water temperatures. Volume of movement during early summer was greatest in the canyon between Tenderfoot Creek and Sheep Creek. Fish in this section frequently entered the lower portions of Tenderfoot Creek, Rock Creek, or Sheep Creek and remained there throughout the summer. Fish that did not enter tributaries generally did not move during summer, indicating that they occupied suitable refuge habitats in the main-stem Smith River. Many fish also moved in the late autumn after spawning by mountain whitefish and brown trout, presumably to overwintering habitat (Ritter 2015). These movements preceded freezing water conditions in the Smith River and its tributaries. Interactions between surface waters and groundwater create dynamic thermal landscapes such as small, hyporheic seeps and tributary junctions that fish can use to avoid exposures to potentially harmful water temperatures (Power et al. 1999, Torgersen et al. 1999, Armstrong et al. 2013, Dugdale et al. 2016); fish in the Smith River watershed appeared to use both. Connectivity allows fish to move among different habitats as conditions change, and movements into cool refuge habitats allow coldwater species to persist in the Smith River where summer water temperatures can exceed normal metabolic optima. Local adaptation also helps fish survive periods of extreme water temperatures (Verhille et al. 2016); fish in the Smith River watershed are probably adapted to the local thermal regime. The ability for fish to move into thermal

refuge habitats will become increasingly important as streams continue to warm at rates that may exceed the ability of fish to adapt to new thermal regimes.

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 much longer than those in smaller, headwater streams and streams with barriers to movement (Young 1996, Bunnell et al. 1998, Young 1999). Warmwater inland fishes such as pallid sturgeon (*Scaphirhynchus albus*) and Colorado pikeminnow (*Ptychocheilus lucius*) historically traversed long reaches of main-stem rivers (Bestgen and Hill 2016, Jordan et al. 2016). Similarly, Arctic grayling and mountain whitefish evolved to move long distances from downstream reaches into headwater streams to access spawning, feeding, and refuge habitats (Pettit and Wallace 1975, Peterson and Ardren 2009). 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 ten times larger.

Most fish made watershed-scale movements (i.e., greater than typical diurnal movements); many travelled up to 10 km with lower numbers of fish travelling ever-greater distances. Individual fish have typically been categorized as “mobile” or “stationary” (or migratory and resident) as judged by study area residency or mathematically derived groupings (Rodríguez 2002, Radinger and Wolter 2014). However, we saw no evidence of distinct, bimodal stationary and mobile life-history patterns as judged by the distances travelled by tagged fish; a continuum was evident. Distances traversed in other inland watersheds are equally diverse (Fausch et al. 2002,

Baxter et al. 2004). Categorizations of animals as stationary or migratory have largely been based on studies that did not monitor movements outside of a small study area and often were based on limited and localized mark-recapture studies (Radinger and Wolter 2014), and may have been influenced by the appeal of simple and distinct categorizations such as anadromous versus landlocked life history forms. Failing to recognize the complexity of animal movements and oversimplifying life histories into mobile or stationary categories risks trivializing the ecological significance of diverse movement behaviors. Researchers designing studies of animal movements should carefully choose appropriate field and analytical techniques and empirically derive relevant descriptors of movement patterns.

Natural mortality and episodic movements undoubtedly led to underestimates of the proportions of fish that moved in the Smith River watershed because some fish died before moving. Most tagged fish that were detected at stationary arrays were not detected for six months or more between relocation events, as many fish appeared to move at seasonal or annual intervals. Natural mortality that occurred prior to when individuals would have undertaken seasonal watershed-scale movements may account for a substantial portion of tagged fish that appeared to not move during our study. Therefore, fish movements longer than typical daily movements (i.e., > 0.5 km) are probably undertaken by the majority of fish in the Smith River watershed that survive to sexual maturity (two to five years; Brown 1971). Our study of large numbers of fish over multiple years suggests that the paradigm that only small proportions of fish move at watershed scales is an artifact of the short durations of most movement studies (Radinger

and Wolter 2014). Moreover, we are unaware of any studies that addressed the influence of natural mortality on observed movements.

Movement patterns revealed both critical movement corridors and partial barriers to movement (Quinn 2005, Berger et al. 2008, Lindström et al. 2014). Identification of movement corridors where the volumes of movements and mover diversity are greatest facilitates 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 and mover diversity were greatest in the main stem and lower reaches of major tributaries of the semi-wilderness canyon geomorphic region. Whereas habitat degradation can make movements among suitable habitats difficult (Hansson et al. 2014), the pristine nature of the canyon maintains natural hydrologic processes that sustain complex habitats and connectivity (Elosegi et al. 2010) allowing fish to move to habitats that were optimal for seasons, environmental conditions, and individual life stages (Fausch et al. 2002). Few fish therefore left the canyon, but large numbers of some groups immigrated into the canyon from the headwaters or prairie. Habitat alterations associated with land-use practices probably contributed to the low volumes of movement and mover diversity in the headwaters and prairie geomorphic regions and suggested that these areas were partial barriers to movement. Land-use activities that destabilize stream channels can decrease habitat suitability for coldwater fishes (Brooks et al. 2003). Fish appeared less willing to traverse habitats that were simplified or altered. Fragmentation of streams is therefore

more pervasive than reported as inferred from absolute barriers, because habitat alteration can create partial barriers to migration.

Periods when fish movements are frequent represent times when protection of connectivity is particularly important. Watershed-scale movements of mountain whitefish and rainbow trout were associated with moderate water temperatures that approximated physiological optima at which swimming ability, metabolic performance, and digestion are maximized (Elliott 1976, Lee et al. 2003, Armstrong et al. 2013, Verhille et al. 2016). However, spawning movements occurred at temperatures that were cooler than species-specific, physiological optima. Similarly, watershed-scale movements were not associated with stream discharges. 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. However, spawning movements of rainbow trout in the Smith River occurred concurrently with peak discharges such that we were unable to determine their separate effects on the timing of movements of rainbow trout. Movements of rainbow trout concurrent with peak discharge were probably coincidental with proximal photoperiod cues that prompted gonadal maturity and spawning (Whitehead et al. 1978, Bromage et al. 1984) that evolved to optimize timing of embryo incubation (Lucas and Baras 2001, Quinn 2005, Keefer et al. 2009). However, those cues most likely have been influenced by long-term seasonal hydrologic trends.

Periods of decreased movement identify conditions such as locally extreme water temperatures that may constitute partial barriers to movement by fish. Fish moved

infrequently during periods of stressful water temperatures in winter and summer when mean daily water temperatures were near freezing or $> 20^{\circ}\text{C}$, indicating that fish remained within thermal refuge habitats, decreased their activity, or both at such times. Fish probably moved to or near refuge habitats prior to the initiation of stressful thermal conditions. Thermal landscapes of rivers can be complex and provide fish with local habitat patches where water temperatures are moderated by groundwater inputs, channel morphology, and tributary junctions (Torgersen et al. 1999, Vatland et al. 2015). Fish move into such local thermal refuges in response to temperature extremes (Kaya et al. 1977, Power et al. 1999, Schaefer et al. 2003, Armstrong et al. 2013, Ritter and Zale 2015), and may move to distant locations ahead of anticipated events (Bentley et al. 2015). 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 $\geq 26^{\circ}\text{C}$ 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 elevated water temperatures will occur more frequently, and connectivity to thermal refuges such as Sheep Creek may be important for reducing the effects of 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). The pin and plank irrigation diversion structures common in central Montana typically do not afford fish passage; such structures could inhibit movement into upstream thermal refuge habitats during periods of elevated water temperatures (Silva et al. 2018). Installation of Denil

fishways (Benjamin Triano, Montana State University, personal communication) or temporarily opening diversion structures during periods of elevated water temperatures could enhance access to thermal refugia.

Tributary use varied by species and life stage. Although many brown and rainbow trout in the Smith River appeared dependent upon tributaries for some portion of their life cycle, fish in tributaries appeared to be less dependent upon the Smith River. Brown trout and rainbow trout tagged in tributaries generally moved less often and over shorter distances than fish 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). However, fish that leave tributary streams for river main stems may have access to food and habitats that are limited in natal tributaries (Schlosser 1995, Chapman et al. 2014). Conversely, mountain whitefish appeared to be more dependent on main-stem habitats. Most mountain whitefish tagged in tributaries used the Smith River during at least some portion of their lives and many mountain whitefish never left main-stem habitats. Spawning occurred in both tributary and main-stem habitats. Nevertheless, many mountain whitefish also temporarily moved into tributaries to access feeding opportunities, thermal refuge habitats, or to spawn (Ritter 2015).

Movements of fish across the Smith River watershed resulted in shifts in biomass that probably altered trophic interactions and nutrient cycling. Movements by fish influence the ecology of streams and adjacent riparian corridors (Wipfli and Baxter 2010) by redirecting nutrients and energy (Lance and Baxter 2011). Fish that move can change

the trophic structure of stream ecosystems by shifting competition for food and influencing nutrient cycles through excretion of nitrogen and phosphorous (Baxter et al. 2004, McIntyre and Flecker 2010). Large numbers of mountain whitefish that moved into tributaries in the spring and fed on emerging and drifting insects, intercepted insects that would otherwise have been available to riparian foragers such as spiders and birds. Movements of fish into thermal refuge habitats along the Smith River and in the lower reaches of tributaries including Tenderfoot and Rock Creeks may have influenced local primary producers through increased availability of excreted organic nitrogen and phosphorous. Spawning rainbow trout in the Smith River watershed transported nutrients and energy from lower elevation habitats into small, tributary streams. Movements of fish out of tributaries into the main-stem Smith River likewise transported nutrients and energy in the opposite direction. Trophic interactions, energy budgets, and nutrient cycles of stream ecosystems may be altered if mobile fishes are replaced by species with lower propensities to move or if barriers to movements are imposed.

Minimal annual emigration of fish from geomorphic regions in the Smith River accumulated over multiple years to result in substantial emigration. Annual probabilities of emigration were less than 10% across all species and geomorphic regions, but cumulative probabilities indicated that up to one-third of mountain whitefish and rainbow trout eventually emigrated from the headwaters or prairie into the canyon, which was used by many individuals of both species for some portion of their life cycle. For example, most rainbow trout spawned in canyon tributaries. Some emigration by mountain whitefish may have simply reflected the inherent high mobility of the species.

Genetic structure of mountain whitefish is generally less variable than that of other native species and is indicative of high rates of movement and emigration (Whiteley et al. 2006). Other inland populations of salmonids also have low seasonal probabilities of emigration, but relatively high cumulative probabilities of emigration (Bowerman and Budy 2012, Uthe et al. 2016).

Annual survival probabilities of populations in the Smith River were similar to those of other salmonids occupying main-stem habitats in western North America (Al-Chokhachy and Budy 2008, Uthe et al. 2016) but lower than in headwater streams (Budy et al. 2007, Uthe et al. 2016). However, not all headwaters are comparable; the headwaters of the Smith River occupy a low gradient, agricultural valley, similar to downstream reaches, whereas typical western headwaters (e.g., Budy et al. 2007, Uthe et al. 2016) are found in high gradient, forested watersheds. Mountain whitefish survived at higher probabilities than either brown trout or rainbow trout. Survival probabilities of mountain whitefish in Idaho were somewhat higher (0.63–0.91) and populations included individuals over 10 years old (Meyer et al. 2011a). High annual survival and longevity of mountain whitefish may help explain the robust persistence of this species across much of its native range.

Summer survival probabilities of mountain whitefish and rainbow trout differed among geomorphic regions with different levels of anthropogenic alterations; survival of mountain whitefish was lower in the prairie than in the canyon and survival of rainbow trout was lower in both the prairie and the headwaters than in the canyon. Land conversion for agricultural uses is common in the headwaters and the prairie, especially

in riparian and floodplain habitats. Altered stream channels and destabilized stream banks homogenize stream habitats, diminish groundwater exchange, and elevate water temperatures (Belsky et al. 1999, Brooks et al. 2003) thereby reducing habitat suitability for coldwater fishes during summer when discharges are low and water temperatures are highest. Summer survival of brown trout, which are more tolerant of high temperatures than mountain whitefish or rainbow trout (Carline and Machung 2001, Bear et al. 2007, Brinkman et al. 2013), did not vary among geomorphic regions.

Survival was not lower during species-specific spawning periods than during other seasons (except perhaps among rainbow trout in the prairie, but they did not spawn there), probably because associated metabolic costs and levels of stress were low in this system. For example, post-spawning mortality of steelhead that migrated short distances into coastal rivers was lower than among populations that migrated long distances to spawn inland (Keefer et al. 2008). Similarly, rainbow trout in the main-stem canyon moved relatively short distances to spawn in canyon tributaries and few brown trout made long distance spawning movements. Whitefish do not select for specific spawning substrates (Pierce et al. 2012, Boyer et al. 2017) and therefore could spawn throughout the watershed. Low metabolic investment associated with spawning appears to have minimized post-spawning mortality among Smith River fishes.

Survival and site fidelity of all three species were both high in the canyon. Site fidelity of terrestrial organisms has been associated with high habitat quality and reproductive success (Lurz et al. 1997, Hoover 2003). Fish in the Smith River that occupy habitats where probabilities of survival are high are influenced less by

environmental disturbances than those that occupy habitats where survival is lower, and fish densities in the canyon are almost certainly more stable than densities in the other two geomorphic regions. Movements during species-specific spawning periods indicated that the probable natal habitat of many fish that were tagged in the prairie and headwaters was the canyon. Emigration of juveniles from portions of the canyon is probably necessary for maintaining fish density and species diversity throughout the Smith River. However, the low probabilities of emigration among sub-adult and adult fish in the canyon suggest that few larger fish emigrate out of the canyon to other geomorphic regions.

The headwaters appears to be an intermediate habitat; probabilities of survival and site fidelity of mountain whitefish and rainbow trout in the headwaters were similar to or lower than in the canyon, but did not differ among brown trout. Brown trout are habitat generalists that have established self-sustaining populations well outside their native range (Klemetsen et al. 2003), which may help explain why their probabilities of survival and site fidelity did not vary. Movement between the headwaters and the canyon appeared to be particularly important for mountain whitefish and rainbow trout as both frequently moved from the headwaters into the canyon during some portion of their life cycle. Rainbow trout survival was relatively low in the headwaters, and most rainbow trout in the headwaters that spawned did so in tributaries in the canyon. Mountain whitefish frequently moved along the Smith River between Tenderfoot Creek in the canyon and just downstream of Camas Creek in the headwaters. These movements may

have homogenized the probabilities of survival among mountain whitefish in the canyon and headwaters.

