Life Histories of Salmonids in the Upper Missouri River Basin

T. David Ritter[1], Jason Mullen[1], Brian J. Tornabene[2], Grant Grisak[3]

[1]Montana Fish, Wildlife and Parks, 4600 Giant Springs Road, Great Falls, MT 59405
[2]Wildlife Biology Program, W.A. Franke College of Forestry & Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812
[3]NorthWestern Energy, 6700 Rainbow Dam Road, Great Falls, MT 59404

Final report for Northwestern Energy FERC Project 2188
Project Number 759-14

March 2021

ACKNOWLEDGEMENTS

This study was truly a collaborative effort among agencies, entities, and individuals and required an enormous amount of time, resources, and dedication. We first thank our co-author and original investigator for this project, Grant Grisak; his devotion to the resource and those who use it is unparalleled and inspirational. We also thank our co-author Jason Mullen for his guidance, patience, and commitment to seeing this project through. In addition to data analysis and review, Brian Tornabene provided enthusiasm and encouragement. We are indebted to Michael Duncan for his thorough review, support, and advice. Michael Lance and Al Zale contributed both writing advice and knowledge of the Smith River system. Katie Vivian provided guidance and insights on salmonid movements and water temperatures. Dave Stagliano contributed data. Numerous individuals assisted with equipment installation and upkeep, fish marking, and data management: Rob Clark, Tracy Elam, Rob Beattie, Mike Schilz, Gabe Madel, Keenen Blackbird, Jonathan Wester, Charlie Williams, Lauren Flynn, Katie Vivian, Dylan Owensby, Colton Wennerberg, and Megan Heinemann. Colin Maas and his Smith River State Park personnel provided insights and support. Finally, this project would not have been possible without the cooperation of private landowners in Cascade, Meagher, and Lewis and Clark counties and the Lewis and Clark National Forest Service.

ABSTRACT

The upper Missouri River below Holter Dam consists of three primary interconnected salmonid populations that provide important recreational sport fisheries. Despite the presence of the myxosporean parasite *Myxobolus cerebralis*, the upper Missouri River rainbow trout *Onchorhynchus mykiss* population is among the most productive fisheries in the state. Previous studies have suggested that diverse life history patterns may explain the resilience of trout populations to the parasite. We used passive integrated transponder (PIT) telemetry to investigate outmigration timing, spawning strategies, straying and homing rates, and aging and growth patterns. Outmigration varied among species and tributaries but was generally bimodal and usually occurred following sudden changes in stream discharge. Our analysis implicated photoperiod and discharge as factors influencing outmigration, but primary drivers in some systems were unclear; multiple linear regression models explained only up to 14% of variation in outmigration. In the upper Missouri River, relatively few tagged fish were observed spawning in tributaries, suggesting mainstem spawning may be widespread. Rainbow trout spawning occurred primarily in the Little Prickly Pear Creek watershed in the Missouri River and Sheep Creek watershed in the Smith River. Brown trout *Salmo trutta* spawning was restricted to the Little Prickly Pear Creek watershed in the Missouri River but was distributed widely among tributaries in the Smith River. Mountain whitefish *Prosopium williamsoni* spawned almost exclusively in the Dearborn River watershed in the Missouri River and in the Sheep Creek and Tenderfoot Creek watersheds in the Smith River. No spawning was observed in the Sun River. Consecutive and alternate year spawning was observed in all species. Stray rates of tributary spawners were much lower than expected based on previous studies of mainstem spawners and ranged from 1% to 7% at the watershed scale and 16% to 51% at the subwatershed scale. Minimum homing rates were generally greater than straying rates, but many fish could not be categorized or were unaccounted for and could have been tributary residents, mortalities, or undetected. Growth rates were highest in the upper Missouri River subbasin and averaged 71 mm (2.8”) per year over an average interval of 3.5 years for rainbow trout and 88 mm (3.5”) per year over an average interval of 3.4 years. Longevity was highest in the Smith River subbasin where rainbow trout potentially reached seven to eight years of age. Mountain whitefish were the longest-lived species reaching over ten years of age. Life history patterns were potentially more diverse than previously thought. Such complexity promotes a resilient and robust fishery in a climatically dynamic system.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER ONE

INTRODUCTION

Knowledge of life history patterns is necessary for effective management of salmonid populations, but such patterns can be complex and vary across biological, spatial, and temporal scales (Bennett et al. 2014; Lance 2019). Life history diversity in potomadromous populations is thought to have evolved in response to dynamic systems in which spatial and temporal availability of resources varies greatly (Gresswell et al. 1994; Northcote 1997). Such populations are therefore more robust because connectivity from diverse movement patterns promotes resilience to environmental disturbances (Dunham and Rieman 1999).

Outmigration timing, spatial and temporal distribution of spawning, and age structure are primary aspects of salmonid life history, but literature on such topics in the context of large inland populations is uncommon (Bennett et al. 2014). Most current knowledge is skewed towards either anadromous populations (Keefer and Caudill 2014) or potomadromous trout of adfluvial populations (Downs et al. 2006; Watschke 2006; Bennet et al. 2014). Accordingly, life history of fluvial salmonids has been identified as an area requiring further investigation (Al-Chokachy and Budy 2008; Bennet et al. 2014).

In the upper Missouri River basin, fluvial salmonid populations support popular recreational fisheries, including the Holter Dam tailwater fishery and the only permitted float in Montana on the Smith River. The Holter Dam tailwater fishery in the upper Missouri River is among the most productive rainbow trout *Onchorhynchus mykiss* populations in Montana and consistently ranks among the most heavily fished waters in the state (183,479 angler days in 2015; Montana Fish, Wildlife & Parks [FWP] 2015). In 1995, the myxosporean parasite

Myxobolus cerebralis that causes whirling disease was discovered in one of the primary rainbow trout spawning tributaries, Little Prickly Pear Creek. The parasite subsequently spread to additional spawning tributaries over the next several years (Grisak 1999; Leathe 2001). Although whirling disease contributed to sharp declines in rainbow trout populations in the Madison and Colorado rivers (Vincent 1996; Nehring and Walker 1996), rainbow trout abundances remain stable in the Missouri River.

The robustness and resilience of this tailwater fishery is thought to be the result of complex life history patterns. Accordingly, investigations on outmigration timing, spawning distribution, and age structure were conducted. Outmigrations of juvenile rainbow trout and brown trout *Salmo trutta* from Little Prickly Pear Creek and the Dearborn River were examined using a rotary screw trap from 1998 to 2002 (Leathe 2001; Leathe et al. 2014). Outmigration patterns were variable and influenced by a variety of environmental factors (Leathe et al. 2014). Scale patterns were used to determine that age-1 outmigration life history was the most common outmigration strategy of juvenile rainbow trout in Little Prickly Pear Creek and the Dearborn River (Munro 2004). Multiple radiotelemetry studies have demonstrated a lack of spawning site fidelity in rainbow trout tagged in the mainstem Missouri River (Grisak et al. 2012b) and evidence of interconnected populations among Missouri River, Sun River, and Smith River rainbow and brown trout (Grisak et al. 2012a). Finally, a 30-year scale aging study on rainbow and brown trout in the upper Missouri River revealed relatively high growth rates based on length at age data.

Though extensive, previous studies were conducted in different years and over relatively short durations, leaving gaps in knowledge of salmonid life history patterns in the basin. A comprehensive understanding would enhance management of salmonids in the basin and could provide insights into the resilience of salmonid populations to environmental disturbances such as whirling disease. In 2013, Northwestern Energy awarded Montana Fish, Wildlife & Parks funding to use passive integrated transponder (PIT) telemetry to monitor fish movement in the upper Missouri, Sun, and Smith rivers. Our goal was to investigate the life histories of rainbow trout, brown trout, and mountain whitefish *Prosopium williamsoni*. Our objectives were to (1) quantify spatiotemporal variability of natal straying and homing rates and identify connectivity among upper Missouri River, Sun River, and Smith River salmonid populations, (2) determine the timing of and factors influencing rainbow and brown trout outmigration, and (3) determine growth rates and age structures of rainbow trout, brown trout, and mountain whitefish populations and compare them to previous age and growth studies.

A concurrent study investigating salmonid movement and connectivity in the Smith River (Lance 2019) provided a unique opportunity to examine inter-subbasin connectivity and compare life history patterns among the upper Missouri, Smith, and Sun rivers. Although funding awarded by Northwestern Energy was not used for this Smith River study, the interconnected nature of the salmonid populations warranted report of some results and comparisons. In addition, a study examining rates of predation on Smith River trout by American white pelicans *Pelecanus erythrorhynchos* was conducted from 2016 through 2017 (Vivian and Mullen 2018). Although this study is referenced in our report and some findings are presented, we did not include detailed results. Details of the pelican predation study and comprehensive annual summaries of this life history study can be found in Vivian and Mullen (2008) and Mullen et al. (2017), Mullen et al. (2018), and Mullen and Vivian (2019), respectively.

Study area

Upper Missouri River

The upper Missouri River is in central Montana and originates at the confluence of the Jefferson, Madison, and Gallatin rivers (Figure 1.1), extending north to Loma, Montana, where the river begins to flow east. The upper Missouri River basin has a drainage area of 36,248 km^2 and has two major tributaries, the Sun River and Smith River. The study area begins at Holter Dam and extends north to the confluence of the Missouri and Sun rivers near Great Falls, Montana (Figure 1.1). In addition to Holter Dam, two other hydroelectric dams (Hauser and Canyon Ferry) regulate discharges in the upper Missouri River; mean daily discharge measured below Holter Dam was 6,639 CFS from 1955 to 2020 (USGS site 06066500). Smaller tributaries in the study area include Little Prickly Pear Creek, Sheep Creek, and the Dearborn River.

Little Prickly Pear Creek flows east into the Missouri River 3.8 km downstream of Holter Dam (Figure 1.1). Draining an area of 1,026 km^2, Little Prickly Pear Creek has two major tributaries, Wolf and Lyons creeks. Mean daily discharge from 1988 to 2020 was 49 CFS (USGS site 06071300). Little Prickly Pear Creek and its tributaries are used heavily as spawning areas by rainbow and brown trout (Grisak 1999; Grisak et al. 2012; Leathe et al. 2014).

The Dearborn River originates on the eastern slope of the Rocky Mountain Front and enters the Missouri River from the west near the town of Craig, Montana (Figure 1.1). The Dearborn River drains an area of 1,418 km^2. Mean daily discharge was 63.6 CFS from 1969 to 2020 (USGS site 06073500). The Dearborn River is an important spawning tributary for rainbow and brown trout (Grisak 1999; Grisak et al. 2012; Leathe et al. 2014).

Sheep Creek begins on the western slope of the Big Belt Mountains before entering the Missouri River 37.8 km downstream of Holter Dam (Figure 1.1). Sheep Creek is a smaller tributary relative to Little Prickly Pear Creek and the Dearborn River, draining an area of 96 km^2.

Discharge data were not available for Sheep Creek. Rainbow and brown trout also use Sheep Creek as a spawning area (Grisak 1999; Grisak et al. 2012; Leathe et al. 2014).

Sun River

The Sun River originates in the Bob Marshall Wilderness on the eastern slope of the Rocky Mountain Front and flows east until its confluence with the Missouri River near Great Falls, Montana. The Sun River drainage area is 4,863 km^2. The study area begins below the Sun River Diversion Dam, which is a complete barrier to movement 5.6 km downstream of Gibson Dam, and extends to the confluence, including one major tributary, Elk Creek (Figure 1.1). The Sun River is used extensively for irrigation and several diversion dams in its lower reaches potentially limit fish movements during low flows (Figure 1.1). Mean daily discharge taken near Simms, Montana from 1987 to 2020 was 205 CFS (USGS site 06085800).

Elk Creek originates in the Lewis and Clark National Forest south of the Sawtooth Range and flows northeast until its confluence with the Sun River near Augusta, Montana (Figure 1.1). The drainage area of Elk Creek is 501 km^2. Discharge data were not available.

Smith River

The Smith River originates near White Sulphur Springs, Montana, and flows northwest for 195 km to its confluence with the Missouri River near Great Falls, Montana (Figure 1.1). The Smith River drains an area of 5,190 km^2 from tributaries flowing out of the Castle, Big Belt, and Little Belt mountains. Mean daily discharge measured near Fort Logan from 1996 to 2020 was 106 CFS (USGS site 06077200). A river corridor managed in partnership with federal, state, and private landowners as Smith River State Park extends from the only recreational put-in at Camp

Baker 95 km to the only take-out at Eden Bridge. Major tributaries of the Smith River include Sheep, Tenderfoot, and Hound creeks (Figure 1.1).

Sheep Creek originates in the Little Belt Mountains, flowing west until entering the Smith River just downstream of Camp Baker (Figure 1.1). The drainage area of Sheep Creek is 504 km^2. The study area included one major tributary, Moose Creek. Discharge data for Sheep Creek were not available. Rainbow trout and mountain whitefish use Sheep Creek and its tributaries extensively for spawning (Lance 2019).

Tenderfoot Creek originates on the western slope of the Little Belt Mountains, entering the east side of the Smith River 26 km downstream of Camp Baker (Figure 1.1) and drains an area of 282 km^2. The study area consisted of Tenderfoot Creek and several tributaries below a waterfall barrier 13.7 km upstream of the confluence with the Smith River that prevents upstream fish movements (Figure 1.1). Discharge data were not available. Rainbow trout and mountain whitefish use lower Tenderfoot Creek extensively for spawning; brown trout spawn there to a lesser extent (Ritter 2015).

Hound Creek is the lowest major tributary of the Smith River, flowing northeast out of the foothills of the Big Belt Mountains until its confluence with the Smith River 2.6 km upstream of the Eden Bridge take-out (Figure 1.1). The drainage area is 592 km^2. Discharge data were not available. Rainbow trout, brown trout, and mountain whitefish moved into Hound Creek during spawning seasons, suggesting some use as a spawning area (Lance 2019).

Fish assemblage

The fish assemblage of the study area includes mountain whitefish, brown trout, rainbow trout, westslope cutthroat trout *Onchorhynchus clarkii lewisi* (mostly restricted to isolated tributaries in the Smith River subbasin), hybridized cutthroat trout, and brook trout *Salvelinus fontinalis*. Other game fishes include burbot *Lota lota*, yellow perch *Perca flavescens*, walleye *Sander vitreus*, and northern pike *Esox lucius.* White suckers *Catostomus commersonii*, longnose suckers *Catostomus catostomus*, and mountain suckers *Catostomus platyrhynchus* are common throughout the study area. Rocky Mountain sculpin *Cottus bondi* and longnose dace *Rhinichthys cataractae* are also common throughout the study area and numerous other non-game species are also present.

FIGURES

Figure 1.1. The upper Missouri, Sun, and Smith rivers and their major tributaries. Yellow dots represent USGS gaging stations used in the study. Black diagonals represent dams or diversions. Green diamonds represent fixed PIT antenna arrays. Shaded buffers represent areas where fish movement was monitored by fixed PIT antenna arrays, portable PIT antennas, and physical recapture events.

CHAPTER TWO

SPATIOTEMPORAL VARABILITY OF NATAL STRAYING AND HOMING RATES AND CONNECTIVITY AMONG UPPER MISSOURI RIVER, SUN RIVER, AND SMITH RIVER SALMONID POPULATIONS

Introduction

Potomadromous trout populations demonstrate a variety of spawning patterns, including adfluvial (outmigration from natal streams as juveniles to lakes; Downs et al. 2006; Watschke 2006), fluvial (outmigration from natal streams as juveniles to larger rivers; Al-Chokachy and Budy 2008; Bennett et al. 2014), and tributary residence (Hilderbrand and Kershner 2000; Ritter 2015). Multiple spawning patterns can occur within populations and even drainages (Gresswell et al. 1994; Al-Chokachy and Budy 2008). In extensive, interconnected river basins, variations within fluvial spawning patterns have been observed. In some populations, individuals move great distances to spawn in mainstem river habitat rather than natal tributaries (DeRito et al. 2010). Adults may share mainstem river habitat to exploit metabolic benefits but home to separate natal streams to spawn (Kershner et al. 2019).

Diversity in spawning patterns has enabled salmonids to colonize dynamic coldwater habitats that experience spatially and temporally variable environmental disturbances (Dunham and Rieman 1999; Kershner et al. 2019). Accordingly, the robustness and productivity of fluvial salmonid populations in the upper Missouri River basin in the presence of whirling disease are thought to be products of highly variable spawning patterns. Radiotelemetry studies investigating the spawning characteristics of rainbow trout showed interannual variation in spawning locations and low spawning site fidelity (Grisak et al. 2012b). Radio-tagged fish spawned in both the mainstem Missouri River and tributaries (Grisak et al. 2012b). Redd counts showed 72% of spawning occurred in tributaries, primarily Little Prickly Pear Creek and its tributaries, but mainstem spawning was more prevalent than observed in previous studies (Grisak et al. 2012b).

In addition to spawning patterns, radiotelemetry studies revealed an interconnectivity among the upper Missouri, Sun, and Smith rivers (Grisak et al. 2012a). Multiple rainbow and brown trout were observed moving from the Missouri River to the Smith River and its tributaries to spawn (Grisak et al. 2012a). The relatively low total number of fish tagged ($N = 43$) suggested that such inter-subbasin movement may not be uncommon (Grisak et al. 2012a).

We used PIT telemetry to monitor fish movement in the upper Missouri, Sun, and Smith rivers. Our goal was to investigate the spawning patterns and movement of rainbow trout, brown trout, and mountain whitefish. Our objectives were to quantify spatiotemporal variability of natal straying and homing rates and identify connectivity among upper Missouri River, Sun River, and Smith River salmonid populations.

Methods

PIT-tagging

A total of 11,936 fish was tagged in the upper Missouri River basin from 2010 to 2019; 3,572 in the upper Missouri River subbasin (Table 2.1), 739 in the Sun River subbasin (Table 2.2), and 7,625 in the Smith River subbasin (Table 2.3). From 2010 to 2012, 777 fish were tagged as part of a Montana State University graduate study investigating Tenderfoot Creek, a major tributary of the Smith River (Ritter 2015). Most of these fish were likely not present from

2014 to 2019; however, some fish tagged in 2012 were active until at least 2018 (Mullen and Vivian 2019).

Fish were collected with boat, barge, and backpack electrofishers, and fyke nets, anesthesized with Aqui-S 20E (Aqui-S New Zealand Ltd.; 10 to 20 mg/L) or MS-222 (tricaine methanesulfonate; 50 mg/L), and implanted with half duplex (HDX) PIT tags. Location, species, and total length (TL) were recorded for each fish at the time of tagging; 20% (2,389 of 11,936) were also weighed. The date when a fish was collected and tagged was recorded as the first observation for each individual. PIT tags were surgically implanted into the abdominal cavity through small incisions made by a small scalpel coated with antiseptic. Most fish were tagged with 23 or 32-mm HDX PIT tags; a small number of fish (217 of 11,936) were tagged with 12-mm HDX PIT tags.

Monitoring fish movement

A network of 23 stationary PIT arrays monitored the movements of PIT-tagged fish throughout the upper Missouri River basin (Table 2.4 and Figure 2.1). Five arrays were installed in the upper Missouri River in the spring of 2014, three arrays were installed in the Sun River in the spring of 2015, and 15 arrays were installed in the Smith River from 2014 to 2016 (Table 2.4 and Figure 2.1). These monitoring stations ran in some combination from 2010 to 2019 (Figure 2.2). The Dearborn River, Little Prickly Pear Creek, Truly Bridge (Smith River), and Hound Creek arrays were damaged by flows in the spring and early summer of 2018. All but Truly Bridge were repaired and reinstalled. Five stations were operated in Tenderfoot Creek from 2010 to 2014, but only one array installed at the mouth of Tenderfoot Creek was maintained after 2013 (Table 2.4 and Figure 2.1; Ritter 2015). Age and growth analyses used data collected prior to

2014 and afterward, but all other analyses were restricted to data collected after 2013. In general, fixed PIT arrays were installed in locations to monitor interchange between tributaries and mainstem rivers. Array locations were not necessarily conducive to monitoring interchange among the Missouri River, Smith River, and Sun River subbasins (Figure 2.1). The Truly Bridge PIT array was in the most favorable location to monitor such movement but was still 14.6 rkm (9.1 miles) from the confluence of the Smith River with the Missouri River (Figure 2.1).

Antenna stations consisted of a PIT-tag reader (Oregon RFID, multi-antenna HDX reader and long-range HDX reader, Portland, Oregon), one to two stream-width antennas, and a tuning board for each antenna (Oregon RFID, standard remote tuner board and long-range tuner board, Portland, Oregon). Antenna arrays were powered by 12-V DC supplied by either solar panels or 120-V AC converters. Antennas were placed in areas where fish would unlikely stay for long periods of time (e.g., riffles and shallow water habitat) to prevent many consecutive detections and to monitor interchange between mainstem river and tributaries (rather than localized use near the antennas). All antennas were oriented flat on the bottom (swim over or flat-bed design; Armstrong et al. 1996) and tuned to best possible vertical read ranges for tags oriented perpendicularly to the antennas. Average tag detection distances of antennas ranged from 0.03 to 1.50 m (Table 2.4) and varied seasonally (Figure 2.3). Detection efficiencies (Zydlewski 2006) of PIT arrays installed in the Smith River ranged from 0.66 to 1.00 (Lance 2019). Detection efficiencies can be used to correct for potential bias associated with variations in detection efficiencies of stationary PIT arrays (e.g., Lance 2019). We did not account for such bias in this study; rather, we provided detection efficiencies as a metric for PIT array performance in addition to tag detection distance.

Mobile PIT arrays were used to actively monitor fish movements and complement the network of fixed monitoring stations. Mobile tracking was conducted using raft, kayak, and pole-mounted antennas (Hill et al. 2006; McKinstry and Mackinnon 2011); methods are explained in detail by Lance (2019). In the upper Missouri and Sun rivers, mobile tracking by raft and kayak was conducted in 2015 and 2016 but discontinued thereafter because of low detection range. A pole-mounted antenna was used in 2016 to scan tributaries and islands of the upper Missouri River and American white pelican *Pelecanus erythrorhynchus* nesting islands in Canyon Ferry and Arod Lake (Vivian and Mullen 2018). In the Smith River, all forms of mobile tracking were used to track fish from 2015 to 2017 (Lance 2019). No mobile tracking was conducted from 2018 onward.

Data analysis

The statistical software programs R (v4.0.2; R Core Team 2019) and SigmaPlot 14 (SigmaPlot 2017) were used for analyzing and plotting trends and comparisons in outmigration timing and magnitude, straying and homing rates, and age and growth rates. Program R was also used for modeling water temperatures. We used geographic information system (GIS) software (QGIS 2021) for spatial analyses and map construction.

Spatial analysis

We divided the study area into hydrologic units based on the hierarchical hydrologic unit code (HUC) system developed by the USGS at four different levels: basin, subbasin, watershed, and subwatershed (Figures 2.4, 2.5, and 2.6). Locations of fish determined by fixed PIT arrays, portable PIT tracking events, and physical capture events were joined with hydrologic units for spatial analysis (Figure 2.7). The upper Missouri River basin encompasses five subbasins: upper Missouri-Dearborn, upper Missouri River, Sun River, Smith River, and Belt Creek. Because the study area included parts of both the upper Missouri-Dearborn and upper Missouri River subbasins, we combined them to simplify analysis and hereafter refer to them collectively as the upper Missouri River subbasins.

Seven of the 42 watersheds in the upper Missouri River subbasins were included in analyses (from upstream to downstream): Rattlesnake Gulch, Little Prickly Pear Creek, Stickney Creek, Dearborn River, Sheep Creek, Castner Coulee, and City of Great Falls (Figure 2.4). Sixteen subwatersheds were included in the study: Medicine Rock, Little Prickly Pear Creek, Lyons Creek, Log Gulch, Wolf Creek, Dog Creek, Dearborn River, Sheep Creek, Finigan Creek, Antelope Creek, Knapp Creek, Lower Chestnut Valley, Nelson Island, Wilson Butte, and City of Great Falls (Figure 2.4). The Dog Creek and Finigan Creek subwatersheds encompass the Cascade and Craig sections, respectively, used by Montana Fish, Wildlife & Parks for annual population sampling (Figure 2.4).

Five of the eight watersheds in the Sun River subbasin were included in analyses: Gibson Reservoir, Elk Creek, Dry Creek, Big Coulee, and Fourmile Creek (Figure 2.5). Location data of fish in the Sun River were too coarse to be analyzed at the subwatershed scale. The Big Coulee watershed encompassed the Simms section used by Montana Fish, Wildlife & Parks for annual population sampling (Figure 2.5).

All 11 Smith River watersheds were included in analyses: North Fork Smith River, South Fork Smith River, Newlan Creek, Sheep Creek, Camas Creek, Rock Creek, Eagle Creek, Tenderfoot Creek, Deep Creek, Hound Creek, and Ming Coulee (Figure 2.6). Nineteen of the 68 subwatersheds in the Smith River basin were included: Big Birch Creek, Newlan Creek, Rock Springs Creek, Camas Creek, Cottonwood Creek, Lower Sheep Creek, Middle Sheep Creek, Upper Sheep Creek, Moose Creek, Blacktail Creek, Rock Creek, Lower Tenderfoot Creek, Two Creek, Bear Gulch, Rocky Coulee, Hound Creek, Boston Coulee, and Goodman Coulee (Figure 2.6). The Blacktail Creek subwatershed encompassed the Eagle Creek section used by Montana Fish, Wildlife & Parks for annual population sampling (Figure 2.6).

Spawning seasons

To determine spawning seasons for rainbow and brown trout, we investigated the detections on tributary antennas of sexually mature fish (Figures 2.8 and 2.9). The spawning seasons defined in this study were broader than in past studies so both upstream and downstream portions of spawning migrations could be included. Some fish were not detected moving upstream into tributaries but were detected moving out, and vice versa. Additionally, some spawning activity was observed during late February, further justifying the use of these date ranges. In the upper Missouri River and Sun River basins, spawning seasons for rainbow and brown trout were defined as February 15 to May 31 and September 1 to November 30, respectively (Figure 2.8). For comparison, Grisak et al. 2012 observed radio-tagged rainbow trout spawning from March 3 to May 5 in the Missouri River from 2008 to 2010. In the Smith River basin, spawning seasons for rainbow trout and brown trout were defined as March 1 to June 31 and September 1 to November 30, respectively (Figure 2.9). Mountain whitefish spawning seasons were identical to those defined for brown trout.

Assumptions

Spawning

- Fish were considered mature if tagging length was over 254 mm (10”) to avoid exclusion of young adult fish (particularly precocious males) making potential spawning movements. Numerous young males exhibited milt when collected (269 rainbow trout ranging from 99 mm (3.9”) to 373 mm (14.7”).
- Fish tagged as juveniles were considered mature the following year unless length at tagging was less than 127 mm (5”). Fish smaller than 127 mm at tagging were considered mature two years later.
- Fish that meet the preceding two criteria and detected on tributary PIT antennas during the spawning season were considered to have spawned.
- Spawning location was defined as the most upstream detection or relocation (including initial tagging) of an individual fish during the spawning season.
- Fish tagged and never redetected were not included in straying and homing rate calculations.

Straying and homing

- If a juvenile fish (less than 254 mm or 10”) was tagged in a tributary, the tributary was assumed to be the natal origin of the individual regardless of the time of year tagging took place.
- If an adult fish (greater than 254 mm or 10”) was tagged in a tributary during the spawning season, this tributary was assumed to be the natal origin of the individual.
- Several fish were detected in more than one tributary during a single spawning season. Initial detections were considered exploratory movements and the final detection was considered the spawning event.

Spawning movements and straying and homing rates

Spawning movements were initially assessed at subwatershed scales based on the resolution of the network of fixed PIT antennas, which included smaller tributaries, such as Lyons and Wolf creeks (Figure 2.4). However, because the natal origins at this scale were difficult to determine in some instances, we also assessed spawning movements at a watershed scale (Figure 2.4). For example, most rainbow trout tagged in Little Prickly Pear Creek were captured in the spring and assigned Little Prickly Pear Creek as their natal stream. However, these fish could have been moving to or from their actual natal origins in the tributaries of Little Prickly Pear Creek (Wolf and Lyons creeks). Analysis at the subwatershed scale could have therefore artificially increased stray rates. In addition, fish tagged in upper subwatersheds that spawned in lower subwatersheds of the same tributary were considered strays. Analysis at the subwatershed scale could have therefore inflated straying rates in the context of fisheries management because fish returns to their natal tributary to spawn are generally considered homing behaviors (Keefer and Caudill 2014). Assessing spawning movements on a watershed scale eliminated these issues for straying and homing analyses but reduced resolution of analysis of spawning effort, so both scales were used. Mainstem spawning was only investigated in the Sun River; results do not include spawning events that occurred in the mainstems of the upper Missouri River (stationary PIT arrays were not installed in the upper Missouri River mainstem) and Smith River.

Straying and homing rates were evaluated by tagging location (at watershed and subwatershed scales), species (rainbow and brown trout), and among years. We investigated straying and homing from 2015 to 2018 when the largest numbers of PIT-tagged fish were present; this also allowed the 2014 tagging class to disperse and prevented any overlap with outmigrating individuals. Because numerous fish spawned multiple times, we used numbers and proportions of spawning events in addition to numbers and proportions of individual fish for calculating stray rates. Only fish tagged in their natal streams that spawned were used in the calculations of stray rates. Spawning events made by fish with unknown natal streams (e.g., tagged in the mainstem river) were addressed separately. Natal origin assignment for mountain whitefish was not possible because no fish met the criteria listed above. However, we did investigate mountain whitefish spawning locations and magnitudes.

Straying analyses could not differentiate returning spawners from tributary residents. Although fish detected on tributary antennas during spawning seasons were likely entering from the mainstem river, the lack of mainstem antennas made this impossible to verify. We therefore calculated minimum homing rates of fish that were documented outside of their natal stream and made distinct homing movements to spawn. At the subwatershed level, this would include individuals tagged in a natal subwatershed, detected in another subwatershed, and then detected at the natal subwatershed again as a returning spawner. Similarly, lack of mainstem antennas meant that analyses could not identify strays that spawned in the mainstem. However, we could not differentiate mainstem spawners from those with unknown life histories. In summary, we calculated both straying and minimum homing rates. Fish that could not be identified as having strayed or homed would be comprised of tributary residents and fish of unknown life histories.

In the Missouri River and Smith River subbasins, tributaries and their respective watersheds and subwatersheds were used as natal locations. Because few fish were tagged in the Sun River and most tagging events occurred outside of spawning seasons, fish tagged in the Sun River subbasin were not assigned natal origins. Moreover, in the Sun River subbasin, fish were only tagged in one tributary, Elk Creek, and in the mainstem Sun River. Therefore, spawning movements were investigated only at the watershed scale. However, discernable spawning movements in the Sun River were not observed for any species; detections during the spawning season were reported instead.

Results

Fish detections

We redetected 42% (5,036 of 11,936) of PIT-tagged fish in the upper Missouri River basin from 2010 to 2020 (Table 2.5); 181 were redetected only at American White Pelican colonies rather than by PIT arrays or recapture events (see Vivian and Mullen 2018 for comprehensive report). We redetected 37% (2,224 of 5,956) of rainbow trout, 33% (812 of 2,495) of brown trout, and 63% (1,785 of 2,846) of mountain whitefish. Of the redetected fish, 77% (3,883) were detected by stationary PIT arrays.

Twenty-eight percent (988 of 3,572) of fish tagged in the upper Missouri River subbasins were redetected (Table 2.5). Twenty-nine percent (724 of 2,487) of rainbow trout, 20% (128 of 633) of brown trout, and 30% (84 of 277) of mountain whitefish were redetected (Table 2.5). Of the 988 total redetected fish, 90% (887) were detected by stationary PIT arrays.

Twenty-one percent (156 of 739) of fish tagged in the Sun River subbasin were redetected (Table 2.5). Twenty percent (30 of 153) of rainbow trout, 20% (72 of 353) of brown trout, and 23% (51 of 223) of mountain whitefish were redetected. Of the 156 total redetected fish, 81% (127) were redetected by stationary PIT arrays.

Fifty-one percent (3,892 of 7,625) of fish tagged in the Smith River subbasin were redetected (Table 2.5). Forty-four percent (1,470 of 3,323) of rainbow trout, 41% (612 of 1,510) of brown trout, and 70% (1,650 of 2,346) mountain whitefish were redetected. Of the 3,892 total redetected fish, 74% (2,871) were detected on stationary PIT arrays.

Natal straying and homing rates

Upper Missouri River

Rainbow trout

A total of 442 (18% of tagged; 61% of redetected) rainbow trout made 601 spawning movements in tributaries of the upper Missouri River from 2014 to 2019 (Table 2.6). Three hundred forty-eight were tagged in their natal streams and accounted for 486 spawning events (Table 2.6). Over the six-year period, 92 fish spawned twice, 25 fish spawned three times, three fish spawned four times, and two fish spawned five times. Seventy-four rainbow trout spawned in at least two consecutive years. Thirty-nine fish had at least a one-year gap between spawning events, six fish had at least a two-year gap, and one fish exhibited a three-year gap between spawning events. The 269 males exhibiting milt when collected ranged from 99 mm (3.9”) to 373 mm (14.7”) and averaged 232 mm (9.2”). Three females were collected with eggs measuring 317 mm (12.5”), 361 mm (14.2”), and 381 mm (15”).

Seventy percent of rainbow trout spawning events occurred in the Little Prickly Pear Creek watershed; the remaining 30% was split evenly between the Dearborn River and Sheep Creek watersheds (Figure 2.10). Wolf Creek was the most used subwatershed (30%), followed by Lyons Creek (21%), and Little Prickly Pear Creek (18%; Figure 2.11). Distribution of spawning effort varied among years (Figure 2.12). No rainbow trout tagged in the Missouri River subbasin were observed spawning in another subbasin. No rainbow trout tagged in another subbasin were observed spawning in the Missouri River subbasin.

At the watershed scale, eight (3%) rainbow trout were observed straying from their natal streams 16 times (5%) from 2015 to 2018 (Table 2.7). Fish tagged in the Sheep Creek watershed had the highest stray rate (15%) relative to other watersheds in the Missouri River subbasin (Table 2.8; Figure 2.13). Of all the straying spawning events, 94% strayed to the Dearborn River watershed and 6% occurred in the Little Prickly Pear Creek watershed (Figure 2.14). All spawning events that strayed from the Sheep Creek watershed occurred in the Dearborn River (Table 2.8). Most rainbow trout tagged in the Missouri River spawned in the Little Prickly Pear Creek watershed (Table 2.9). Stray rates were consistent among years (Figure 2.15).

Thirteen (5%) rainbow trout were documented outside of their natal watershed and made distinct homing movements back to their natal watershed to spawn 19 times (5%). Minimum homing rates were 6% for fish tagged in the Little Prickly Pear Creek and Sheep Creek watersheds. All rainbow trout that did not return to Sheep Creek spawned in the Dearborn River. One rainbow trout that was tagged in the Dearborn River spawned in the Little Prickly Pear Creek watershed.

At the subwatershed scale, 66 (25%) rainbow trout were observed straying from their natal origins 84 times (24%) from 2015 to 2018 (Table 2.10). Rainbow trout tagged in Little Prickly Pear Creek had the highest stray rate (56%) relative to other subwatersheds in the Missouri River subbasin (Table 2.11; Figure 2.16). Except for 1% that spawned in the Dearborn River, all spawning events that strayed from the Little Prickly Pear Creek subwatershed occurred in Lyons (43%) and Wolf creeks (12%). The next highest stray rate was by fish tagged in the Lyons Creek subwatershed (28%; Table 2.11; Figure 2.16). All fish that strayed from the Lyons Creek subwatershed spawned in the Little Prickly Pear Creek subwatershed (Table 2.11). Most spawning events made by rainbow trout tagged in the Missouri River occurred in the Little Prickly Pear Creek subwatershed, but 14% of the fish tagged in the Log Gulch subwatershed spawned in the Dearborn River (Table 2.12). Stray rates remained consistent among years for the Dearborn River, Sheep Creek, and Wolf Creek subwatersheds (Figure 2.15). Stray rates were lower for fish tagged in Lyons Creek in 2015 and Little Prickly Pear Creek in 2017 (Figure 2.15).

Fifty-seven (21%) rainbow trout were documented outside of their natal subwatershed and made distinct homing movements to spawn 79 times (22%). Minimum homing rates at the subwatershed scale were highest for fish tagged in the Wolf Creek subwatershed (66%). Rainbow trout tagged in the Lyons Creek subwatershed had the lowest minimum homing rate (0%); all nine individuals spawned in the Little Prickly Pear Creek subwatershed. Fish tagged in the Little Prickly Pear Creek subwatershed and Sheep Creek subwatershed had minimum homing rates of 7% and 6%, respectively.

Brown trout

A total of 41 (7% of tagged; 32% of redetected) brown trout made 54 spawning movements in tributaries of the upper Missouri River from 2014 to 2019 (Table 2.6). Fourteen were tagged in their natal streams and accounted for 18 spawning events. Over the six-year period, seven fish spawned twice and two fish spawned four times. All fish that spawned multiple times did so in consecutive years; there were no gaps between spawning events observed. Four brown trout were collected as ripe males that ranged from 300 mm (11.8”) to 493 mm (19.4”) and averaged 432 mm (17.0”).

All brown trout spawning occurred in the Little Prickly Pear Creek watershed (Figure 2.17). Within this watershed, most spawning occurred in the Little Prickly Pear Creek subwatershed (68%), followed by the Wolf Creek (19%) and Lyons Creek (13%) subwatersheds (Figure 2.17). No brown trout tagged in the Missouri River subbasin were observed spawning in another subbasin. No brown trout tagged in another subbasin were observed spawning in the Missouri River subbasin.

At the watershed scale, only one (7%) brown trout was observed straying from its natal stream in 2016 (Table 2.7). This individual was tagged in the Sheep Creek watershed and strayed to the Little Prickly Pear Creek watershed (Table 2.8). All brown trout that were tagged in the Missouri River spawned in the Little Prickly Pear Creek watershed (Table 2.9).

At the subwatershed scale, 7 (50%) brown trout were observed straying from their natal origins (Table 2.10). Three of the seven brown trout tagged in the Little Prickly Pear Creek subwatershed strayed to Wolf Creek (Table 2.11). One brown trout tagged in Sheep Creek and Wolf Creek strayed to Little Prickly Pear Creek and one brown trout tagged in Lyons Creek strayed to Wolf Creek (Table 2.11). Five of the seven straying events occurred in 2016 (Table 2.10).

One (6%) brown trout documented outside of its natal watershed made a distinct homing movement to spawn. However, only two total brown trout were documented outside of their natal watershed; the other individual was tagged in the Sheep Creek watershed and spawned in Little Prickly Pear Creek. The other individual was tagged in Little Prickly Pear Creek and returned to spawn there. No brown trout documented outside of their natal subwatershed made distinct homing movements to spawn; all individuals spawned in subwatersheds other than those in which they were tagged (minimum homing rates were 0%).

Mountain whitefish

A total of 49 (18% of tagged; 58% of redetected) mountain whitefish made 86 spawning events in the upper Missouri River from 2014 to 2019 (Table 2.6). Over the six-year period, 19 fish spawned twice and eight fish spawned three times. Four fish had a one-year gap between spawning events. All eight fish that spawned three times did so in consecutive years. Twelve males were collected exhibiting milt with tagging lengths ranging from 361 mm (14.2”) to 460 mm (18.1”) and averaging 401 mm (15.8”). One female measuring 442 mm (17.4”) was collected with eggs.

Almost all mountain whitefish spawning occurred in the Dearborn River watershed (98%); 2% occurred in the Little Prickly Pear Creek watershed (Figure 2.18). One mountain whitefish that was tagged in the Deep Creek watershed in the Smith River subbasin spawned in the Dearborn River twice in 2017 and 2018.

All 14 mountain whitefish that were tagged in the Dearborn River watershed returned to spawn (Table 2.9). No mountain whitefish tagged in the Sheep Creek watershed returned to spawn in Sheep Creek; 96% spawned in the Dearborn River watershed and the remaining 4% spawned in Little Prickly Pear Creek (Table 2.9). Of all the mountain whitefish tagged in the Missouri River (N = 230), three were detected spawning and all in the Dearborn River (Table 2.9).

Sun River

Rainbow trout

A total of six rainbow trout were redetected seven times during the spawning season in the Sun River subbasin from 2015 to 2018 (Table 2.6). However, only two of these detections were upstream movements to the Dry Creek watershed. All other detections inferred downstream movements. All seven individuals were tagged in Sun River watersheds; no rainbow trout tagged in another subbasin were observed spawning in the Sun River. No rainbow trout tagged in the Sun River subbasin were observed spawning in another subbasin.

Brown trout

A total of 30 brown trout were detected 33 times during the spawning season in the Sun River subbasin from 2015 to 2017 (Table 2.6). Most (18) of these detections inferred no movement up or down. Twelve fish were detecting moving downstream, eight of which moved downstream out of Elk Creek. Only two fish were detected moving upstream, one moved into Elk Creek. All 30 individuals were tagged in Sun River watersheds; no brown trout tagged in another subbasin were observed spawning in the Sun River. No brown trout tagged in the Sun River subbasin were observed spawning in another subbasin.

Mountain whitefish

A total of seven mountain whitefish were detected ten times during the spawning season in the Sun River subbasin from 2015 to 2017 (Table 2.6). Most (eight) detections did not infer movement up or downstream. Only one individual was detected moving upstream and only one individual was detected moving downstream. All seven individuals were tagged in Sun River watersheds; no mountain whitefish tagged in another subbasin were observed spawning in the Sun River. No mountain whitefish tagged in the Sun River subbasin were observed spawning in another subbasin.

Smith River

Rainbow trout

A total of 750 (23% of tagged; 51% of redetected) rainbow trout made 951 spawning movements in tributaries of the Smith River from 2014 to 2019 (Table 2.6). Three hundred ninety-three were tagged in their natal streams accounting for 499 spawning events (Table 2.6).

Over the six-year period, 129 fish spawned twice, 28 spawned three times, four fish spawned four times, and one fish spawned five times. One hundred thirty-four spawned at least two consecutive years, 28 fish spawned at least three consecutive years, five fish spawned four consecutive years, and one fish spawned five years in a row.

Most rainbow trout spawning events occurred in the Sheep Creek (78%) and Tenderfoot Creek (17%) watersheds (Figure 2.19). At the subwatershed scale, 32% of spawning events occurred in lower Sheep Creek, 24% occurred in Moose Creek, 22% occurred in upper Sheep Creek, 17% occurred in Tenderfoot Creek, and 3% occurred in Big Birch Creek (Figure 2.20). No rainbow trout tagged in the Smith River subbasin were observed spawning in another subbasin. No rainbow trout tagged in another subbasin were observed spawning in the Smith River subbasin.

At the watershed scale, nine (2%) rainbow trout were observed straying from their natal origins nine (2%) times in 2016 (Table 2.13). All individuals that strayed were tagged in the Sheep Creek watershed. Six of these straying events occurred in the Rock Creek watershed and the remaining three occurred in the Tenderfoot Creek watershed. Fifty-nine percent of rainbow trout tagged in the Smith River mainstem spawned in the Sheep Creek watershed, 38% spawned in the Tenderfoot Creek watershed, 2% spawned in Rock Creek, and the remaining 1% spawned in Hound and Camas creeks.

Sixty (15%) rainbow trout were documented outside of their natal watershed and made distinct homing movements to spawn 80 times (17%). Most of these fish were tagged in the Sheep Creek watershed where the minimum homing rate was 16%. Two fish tagged in the Tenderfoot Creek watershed returned to spawn four times. One rainbow trout tagged in the Newlan Creek watershed returned to spawn.

At the subwatershed scale, 198 (51%) rainbow trout were observed straying from their natal origins 232 (48%) times from 2015 to 2018 (Table 2.14). All rainbow trout that strayed were either tagged in the upper Sheep Creek (106) or Moose Creek (92) subwatersheds (Table 2.14). Rainbow trout tagged in the upper Sheep Creek subwatershed had a 47% stray rate, whereas those tagged in the Moose Creek subwatershed had a 42% stray rate (Table 2.15). Of those tagged in the upper Sheep Creek subwatershed, 25% strayed to Moose Creek and 21% strayed to lower Sheep Creek (Table 2.15). Of those tagged in the Moose Creek subwatershed, 21% strayed to upper Sheep Creek and 18% strayed to lower Sheep Creek (Table 2.15). Nearly half (48%) of all spawning events made by rainbow trout tagged in the mainstem Smith River occurred in the lower Sheep Creek subwatershed, a third (33%) occurred in the lower Tenderfoot Creek subwatershed, and 7% occurred in Big Birch Creek (Figure 2.21).

Ninety-three (24%) rainbow trout documented outside of their natal subwatershed made distinct homing movements to spawn 103 times (22%). Fish tagged in the Tenderfoot Creek subwatershed had the highest minimum homing rate (100%), but only two fish were tagged there that were documented elsewhere. Fish tagged in the upper Sheep Creek subwatershed had the lowest minimum homing rate (14%). Fish tagged in the Moose Creek subwatershed had a minimum homing rate of 30%. One fish tagged in Newlan Creek that was documented elsewhere returned to spawn there.

Stray rates of fish tagged in the upper Sheep Creek and Moose Creek subwatersheds varied among years (Figure 2.22). Stray rates were highest for upper Sheep Creek in 2016 and 2018 (Figure 2.22). For fish tagged in the Moose Creek subwatershed, stray rates were highest in 2017 and 2018 (Figure 2.22).

Brown trout

A total of 157 (10% of tagged; 26% of redetected) brown trout made 199 spawning movements in tributaries of the Smith River from 2014 to 2019 (Table 2.6). Seventy were tagged in their natal streams accounting for 100 spawning events (Table 2.6). Over the six-year period, 29 brown trout spawned twice, five fish spawned three times, and one fish spawned four times. Twenty fish spawned for at least two consecutive years and four fish spawned for three years in a row.

Brown trout spawning effort varied among Smith River watersheds and subwatersheds (Figures 2.23 and 2.24). Thirty-eight percent of brown trout spawning events occurred in the Sheep Creek watershed, 18%, occurred in the Rock Creek watershed, 13% occurred in the Hound Creek watershed, 11% occurred in the South Fork Smith River watershed, 10% occurred in the Tenderfoot Creek watershed, and the remaining 10% was split evenly between the Camas Creek and Newlan Creek watersheds (Figure 2.23). At the subwatershed scale, 19% of spawning events occurred in both the upper and lower Sheep Creek subwatersheds, followed closely by Lower Rock Creek (18%; Figure 2.24). Lower Hound Creek, Big Birch Creek, and lower Tenderfoot Creek had 13%, 11%, and 10% of brown trout spawning events, respectively (Figure 2.24). The remaining 10% was split evenly between the lower Camas Creek and lower Newlan Creek subwatersheds (Figure 2.24).