The lowest probabilities of survival were in the prairie, indicating poor habitat and environmental conditions there for these coldwater species. Therefore, many mountain whitefish and rainbow trout emigrated to the canyon from the prairie at some point. Few fish passed downstream through the prairie into the Missouri River, where better environmental conditions exist. Accordingly, the prairie probably forms a partial barrier to migration, if not an ecological trap. Improved habitat conditions in the prairie may increase survival there and could promote higher rates of movement among the Smith River and adjacent watersheds. Despite the apparent deficiencies of the prairie, dispersal into it from the canyon may increase abundances at meta-population scales and enhance the fitness of individual fish through release from density dependent regulation (Pulliam 1988, McMahon and Matter 2006). Relationships between site fidelity and habitat quality can be difficult to identify because of interactions among habitat quality, habitat heterogeneity, density of individuals, and social behaviors (Lanyon and Thompson 1986, Switzer 1993, McMahon and Matter 2006). Further study is needed to understand how factors such as habitat quality influence site fidelity and survival patterns of stream-dwelling fishes.

Predation by American white pelicans contributed to mortality of fish in the Smith River watershed. Over 1,500 white pelicans nest at nearby Canyon Ferry Reservoir (King and Anderson 2005) and frequently feed on fish in the Smith River during spring and early summer. White pelicans consumed from 20 to 70% of tagged Yellowstone cutthroat

trout annually in the Blackfoot River in southeast Idaho (Teuscher et al. 2015) and recoveries of PIT tags at the Canyon Ferry nesting colony suggest that predation rates in the Smith River watershed were similar (Vivian and Mullen 2018). Pelicans elsewhere concentrate their feeding efforts on fish concentrated during spawning migrations (Scoppettone et al. 2014, Teuscher et al. 2015), but pelicans were generally not observed feeding in Smith River tributaries where rainbow trout spawned and were gone when brown trout and mountain whitefish spawned in autumn.

The movement behaviors of the salmonids in the Smith River probably are reflective of their origins. Mountain whitefish are native to the Smith River and developed diverse and mobile life history patterns compatible with the ecology and hydrology of the Smith River watershed. Rainbow trout and brown trout originated from hatchery stocks that were cultured in the late 19th century from wild populations in western North America (rainbow trout) and western Europe (brown trout; Montana Fish, Wildlife and Parks 2013, Needham and Behnke 1962, MacCrimmon and Marshall 1968). Streams in western North America were relatively pristine during the 19th century, but streams in Europe had already been influenced by deforestation, land conversion, and modifications associated with growing transportation corridors and the industrial revolution (Amisah and Cowx 2000, Roni and Beechie 2013). These activities led to declines in migratory populations of brown trout prior to their initial domestication (Klemetsen et al. 2003). The decreased propensity for brown trout in the Smith River watershed to move at watershed-scales relative to rainbow trout and mountain whitefish suggests that selective pressures against mobile life histories influenced the behaviors of

subsequent generations of brown trout in the Smith River watershed. Offspring of individuals translocated from populations with mobile life histories tend to exhibit more migratory behaviors than fish translocated from sessile populations (Jonsson 1982, Palm and Ryman 1999). Conservation measures aimed at restoring mobile life history patterns to populations affected by long-term fragmentation and loss of heritable movement behaviors may be most successful if passive measures such as the construction of fish passage structures are paired with active measures such as translocation of migratory individuals from areas where they persist. However, some naturalized populations such as brown trout in South America can develop highly mobile life histories independently in response to resource limitations (O'Neal and Stanford 2011).

Human understanding of fish movements along stream networks has differed among cultures and has changed through time. Historically, hunter-gatherer societies understood that fish can move long distances along streams. For example, Native Americans in North America created weirs along streams of the Pacific Northwest in anticipation of returning salmon (Jones 2005). However, agrarian and industrial cultures lacking a direct understanding of the ecology of fishes altered landscapes and often suppressed movements of fish along stream networks (Wilson 2015). Interest in the movement behaviors of fish grew throughout the mid twentieth century, but inadequate technology for monitoring movements led to a perception that many species moved little (Gerking 1959). This perception influenced burgeoning fisheries management policies that viewed fish populations in streams as discrete units that resided within relatively small geographic areas. By the late twentieth century, advanced methods for monitoring

the movement behaviors of fish were helping researchers to understand that existing ideas about movement behaviors of stream-dwelling fishes underestimated the true extent of fish movement along stream corridors (Pettit and Wallace 1975, Gowan et al. 1994, Schlosser and Angermeier 1995). Our expansive use of PIT technology adds to the understanding that unconstrained movements of stream-dwelling salmonids are complex, connect distant parts of stream networks, provide fish access to diverse habitats and resources, and influence population dynamics through connections among habitats with vital rates that differ.

Recognition of the effects of barriers on stream-dwelling fish populations has led fisheries and watershed managers to begin to address the problems they impose (Lucas and Baras 2001, Idaho Department of Fish and Game 2007, Peterson and Ardren 2009, Jordan et al. 2016, Osmundson and White 2017). Careful management of connectivity along river corridors preserves biodiversity while optimizing economic benefits derived from rivers (Winemiller et al. 2016). However, most restoration of connectivity is associated with highly migratory species such as Pacific salmon (e.g., Oregon plan for salmon and watersheds; State of Oregon 1997); management plans for connectivity along inland streams are rare. Efforts aimed at protecting and restoring life history patterns of inland fishes first need identification of critical movement corridors for multiple species across entire watersheds, such as the canyon geomorphic region of the Smith River. Management plans can then specify actions for protecting connectivity in critical areas where the volume of movement and mover diversity are greatest.

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. 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. Similarly, recovery efforts directed at improving or re-establishing populations of imperiled fishes may be most successful if target populations have access to sufficiently large habitats with suitable movement corridors such that they can express their full range of life history patterns (Rosenfeld and Hatfield 2006). However, many imperiled fish species are restricted to small habitats (Schaefer et al. 2003, Uthe et al. 2016) where risks of extinction and loss of genetic diversity are high (Dunham et al. 1997, Yamamoto et al. 2004). If managers can maintain or re-establish movement corridors among isolated groups of fish, then imperiled species are more likely to maintain mobile life history patterns necessary for metapopulation function and population resilience. Reintroduction efforts will have the highest probability of success in systems that have 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 socially acceptable, will allow the full range of movement behaviors present in a population, the expression of which should maximize population abundance, productivity, and persistence (Yamamoto et al. 2004, Hitt et al. 2012).

CONCLUSIONS

Watershed-scale movements by fish in the Smith River were common, diverse, and overlapped, thereby connecting distant groups of fish. Volume of movements of each species peaked at specific locations and during specific seasons. Patterns of survival also varied among species and locations, and movements throughout the Smith River watershed connected fish populations in habitats with relatively high survival, where populations were probably most stable, to habitats where survival was lower but per capita resource availability was may be higher. Studies restricted in scope to single species or seasons of interest risk mischaracterizing vital rates and the diversity of movements expressed by a fish assemblage. Accounting for the diversity and spatial extent of movement patterns expressed by all species in a fish assemblage will 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 management of highly migratory anadromous fishes, which seeks to facilitate unhindered movements.

TABLES AND FIGURES

Table 1

Species	Headwaters		Canyon		Prairie		Total
	Smith	Trib	Smith	Trib	Smith	Trib	
Rainbow trout	85	7	682	2,465	54	24	3,317
Mountain whitefish	425	5	616	1,077	212	11	2,346
Brown trout	275	71	401	323	72	367	1,509
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 (ling)	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

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

Table 2

Species	Pre-2014	2014	2015	2016	2017	2018
<i>Canyon</i>						
Brown trout	70	286	213	89	66	0
Mountain whitefish	290	863	245	107	184	0
Rainbow trout	358	2,281	258	134	116	0
<i>Headwaters</i>						
Brown trout	0	145	40	53	108	0
Mountain whitefish	0	194	0	60	176	0
Rainbow trout	0	26	4	23	39	0
<i>Prairie</i>						
Brown trout	0	387	0	26	26	0
Mountain whitefish	0	112	0	58	53	0
Rainbow trout	0	24	0	34	20	0

Table 2. Numbers of fish captured and marked with PIT tags by geomorphic region, species, and year when fish were tagged.

Table 3

Stationary array	Antenna size	$E_{in situ}$	$p_{operational}$	Observed movements (n)	Simulated movements (n)
Smith River at Truly Bridge*	Large	0.70 (0.64, 0.75)	0.96	231	92
Hound Creek*	Medium	0.96 (0.91, 1.00)	0.91	1782	75
Smith River at Merganser Bend	Large	0.66 (0.48, 0.84)	0.76	337	93
Smith River at Castle Bar	Large	0.75 (0.68, 0.81)	0.83	733	202
Tenderfoot Creek	Medium	0.98 (0.87, 1.00)	0.67	3811	67
Rock Creek*	Small	0.79 (0.67, 0.90)	0.67	284	54
Sheep Creek lower	Medium	0.78 (0.71, 0.85)	0.84	5001	770
Sheep Creek upper	Medium	0.71 (0.60, 0.81)	0.82	3097	1080
Moose Creek*	Medium	0.96 (0.91, 1.00)	0.81	4274	159
Smith River upstream of Sheep Creek	Medium	1.00 (0.95, 1.00)	0.92	995	0
Benton Creek*	Small	0.79 (0.67, 0.90)	0.70	38	8
Camas Creek*	Medium	0.96 (0.91, 1.00)	0.70	304	12
Smith River downstream of Big Birch Creek*	Medium	0.96 (0.91, 1.00)	0.86	470	19
Newlan Creek*	Small	0.79 (0.67, 0.90)	0.94	161	25
Big Birch Creek*	Small	0.79 (0.67, 0.90)	0.94	813	114

Table 3. Estimated detection efficiencies ($E_{in situ}$) of stationary PIT arrays in the Smith River watershed, the proportions of time each array was operational ($p_{operational}$), the numbers of observed movements of tagged fish, and the numbers of simulated movements of fish missed by arrays. Numbers in parentheses indicate lower and upper 95% confidence limits. Asterisks indicate sites where detection efficiencies were estimated by pooling sites with similar-sized antennas.

Table 4

Parameter	Description	Tested parameter structures
S	Probability of survival from one primary period to the next	Season, year, and constant
F	Probability that an animal remains in the study area	Fixed to values estimated from observed movements
p	Probability of detection	Session (differs among primary occasions but not within), season, and constant
c	Trap response	Assumed no trap response, $c = p$
r	Probability of dead recovery	Time varying with the first period fixed to 0
R	Probability of live resight given the animal remained alive	Time, season, and constant
R'	Probability of live resight given the animal died later in the sampling period but was not recovered	Time, season, and constant
a''	Probability that an animal is available for capture given it was available in the previous period	Time, season, and constant
a'	Probability that an animal is available for capture given it was not available in the previous period	Assumed random emigration, $a'' = a'$

Table 4. Parameters in the robust-design model used to estimate probabilities of survival. Listed with each parameter are the candidate model structures that were tested.

Table 5

Model	Number of parameters	AICc	Δ AICc	Model weight
<i>Brown trout - prairie</i>				
$S_{(.)} r_{(time)} R_{(time)} R'_{(time)} a''_{(season)} a'_{(= a'')} F_{(fixed)} p_{(session)}$ $C(= p)$	52	3,634.25	0.00	0.75
$S_{(year)} r_{(time)} R_{(time)} R'_{(time)} a''_{(season)} a'_{(= a'')} F_{(fixed)} p_{(session)}$ $C(= p)$	53	3,636.76	2.52	0.21
$S_{(season)} r_{(time)} R_{(time)} R'_{(time)} a''_{(season)} a'_{(= a'')} F_{(fixed)}$ $p_{(session)} C(= p)$	54	3,640.14	5.90	0.04
<i>Brown trout - canyon</i>				
$S_{(season)} r_{(time)} R_{(time)} R'_{(time)} a''_{(time)} a'_{(= a'')} F_{(fixed)} p_{(session)}$ $C(= p)$	19	7,946.99	0.00	0.99
<i>Brown trout - headwaters</i>				
$S_{(season)} r_{(time)} R_{(time)} R'_{(season)} a''_{(season)} a'_{(= a'')} F_{(fixed)}$ $p_{(session)} C(= p)$	45	4,824.76	0.00	0.97
<i>Mountain whitefish - prairie</i>				
$S_{(season)} r_{(time)} R_{(time)} R'_{(time)} a''_{(.)} a'_{(= a'')} F_{(fixed)} p_{(session)}$ $C(= p)$	52	4,048.75	0.00	0.99
<i>Mountain whitefish - canyon</i>				
$S_{(.)} r_{(time)} R_{(time)} R'_{(time)} a''_{(time)} a'_{(= a'')} F_{(fixed)} p_{(session)} C(= p)$	60	32,064.84	0.00	0.90
$S_{(season)} r_{(time)} R_{(time)} R'_{(time)} a''_{(time)} a'_{(= a'')} F_{(fixed)} p_{(session)}$ $C(= p)$	62	32,069.22	4.38	0.10

Table 5. Model structure and AICc values for survival models with the lowest AICc scores (Δ AICc < 7.00). Separate models were run for each species in each geomorphic region. Headings above each group of candidate models correspond to the species and geomorphic region of the reported models.

Table 5 - continued

Model	Number of parameters	AIC _c	ΔAIC _c	Model weight
<i>Mountain whitefish - headwaters</i>				
$S_{(\text{season})} r_{(\text{time})} R_{(\text{time})} R'_{(\text{time})} a''_{(\text{time})} a'_{(= a'')} F_{(\text{fixed})} p_{(\text{session})} C_{(= p)}$	62	9,103.48	0.00	1.00
<i>Rainbow trout - prairie</i>				
$S_{(\text{season})} r_{(\text{time})} R_{(.)} R'_{(.)} a''_{(.)} a'_{(= a'')} F_{(\text{fixed})} p_{(\text{session})} C_{(= p)}$	30	939.78	0.00	0.98
<i>Rainbow trout - canyon</i>				
$S_{(\text{season})} r_{(\text{time})} R_{(\text{time})} R'_{(\text{time})} a''_{(\text{time})} a'_{(= a'')} F_{(\text{fixed})} p_{(\text{session})} C_{(= p)}$	62	35,864.62	0.00	1.00
<i>Rainbow trout - headwaters</i>				
$S_{(.)} r_{(\text{time})} R_{(\text{season})} R'_{(.)} a''_{(\text{season})} a'_{(= a'')} F_{(\text{fixed})} p_{(\text{session})} C_{(= p)}$	32	1,742.13	0.00	0.48
$S_{(\text{season})} r_{(\text{time})} R_{(\text{season})} R'_{(.)} a''_{(\text{season})} a'_{(= a'')} F_{(\text{fixed})} p_{(\text{session})} C_{(= p)}$	34	1,742.38	0.25	0.42
$S_{(\text{year})} r_{(\text{time})} R_{(\text{season})} R'_{(.)} a''_{(\text{season})} a'_{(= a'')} F_{(\text{fixed})} p_{(\text{session})} C_{(= p)}$	33	1,745.24	3.11	0.10

Table 5 - continued. Model structure and AIC_c values for survival models with the lowest AIC_c scores (ΔAIC_c < 7.00). Separate models were run for each species in each geomorphic region. Headings above each group of candidate models correspond to the species and geomorphic region of the reported models.