At the watershed scale, two (6%) brown trout tagged in the Sheep Creek watershed were observed straying in 2015 (Table 2.13). One of these fish spawned in Rock Creek watershed and one spawned in the Newlan Creek watershed. At the subwatershed scale, 11 (33%) brown trout were observed straying: five in 2015, five in 2016, and one in 2018 (Table 2.14). Nine fish were tagged in upper Sheep Creek and two were tagged in lower Sheep Creek. Of the fish tagged in lower Sheep Creek, one strayed to upper Sheep Creek and one strayed to lower Rock Creek (Table 2.15). Of the fish tagged in upper Sheep Creek, five individuals strayed to lower Sheep Creek and one strayed to lower Newlan Creek (Table 2.15). Spawning locations of brown trout tagged in the mainstem Smith River varied among subwatersheds; most occurred in lower Rock Creek (35%), Big Birch Creek (22%), and lower Tenderfoot Creek (15%; Figure 2.25).

Nine (13%) brown trout documented outside of their natal watershed made distinct homing movements to spawn 12 times (12%). Six (9%) brown trout documented outside of their natal subwatershed made distinct homing movements to spawn nine times (9%). Fish tagged in the upper Sheep Creek subwatershed had minimal homing rates of 0%. All fish tagged in Hound Creek, Tenderfoot Creek, and Newlan Creek that were documented elsewhere returned to their natal subwatersheds to spawn.

Mountain whitefish

A total of 734 (31% of tagged; 45% of redetected) mountain whitefish made 1,344 spawning movements in Smith River tributaries from 2014 to 2019 (Table 2.6). Three hundred thirty-eight were tagged in their natal streams and accounted for 678 spawning events (Table 2.6). Over the six-year period, 192 fish spawned twice, 98 spawned three times, 62 spawned four times, and nine fish spawned five times. Three hundred and three mountain whitefish spawned for at least two consecutive years, 143 spawned for at least three consecutive years, 55 spawned for at least four consecutive years, and one fish spawned five years in a row.

Most mountain whitefish spawning occurred in the Sheep Creek (61%) and Tenderfoot Creek watersheds (42%) from 2014 to 2019 (Figure 2.26). The Hound Creek, Rock Creek, and South Fork Smith River watersheds each accounted for 2% of the mountain whitefish spawning events (Figure 2.26). At the subwatershed scale, most spawning occurred in the lower Tenderfoot Creek watershed (32%), followed by lower Sheep Creek (25%), Moose Creek (24%), and upper Sheep Creek (12%; Figure 2.27). The lower Hound Creek, lower Rock Creek, and Big Birch Creek subwatersheds each accounted for 2% of the mountain whitefish spawning effort (Figure 2.27). One mountain whitefish that was tagged in the Deep Creek watershed (mainstem Smith River) spawned twice in the Dearborn River in 2017 and 2018 (Figure 2.28). No mountain whitefish tagged in the Sun River or Missouri River subbasins spawned in the Smith River subbasin.

At the watershed scale, four (1%) mountain whitefish were observed straying from their natal origins seven (1%) times from 2015 to 2018. Four of these straying events were made by fish tagged ($N = 2$) in the Sheep Creek watershed and occurred in Tenderfoot Creek. The other three were made by fish tagged ($N = 2$) in Tenderfoot Creek and occurred in the Sheep Creek watershed. At the subwatershed scale, 85 (25%) mountain whitefish strayed 144 (22%) times. Fish tagged in the upper Sheep Creek subwatershed had the highest stray rate (42%) relative to other subwatersheds in the Smith River subbasin (Table 2.15). All straying events made by these fish occurred in the Moose Creek subwatershed (Table 2.15). Fish tagged in the Moose Creek subwatershed also had a high stray rate (22%); except for 1% that strayed to the lower Sheep Creek subwatershed, all of these straying events occurred in the upper Sheep Creek subwatershed (Table 2.15). Forty-one percent of spawning events made by mountain whitefish tagged in the mainstem Smith River occurred in the lower Tenderfoot Creek subwatershed, 25% occurred in lower Sheep Creek, and 14% occurred in the upper Sheep Creek subwatershed (Figure 2.28). Stray rates were consistent among years (Figure 2.29).

Thirty-seven (11%) 39 mountain whitefish documented outside of their natal watershed made distinct homing movements to spawn 64 times (10%). Minimum homing rates for fish tagged in the Tenderfoot Creek and Sheep Creek watersheds were 39% and 8%, respectively. One hundred fifty-four (46%) mountain whitefish were documented outside of their natal subwatershed and made distinct homing movements to spawn 182 times (27%). Minimum homing rates were highest in the Tenderfoot Creek subwatershed (39%) and lowest in the Moose Creek subwatershed (29%). Fish tagged in the lower Sheep Creek subwatershed had a minimum homing rate of 25%.

Connectivity among salmonid populations

Eight fish were redetected in subbasins different from those in which they were tagged. Two fish (one rainbow trout and one Burbot) were tagged in the upper Missouri River subbasins and redetected in the Smith River subbasin. The rainbow trout was tagged in the Wilson Butte subwatershed in the mainstem Missouri River in the spring of 2016 and redetected in the Goodman Coulee subwatershed in the mainstem Smith River the following spring, eventually spawning in Tenderfoot Creek that same year. The Burbot was tagged in the Wilson Butte subwatershed in the mainstem Missouri River in March of 2016 and redetected three months later in the Goodman Coulee subwatershed in the mainstem Smith River. One rainbow trout was tagged in the Missouri River subbasin (City of Great Falls subwatershed, mainstem river) in autumn of 2015 and redetected twice in the Sun River subbasin (Fourmile Creek watershed, mainstem Sun River) in the summers of 2016 and 2017. Four fish tagged in the Smith River subbasin were redetected in the Missouri River subbasin. Three brown trout, all tagged in the lower Hound Creek subwatershed in July of 2014, were later redetected in the upper Missouri

River subbasins; two were redetected in the lower Dearborn River subwatershed later that year and one was redetected in the Sheep Creek subwatershed in 2015. One mountain whitefish was tagged in the Rocky Coulee subwatershed of the mainstem Smith River in 2016 and redetected spawning in the lower Dearborn River subwatershed in the autumns of 2017 and 2018. One mountain whitefish tagged in the Smith River subbasin (Two Creek subwatershed, mainstem Smith River) in the summer of 2014 was redetected in the Sun River subbasin (Fourmile Creek watershed, mainstem Sun River) in December 2015. This same individual returned to the Smith River subbasin the following summer, redetected in the same subwatershed it was tagged in.

A total of 107 fish was detected on the Truly Bridge fixed PIT array: eight rainbow trout, three brown trout, 90 mountain whitefish, one Burbot, four White Suckers, and one Longnose Sucker. Of the seven fish that were observed leaving or entering the Smith River subbasin, four (one rainbow trout, two mountain whitefish, and one Burbot) were redetected. All three brown trout that moved from the Smith River subbasin to the Missouri River subbasin were not detected by the Truly Bridge array.

Discussion

Stray rates were lower than expected based on work previously done in the upper Missouri River. Rainbow trout radio-tagged in the mainstem Missouri River from 2009 to 2011 lacked spawning site fidelity and only 8% of those that spawned in tributaries did so in consecutive years (Grisak et al. 2012b). The longer duration of our monitoring effort may have allowed more alternate-year spawners to return to natal tributaries, thereby reducing stray rates. Indeed, we observed multi-year spawning by all study species in the upper Missouri River and

Smith River subbasins. Minimum homing rates were generally greater than straying rates, but many fish could not be categorized or were unaccounted for and could have been tributary residents, mortalities, or undetected.

Our network of PIT antennas may have only been able to monitor specific life histories or fragments thereof. Multiple life histories were observed for all three study species in the Smith River (Ritter 2015; Lance 2019) and radiotelemetry studies across upper Missouri River subbasins provided evidence for variation in spawning migration patterns and distribution (Grisak 2012; Grisak et al. 2012a; Grisak et al. 2012b). Mainstem spawning was not investigated in the upper Missouri River or Smith River subbasins, nor were any fish assigned mainstem natal origins, although we know mainstem spawning takes place (Grisak 2012; Grisak et al. 2012b).

Widespread mainstem spawning could explain why such small proportions of spawning fish were observed. Stray rates of the overall population (rather than just those that spawn in tributaries) could therefore be higher than observed because fish with tributary origins that spawned in the mainstem could not be detected. Still, previous work suggested most rainbow trout spawning occurs in tributaries in the upper Missouri River subbasin where our network was installed; Grisak et al. (2012b) reported that only 28% of redds surveyed from 2007 to 2010 were found in the mainstem. However, this was a 64% increase from historical numbers (Grisak et al. 2012b), so if this trend continued, mainstem spawning by rainbow trout in the Missouri River could have been even more prevalent during our study. Redd count data from 2015 suggest this was the case as it was estimated 39% of rainbow trout redds were in the mainstem in 2015 (J. A. Mullen, unpublished data).

Minimum homing rates provided more insights into fluvial spawning patterns by excluding resident fish. However, there remained a large proportion of spawning individuals with known natal origins that could not be categorized as making straying or homing movements. Some fish may have remained tributary residents rather than migrating out to the mainstem. Tributary residence was observed in the Smith River subbasin by rainbow and brown trout and mountain whitefish (Ritter 2015; Lance 2019). Tributary residents could have been interpreted as returning spawners in our straying analyses, thereby lowering straying rates (thus we evaluated minimum homing rates of fish that were documented outside of the natal stream as an alternative). Previous otolith microchemistry and scale growth studies did not include tributary residents because fish were sampled as they outmigrated or in the mainstem Missouri River (Munro 2004; Leathe et al. 2014). Stream residents generally show physical signs of sexual maturity at smaller sizes than their migratory counterparts (Meyer et al. 2003) and we observed numerous ripe male rainbow trout at lengths much smaller than would be expected for migratory individuals.

Low proportions of detected spawning individuals may also be a result of low detection rates of PIT arrays and mortality. Detection ranges were generally lowest during spring flows, which also coincided with rainbow trout spawning migrations and contributed to low numbers of outmigrants. In contrast, detection ranges were relatively high during brown trout and mountain whitefish spawning seasons. We would therefore expect proportions of spawning rainbow trout to be lowest relative to total numbers tagged, but this was not observed. Mortality, especially resulting from predation, may partly explain such low proportions, especially in the Smith River; predation rates of American white pelicans on PIT tagged fish in the Smith River ranged from 12.3% to 66.1% annually (Vivian and Mullen 2018). However, pelican predation rates on PIT-tagged fish in the Missouri and Sun rivers were much lower (Vivian and Mullen 2018).

The Dearborn River and Little Prickly Pear Creek and its tributaries are critical to the reproductive success of rainbow trout. If straying among Little Prickly Pear Creek subwatersheds did occur, it was almost always to another tributary within the same watershed (e.g., Wolf Creek, Lyons Creek, or Little Prickly Pear Creek itself). Furthermore, spawning efforts were highest in the Little Prickly Pear Creek watershed for rainbow trout tagged in both tributaries and mainstem alike. Interestingly, spawning location of fish tagged in the mainstem was not necessarily the closest tributary; some rainbow trout tagged in the vicinity (<8.5 rkm) of Little Prickly Pear Creek moved downstream to spawn in the Dearborn River. This same pattern was reported in radio-tagged rainbow trout by Grisak et al. (2012b) and could be indicative of homing behavior considering the energy required to bypass a proximal spawning tributary in favor of one more distant. Similar movements were observed in rainbow trout that strayed from the Dearborn River; rather than spawning in nearby Sheep Creek, strays spawned exclusively in the Little Prickly Pear Creek watershed. Curiously, fish that strayed from Sheep Creek did not show a similar pattern and spawned exclusively in the Dearborn River.

Relative to other tributaries in the Missouri River subbasin, Little Prickly Pear Creek and its tributaries are most important for brown trout spawning success. Indeed, all observed brown trout spawning occurred in the Little Prickly Pear Creek watershed, whereas no brown trout were observed making spawning movements in the Dearborn River despite tagging 131 fish in the tributary itself and 68 in the closest downstream mainstem subwatershed, Dog Creek. Correspondingly, Grisak et al. (2012a) observed no radio-tagged brown trout spawning in the Dearborn River, although some individuals may have spawned at the confluence with the Missouri River. Furthermore, no outmigration from the Dearborn River was observed and very few juveniles were tagged; Leathe et al. (2014) reported lower numbers of brown trout outmigrants from the Dearborn River compared to Little Prickly Pear Creek.

Proportionally, Sheep Creek has less spawning than other major tributaries to the Missouri River, especially for rainbow and brown trout. Sheep Creek had the lowest proportion of spawning effort relative to other tributaries for all study species, despite tagging 424 rainbow trout and 72 brown trout there (no mountain whitefish were tagged there). Grisak et al. (2012b) also observed the lowest proportion of rainbow trout redds in Sheep Creek. In addition, fish tagged in Sheep Creek had the highest stray rate, suggesting that other tributaries provided preferential spawning habitat regardless of natal origins. Unsurprisingly, Sheep Creek was the only tributary that was never a straying destination of fish with natal origins elsewhere. Early and rapid outmigrations of juvenile trout could have contributed to the high stray rates of natal fish; juvenile dispersal has been associated with propensity to stray in Chinook Salmon (Hamann and Kennedy 2012).

The Sun River supports reduced populations of rainbow and brown trout compared to the Missouri and Smith rivers, mainly because of poor habitat conditions (i.e., high water temperatures and low flows during critical times of the year). Whereas trout redds have been documented in the Sun River (J. A. Mullen, personal observation), we did not detect spawning movements made by fish tagged in the Sun River. The lack of spawning movement detections was likely related to the large distance between the PIT antenna arrays, but we did observe some downstream movements during the early portions of spawning seasons. This pattern was similar to a previous study; rather than spawning in the Sun River, Grisak et al. (2012b) observed fish tagged in the lower Sun River moving downstream to spawn in the mainstems and tributaries of the Missouri or Smith rivers.

Straying rates and spawning patterns were generally similar for all species in the Smith River as compared to the those observed in the upper Missouri River. Rainbow trout spawning occurred primarily in one tributary watershed encompassing many smaller tributaries. This coupled with the combination of low and high stray rates at the watershed and subwatershed scales suggests that the Sheep Creek watershed in the Smith River is analogous to the Little Prickly Pear Creek watershed in the Missouri River as far as importance to rainbow trout reproduction. Similar to that observed in the Little Prickly Pear Creek watershed in the Missouri River, straying that occurred at the subwatershed level was almost always to other subwatersheds within the same watershed. Unlike that observed in the Missouri River, brown trout spawning effort was widely distributed among tributaries in the Smith River. Regardless, stray rates of brown trout remained low at both watershed and subwatershed scales; homing abilities of brown trout are well-known (Harcup et al. 1984; Armstrong and Herbert 1997).

Spawning efforts of mountain whitefish were not widely distributed among tributaries in either subbasin, occurring primarily in the Sheep Creek and Tenderfoot Creek watersheds in the Smith River and Dearborn River in the Missouri River. Consistent with that observed with other species in the study area, stray and return rates of mountain whitefish were low at both spatial scales. Unsurprisingly, mountain whitefish in other systems have exhibited strong homing abilities (Pettit and Wallace 1975; Davies and Thompson 1976; Benjamin et al. 2014). However, the homing abilities we observed were much stronger than expected; homing rates were never lower than 75% at either scale, whereas homing proportions observed in other studies ranged from 37% to 49% (Pettit and Wallace 1975; Benjamin et al. 2014). Again, not including mainstem spawners may have resulted in lowered stray rates; mountain whitefish have been observed spawning in the mainstem Smith River (Lance 2019). Furthermore, in the upper

Missouri River, most mountain whitefish were tagged in either the Dearborn River or the mainstem Missouri River in subwatersheds near the mouth of the Dearborn River. These were the few locations where they could reliably be sampled, which also supports their diminished use of other tributaries for reproduction.

Inter-subbasin connectivity is likely higher than we observed. Our network of stationary PIT arrays was designed to monitor interchange between mainstem rivers and tributaries, but not necessarily inter-subbasin movements. Whereas the Sun and Smith rivers were small enough to install mainstem antennas, the width of the Missouri River precluded effective use of PIT telemetry. Furthermore, our PIT array network was sparsest in the area surrounding the confluences of the Sun and Smith rivers with the Missouri River; mainstem antennas in the Sun and Smith rivers were 32 rkm and 14.6 rkm upstream of their mouths, respectively. These antennas (Durocher and Truly Bridge) also exhibited some of the lowest detection ranges observed in the study. Tagged fish that were detected making inter-subbasin movements therefore probably represented even more untagged fish than typically accepted. Radiotelemetry studies unhindered by spatial limitations observed larger proportions of tagged fish making such movements, though sample size was low (N = 43; Grisak et al. 2012b). These studies also monitored the movements of fish tagged in mainstem river habitat, whereas we tagged most fish in tributaries (only 128 rainbow trout were tagged in the mainstem Missouri River compared to 2,358 tagged in tributaries).

Despite the low number of fish detected making such movements, some patterns were apparent. This study confirms the inter-basin connectivity of the Missouri River downstream of Cascade with the Smith and Sun rivers that was also observed in past radio telemetry studies. Only 7 rainbow trout and 16 burbot were tagged downstream of Cascade; one rainbow trout and one burbot were detected in the Smith River and one rainbow trout was detected in the Sun River. Although radiotelemetry studies reported only fish tagged in the Missouri and Sun rivers making inter-subbasin movements, we observed more fish moving from the Smith River to the Missouri River. Interestingly, Hound Creek may play an important role in movements between the Smith River and Missouri and Sun rivers. Grisak et al. (2012b) observed two brown trout tagged in the Missouri and Sun rivers spawning in Hound Creek, one of which overwintered there. In contrast, the three brown trout we detected were tagged in Hound Creek and moved to the Dearborn River and Sheep Creek. In addition to spawning areas, Hound Creek may provide an oasis of preferential habitat in the lower prairie region of the Smith River, which is heavily affected by agriculture (Lance 2019).

TABLES

Table 2.1. Number of fish tagged by species and subwatershed in the Missouri River subbasin from 2014 to 2016. Superscripts represent subwatersheds that include locations of annual population sampling. Miscellaneous species include Mountain Sucker, Yellow Perch, and Walleye.

	Species								
Subwatershed	Rainbow Trout	Brown Trout	Mountain Whitefish	Brook Trout	Burbot	White Sucker	Longnose Sucker	Misc	Total
Tributary									
Dearborn River	390	131	46	-	-	40	46	2	655
Sheep Creek	424	72	-	-	-	2	-	-	498
Little Prickly Pear Creek watershed									
Little Prickly Pear Creek	521	86	1	-	-	9	2	-	619
Wolf Creek	760	94	-	-	-	-	-	-	853
Lyons Creek	263	114	-	-	-	1	-	-	377
Subtotal	2,358	495	47	-	-	52	48	2	3,002
Mainstem									
City of Great Falls	3	6	7	-	1	2	1	1	21
Dog Creek[1]	66	68	4	-	-	23	1	-	162
Finigan Creek[2]	8	4	-	-	-	-	-	-	12
Log Gulch	37	59	114	-	1	-	-	-	211
Prewett Creek	10	-	105	-	-	26	1	1	143
Wilson Butte	4	1	-	-	15	-	1	-	22
Subtotal	128	138	230	-	17	51	4	2	570
Total	2,487	633	277	-	17	103	52	4	**3,572**

[1] Craig annual population sampling section.
[2] Cascade annual population sampling section.

Table 2.2. Number of fish tagged by species and subwatershed in the Sun River subbasin from 2015 to 2016. Superscripts represent subwatersheds that include locations of annual population sampling. Miscellaneous species include Mountain Sucker, Yellow Perch, and Walleye.

	Species							
Subwatershed	Rainbow Trout	Brown Trout	Mountain Whitefish	Brook Trout	Burbot	White Sucker	Longnose Sucker	Total
Tributary								
Elk Creek	9	125	46	3	-	2	-	142
Mainstem								
City of Simms[1]	96	128	145	-	-	5	-	374
Cutting Shed Coulee	48	100	76	-	-	-	-	223
Subtotal	144	228	221	-	-	5	-	597
Total	153	353	223	3	-	8	-	**739**

[1] Simms annual population sampling section.

Table 2.3. Number of fish tagged by species and subwatershed in the Smith River subbasin from 2010 to 2017. Superscripts represent subwatersheds that include locations of annual population sampling.

	Species								
Subwatershed	Rainbow Trout	Brown Trout	Mountain Whitefish	Brook Trout	Burbot	White Sucker	Longnose Sucker	Mountain Sucker	Total
Tributary									
Big Birch Creek	8	56	10	11	-	3	-	-	88
Hound Creek	24	367	11	-	-	48	19	-	469
Newlan Creek	1	21	5	33	8	46	-	-	114
Sheep Creek watershed									
Lower Sheep	51	26	120	1	-	9	1	-	208
Middle Sheep	689	77	52	13	-	2	-	-	833
Upper Sheep	284	40	40	4	-	2	-	-	370
Moose Creek	908	6	271	21	-	-	-	-	1,204
Rock Creek	13	68	17	-	-	-	-	-	98
Tenderfoot Creek	483	85	460	94	-	-	-	-	1,122
Subtotal	2,455	706	986	166	8	110	20	-	4,451
Mainstem									
Bear Gulch	42*	48	59	-	-	-	2	-	151
Blacktail Creek[1]	376	172	258	-	6	5	7	-	824
Boston Coulee	18*	38	129	-	-	8	7	-	200
Cottonwood Creek[2]	56*	93	211	7	3	6	6	-	381
Rock Springs Creek	38*	178	235	8	2	23	-	-	484
Rocky Coulee	56	47	113	-	-	3	2	-	221
Two Creek	277*	187	356	-	13	12	12	1	858
Subtotal	864	763	1,360	15	24	57	36	-	3,119
Total	3,323	1,510	2,346	192	32	167	56	1	**7,625**

[1] Eagle Creek annual population sampling section.
[*] Includes one Westslope Cutthroat Trout. A total of five was tagged in the Smith River subbasin.

Table 2.4. Locations, average detection ranges, and detection efficiencies of stationary PIT arrays in the upper Missouri River, Sun River, and Smith River subbasins.