Table 6

Model terms	Estimate	Std. Error	<i>t</i> -value	<i>P</i> -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

Dispersion parameter = 5.174, $n = 18$, $p = 8$

Deviance = 55.948 Null Deviance = 1195.770 (Difference = 1139.823)

Table 6. Coefficient estimates, dispersion parameter, and goodness-of-fit statistics for the binomial model evaluating differences in the proportions of fish that moved. Coefficient estimates and standard errors are in the logit scale. The baseline group against which all comparisons were made is brown trout in the Smith River.

Table 7

Model	QAIC	Δ QAIC
<i>Brown trout</i>		
temperature + temperature ² + discharge ²	1884.64	0.00
temperature + temperature ²	1886.97	2.32
discharge ² + year	1910.30	25.66
temperature + temperature ² + spawning	1914.70	30.06
temperature + temperature ² + discharge + discharge ²	1916.68	32.04
<i>Mountain whitefish</i>		
temperature + temperature ² + spawning	3126.58	0.00
temperature + temperature ² + discharge + spawning	3131.75	5.18
temperature + discharge + spawning	3146.53	19.95
temperature + discharge + discharge ² + spawning	3149.63	23.05
temperature + temperature ² + discharge ² + spawning	3156.57	30.00
<i>Rainbow trout</i>		
temperature + temperature ² + discharge + discharge ² + spawning + year	2086.38	0.00
temperature + temperature ² + spawning	2094.16	7.78
temperature + temperature ² + discharge ² + spawning	2100.48	14.10
temperature + temperature ² + discharge + spawning	2108.07	21.69
temperature + temperature ² + discharge + discharge ² + spawning	2137.10	50.72

Table 7. Model structure and associated QAIC values of the five best-supported models predicting the weekly number of unique tagged fish passing stationary arrays. The timing of movements was modelled separately for each species.

Table 8

Predictor	Brown trout		Mountain whitefish		Rainbow trout	
	Estimate	SE	Estimate	SE	Estimate	SE
Temperature	0.1287 (-0.0438, 0.3012)	0.0880	0.1341 (0.0432, 0.2249)	0.0463	0.1571 (0.0401, 0.2742)	0.0597
Temperature ²	-0.0055 (-0.0132, 0.0022)	0.0039	-0.0044 (-0.0083, -0.0005)	0.0020	-0.0058 (-0.0107, -0.0009)	0.0025
Discharge	--	--	--	--	-0.0137 (-0.1121, 0.0848)	0.0502
Discharge ²	-0.0011 (-0.0037, 0.0015)	0.0013	--	--	-0.0008 (-0.0053, 0.0037)	0.0023
Spawning	--	--	0.9247 (0.3728, 1.4766)	0.2816	0.5203 (0.1068, 0.9338)	0.2110
2014	--	--	--	--	0.5671 (-5.9649, 7.0992)	3.3327
2015	--	--	--	--	1.1496 (-5.3764, 7.6755)	3.3296
2016	--	--	--	--	1.0163 (-5.5138, 7.5464)	3.3317
2017	--	--	--	--	0.8068 (-5.7405, 7.3540)	3.3405

Table 8. Estimated coefficients of predictors of weekly counts of movements by PIT-tagged fish in the Smith River. Cells denoted with a double hyphen are predictors that were not supported by model selection and therefore were not included in the final models. Estimated coefficients are in natural log scale with 95% confidence limits listed in parentheses. Predictors with confidence limits that did not overlap zero were considered strongly supported.

Table 9

	<i>S_{annual}</i>	SE	95% low	95% high
<i>Brown trout</i>				
Prairie	0.16	0.012	0.15	0.18
Canyon	0.32	0.018	0.29	0.36
Headwaters	0.38	0.031	0.33	0.44
<i>Mountain whitefish</i>				
Prairie	0.38	0.030	0.33	0.44
Canyon	0.54	0.006	0.53	0.56
Headwaters	0.51	0.023	0.47	0.56
<i>Rainbow trout</i>				
Prairie	0.08	0.024	0.07	0.09
Canyon	0.39	0.010	0.37	0.41
Headwaters	0.25	0.040	0.19	0.31

Table 9. Estimates of annual survival (S_{annual}) of brown trout, mountain whitefish, and rainbow trout in the three geomorphic regions of the Smith River watershed with standard errors (SE) and confidence limits (95%).

Table 10

Season	S_{season}	SE	95% low	95% high	S model
<i>Brown trout</i>					
<i>Prairie</i>					
Spring	0.55	0.022	0.50	0.59	Constant
Summer	0.55	0.022	0.50	0.59	Constant
Autumn	0.55	0.022	0.50	0.59	Constant
<i>Canyon</i>					
Spring	0.69	0.032	0.63	0.75	Season
Summer	0.60	0.030	0.54	0.65	Season
Autumn	0.78	0.042	0.69	0.85	Season
<i>Headwaters</i>					
Spring	0.60	0.031	0.53	0.66	Season
Summer	0.64	0.032	0.57	0.70	Season
Autumn	0.99	0.004	0.99	1.00	Season
<i>Mountain whitefish</i>					
<i>Prairie</i>					
Spring	0.87	0.045	0.76	0.94	Season
Summer	0.58	0.038	0.50	0.65	Season
Autumn	0.76	0.040	0.67	0.83	Season
<i>Canyon</i>					
Spring	0.82	0.006	0.80	0.83	Constant
Summer	0.82	0.006	0.80	0.83	Constant
Autumn	0.82	0.006	0.80	0.83	Constant
<i>Headwaters</i>					
Spring	0.90	0.026	0.83	0.94	Season
Summer	0.62	0.034	0.55	0.68	Season
Autumn	0.92	0.029	0.84	0.96	Season
<i>Rainbow trout</i>					
<i>Prairie</i>					
Spring	0.30	0.070	0.18	0.45	Season
Summer	0.36	0.055	0.26	0.47	Season
Autumn	0.73	0.083	0.54	0.86	Season
<i>Canyon</i>					
Spring	0.72	0.017	0.68	0.75	Season
Summer	0.56	0.013	0.54	0.59	Season
Autumn	0.98	0.007	0.96	0.99	Season
<i>Headwaters</i>					
Spring	0.58	0.063	0.45	0.70	Season
Summer	0.55	0.069	0.42	0.68	Season
Autumn	0.77	0.059	0.64	0.87	Season

Table 10. Estimates of seasonal survival (S_{season}) and best supported model structures of S of brown trout, mountain whitefish, and rainbow trout in the three geomorphic regions of the Smith River watershed with standard errors (SE) and confidence limits (95%).

Figure 1

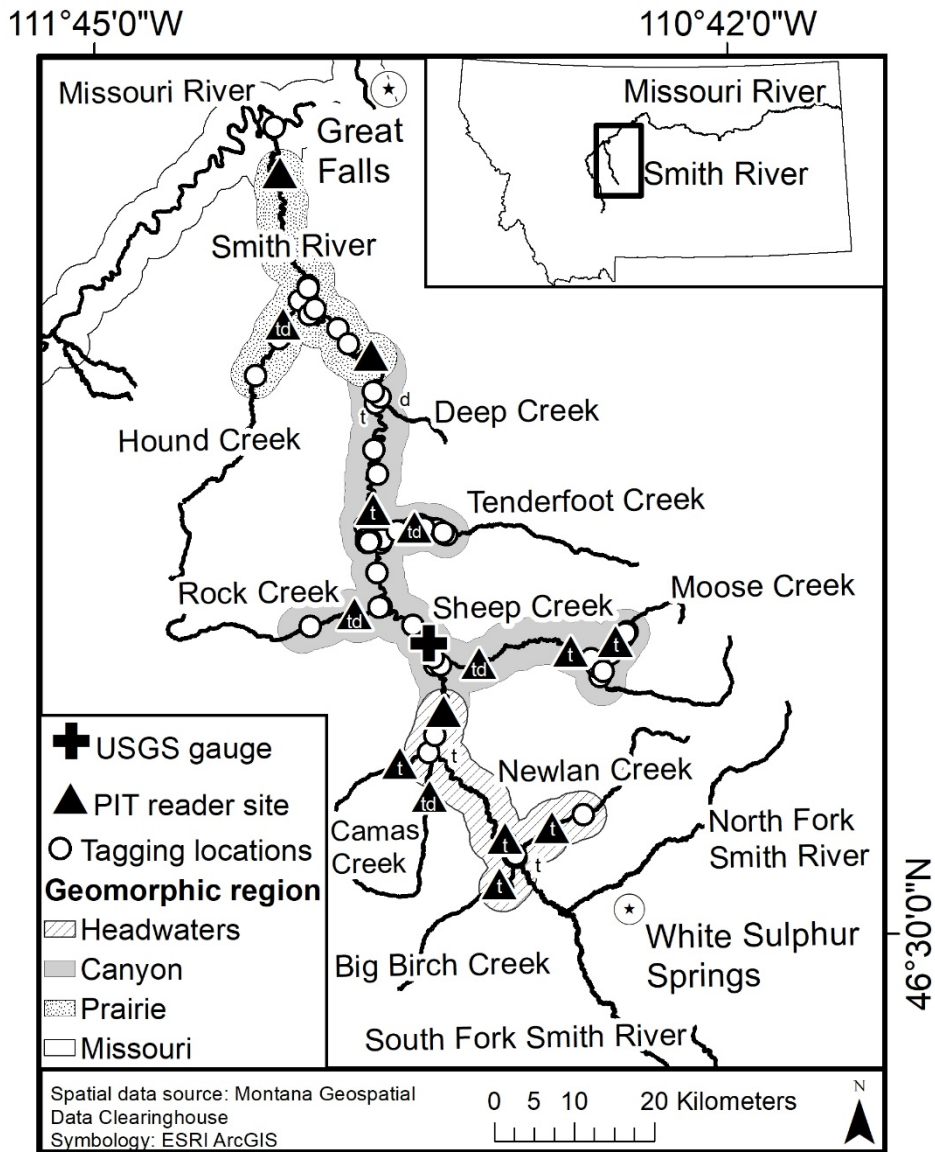


FIGURE 1. The Smith River watershed in central Montana. Shaded buffers depict areas where fish movements were monitored by stationary PIT arrays, mobile PIT array surveys, and physical recaptures. The shade of each buffer depicts the extent of each geomorphic region. Streams outside of the buffers are areas where movements of fish were not monitored because they were upstream of tagging locations, stationary PIT tag arrays, or mobile PIT tag survey reaches. Letters on reader-site symbols (▲) designate the locations of in-stream temperature loggers (t) and stream depth loggers (d).

Figure 2

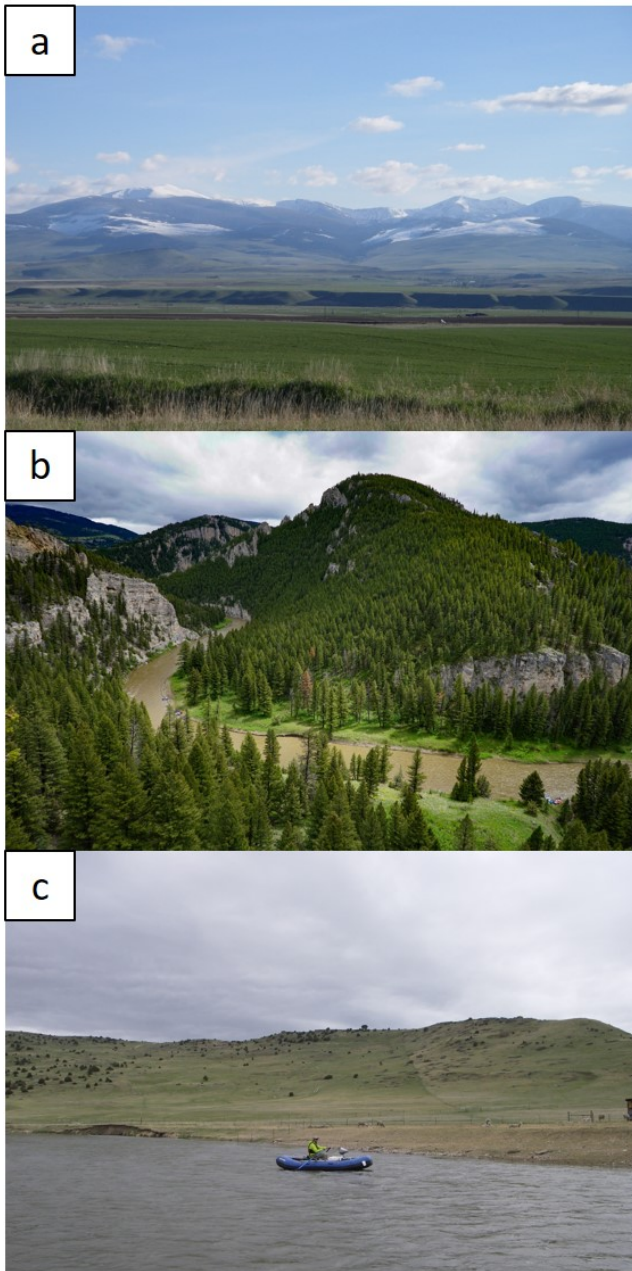


Figure 2. Photos of the three geomorphic regions of the Smith River watershed. The headwaters (a) is a broad valley bounded by mountains similar to other watersheds in the northern Rocky Mountains. The Smith River and its tributaries in the canyon (b) flow through steep timbered canyons with many cliffs exceeding 100 m. The prairie (c) region of the Smith River joins the Missouri River at the edge of the Great Plains.

Figure 3

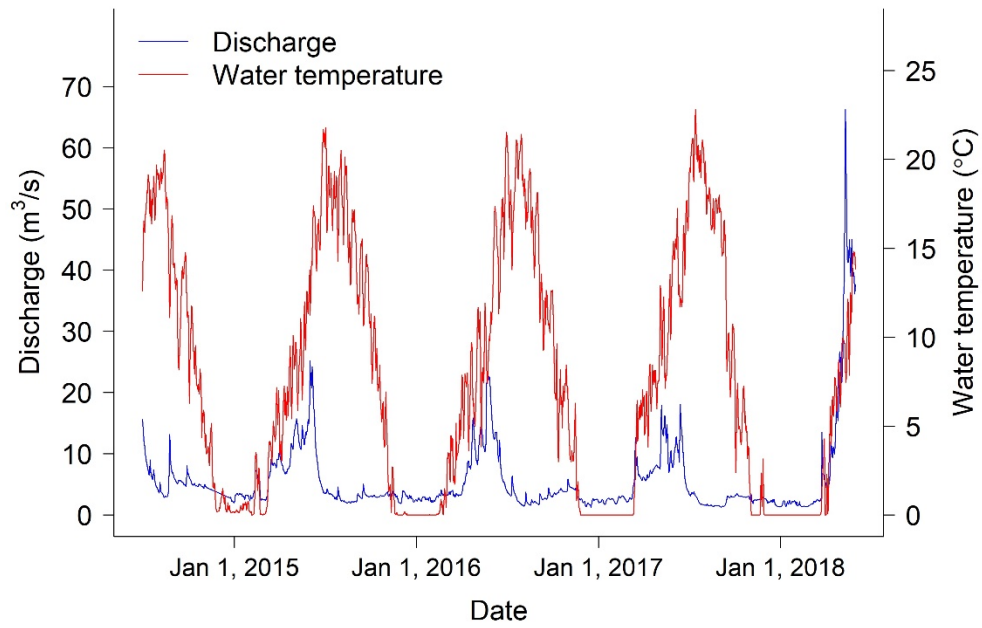


Figure 3. Mean daily water temperatures and discharges of the Smith River at the USGS stream monitoring station downstream of Sheep Creek from July 1, 2014, to May 31, 2018 (USGS station 06077200).

Figure 4

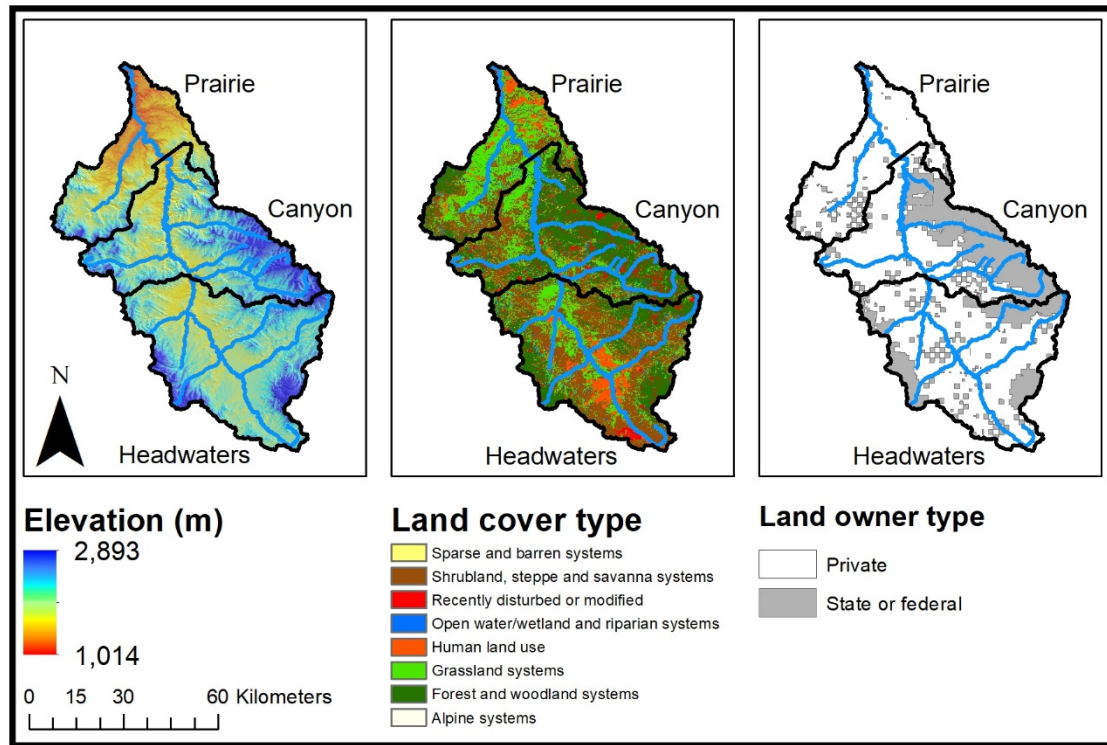


Figure 4. Elevation, land cover, and land ownership across the three geomorphic regions of the Smith River watershed. Areas outlined in black are the three geomorphic regions of the Smith River watershed, and blue lines are the stream network. Data source: Montana Geographic Information Clearinghouse (<http://geoinfo.msl.mt.gov/>).

Figure 5

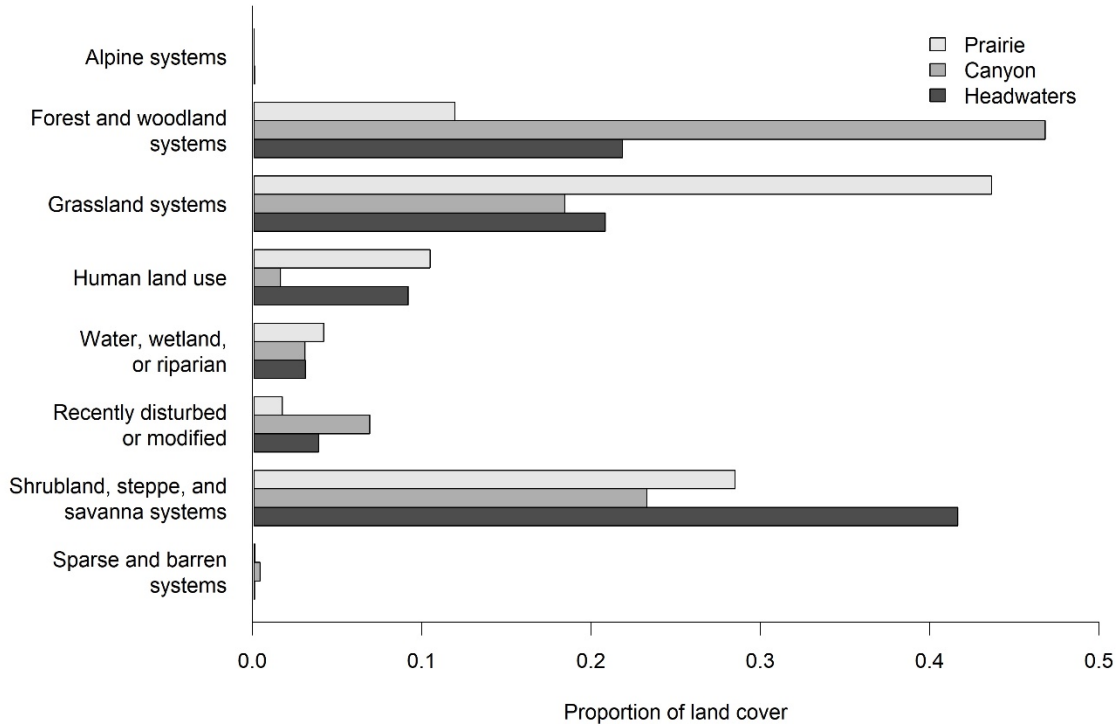


Figure 5. Proportion of land cover by type and geomorphic region across the Smith River watershed. “Human land use” predominantly indicates tilled agriculture, and “recently disturbed or modified” includes recently mountain pine beetle-killed forest stands.

Figure 6

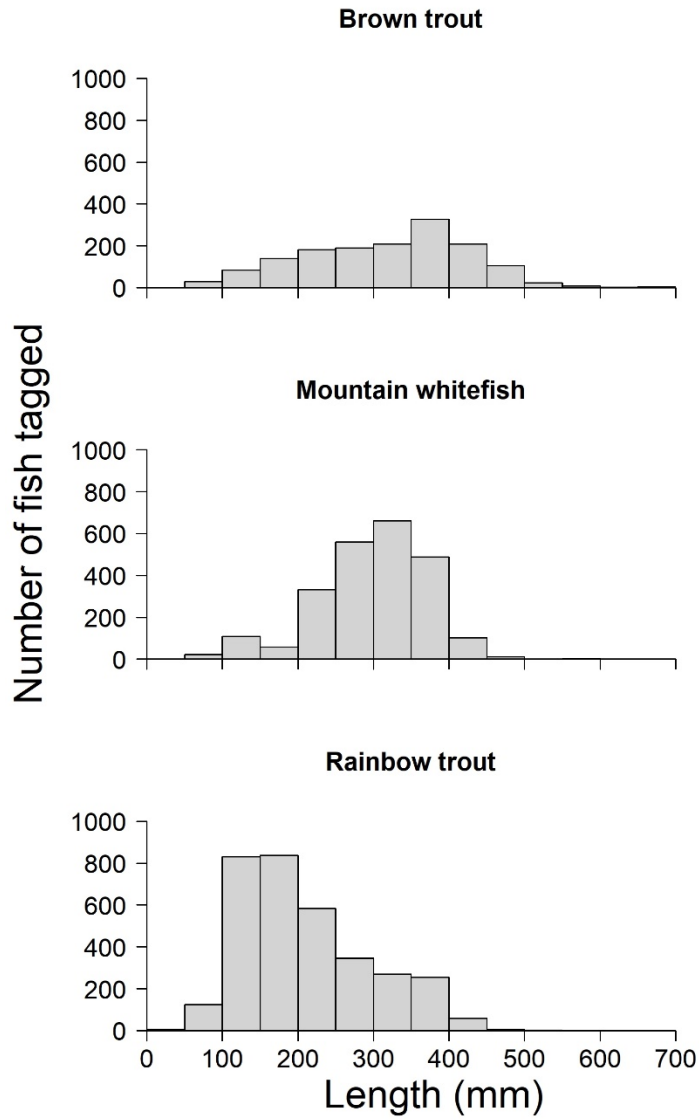


Figure 6. Length frequency distributions of fish captured in the Smith River watershed and marked with half-duplex PIT tags.

Figure 7

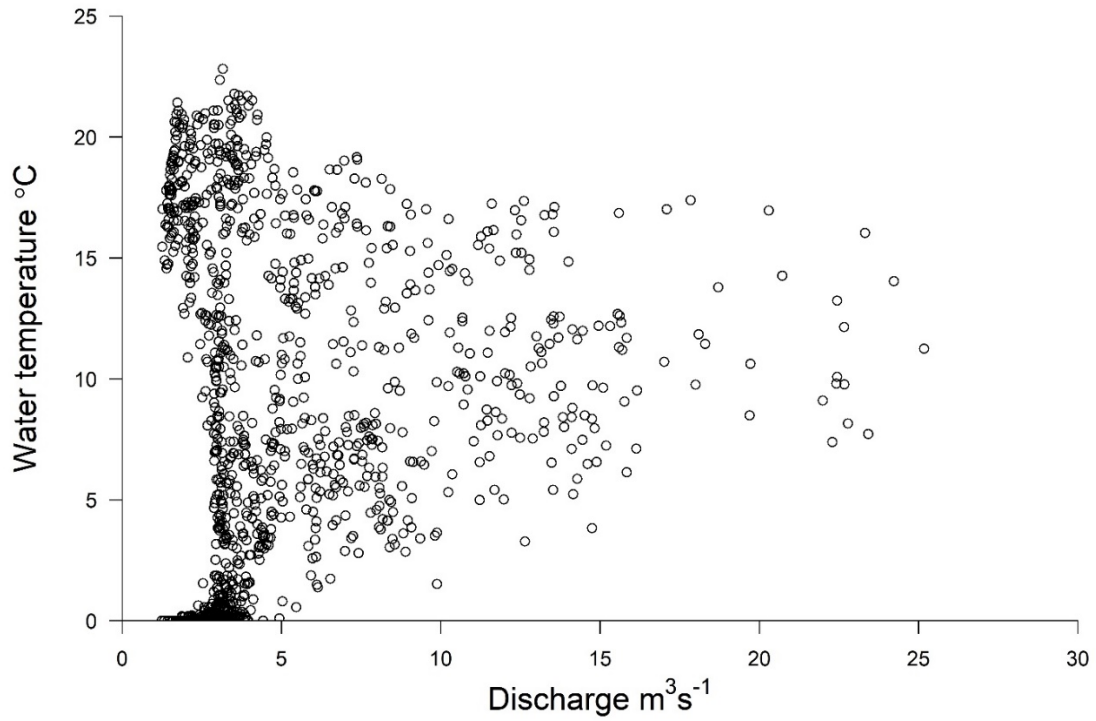


Figure 7. The relationship between discharges and water temperatures of the Smith River at the USGS gauge downstream of Sheep Creek. Each point depicts the mean daily value of discharge and water temperature recorded from July 1, 2014, to November 3, 2017.

Figure 8

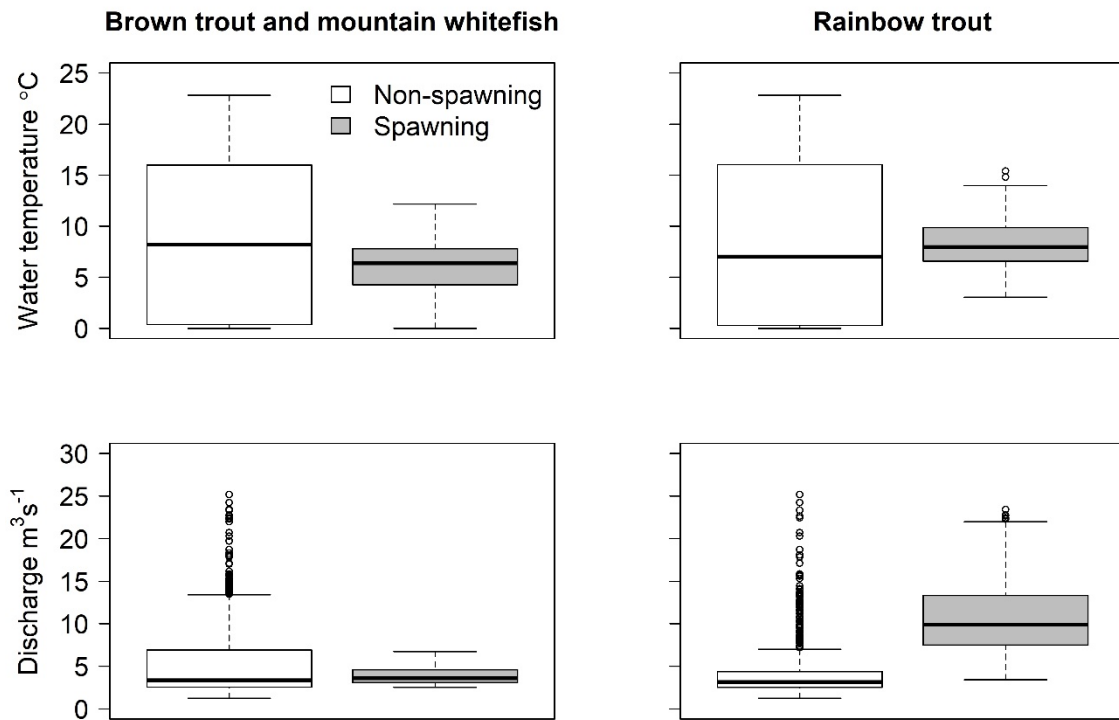


Figure 8. Box and whisker plots of water temperatures and discharges of the Smith River at the USGS gauge downstream of Sheep Creek relative to species-specific spawning periods. Gray boxes are observations during spawning periods, and white boxes are observations during non-spawning periods. Brown trout and mountain whitefish spawned concurrently in the Smith River watershed.