Stationary PIT array	GPS coordinates (UTM)	Tag detection distance (inches)	Detection efficiency	Physical location
		Missouri River		
Lyons Creek	46.93827, -112.12581	28.5 (6 – 54)	-	Just upstream of confluence with Little Prickly Pear Creek
Wolf Creek	47.00597, -112.08026	29 (6 – 60)	-	Just upstream of confluence with Little Prickly Pear Creek
Little Prickly Pear Creek	47.02251, -112.02018	17 (2 – 42)		Just upstream of confluence with Missouri River
Dearborn River	47.13017, -111.91295	6.3 (2.5 – 9)	-	Just upstream of confluence with Missouri River
Sheep Creek	47.17681, -111.81165	17.7 (4 – 36)	-	Just upstream of confluence with Missouri River
		Sun River		
HWY 287	47.54768, -112.36674	8.6 (4.5 – 18)	-	Just upstream of Hwy 287 near Augusta, Montana at rkm 109
Elk Creek	47.51229, -112.33641	30 (4 – 48)	-	rkm 4.5
Durocher	47.54413, -111.57848	7.2 (3 – 18)	-	Upstream of Vaughn, Montana at rkm 32
		Smith River		
Big Birch Creek	46.58884, -111.05305	-	0.79	Just upstream of confluence with Smith River
Newlan Creek	46.59094, -111.05070	-	0.79	Just upstream of confluence with Smith River
Canyon Ranch	46.60810, -111.06760	-	0.96	rkm 172
Benton Creek	46.70542, -111.19305	-	0.79	Just upstream of confluence with Smith River
Camas Creek	46.70542, -111.19305	-	0.96	Just upstream of confluence with Smith River
Smith River at Beaver Creek	46.75143, -111.16839	-	1.00	rkm 141
Moose Creek	46.80292, -110.91484	-	0.96	Just upstream of confluence with Sheep Creek
Upper Sheep Creek	46.81047, -110.92272	-	0.71	1 rkm downstream of Moose Creek
Lower Sheep Creek	46.80443, -111.17403	-	0.78	0.9 rkm upstream of confluence with Smith River
Rock Creek	46.86935, -111.27185	-	0.79	Just upstream of confluence with Smith River
Tenderfoot Creek	46.94185, -111.29404	-	0.98	Just upstream of confluence with Smith River
Castle Bar	46.97789, -111.28427	-	0.75	rkm 97
Merganser Bend	47.14734, -111.294	-	0.66	Just downstream of Merganser Bend boat camp
Hound Creek	47.21261, -111.40371	18.5 (4 – 36)	0.96	rkm 2.4
Truly Bridge	47.35658, -111.44140	7.4 (1 – 18)	0.70	rkm 14.6

Table 2.5. Numbers of fish redetected by stationary PIT arrays, mobile tracking, and physical recapture events organized by year, species, and subbasin tagged. Totals include numbers of unique individuals redetected across years; because many individuals were redetected multiple years, these values may not be mathematical sums.

	Species								
Year	Rainbow Trout	Brown Trout	Mountain Whitefish	Brook Trout	Westslope Cutthroat	Burbot	White Sucker	Longnose Sucker	**Subtotal**
				Missouri River					
2014	398	49	21	-	-	-	15	16	499
2015	177	36	62	-	-	-	5	2	282
2016	249	62	48	-	-	1	11	-	372
2017	128	14	29	-	-	-	10	-	181
2018	36	8	8	-	-	-	3	-	55
2019	6	1	-	-	-	-	-	-	7
2020	-	2	-	-	-	-	-	-	2
Subtotal	724	128	84	-	-	-	33	18	**988**
				Sun River					
2015	25	48	33	-	-	-	1	-	107
2016	6	40	25	1	-	-	1	-	73
2017	2	15	6	-	-	-	1	-	24
2018	1	5	4	-	-	-	-	-	10
2019	-	3	2	-	-	-	-	-	5
2020	-	2	-	-	-	-	-	-	2
Subtotal	30	72	51	1	-	-	2	-	**156**
				Smith River					
2010	16	7	1	1	-	-	-	-	25
2011	38	13	10	1	-	-	-	-	62
2012	46	15	161	2	-	-	-	-	224
2013	34	5	42	-	-	-	-	-	81
2014	73	47	392	2	-	2	22	1	539
2015	526	134	675	4	-	3	31	5	1,378
2016	608	264	738	11	1	10	22	15	1,669
2017	607	299	912	7	4	9	23	23	1,884
2018	122	48	285	-	1	2	8	4	470
2019	24	6	70	-	-	-	2	-	102
2020	-	1	-	-	-	-	-	-	1
Subtotal	1,470	612	1,650	28	5	15	81	31	3,892
TOTAL	2,224	812	1,785	29	5	16	116	49	**5,036**

Table 2.6. Numbers of spawning events made by rainbow trout, brown trout, and mountain whitefish in the upper Missouri River, Sun River, and Smith River subbasins from 2014 to 2019. Ordinary text indicates the total number of spawning events made whereas italicized text indicates the number of spawning events made by fish with determined natal origins. *Spawning movements could not be inferred in the Sun River; detections during spawning seasons are reported instead.

	Year						
Subbasin tagged	2014	2015	2016	2017	2018	2019	Total
			Rainbow Trout				
Upper Missouri River	154 *(127)*	138 *(107)*	150 *(116)*	117 *(101)*	36 *(29)*	6 *(6)*	601 *(486)*
Sun River*	-	-	5	1	1	-	7
Smith River	18 *(10)*	223 *(135)*	383 *(230)*	198 *(74)*	106 *(39)*	23 *(11)*	951 *(499)*
			Brown Trout				
Upper Missouri River	2 *(0)*	18 *(6)*	22 *(8)*	8 *(2)*	3 *(2)*	1 *(0)*	54 *(18)*
Sun River*	-	18	5	10	-	-	33 *(0)*
Smith River	68 (*59)*	47 *(20)*	52 *(16)*	23 *(3)*	6 *(1)*	3 *(1)*	199 *(100)*
			Mountain Whitefish				
Upper Missouri River	-	37 *(0)*	27 *(0)*	20 *(0)*	2 *(0)*-	-	86 *(0)*
Sun River*	-	3	2	5	-	-	10 *(0)*
Smith River	524 *(325)*	346 *(186)*	249 *(112)*	131 *(37)*	49 *(10)*	45 *(8)*	1,344 *(678)*

Table 2.7. Number of straying events by rainbow and brown trout tagged in upper Missouri River watersheds from 2015 to 2018. N_{st} represents the total number of observed spawning fish that strayed.

		Year				
Watershed tagged	N_{st}	2015	2016	2017	2018	Total
			Rainbow Trout			
Dearborn River	1	1	-	-	-	1
Sheep Creek	6	4	4	4	2	14
Little Prickly Pear Creek	1	-	1	-	-	1
Total	8	5	5	4	2	**16**
			Brown Trout			
Dearborn River	0	-	-	-	-	-
Sheep Creek	1	-	1	-	-	1
Little Prickly Pear Creek	0	-	-	-	-	-
Total	1	-	1	-	-	**1**

Table 2.8. Percentages of rainbow and brown trout spawning events that returned to or strayed from upper Missouri River watersheds from 2015 to 2018 with known natal origins. *N* represents the number of observed spawning fish and N_{sp} represents the number of spawning events. Bold values indicate homing percentages. One mountain whitefish tagged in the Smith River drainage was observed spawning in the Dearborn River.

			Returning watershed (%)		
Watershed tagged	*N*	N_{sp}	Dearborn River	Sheep Creek	Little Prickly Pear Creek
				Rainbow Trout	
Dearborn River	28	35	**97**	-	3
Sheep Creek	64	95	15	**85**	-
Little Prickly Pear Creek	174	223	1	-	**99**
				Brown Trout	
Dearborn River	0	0	-	-	-
Sheep Creek	1	1	-	-	1.00
Little Prickly Pear Creek	13	17	-	-	**1.00**

Table 2.9. Percentages of rainbow trout, brown trout, and mountain whitefish spawning events that returned to or strayed from upper Missouri River watersheds from 2015 to 2018 with unknown natal origins. *N* represents the number of observed spawning fish and N_{sp} represents the number of spawning events. Bold values indicate homing percentages. One mountain whitefish tagged in the Smith River drainage was observed spawning in the Dearborn River.

			Returning watershed (%)		
Watershed tagged	*N*	N_{sp}	Dearborn River	Sheep Creek	Little Prickly Pear Creek
				Rainbow Trout	
Dearborn River	34	43	**93**	2	5
Sheep Creek	1	1	-	**100**	-
Little Prickly Pear Creek	27	27	-	-	**100**
City of Great Falls (MR)	0	0	-	-	-
Rattlesnake Gulch (MR)	16	22	9	2	89
Stickney Creek (MR)	16	22	5	5	90
				Brown Trout	
Dearborn River	0	0	-	-	-
Sheep Creek	0	0	-	-	-
Little Prickly Pear Creek	1	1	-	-	**100**
City of Great Falls	0	0	-	-	-
Rattlesnake Gulch (MR)	9	11	-	-	100
Stickney Creek (MR)	14	21	-	-	100
				Mountain Whitefish	
Dearborn River	14	25	**100**	-	-
Sheep Creek	32	53	96	-	4
Little Prickly Pear Creek	0	0	-	-	-
City of Great Falls (MR)	1	1	100	-	-
Rattlesnake Gulch (MR)	2	6	100	-	-
Stickney Creek (MR)	0	0	-	-	-

Table 2.10. Number of straying events by rainbow and brown trout tagged in upper Missouri River subwatersheds. N_{st} represents the total number of observed spawning fish that strayed.

Subwatershed tagged	N_{st}	Year				Total
		2015	2016	2017	2018	
				Rainbow Trout		
Dearborn River	1	1	-	-	-	1
Sheep Creek	6	4	4	4	2	14
Little Prickly Pear Creek	40	14	24	7	3	48
Wolf Creek	10	2	3	3	3	11
Lyons Creek	9	2	3	5	-	10
Total	66	23	34	19	8	**84**
				Brown Trout		
Dearborn River	0	-	-	-	-	-
Sheep Creek	1	-	1	-	-	1
Little Prickly Pear Creek	3	1	1	-	1	3
Wolf Creek	2	-	2	-	-	2
Lyons Creek	1	-	1	-	-	1
Total	7	1	5	-	1	**7**

Table 2.11. Percentages of rainbow and brown trout spawning events that returned to or strayed from upper Missouri River subwatersheds from 2015 to 2018 with known natal origins. *N* represents the number of observed spawning fish and N_{sp} represents the number of spawning events. Bold values indicate homing proportions. Bold values indicate homing proportions.

			Returning subwatershed (%)				
Subwatershed tagged	*N*	N_{sp}	Dearborn River	Sheep Creek	Little Prickly Pear Creek	Wolf Creek	Lyons Creek
					Rainbow Trout		
Dearborn River	28	35	**97**	-	3	-	-
Sheep Creek	64	95	15	**85**	-	-	-
Little Prickly Pear Creek	70	86	1	-	**44**	12	43
Wolf Creek	74	101	-	-	6	**89**	5
Lyons Creek	30	36	-	-	28	-	**72**
					Brown Trout		
Dearborn River	0	0	-	-	-	-	-
Sheep Creek	1	1	-	-	1.00	-	-
Little Prickly Pear Creek	6	7	-	-	**57**	43	-
Wolf Creek	3	3	-	-	33	**67**	-
Lyons Creek	4	4	-	-	-	25	**75**

Table 2.12. Percentages of rainbow trout, brown trout, and mountain whitefish spawning events that returned to or strayed from upper Missouri River subwatersheds from 2015 to 2018 with unknown natal origins. *N* represents the number of observed spawning fish and N_{sp} represents the number of spawning events. Bold values indicate homing proportions.

			Returning subwatershed (%)				
Subwatershed tagged	*N*	N_{sp}	Dearborn River	Sheep Creek	Little Prickly Pear Creek	Wolf Creek	Lyons Creek
					Rainbow Trout		
Dearborn River	34	43	**93**	2	2	2	-
Sheep Creek	0	0	-	-	-	-	-
Little Prickly Pear Creek	0	0	-	-	-	-	-
Lyons Creek	0	0	-	-	-	-	-
Wolf Creek	0	0	-	-	-	-	-
City of Great Falls (MR)	0	0	-	-	-	-	-
Dog Creek (MR)	16	22	5	5	50	18	22
Finigan Creek (MR)	1	1	-	100	-	-	-
Log Gulch (MR)	16	22	14	-	59	18	9
Prewett Creek (MR)	0	0	-	-	-	-	-
					Brown Trout		
Dearborn River	0	0	-	-	-	-	-
Sheep Creek	0	0	-	-	-	-	-
Little Prickly Pear Creek	0	0	-	-	-	-	-
Lyons Creek	1	1	-	-	-	-	**100**
Wolf Creek	0	0	-	-	-	-	-
City of Great Falls (MR)	0	0	-	-	-	-	-
Dog Creek (MR)	14	21	-	-	95	5	-
Finigan Creek (MR)	0	0	-	-	-	-	-
Log Gulch (MR)	9	11	-	-	91	9	-
Prewett Creek (MR)	0	0	-	-	-	-	-
					Mountain Whitefish		
Dearborn River	14	24	**100**	-	3	-	-
Sheep Creek	0	0	-	-	-	-	-
Little Prickly Pear Creek	0	0	-	-	-	-	-
Lyons Creek	0	0	-	-	-	-	-
Wolf Creek	0	0	-	-	-	-	-
City of Great Falls (MR)	1	1	100	-	-	-	-
Dog Creek (MR)	0	0	-	-	-	-	-
Finigan Creek (MR)	0	0	-	-	-	-	-
Log Gulch (MR)	2	6	100	-	-	-	-
Prewett Creek (MR)	32	53	96	-	4	-	-

Table 2.13. Number of straying events by rainbow and brown trout tagged in Smith River watersheds from 2015 to 2018. N_{st} represents the total number of observed spawning fish that strayed.

		Year				
Watershed tagged	N_{st}	2015	2016	2017	2018	Total
			Rainbow Trout			
Hound Creek	0	-	-	-	-	-
Tenderfoot Creek	0	-	-	-	-	-
Rock Creek	0	-	-	-	-	-
Sheep Creek	9	-	9	-	-	9
Camas Creek	0	-	-	-	-	-
Newlan Creek	0	-	-	-	-	-
South Fork Smith River	0	-	-	-	-	-
Total	9	-	9	-	-	**9**
			Brown Trout			
Hound Creek	0	-	-	-	-	-
Tenderfoot Creek	0	-	-	-	-	-
Rock Creek	0	-	-	-	-	-
Sheep Creek	2	2	-	-	-	2
Camas Creek	0	-	-	-	-	-
Newlan Creek	0	-	-	-	-	-
South Fork Smith River	0	-	-	-	-	-
Total	2	-	-	-	-	**2**

Table 2.14. Number of straying events by rainbow and brown trout tagged in Smith River subwatersheds from 2015 to 2018. N_{st} represents the total number of observed spawning fish that strayed.

		Year				
Subwatershed tagged	N_{st}	2015	2016	2017	2018	Total
			Rainbow Trout			
Lower Hound Creek	0	-	-	-	-	-
Lower Tenderfoot Creek	0	-	-	-	-	-
Lower Rock Creek	0	-	-	-	-	-
Lower Sheep Creek	0	-	-	-	-	-
Upper Sheep Creek	106	36	56	22	14	128
Moose Creek	92	23	42	24	15	104
Benton Gulch	0	-	-	-	-	-
Lower Camas Creek	0	-	-	-	-	-
Big Birch Creek	0	-	-	-	-	-
Lower Newlan Creek	0	-	-	-	-	-
Total	198	59	98	46	29	**232**
			Brown Trout			
Lower Hound Creek	0	-	-	-	-	-
Lower Tenderfoot Creek	0	-	-	-	-	-
Lower Rock Creek	0	-	-	-	-	-
Lower Sheep Creek	2	1	-	-	1	2
Upper Sheep Creek	9	4	5	-	-	9
Moose Creek	0	-	-	-	-	-
Benton Gulch	0	-	-	-	-	-
Lower Camas Creek	0	-	-	-	-	-
Big Birch Creek	0	-	-	-	-	-
Lower Newlan Creek	0	-	-	-	-	-
Total	11	5	5	-	1	**11**

Table 2.15. Proportions of rainbow and brown trout and mountain whitefish spawning events that returned to or strayed from Smith River subwatersheds from 2015 to 2018. *N* represents the number of observed spawning fish and N_{sp} represents the number of spawning events. Bold values indicate homing proportions.

			Returning subwatershed (%)						
Subatershed tagged	*N*	N_{sp}	Lower Hound Creek	Lower Tenderfoot Creek	Lower Rock Creek	Lower Sheep Creek	Upper Sheep Creek	Moose Creek	Lower Newlan Creek
						Rainbow Trout			
Lower Hound Creek	1	1	**100**	-	-	-	-	-	-
Lower Tenderfoot Creek	15	18	-	**100**	-	-	-	-	-
Lower Rock Creek	1	1	-	-	-	**100**	-	-	-
Lower Sheep Creek	3	3	-	-	-	**100**	-	-	-
Upper Sheep Creek	168	214	-	-	1	21	**53**	25	-
Moose Creek	201	250	-	1	2	18	21	**58**	-
Lower Newlan Creek	1	1	-	-	-	-	-	-	**100**
						Brown Trout			
Lower Hound Creek	14	20	**100**	-	-	-	-	-	-
Lower Tenderfoot Creek	2	3	-	**100**	-	-	-	-	-
Lower Rock Creek	0	0	-	-	-	-	-	-	-
Lower Sheep Creek	18	25	-	-	4	**92**	4	-	-
Upper Sheep Creek	29	42	-	-	-	12	**86**	-	2
Moose Creek	0	0	-	-	-	-	-	-	-
Lower Newlan Creek	7	9	-	-	-	-	-	-	**100**
						Mountain Whitefish			
Lower Hound Creek	0	0	-	-	-	-	-	-	-
Lower Tenderfoot Creek	22	41	-	**93**	-	5	2	-	-
Lower Rock Creek	0	0	-	-	-	-	-	-	-
Lower Sheep Creek	111	193	-	2	-	**94**	4	-	-
Upper Sheep Creek	26	45	-	-	-	-	**76**	24	-
Moose Creek	178	390	-	-	-	1	21	**78**	-
Lower Newlan Creek	1	1	-	-	-	-	-	-	**100**

FIGURES

Figure 2.1. The upper Missouri, Sun, and Smith rivers and their major tributaries. Yellow dots represent USGS gaging stations used in the study. Black diagonals represent dams or diversions. Green diamonds represent fixed PIT antenna arrays. Shaded buffers represent areas where fish movement was monitored by fixed PIT antenna arrays, portable PIT antennas, and physical recapture events.

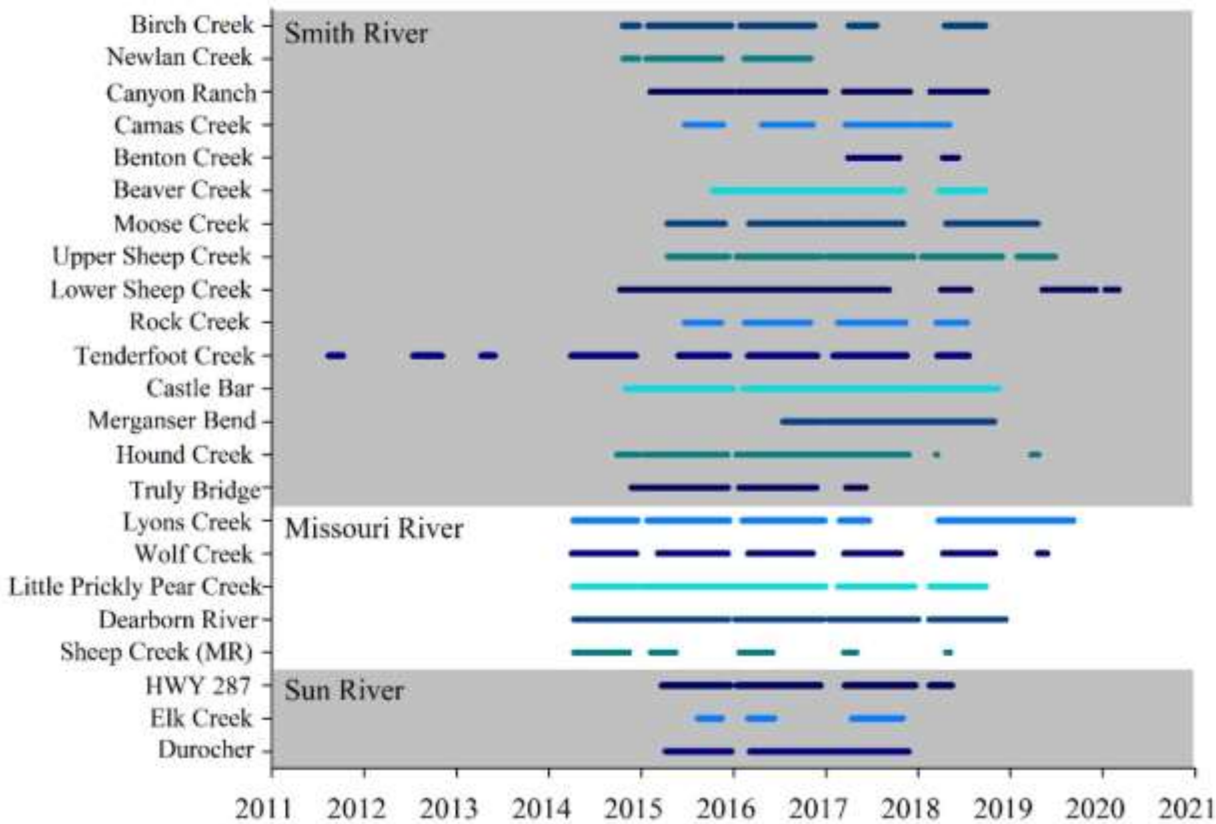


Figure 2.2. Operation timelines of stationary PIT arrays in the Smith, Sun, and upper Missouri River subbasins from 2011 to 2020.

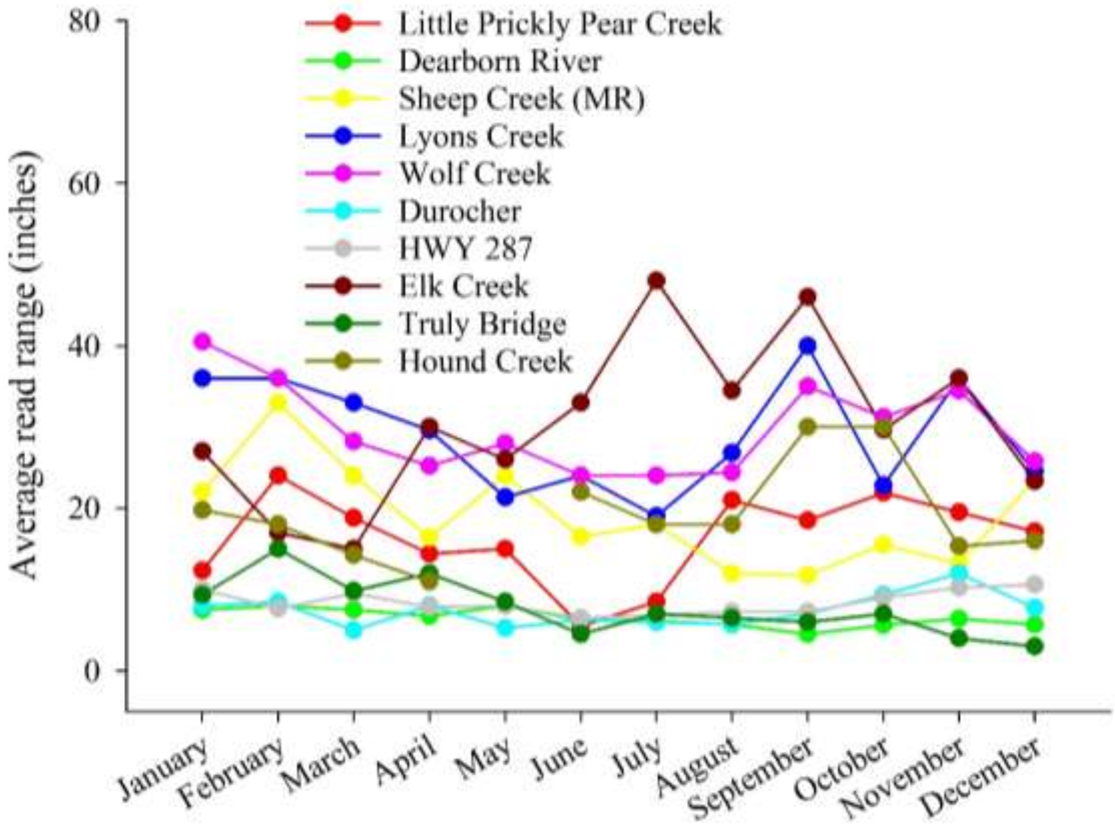


Figure 2.3. Average read ranges of fixed PIT arrays by month from 2015 to 2019.