Figure 9

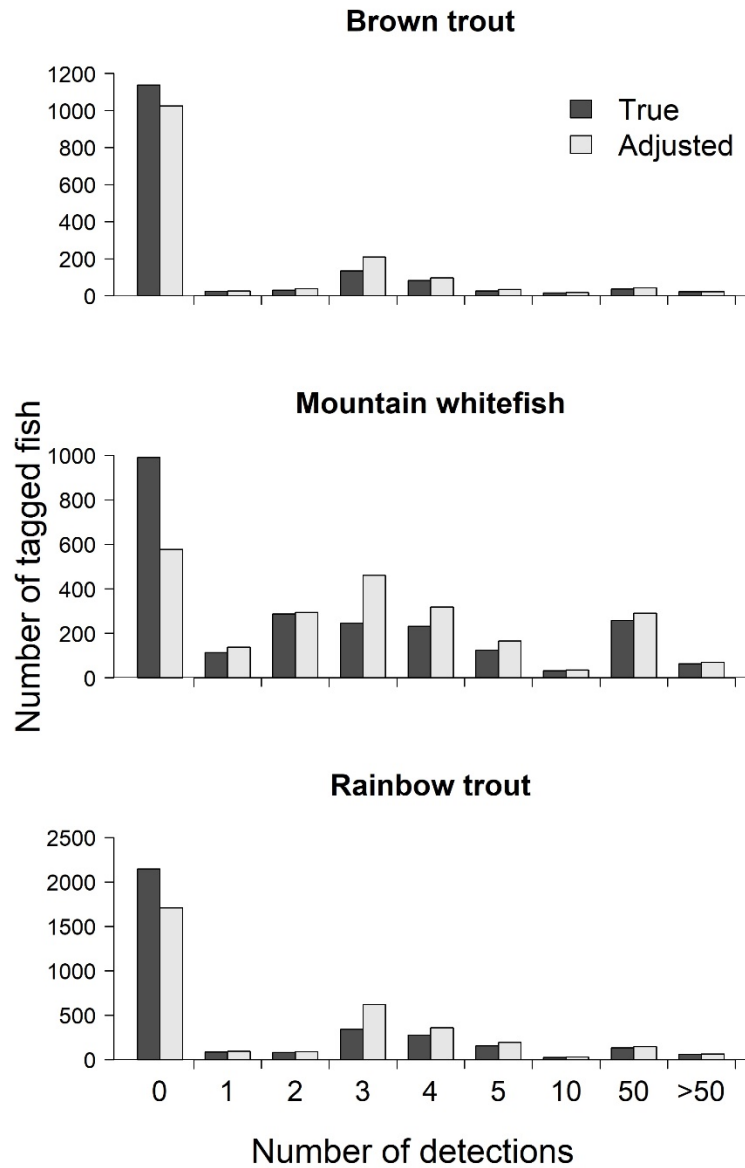


Figure 9. Frequency distributions of numbers of detections of tagged fish at stationary PIT arrays in the Smith River watershed. Bars in the zero column denote the numbers of fish not detected during the study after they were tagged and released. Dark gray bars are the true frequencies of detections, and light gray bars are the frequencies of detections adjusted to account for imperfect detection efficiencies of stationary PIT arrays.

Figure 10

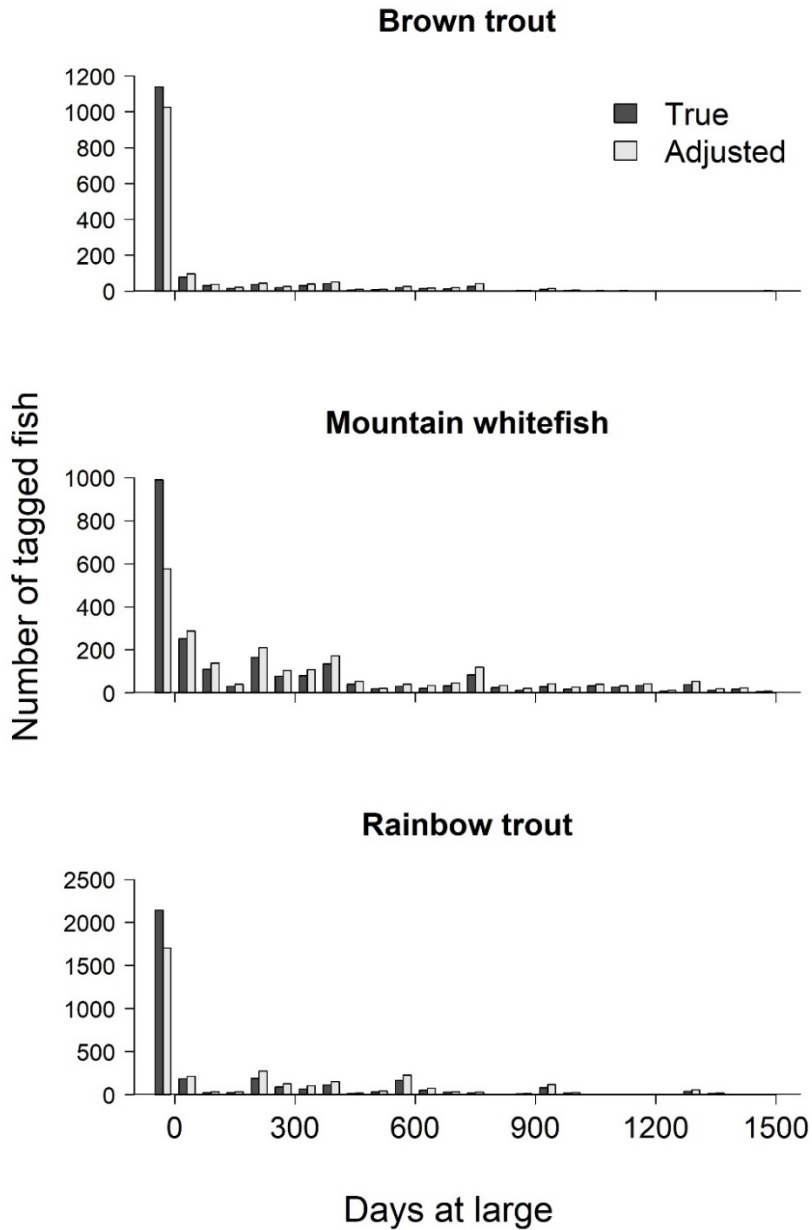


Figure 10. Frequency distributions of the numbers of days at large of fish tagged in the Smith River watershed confirmed by movements past stationary PIT arrays. Bars to the left of the zero mark are numbers of fish not detected after initial capture and release. Dark gray bars are the true frequencies of days at large, and light gray bars are the frequencies of days at large adjusted to account for imperfect detection efficiencies of stationary PIT arrays. Fish remaining at large more than 1,500 days were rare (no brown trout, 38 mountain whitefish, 3 rainbow trout) and are not shown.

Figure 11

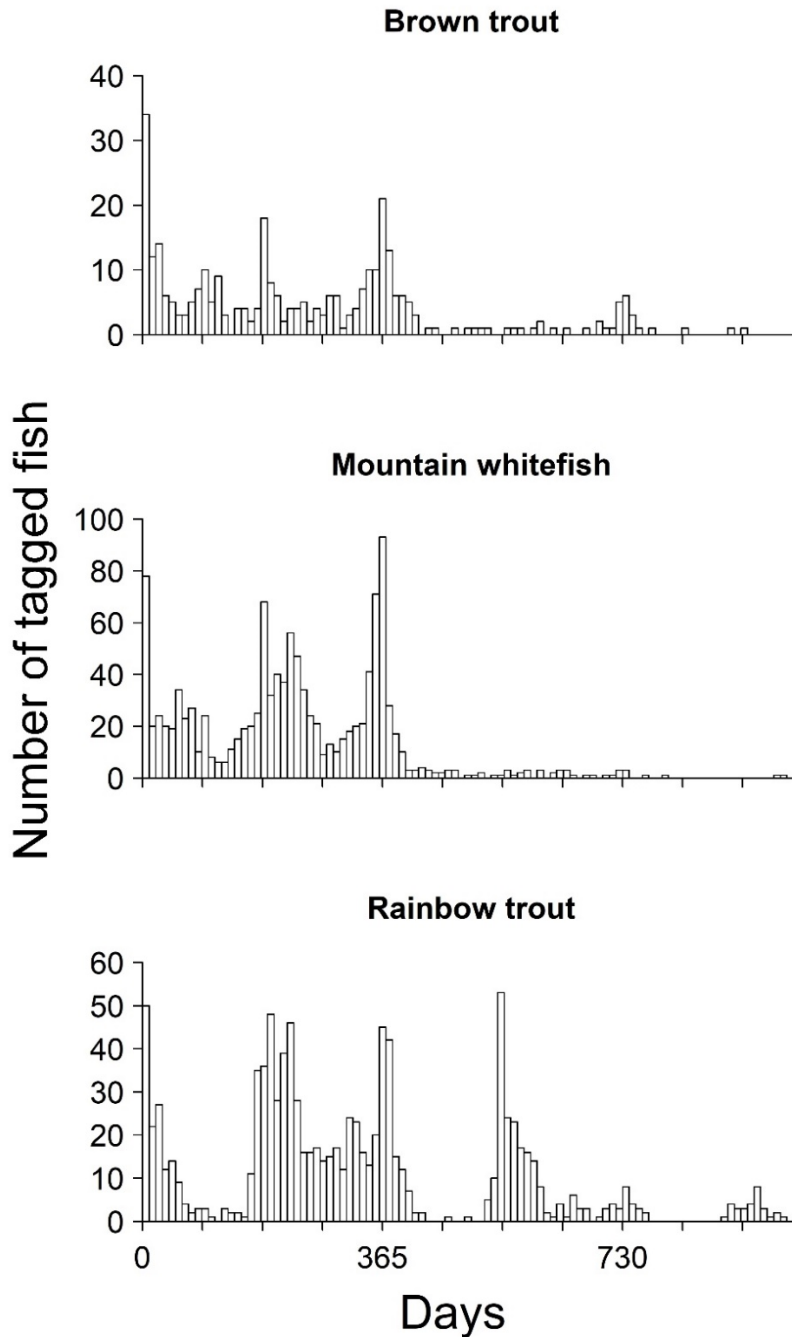


Figure 11. Frequency distributions of maximum durations between successive relocations of tagged fish detected at least once at a stationary PIT array in the Smith River watershed. Detections during mobile surveys and simulated movements past stationary arrays are excluded.

Figure 12

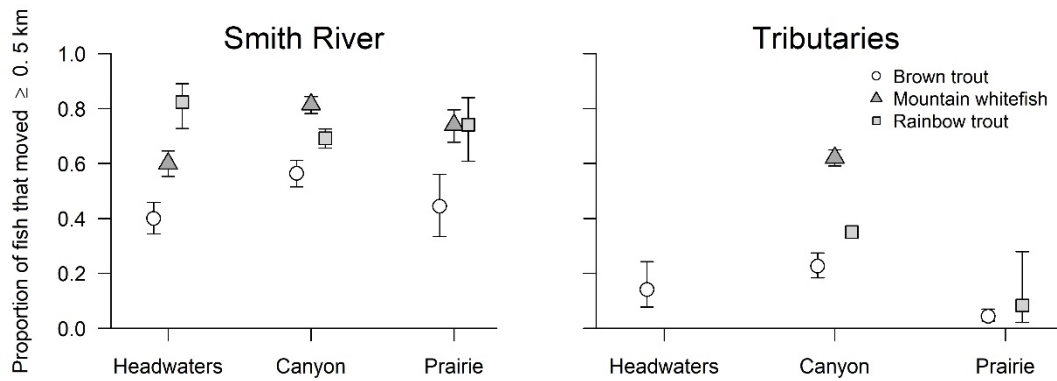


Figure 12. Proportions of brown trout, rainbow trout, and mountain whitefish that moved after tagging and release in the Smith River (left panel) or in tributaries of the Smith River (right panel) grouped by the geomorphic regions in which they were tagged. Groups represented by fewer than 20 fish were omitted (Table 1). Error bars represent 95% confidence intervals.

Figure 13

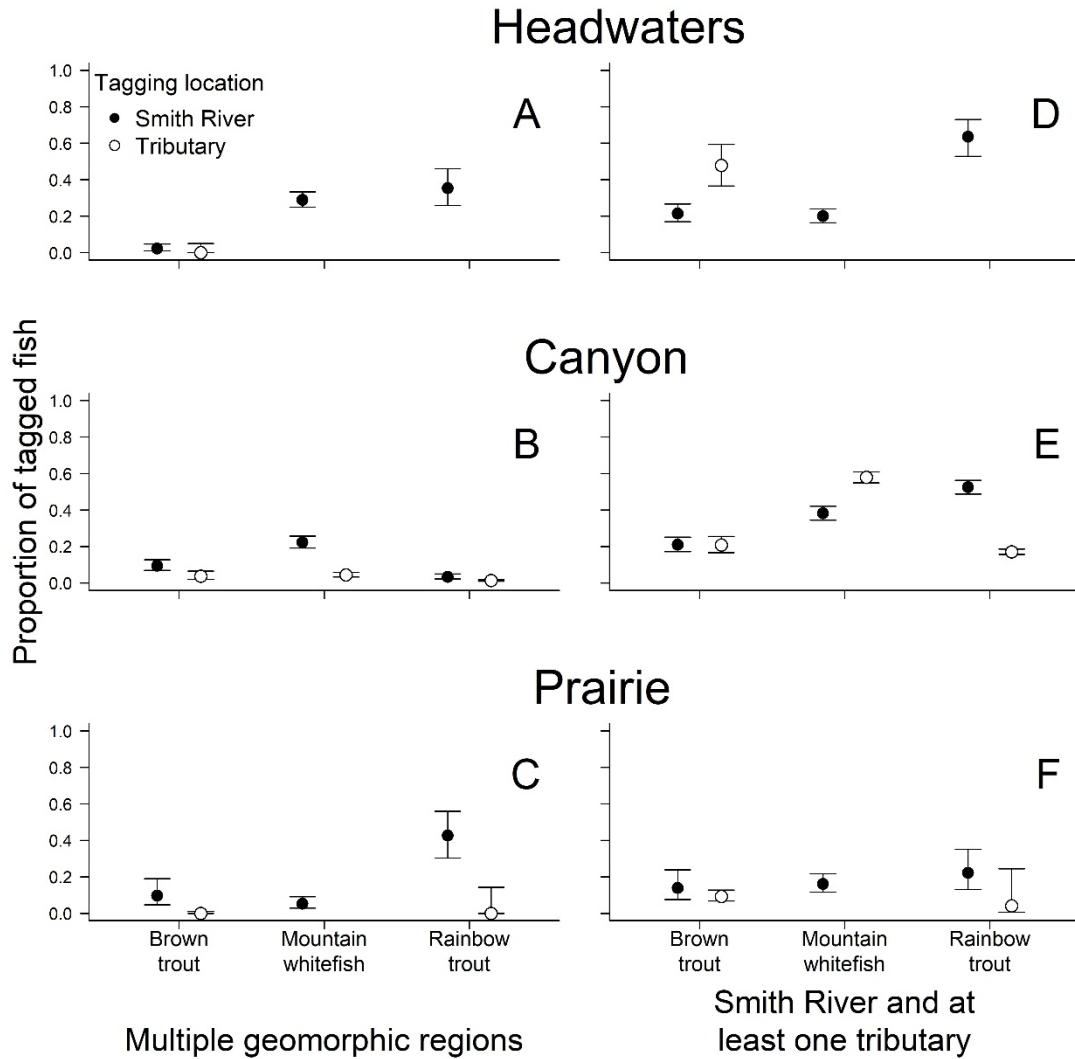


Figure 13. The proportions of tagged fish that occupied multiple geomorphic regions (left panels) and the proportions of fish that occupied the Smith River and at least one tributary (right panels). Each row of graphs represents fish tagged in the same geomorphic region. Letters in each panel correspond to in-text figure citations. Symbol fills denote whether fish were tagged in the Smith River (solid circles) or a tributary of the Smith River (open circles). Groups represented by fewer than 20 fish were omitted (Table 1). Error bars are 95% confidence limits.

Figure 14

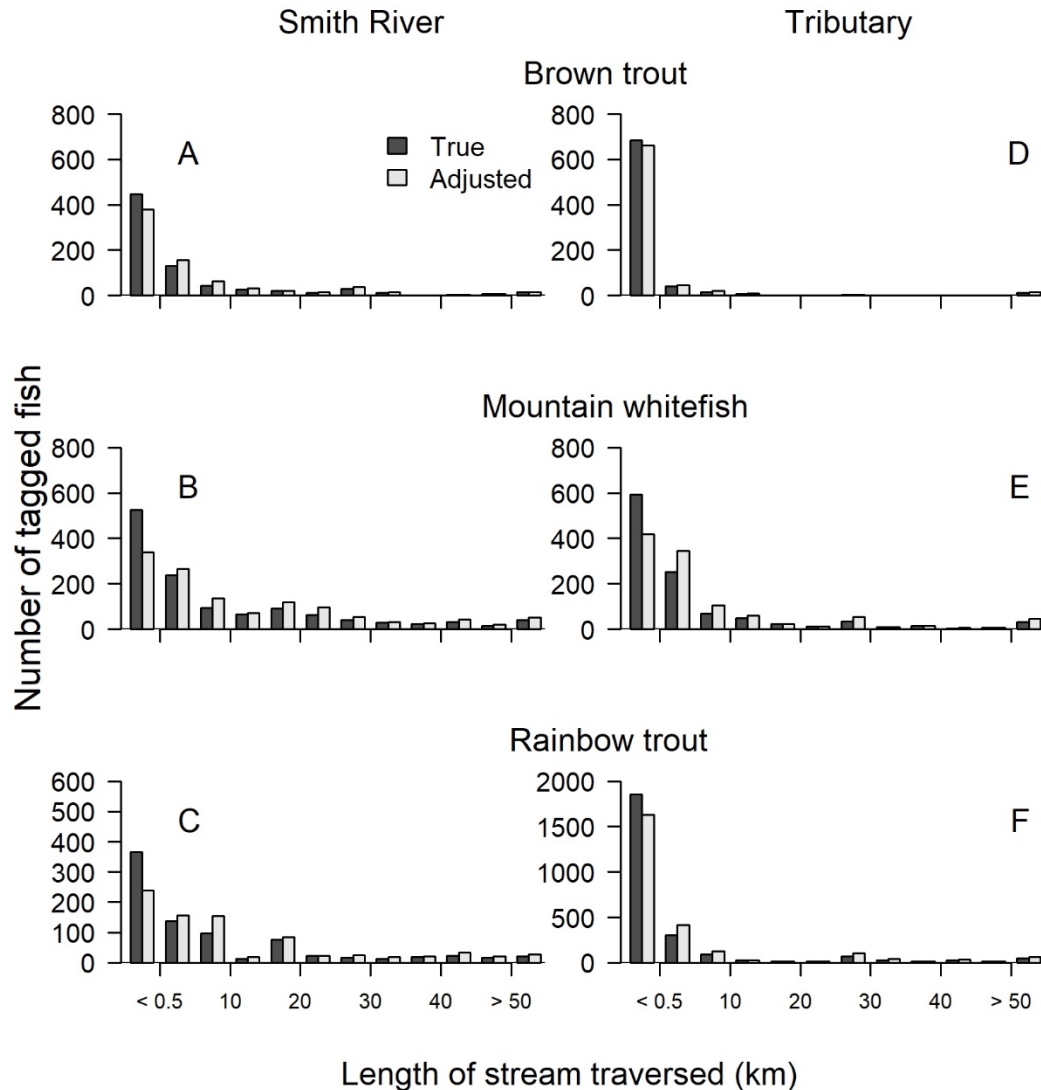


Figure 14. Frequency distributions of numbers of tagged fish that traversed minimum specified lengths of stream network (km). Panels A, B, and C represent fish tagged in the main-stem Smith River, and panels D, E, and F represent fish tagged in tributaries of the Smith River. Dark gray bars are the true frequencies of fish traversing specified lengths of stream, and light gray bars are the frequencies adjusted to account for imperfect detection efficiencies of stationary PIT arrays.

Figure 15

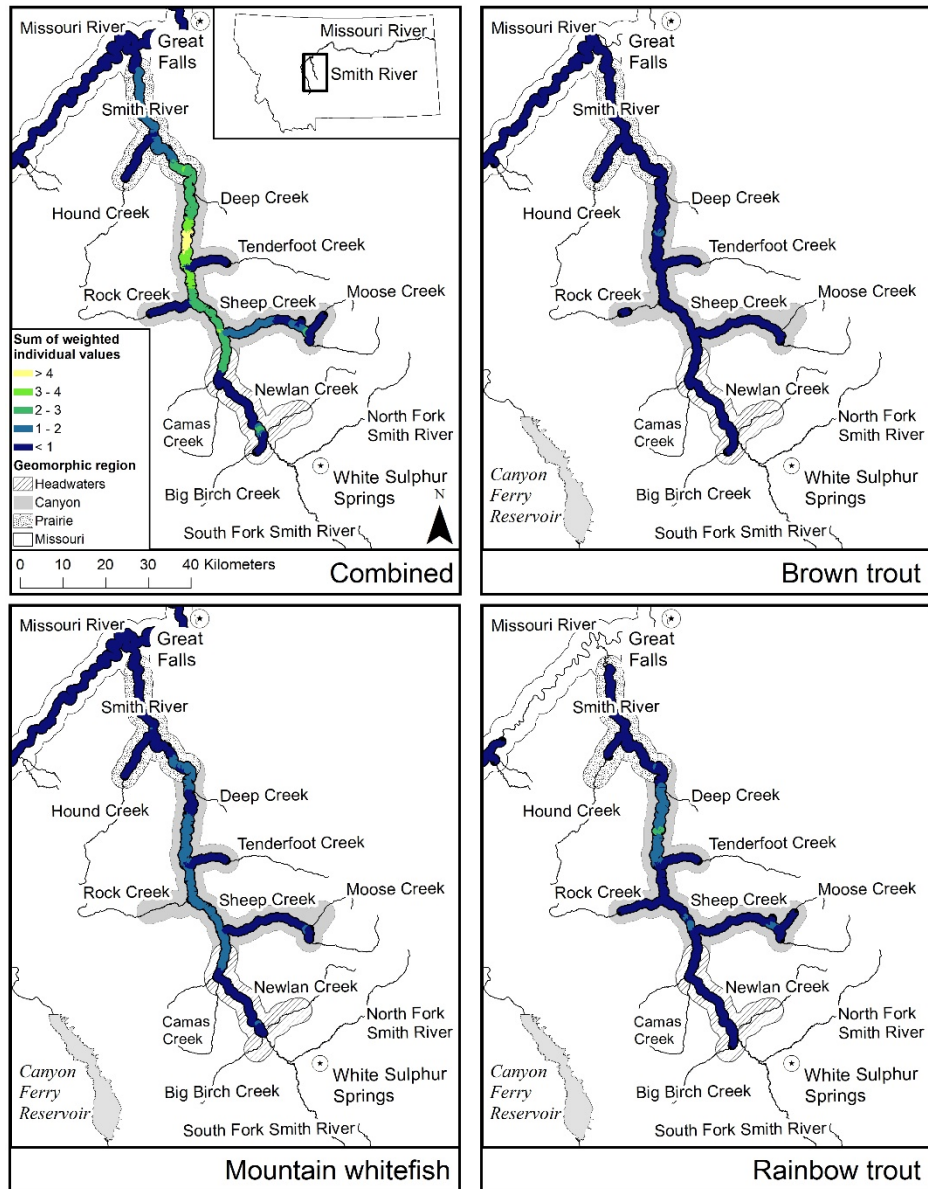


Figure 15. Volumes of movement of tagged fish in the Smith River watershed. Each panel depicts the volume of movement as the sum of weighted individual values (WIV) of fish that passed along the stream network. The top-left panel depicts the volume of movement of all three species combined, and the other three panels depict the volumes of movement of each species individually. Thin black lines are stream segments where movement was not observed.

Figure 16

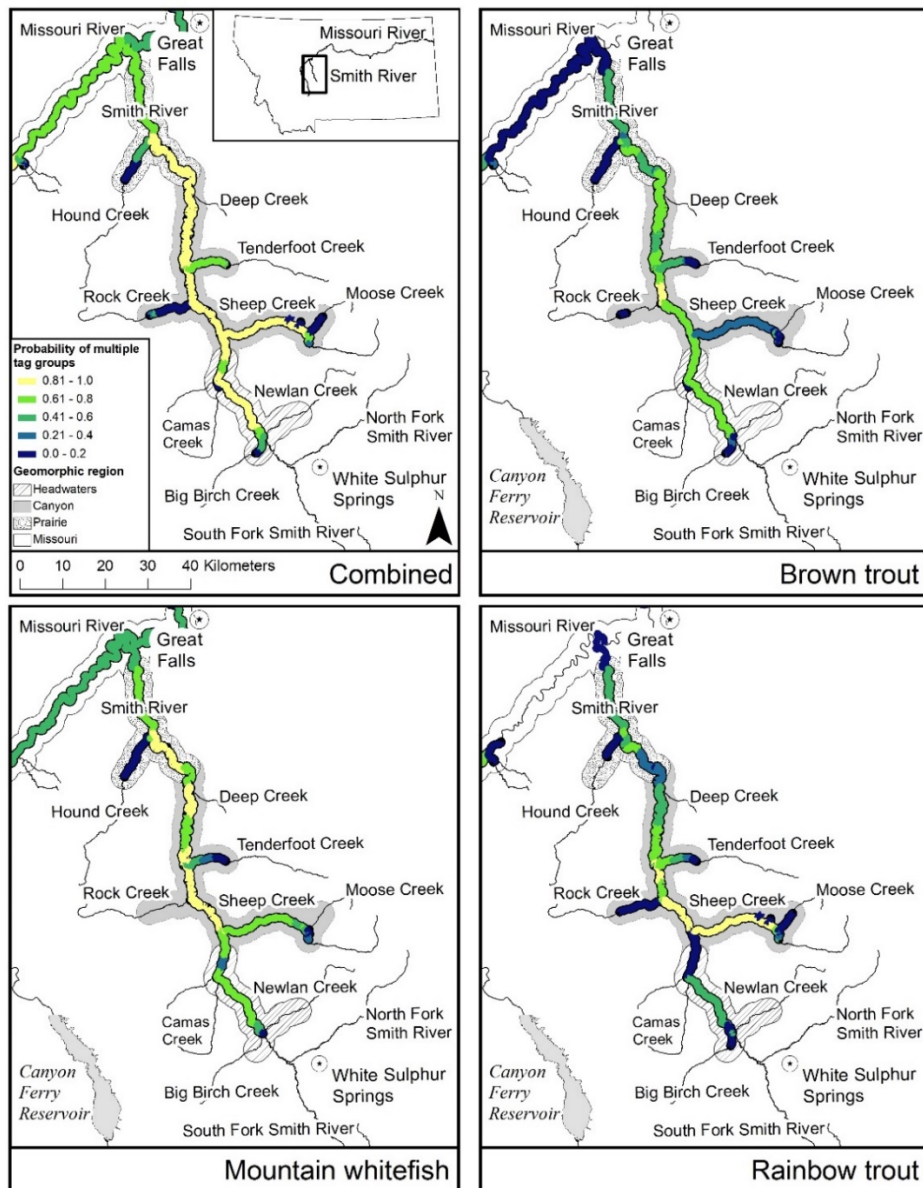


Figure 16. Mover diversity across the Smith River watershed. Shading depicts the probability that two fish passing through a given section of the stream network originated from different tag groups. A tag group consisted of all fish of the same species captured and tagged in the same 15-km stream segment at any time during the study. The top-left panel depicts the probability that passing fish came from different tag groups and includes movements by all three fish species. The remaining three panels depict the probabilities that two fish of the same species passing through a given section of stream were from different tag groups. Thin black lines are stream segments where movement was not observed.