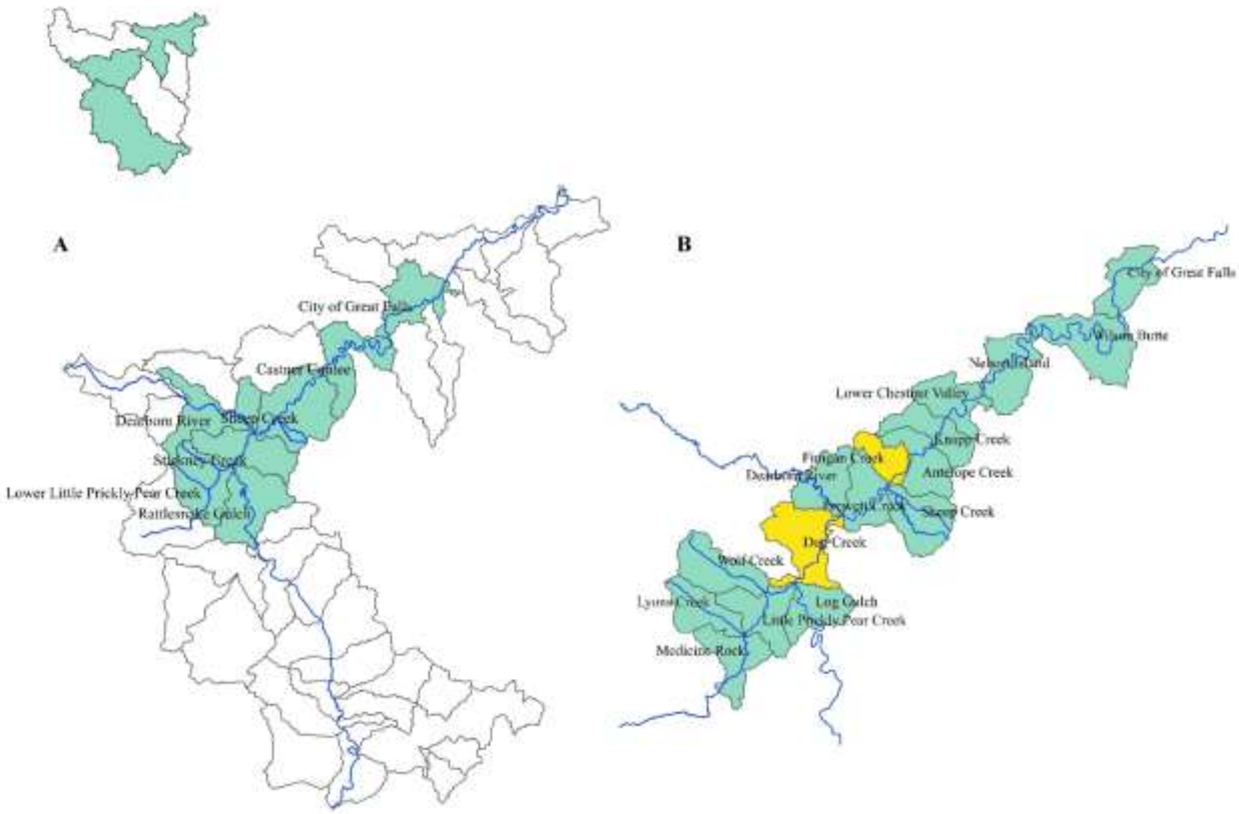


Figure 2.4. The upper Missouri River subbasin watersheds (A) and subwatersheds (B). Light green areas represent watersheds and subwatersheds that were included in the study area. Yellow areas represent subwatersheds that encompassed Montana Fish, Wildlife & Parks annual population sampling sections.

Figure 2.5. Watersheds of the Sun River subbasin. Light green areas represent watersheds and that were included in the study area. The yellow area represents the watershed that encompassed Montana Fish, Wildlife & Parks annual population sampling section at Simms.

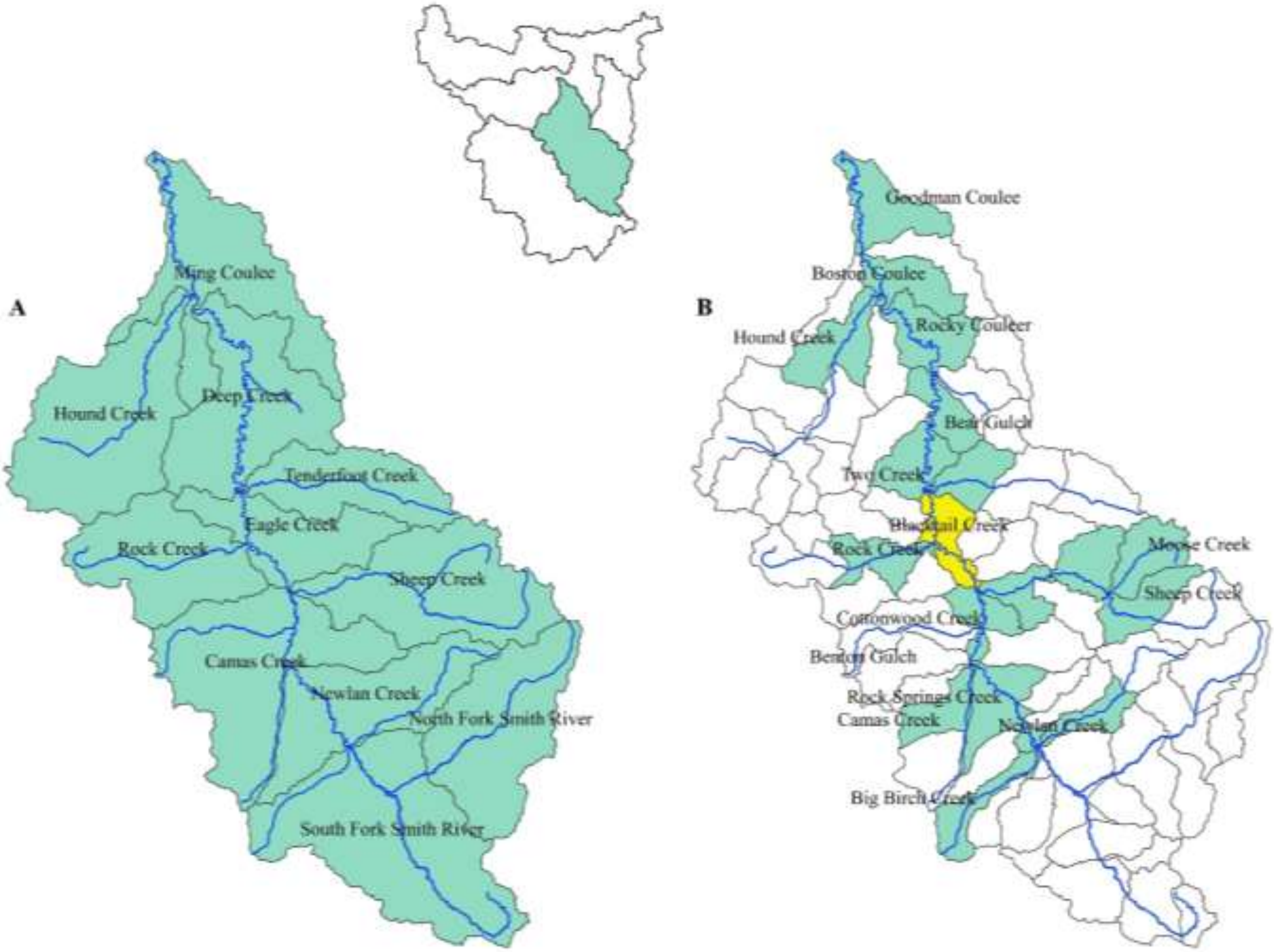


Figure 2.6. Smith River subbasin watersheds (A) and subwatersheds (B). Light green areas represent watersheds and subwatersheds that were included in the study area. The yellow area represents the subwatershed that encompassed Montana Fish, Wildlife & Parks annual population sampling section near Eagle Creek.

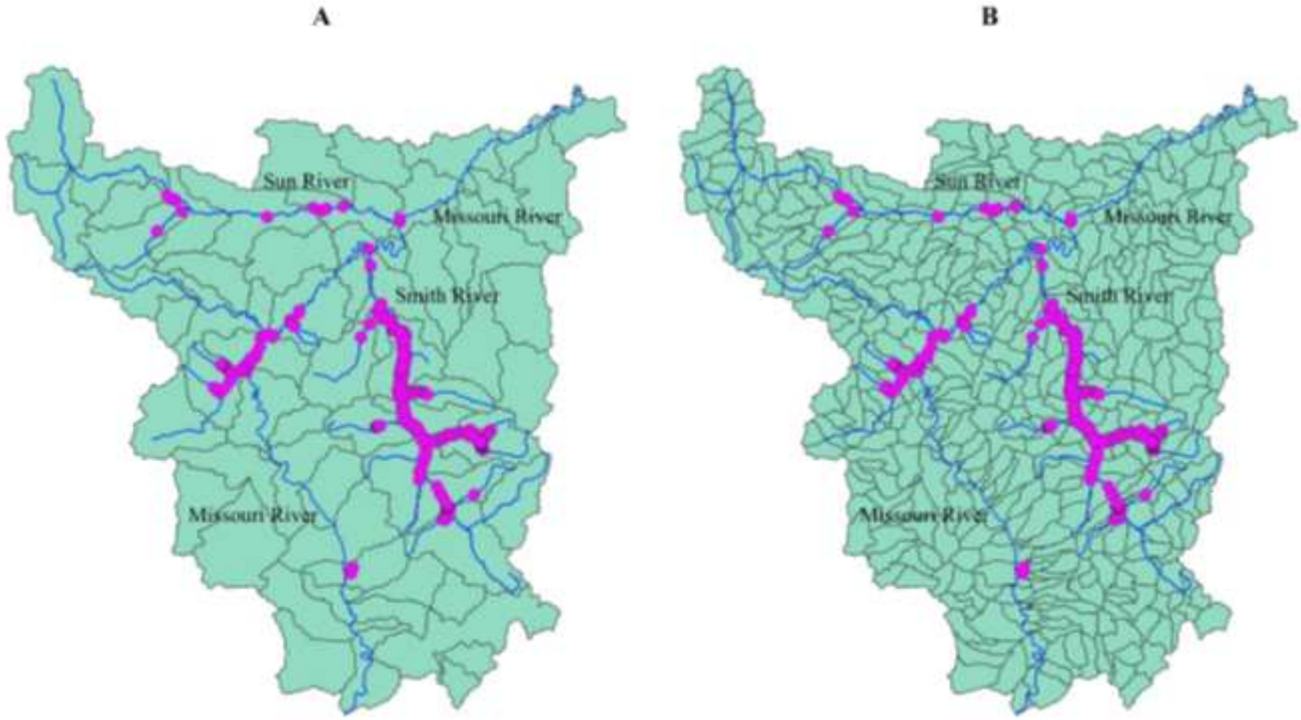


Figure 2.7. Location data of PIT-tagged fish, represented by pink dots, within watersheds (A) and subwatersheds (B) of the upper Missouri River basin.

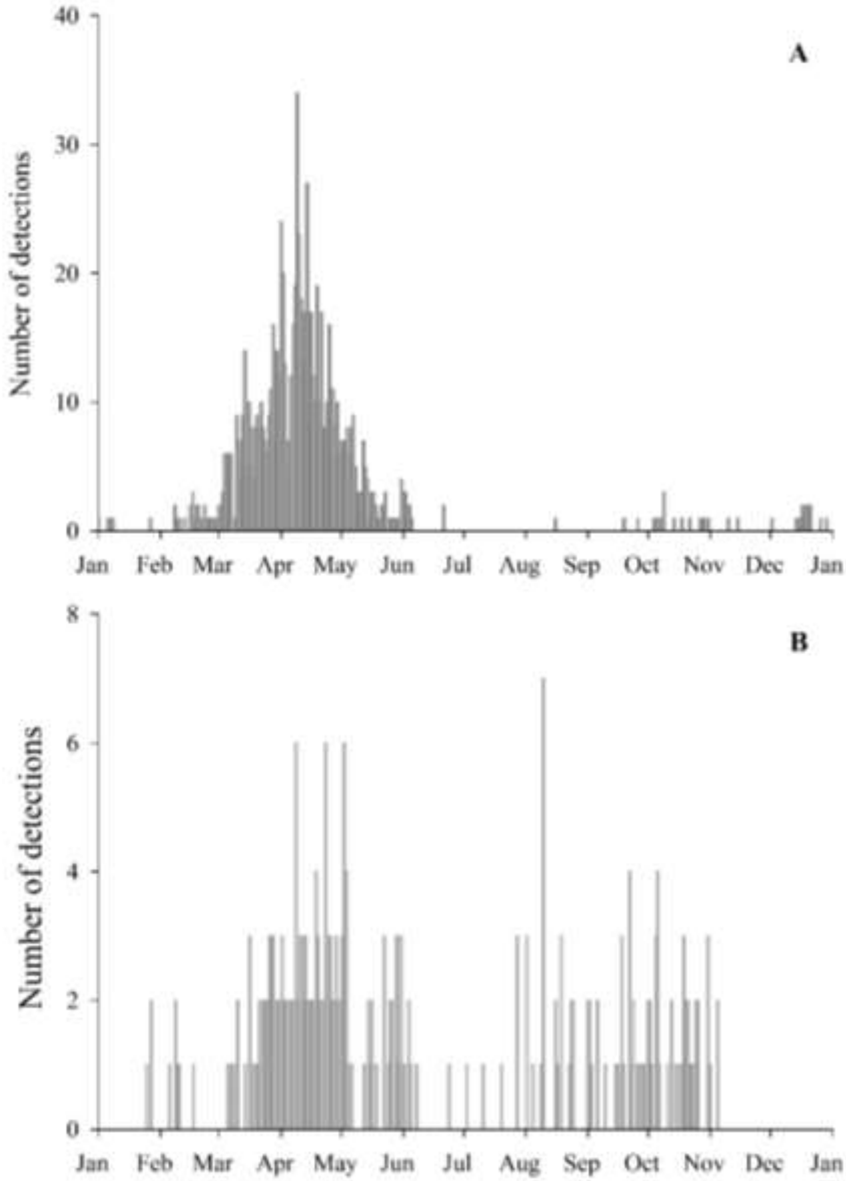


Figure 2.8. Detections of mature (TL > 300 mm) PIT-tagged rainbow trout (A) and brown trout (B) on all upper Missouri River tributary PIT antennas from 2014 to 2019.

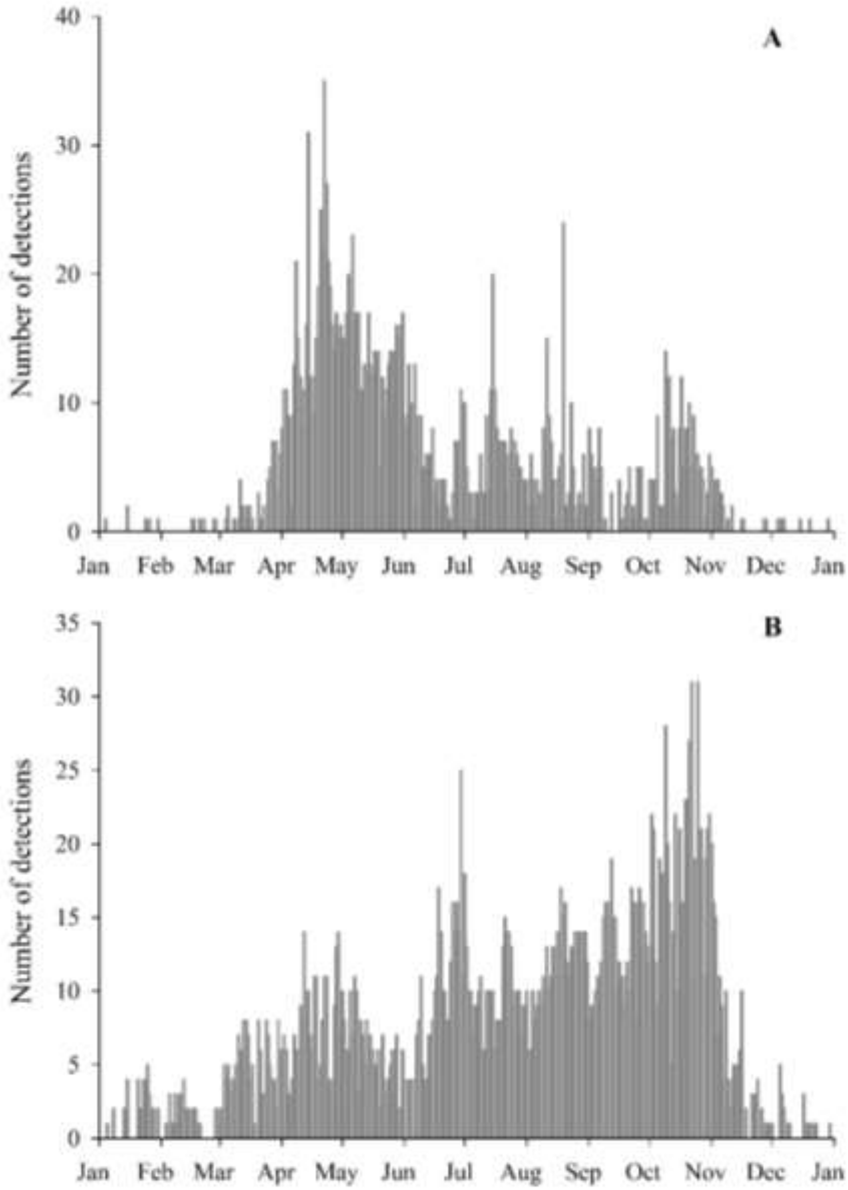


Figure 2.9. Detections of mature (TL > 300 mm) PIT-tagged rainbow trout (A) and brown trout (B) on all Smith River tributary PIT antennas from 2010 to 2019.

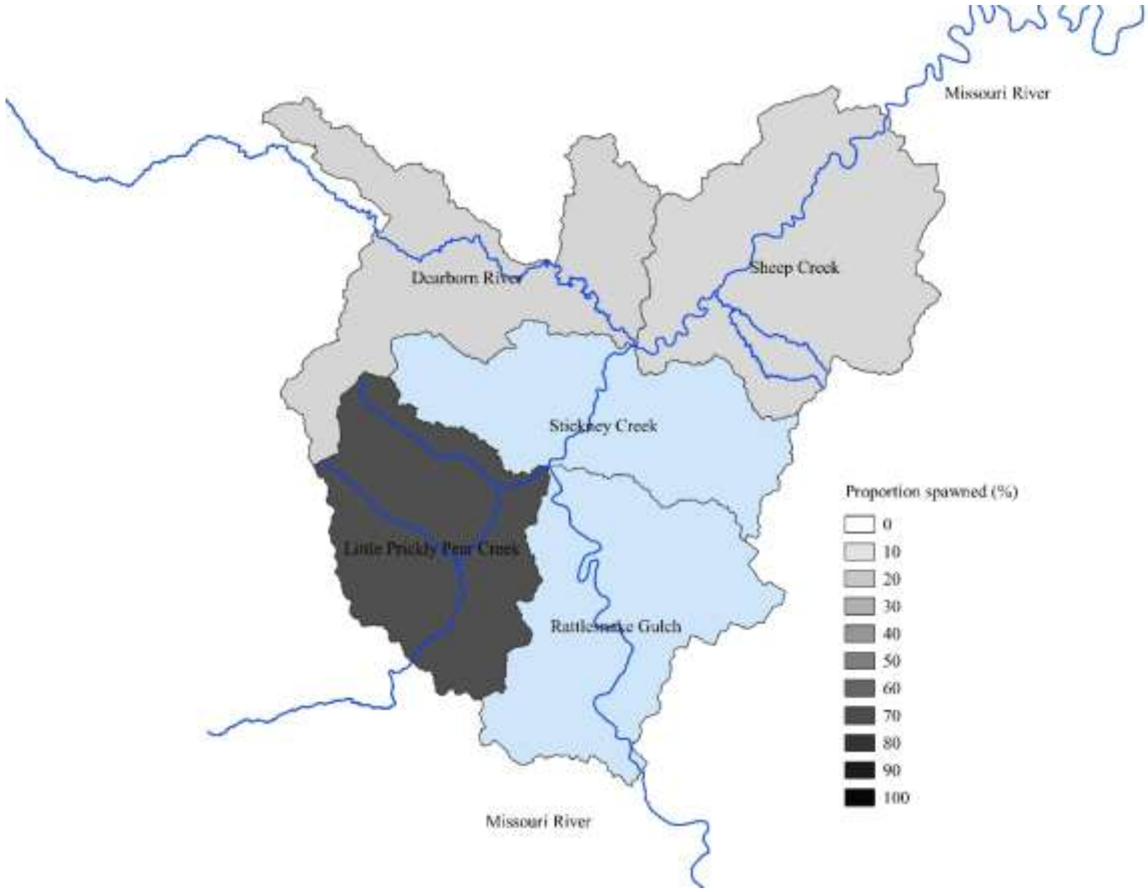


Figure 2.10. Proportion of spawning events made by rainbow trout from 2014 to 2019 by watershed in the upper Missouri River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

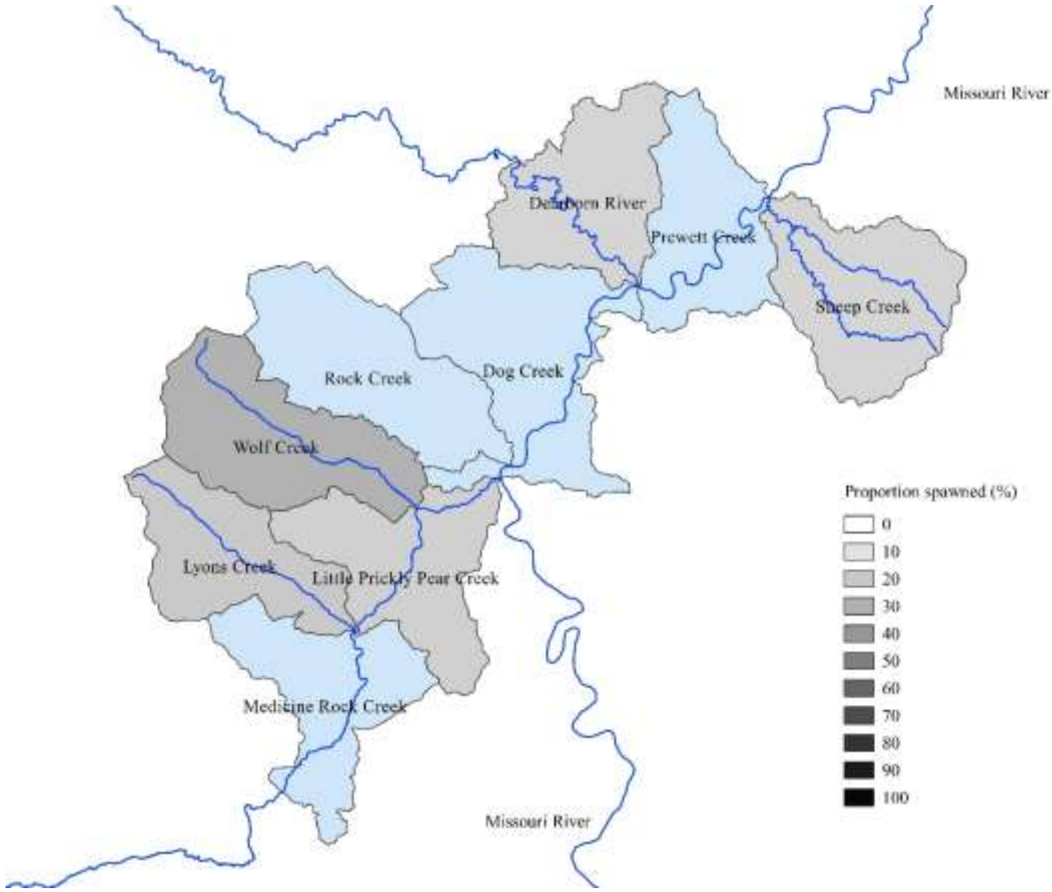


Figure 2.11. Proportion of spawning events made by rainbow trout from 2014 to 2019 by subwatershed in the upper Missouri River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent subwatersheds that were not part of the analysis.