Figure 17

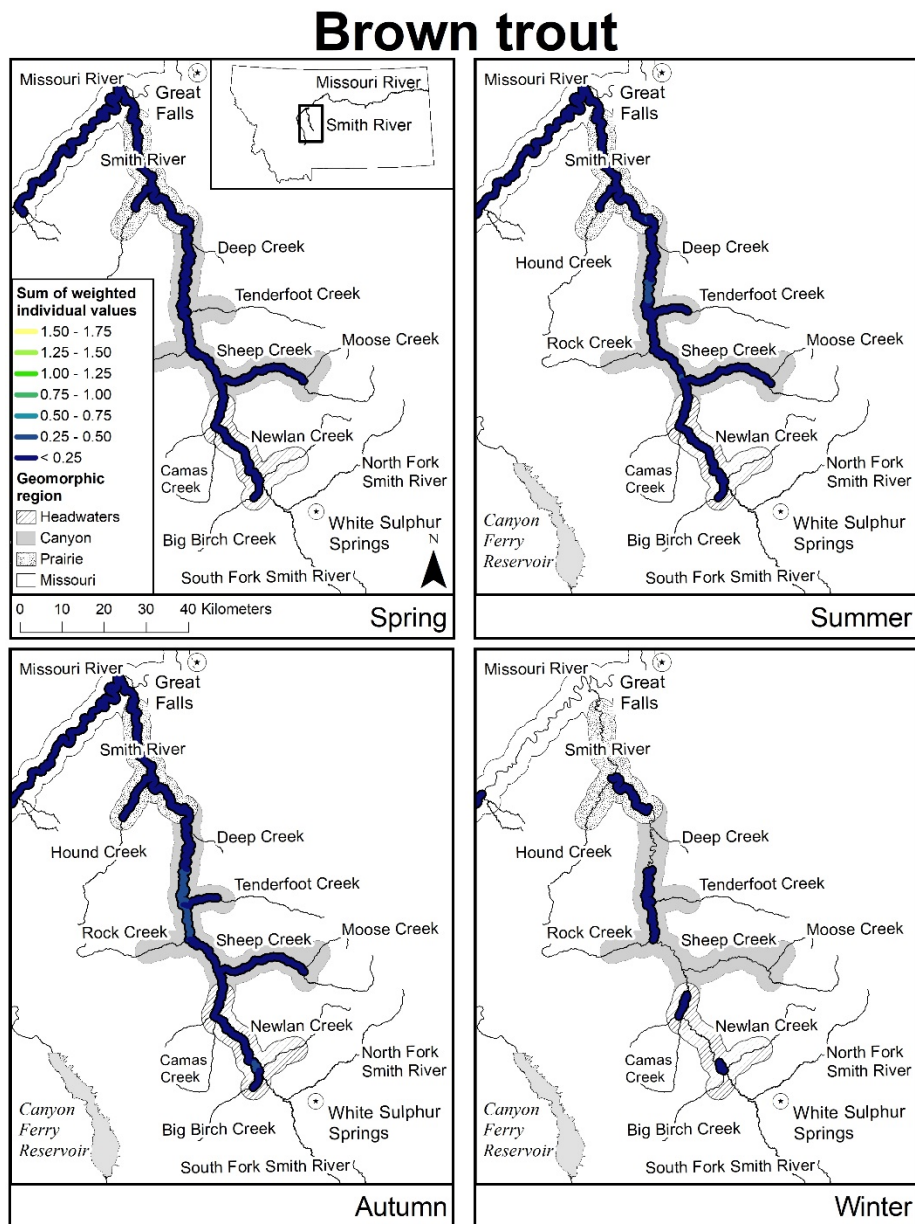


Figure 17. Seasonal patterns of the volumes of movement by brown trout throughout the Smith River watershed. Each panel depicts the volume of movement as the sum of weighted individual values (WIV) of fish that passed along the stream network. Thin black lines are stream segments where movement was not observed.

Figure 18

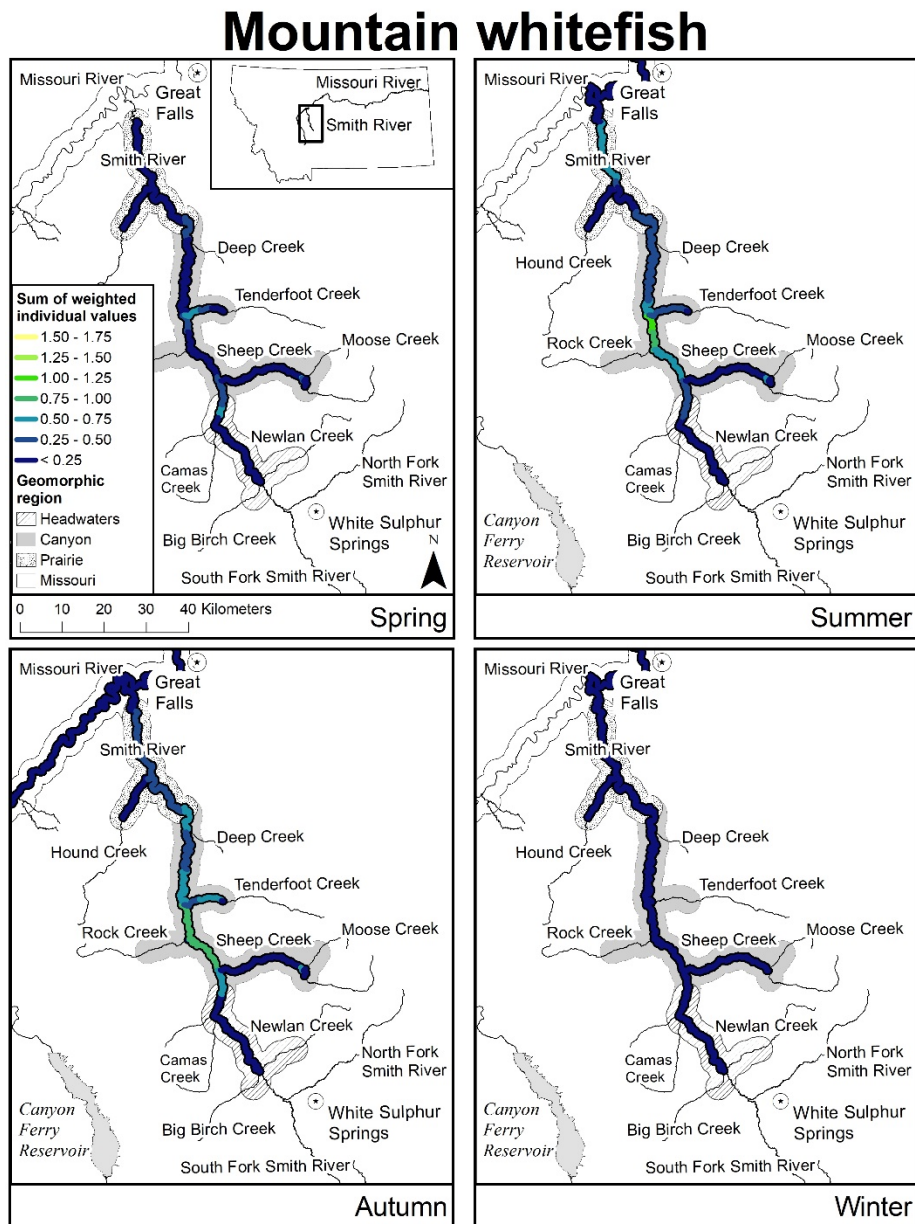


Figure 18. Seasonal patterns of the volumes of movement by mountain whitefish throughout the Smith River watershed. Each panel depicts the volume of movement as the sum of weighted individual values (WIV) of fish that passed along the stream network. Thin black lines are stream segments where movement was not observed.

Figure 19

Rainbow trout

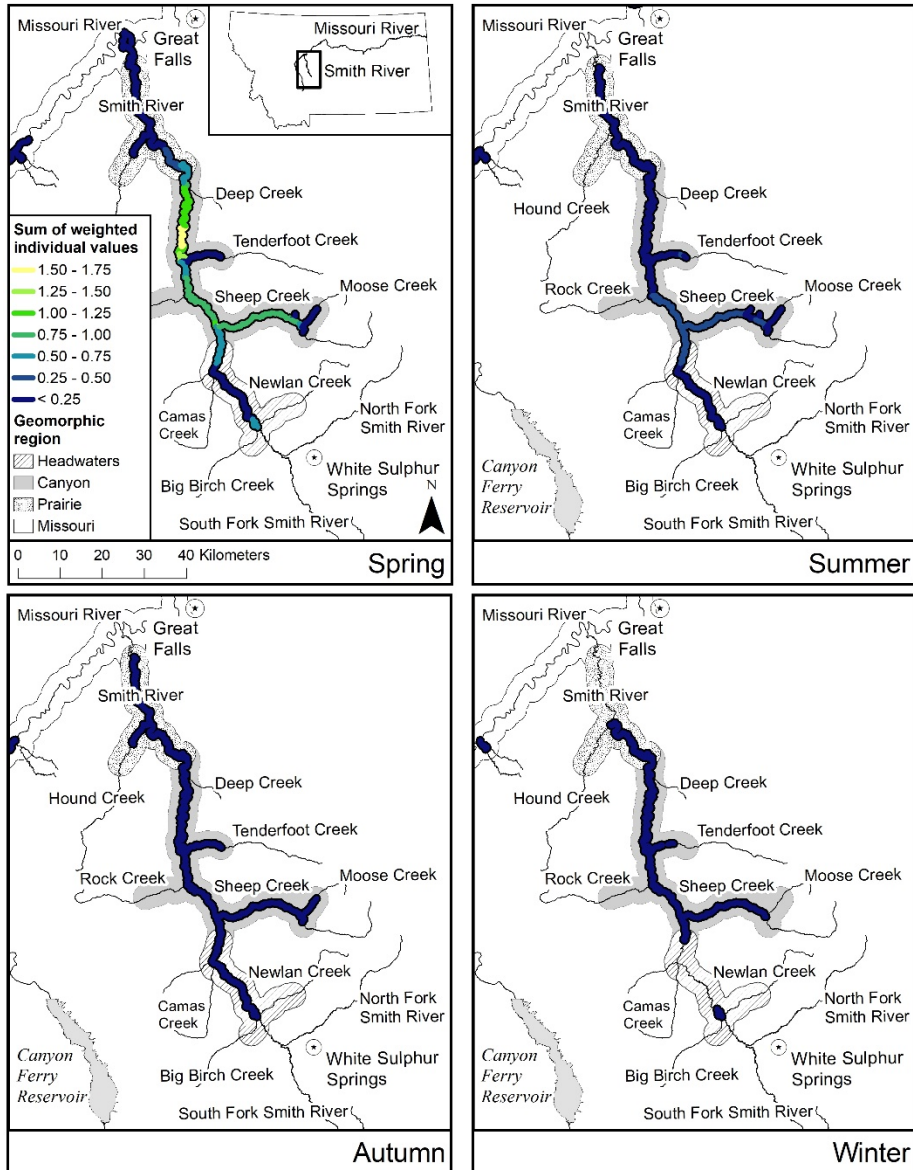


Figure 19. Seasonal patterns of the volumes of movement by rainbow trout throughout the Smith River watershed. Each panel depicts the volume of movement as the sum of weighted individual values (WIV) of fish that passed along the stream network. Thin black lines are stream segments where movement was not observed.

Figure 20

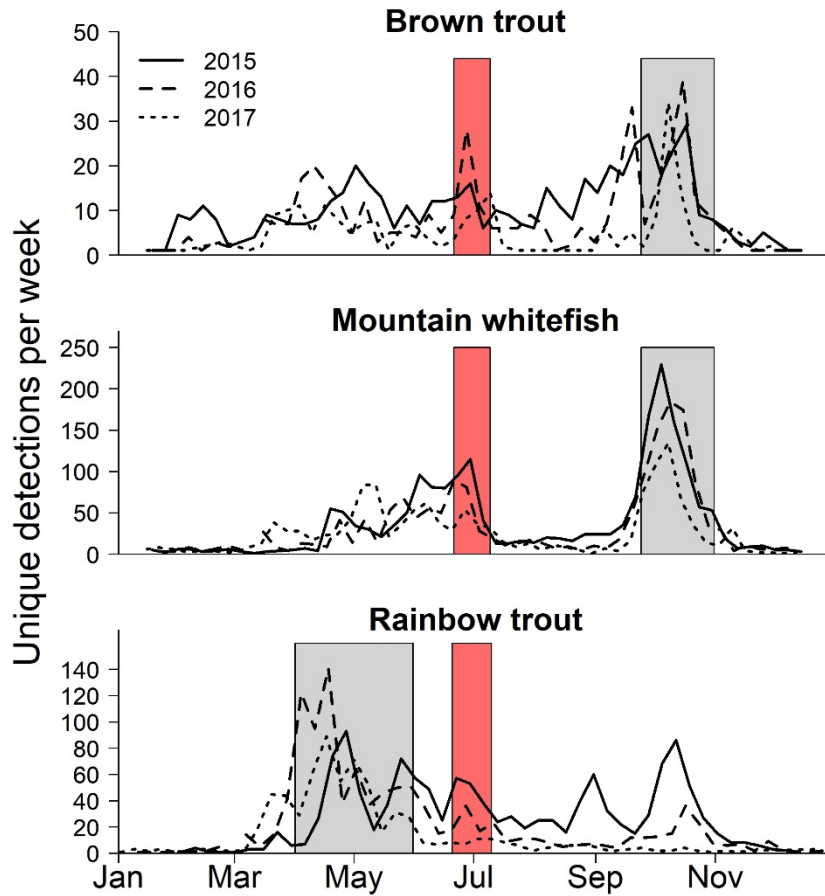


Figure 20. Observed weekly counts of unique tagged fish detected by stationary PIT arrays in the Smith River watershed, 2015-2017. Weekly counts in 2014 and 2018 were not plotted because we did not monitor movements year-round in 2014 or 2018. Shaded gray boxes indicate species-specific spawning periods. Shaded red boxes indicate periods when discharge of the Smith River decreased to base levels and water temperatures increased to peaks.

Figure 21

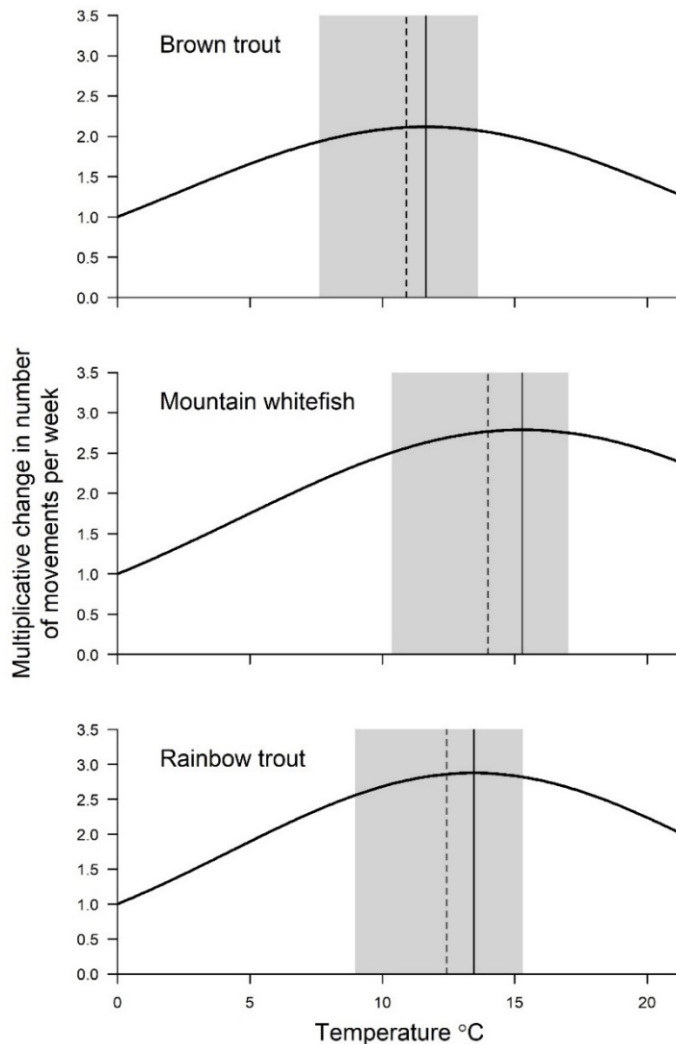


Figure 21. Predicted effects of mean weekly temperatures on the magnitude of fish movement in the Smith River. The y-axis is the estimated multiplicative change in the number of tagged fish detected moving past stationary array sites relative to when water temperature is near 0°C. The x-axis is the weekly mean water temperature of the Smith River at the USGS stream monitoring station downstream of Sheep Creek. Solid, vertical black lines represent the temperatures at the USGS monitoring station downstream of Sheep Creek at which the effect of movement was greatest for each species. The vertical dashed lines are the calculated mean water temperatures of the entire watershed and the shaded gray areas are the ranges of water temperatures across the watershed when water temperatures at the USGS station were equal to the temperatures depicted by the solid black lines.

Figure 22

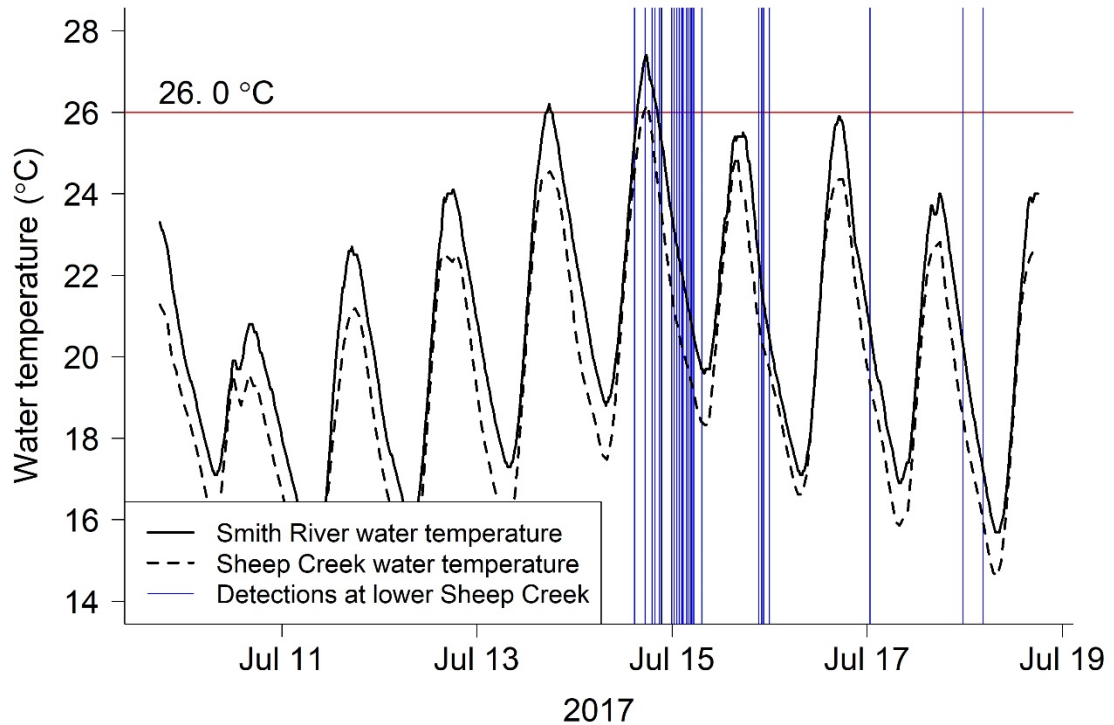


Figure 22. Fish detected at the lower Sheep Creek PIT array after a period of sustained water temperatures in excess of 26°C in the Smith River. Black lines are the water temperatures of the Smith River at the USGS gauge downstream of Sheep Creek (solid) and Sheep Creek at the lower Sheep Creek PIT array (dashed) 2.5 km upstream from the confluence with the Smith River. Vertical blue lines mark when tagged fish were detected passing the lower Sheep Creek PIT array.

Figure 23

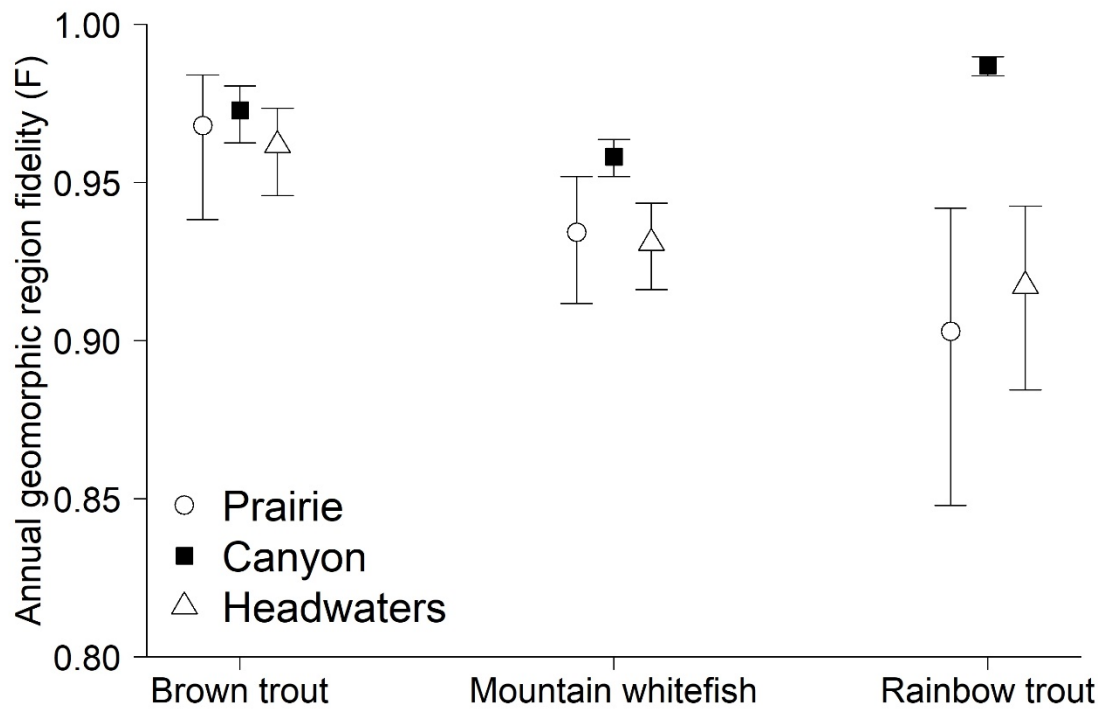


Figure 23. Estimated annual probabilities of geomorphic region fidelity by species and geomorphic region of origin. Error bars represent 95% confidence intervals. Note y-axis values range between 0.8 and 1.

Figure 24

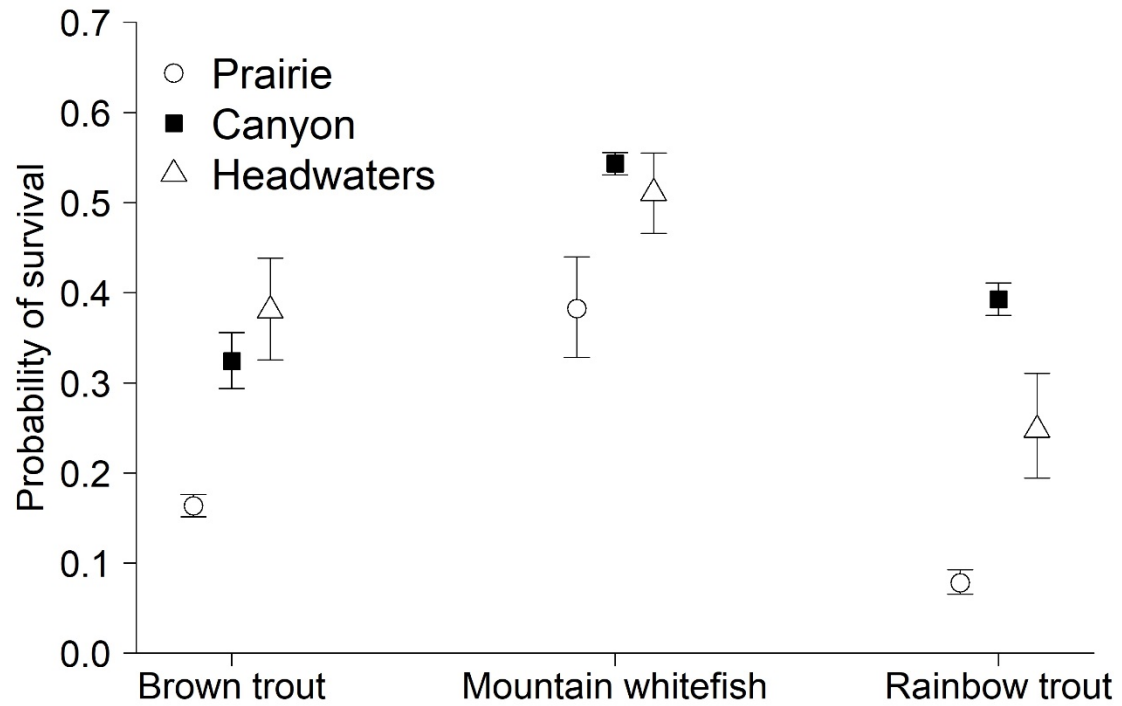


Figure 24. Annual survival probabilities of PIT-tagged fish in the Smith River. Points are survival estimates of each species of fish in each of the three geomorphic regions of the Smith River. Error bars are 95% confidence intervals of each survival estimate.

Figure 25

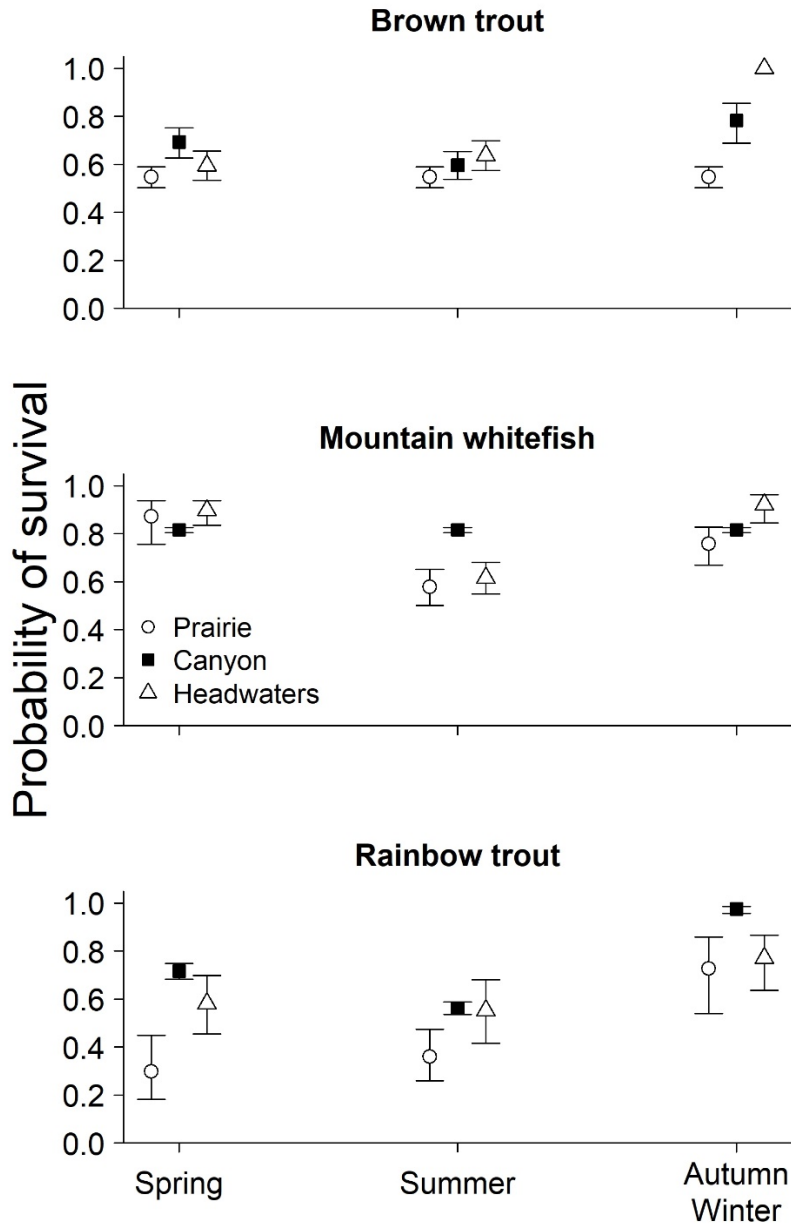


Figure 25. Seasonal survival probabilities of PIT-tagged fish in the Smith River watershed. Points are estimated survival probabilities for each season, and error bars are 95% confidence intervals.

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