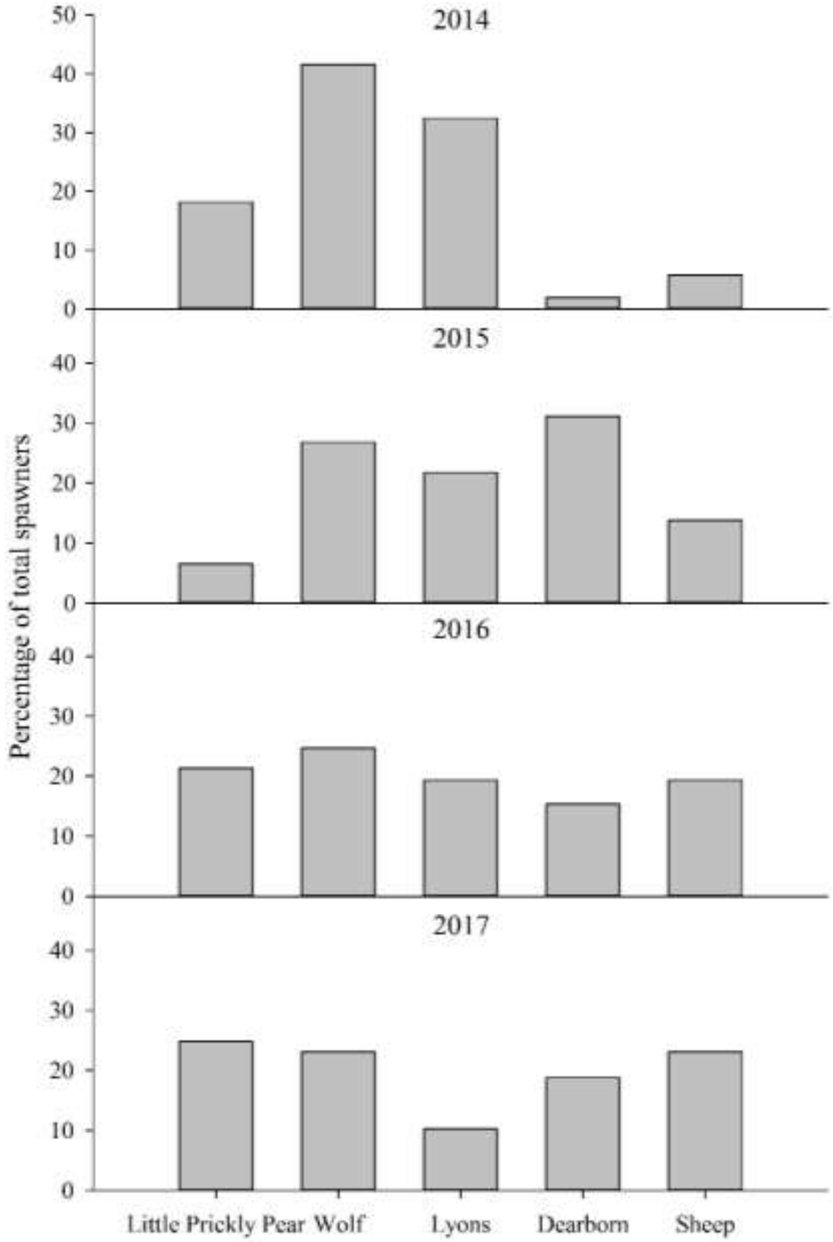


Figure 2.12. Distribution of spawning effort by PIT-tagged rainbow trout in tributary subwatersheds of the upper Missouri River subbasin from 2014 to 2017.

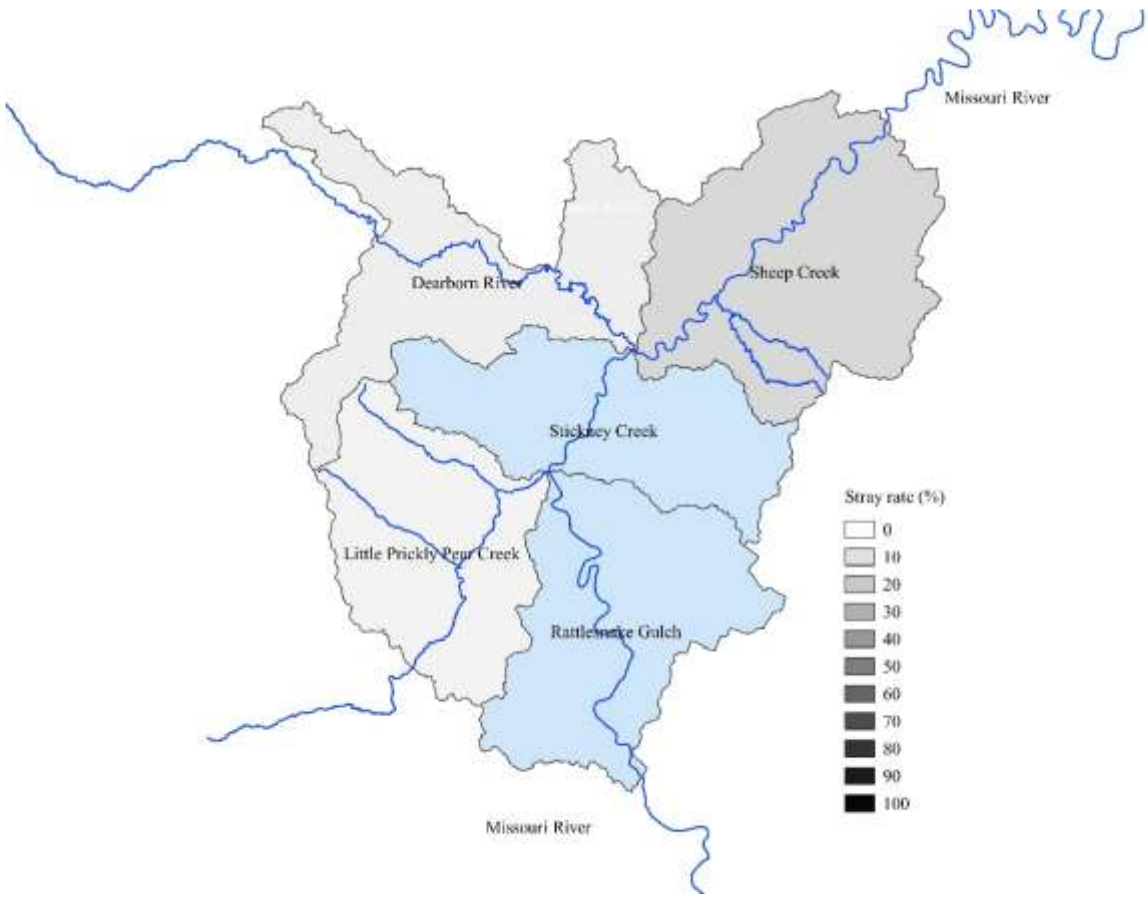


Figure 2.13. Stray rates of rainbow trout with known natal origins by watershed tagged in the upper Missouri River subbasin from 2015 to 2018. Stray rate is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

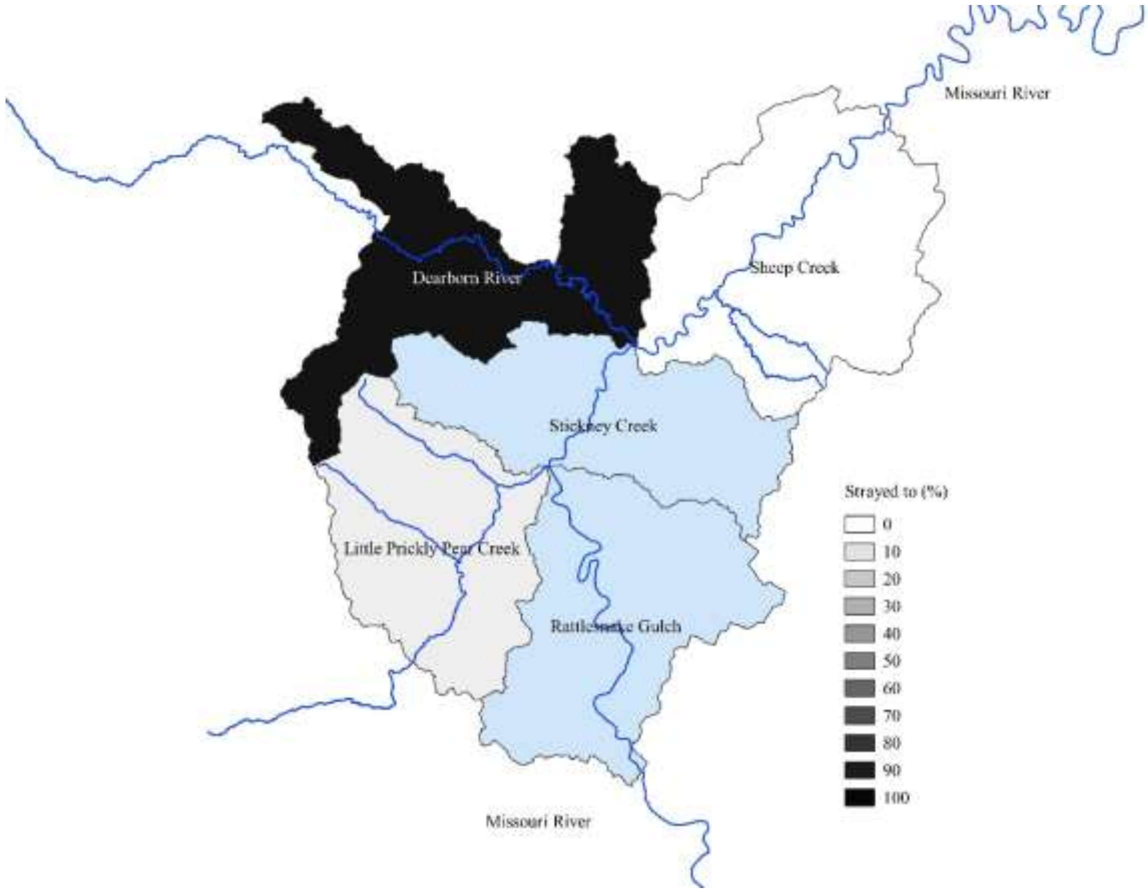


Figure 2.14. Straying destinations by watershed of rainbow trout that strayed from their natal streams from 2014 to 2018 in the upper Missouri River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

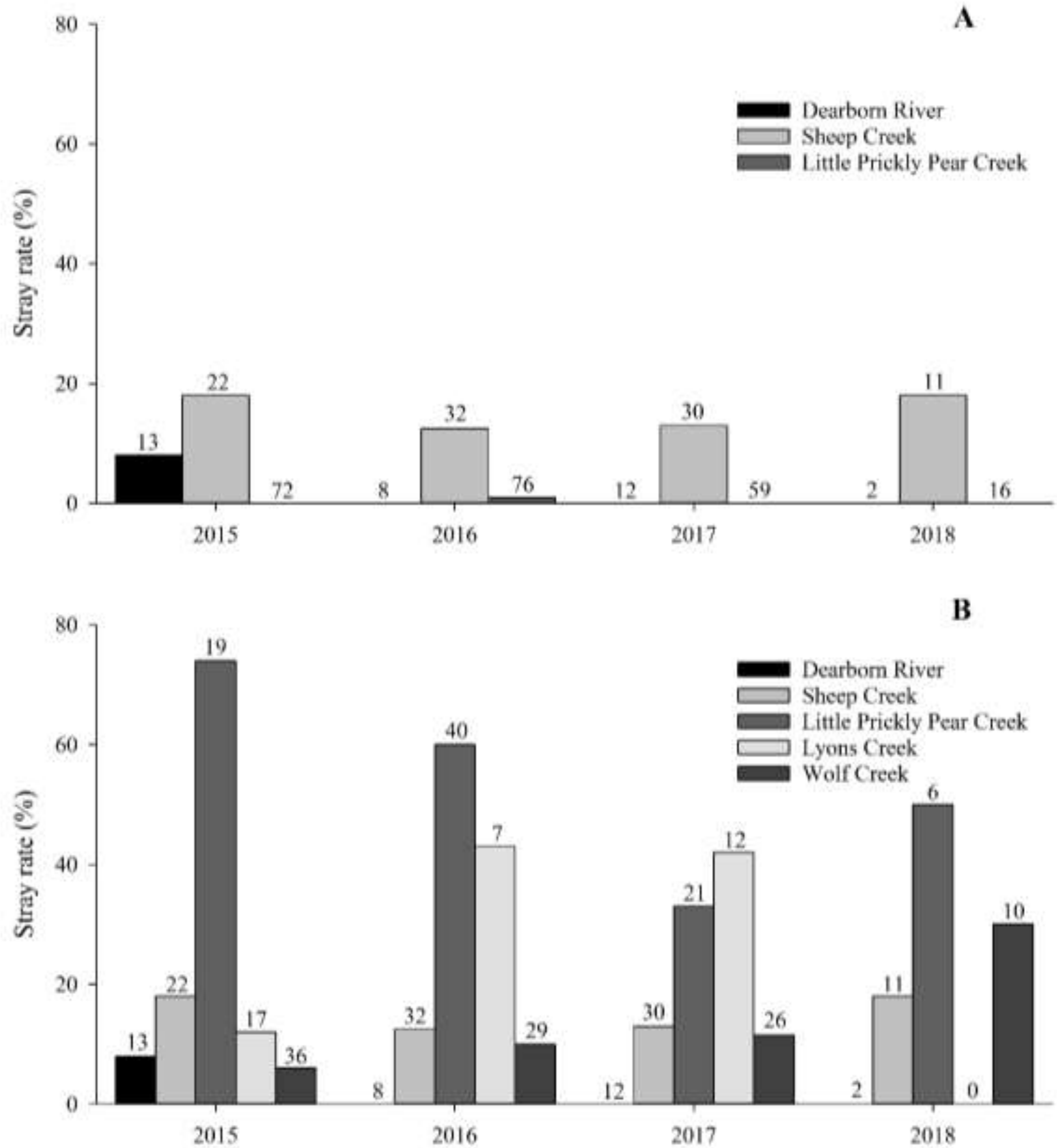


Figure 2.15. Stray rates of rainbow trout tagged in upper Missouri River (A) watersheds and (B) subwatersheds. Numbers above bars represent the total number of spawning events made by fish with known natal origins for each watershed and subwatershed for that year.

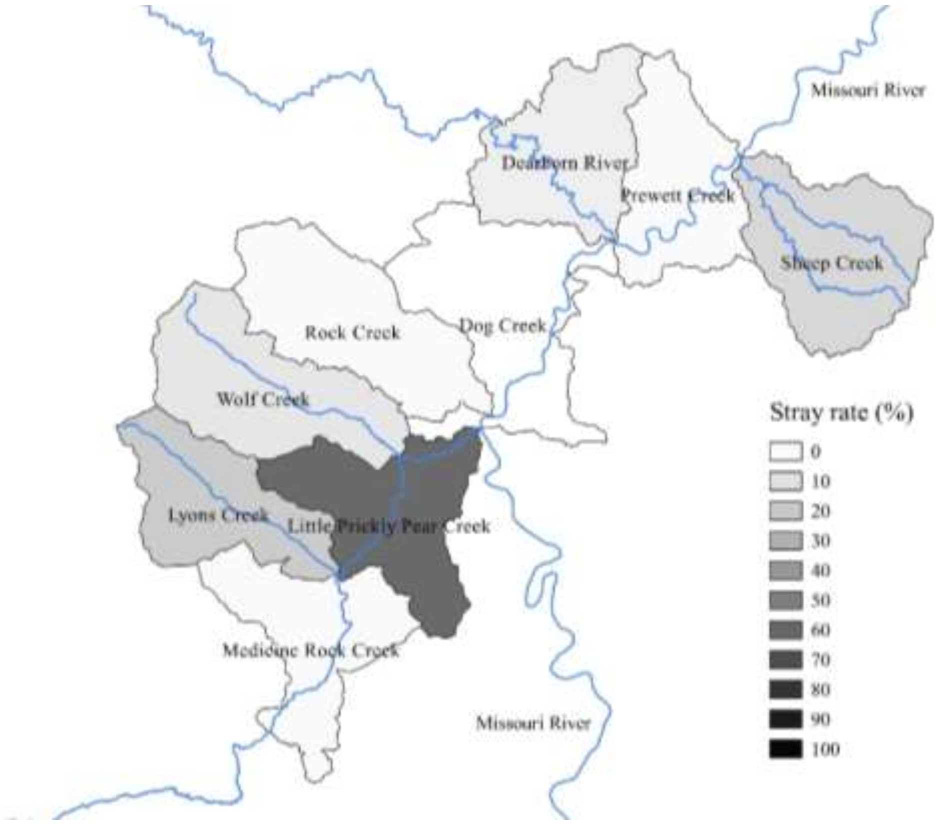


Figure 2.16. Stray rates of rainbow trout with known natal origins by subwatershed tagged in the upper Missouri River subbasin from 2015 to 2018. Stray rate is represented by the gray gradient, with darker shades indicating a higher percentage.

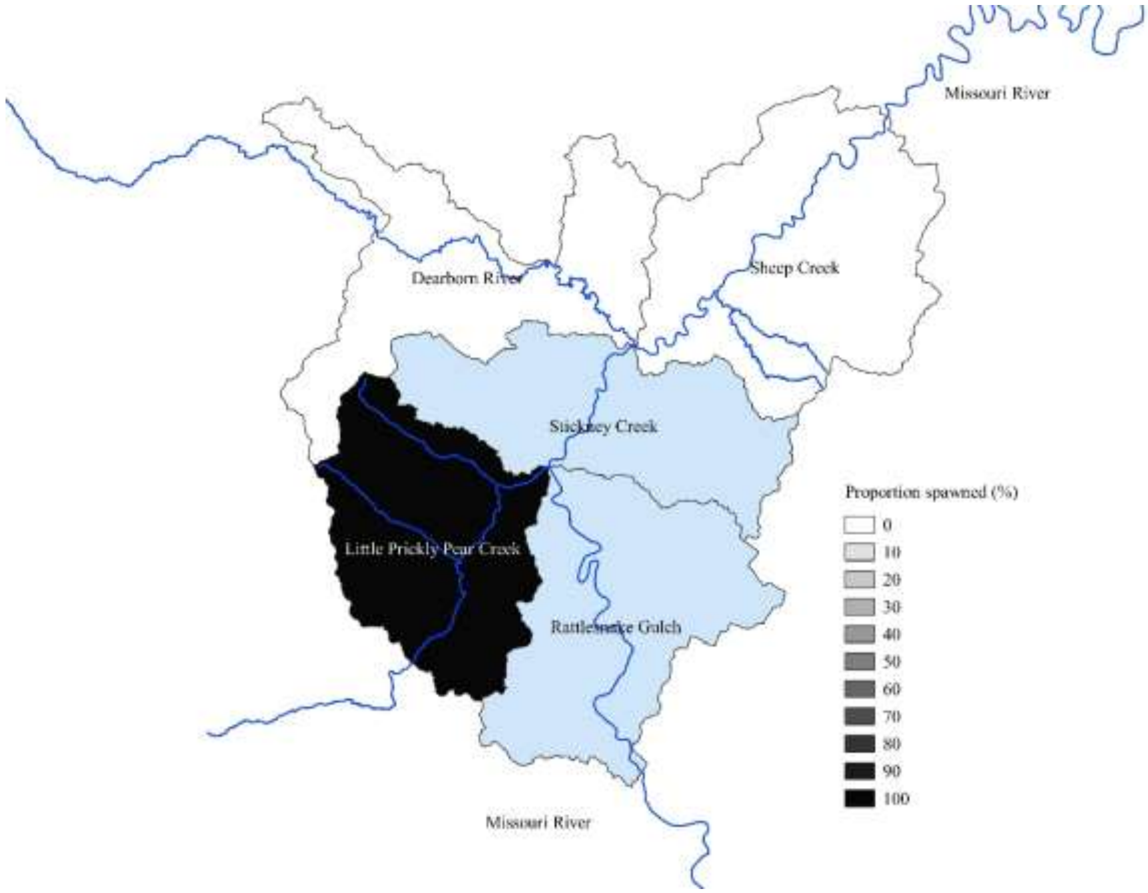


Figure 2.17. Proportion of spawning events made by brown trout from 2014 to 2019 by watershed in the upper Missouri River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

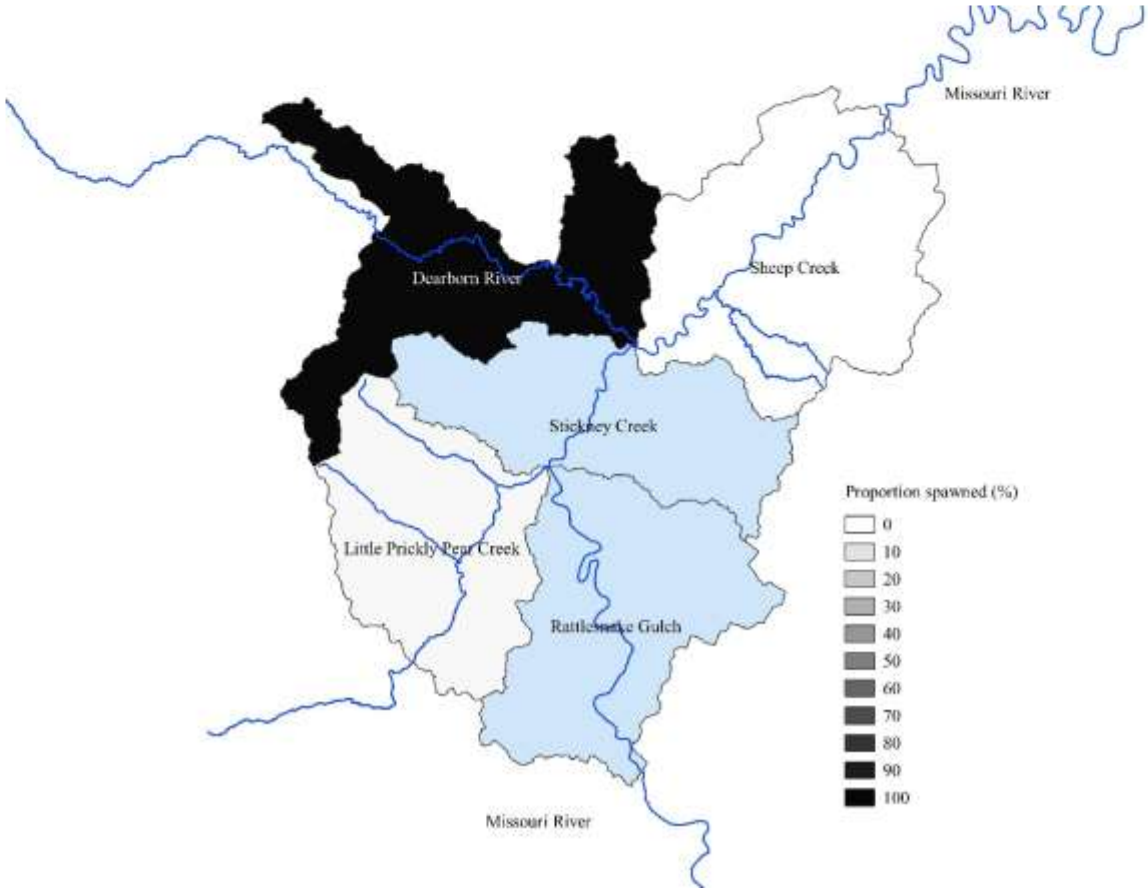


Figure 2.18. Proportion of spawning events made by mountain whitefish from 2014 to 2019 by subwatershed in the upper Missouri River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

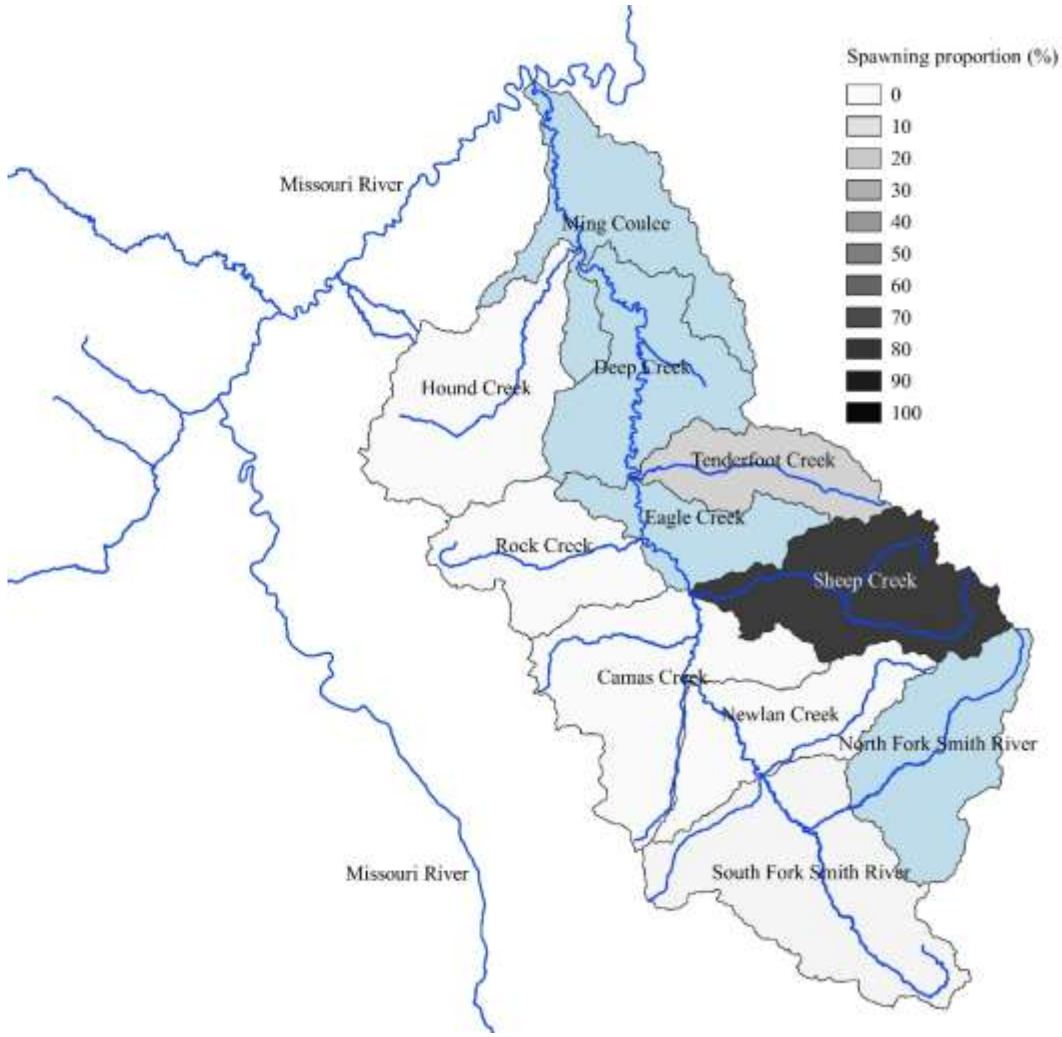


Figure 2.19. Proportion of spawning events made by rainbow trout from 2014 to 2019 by watershed in the Smith River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

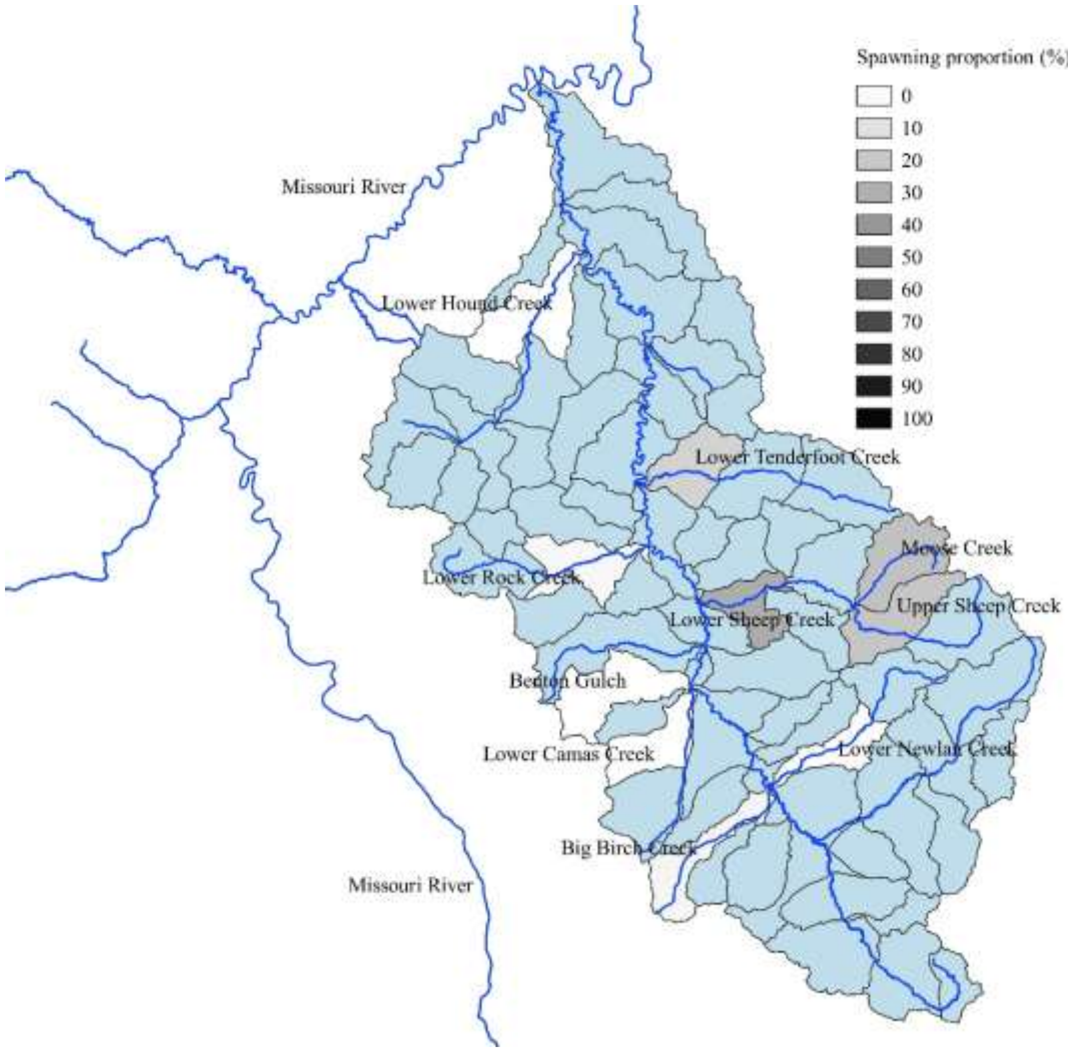


Figure 2.20. Proportion of spawning events made by rainbow trout from 2014 to 2019 by subwatershed in the Smith River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

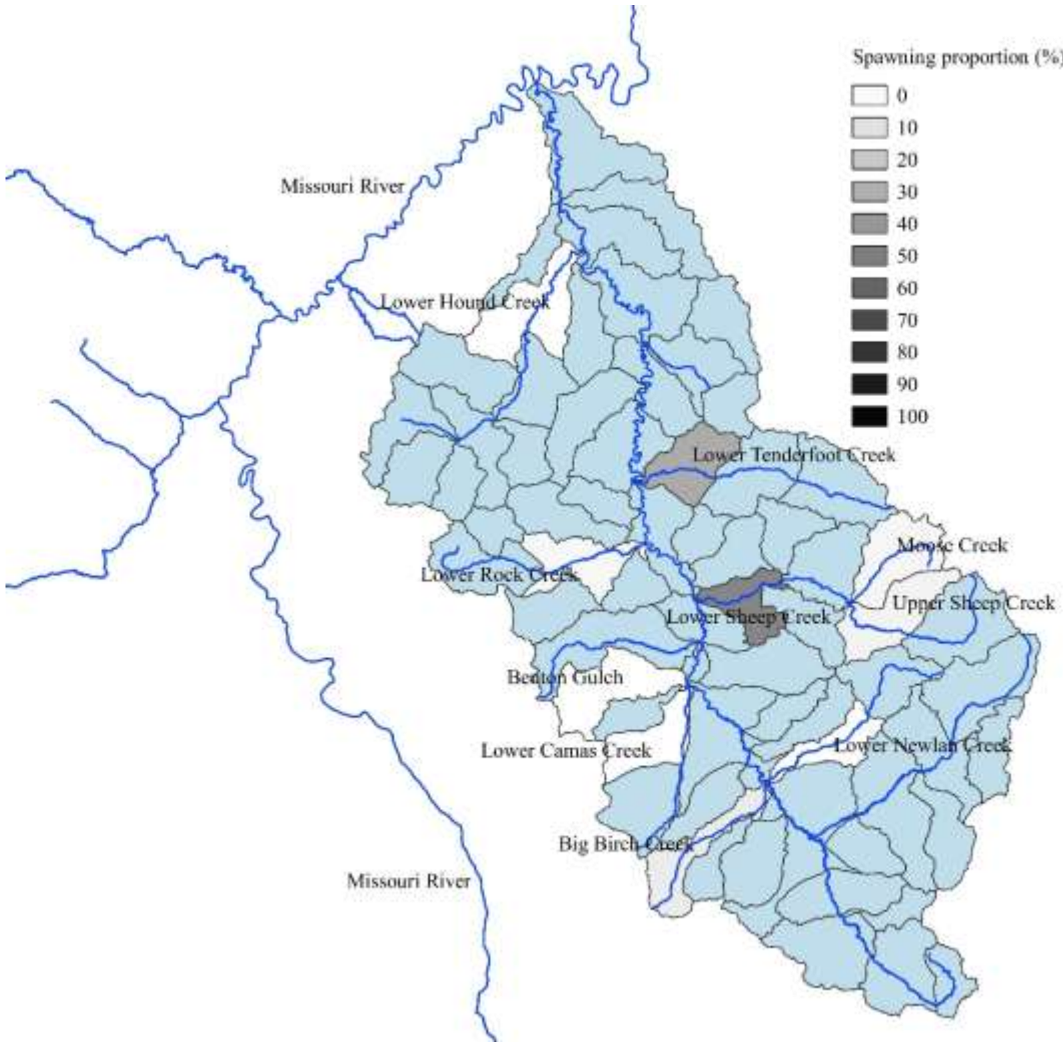


Figure 2.21. Proportion of spawning events made by rainbow trout tagged in the mainstem Smith River from 2014 to 2019 by subwatershed in the Smith River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

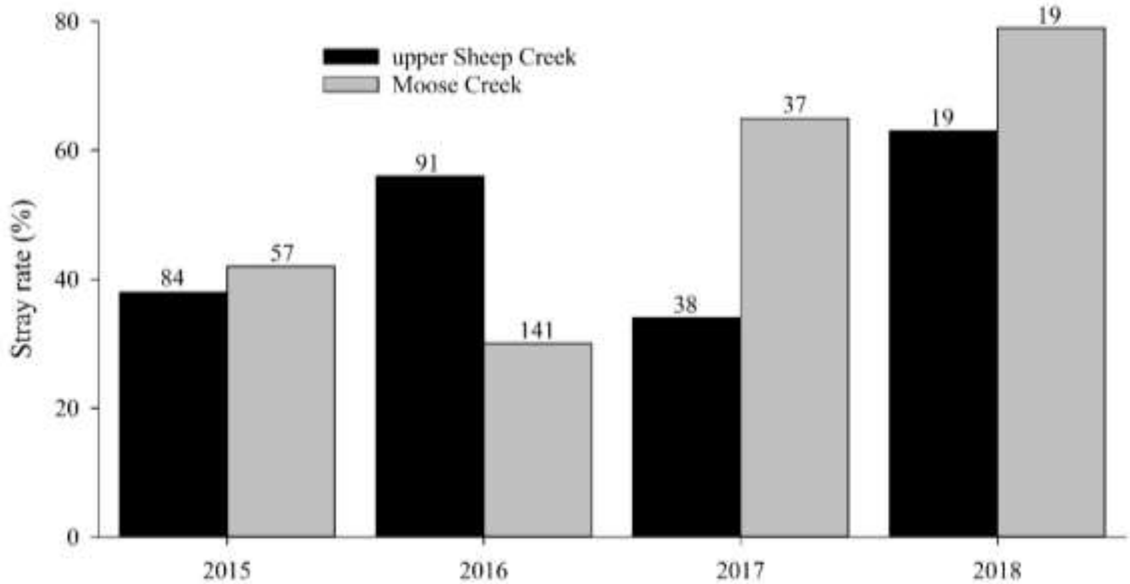


Figure 2.22. Stray rates of rainbow trout tagged in the upper Sheep Creek and Moose Creek subwatersheds from 2015 to 2018. Numbers above bars represent the total number of spawning events made by fish with known natal origins for each subwatershed for that year.

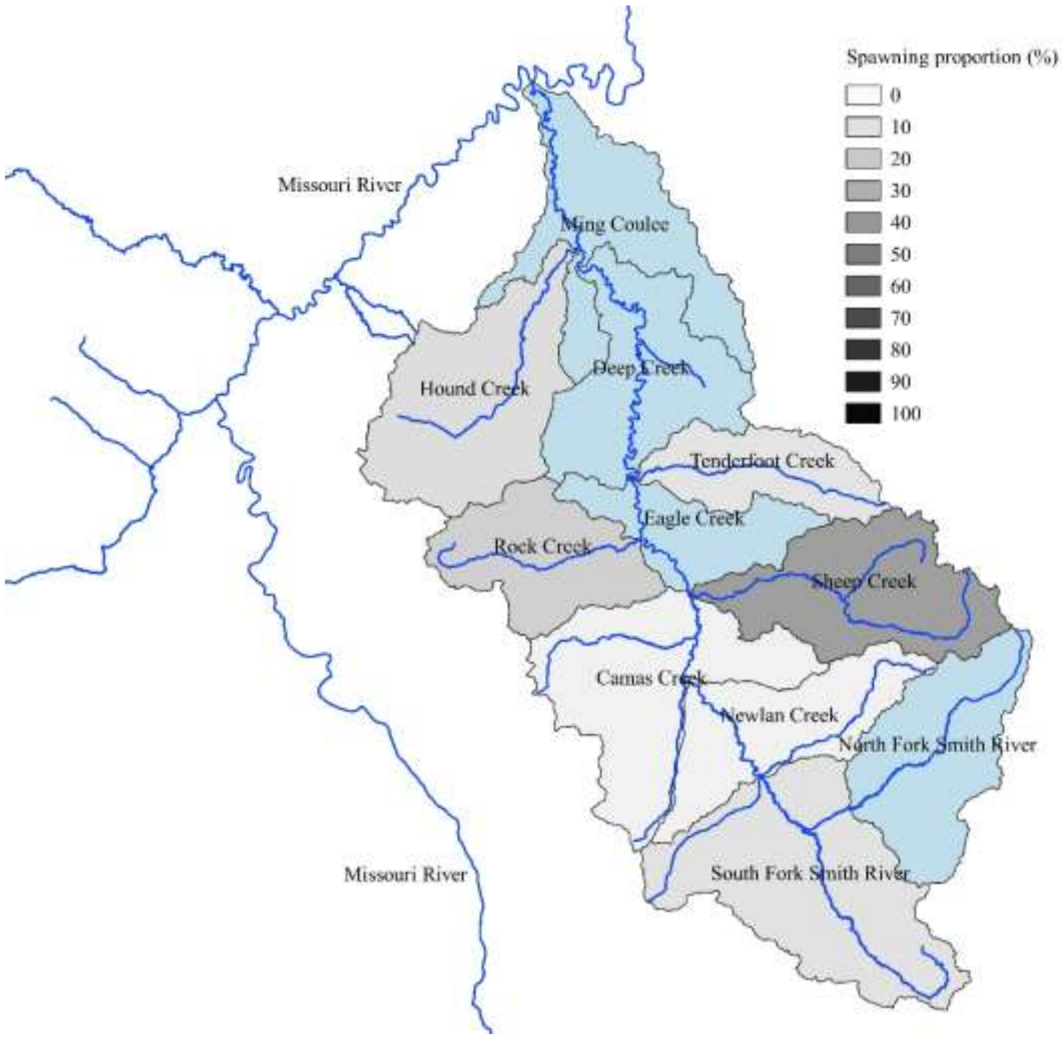


Figure 2.23. Proportion of spawning events made by brown trout in Smith River watersheds from 2014 to 2019. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

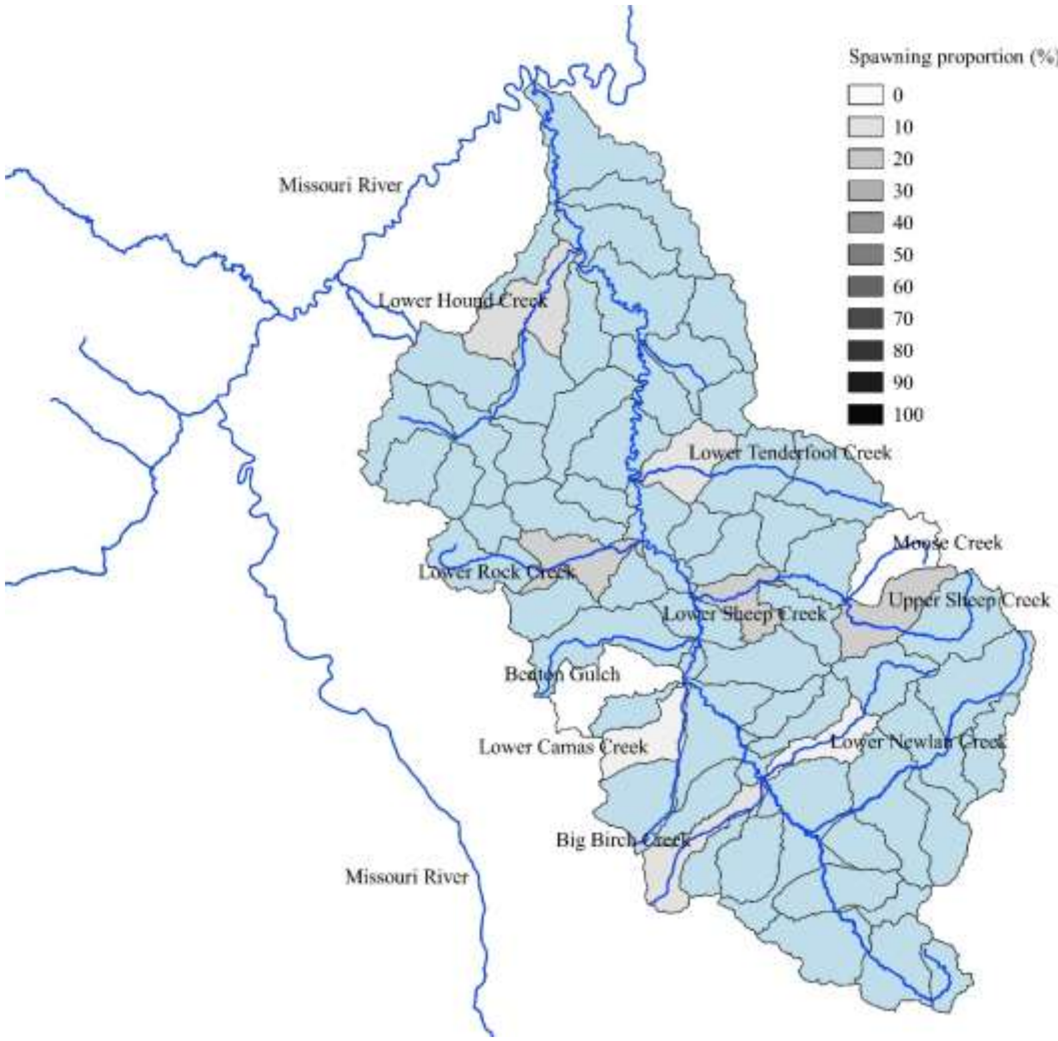


Figure 2.24. Proportion of spawning events made by brown trout in Smith River subwatersheds from 2014 to 2019. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

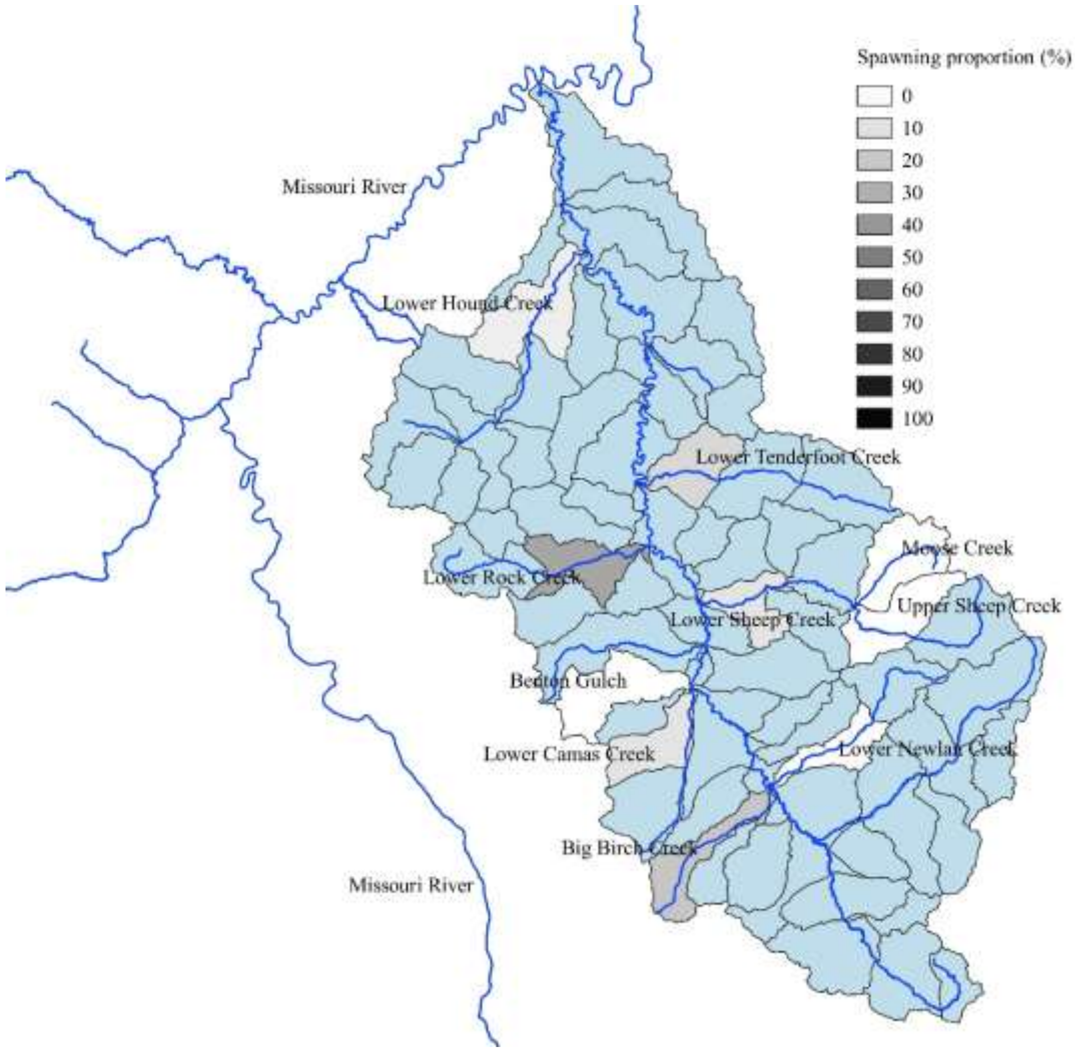


Figure 2.25. Proportion of spawning events made by brown trout tagged in the mainstem Smith River by subwatershed from 2014 to 2019. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

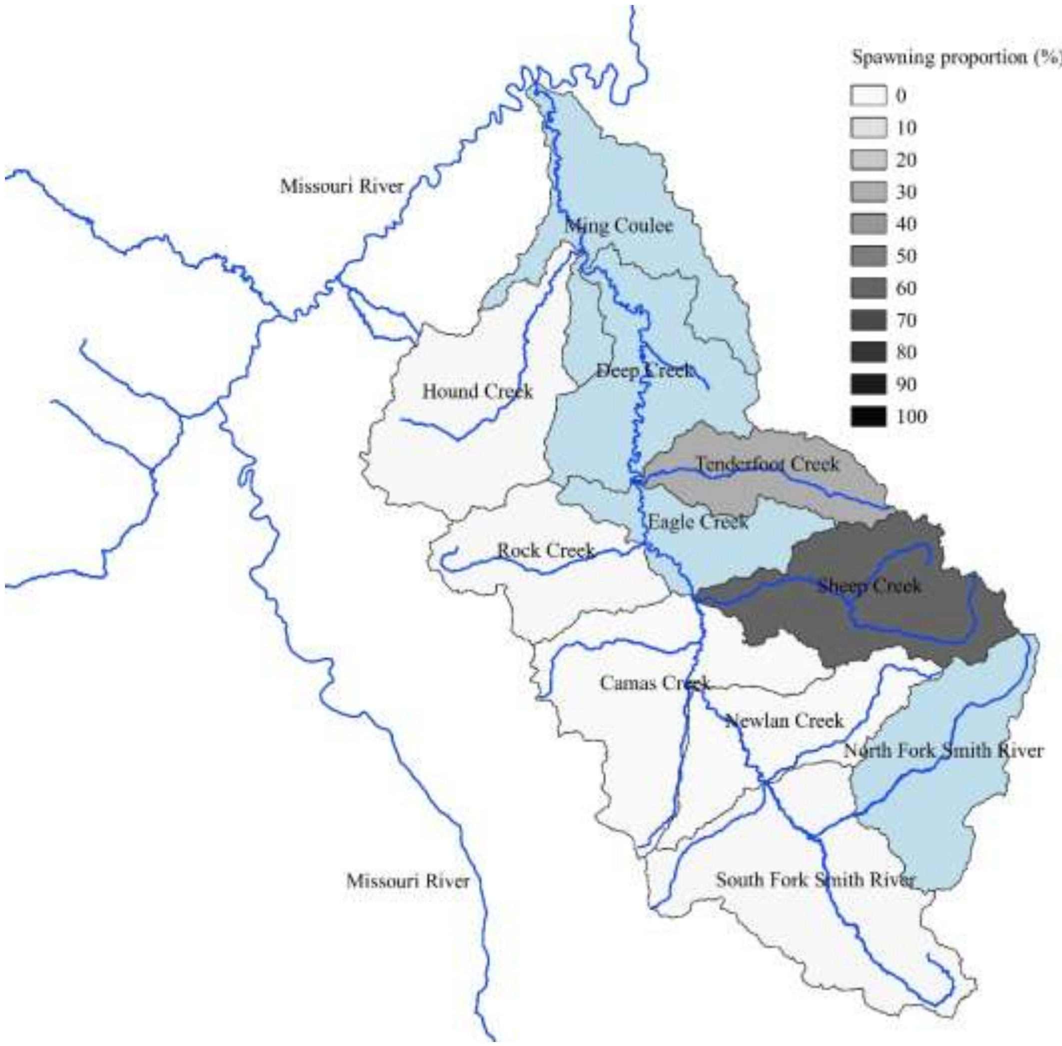


Figure 2.26. Proportion of spawning events made by mountain whitefish in Smith River watersheds from 2014 to 2019. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

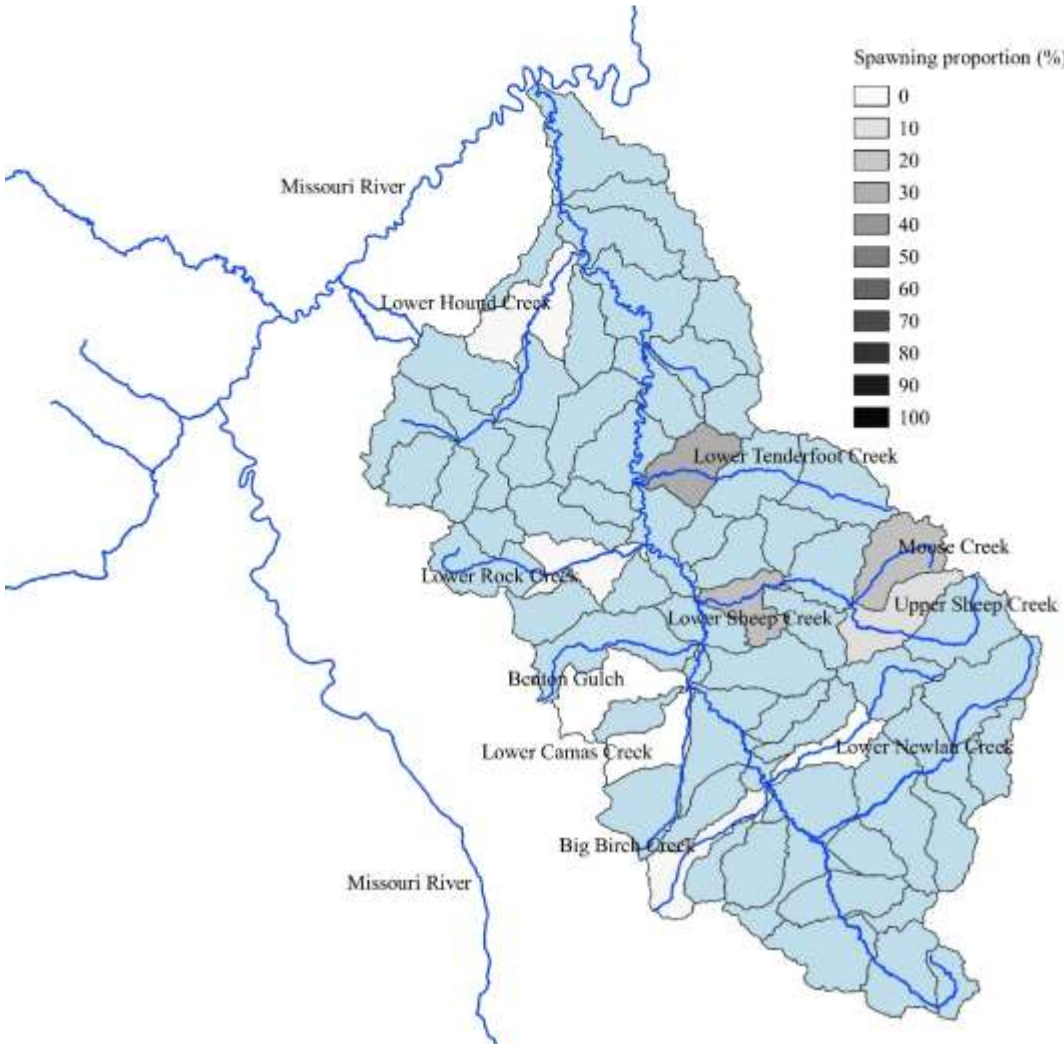


Figure 2.27 Proportion of spawning events made by mountain whitefish in Smith River subwatersheds from 2014 to 2019. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

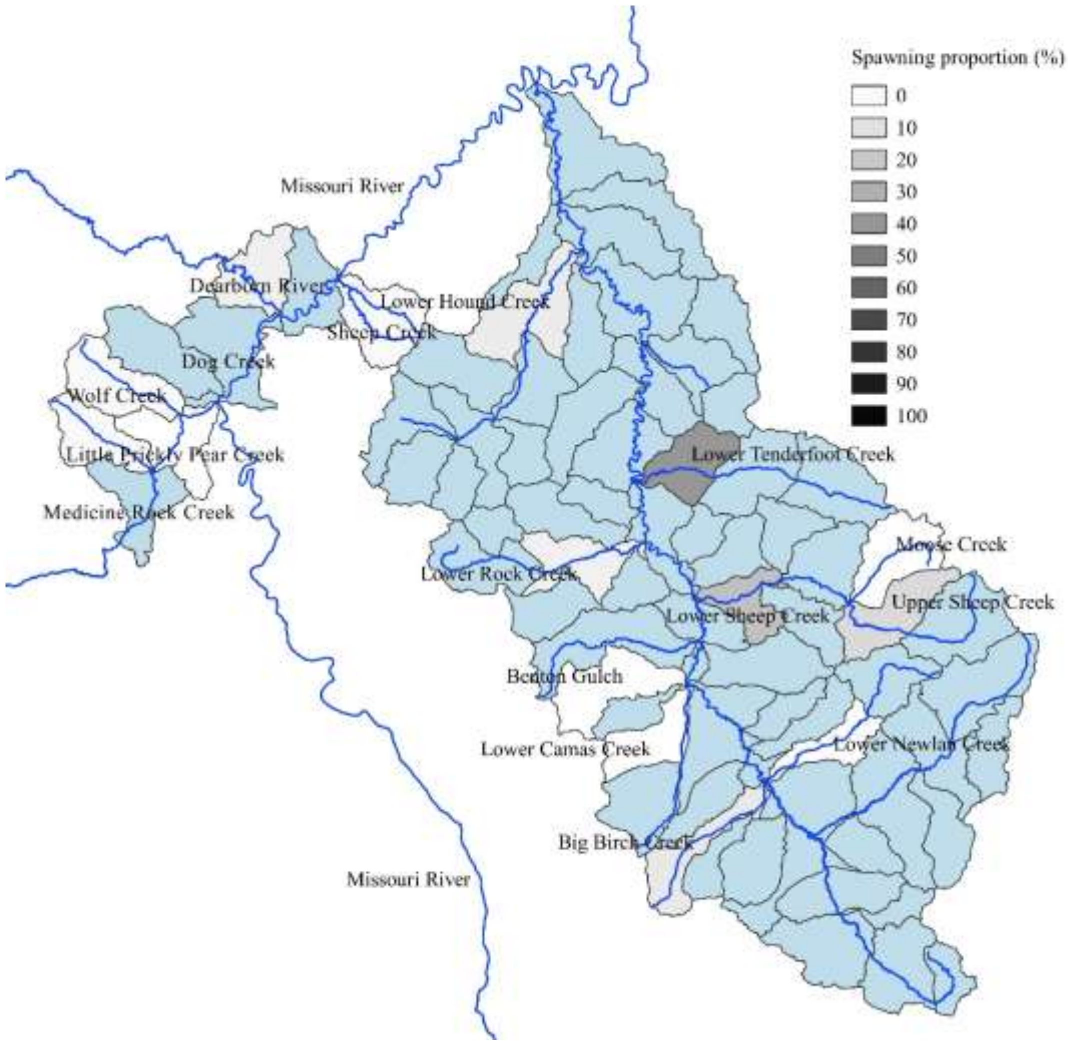


Figure 2.28. Proportion of spawning events made by mountain whitefish tagged in the mainstem Smith River by subwatershed from 2014 to 2019. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

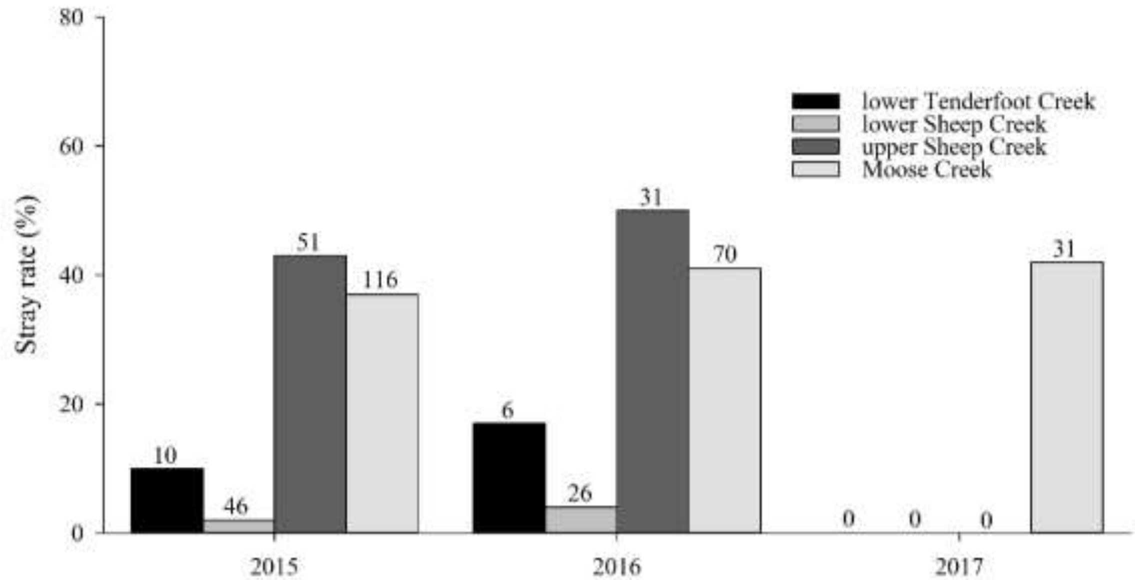


Figure 2.29. Stray rates of mountain whitefish tagged in the lower Tenderfoot Creek, lower Sheep Creek, upper Sheep Creek, and Moose Creek subwatersheds from 2015 to 2017. Numbers above bars represent the total number of spawning events made by fish with known natal origins for each subwatershed for that year.

CHAPTER THREE

TIMING OF AND FACTORS INFLUENCING OUTMIGRATION OF RAINBOW AND BROWN TROUT

Introduction

Successful management of fluvial salmonid populations necessitates an understanding of the requirements of all life history aspects. In addition to spawning and migration patterns, a critical component of fluvial salmonid life history is outmigration, the early rearing of juvenile salmonids in natal streams and subsequent migration to larger rivers. Not surprisingly, fluvial outmigration patterns vary among and within species and populations (Northcote 1997; Munro 2004).

In the upper Missouri River, studies investigating outmigration were conducted as part of an effort to better understand the resilience of trout populations to the parasite *Myxobolus cerebralis* (Leathe et al. 2002; Leathe et al. 2014; Munro 2004). Although two ages of rainbow trout outmigrate, most individuals spend their first year in their natal streams, Little Prickly Pear Creek and the Dearborn River, before migrating to the mainstem Missouri River (Leathe et al. 2002; Munro 2004; Leathe et al. 2014). Timing and magnitude of outmigration for age-0 and age-1 rainbow and brown trout were highly variable and not well-defined, although spring and autumnal pulses in movement occurred (Leathe et al. 2014).

Variation in outmigration patterns may be in response to biological and environmental factors (Leathe et al. 2014). Leathe et al. (2014) reported associations with increasing photoperiod, water temperatures from 7.5 to 12.5 °C, and abrupt increases in stream discharge. However, the variation in timing and magnitude was such that modeling efforts explained no more than 41% of the outmigration, with the limited amount attributed to a combination of highly variable environmental factors and genetic plasticity (Leathe et al. 2014).

Continued efforts to understand the abiotic cues that drive outmigration would provide insights into the adaptations employed by upper Missouri River trout and enhance management of their populations. We used PIT telemetry rather than rotary screw traps to monitor the movements of juvenile rainbow and brown trout in the upper Missouri and Smith rivers. Our objective was to determine the timing of and factors influencing rainbow and brown trout outmigration from natal tributaries.

Methods

Abiotic factors

Temperature and discharge data for the Dearborn, (USGS site 06073500; Figures 3.1 and 3.2), Smith (USGS site 06076690; Figures 3.1 and 3.3), and Sun (USGS site 06085800; Figures 3.1 and 3.4) rivers were collected by USGS gaging stations. Discharge and temperature data measured in the Dearborn River were used as surrogates to describe hydrologic and thermal regimes in the Missouri River because of modified temperatures and discharges below Holter Dam. Discharge data were collected for Little Prickly Pear Creek (USGS site 06071300; Figures 3.1 and 3.5) at the USGS gage station. In addition to collected data, we modeled water temperatures for the Dearborn River, Little Prickly Pear Creek, Lyons Creek, and Wolf Creek (see ‘Temperature modeling’ below).

Daily air temperatures were collected at the Global Historical Climatology Network (GHCN) weather station in Helena, Montana (Station USR0000MHEL; available at http://www.ncdc.noaa.gov). Photoperiod was calculated using the National Ocean and

Atmospheric Administration (NOAA) solar calculator, accessed online (https://www.esrl.noaa.gov/gmd/grad/solcalc). Lunar phase and moon age information was accessed online from National Aeronautics and Space Administration's scientific visualization studio (https://svs.gsfc.nasa.gov).

PIT-tagging

A large sampling effort was made in 2014 to tag juvenile rainbow and brown trout in the major tributaries of the upper Missouri and Smith rivers to investigate outmigration timing and magnitude. Totals of 1,675 and 288 juvenile rainbow and brown trout were tagged in upper Missouri River tributaries in 2014, respectively (Table 3.1). Totals of 1,558 and 169 juvenile rainbow and brown trout were tagged in Smith River tributaries in 2014, respectively (Table 3.2). Tagging was primarily conducted in the Missouri River in the spring, in the spring and autumn in the Dearborn River, and late summer and autumn in Smith River tributaries.

Fish were collected with boat, barge, and backpack electrofishers, and fyke nets, anesthesized with Aqui-S 20E (Aqui-S New Zealand Ltd.; 10 to 20 mg/L) or MS-222 (tricaine methanesulfonate; 50 mg/L), and implanted with HDX PIT tags. Location, species, and total length (TL) were recorded for each fish at the time of tagging; 20% (2,389 of 11,936) were also weighed. The date when a fish was collected and tagged was recorded as the first observation for each individual. PIT tags were surgically implanted into the abdominal cavity through small incisions made by a small scalpel coated with antiseptic.

Monitoring fish movement

A network of 23 stationary PIT arrays monitored the movements of PIT-tagged fish throughout the upper Missouri River basin (Table 3.3 and Figure 3.1). Five arrays were installed in the upper Missouri River subbasins in the spring of 2014, three arrays were installed in the Sun River subbasin in the spring of 2015, and 15 arrays were installed in the Smith River subbasin from 2014 to 2016 (Table 3.3 and Figure 3.1). These monitoring stations ran in some combination from 2010 to 2019 (Figure 3.6). The Dearborn River, Little Prickly Pear Creek, Truly Bridge, and Hound Creek arrays were damaged by flows in the spring and early summer of 2018. All but Truly Bridge were repaired and reinstalled. Five stations were operated in Tenderfoot Creek from 2010 to 2014, but only one array installed at the mouth of Tenderfoot Creek was maintained after 2013 (Table 3.3 and Figure 3.1; Ritter 2015). Age and growth analyses used data collected prior to 2014 and afterward, but all other analyses were restricted to data collected after 2013. In general, fixed PIT arrays were installed in locations to monitor interchange between tributaries and the mainstem within subbasins (Figure 3.1).

Antenna stations consisted of a PIT-tag reader (Oregon RFID, multi-antenna HDX reader and long-range HDX reader, Portland, Oregon), one to two stream-width antennas, and a tuning board for each antenna (Oregon RFID, standard remote tuner board and long-range tuner board, Portland, Oregon). Antenna arrays were powered by 12-V DC supplied by either solar panels or 120-V AC converters. Antennas were placed in areas where fish would unlikely stay for long periods of time (e.g., riffles and shallow water habitat) to prevent many consecutive detections and to monitor interchange between mainstem river and tributaries (rather than localized use near the antennas). All antennas were oriented flat on the bottom (swim over or flat-bed design; Armstrong et al. 1996) and tuned to best possible vertical read ranges for tags oriented perpendicularly to the antennas. Average tag detection distances of antennas ranged from 0.03 to

1.50 m (Table 3.3) and varied seasonally (Figure 3.7). Detection efficiencies (Zydlewski 2006) of PIT arrays installed in the Smith River ranged from 0.66 to 1.00 (Lance 2019). Detection efficiencies can be used to correct for potential bias associated with variations in detection efficiencies of stationary PIT arrays (e.g., Lance 2019). We did not account for such bias in this study; rather, we provided detection efficiencies as a metric for PIT array performance in addition to tag detection distance.

Mobile PIT arrays were used to actively monitor fish movements and complement the network of fixed monitoring stations. Mobile tracking was conducted using raft, kayak, and pole-mounted antennas (Hill et al. 2006; McKinstry and Mackinnon 2011); methods are explained in detail by Lance 2019. In the upper Missouri and Sun rivers, mobile tracking by raft and kayak was conducted in 2015 and 2016 but discontinued thereafter because of low detection range. A pole-mounted antenna was used in 2016 to scan tributaries and islands of the upper Missouri River and American white pelican *Pelecanus erythrorhynchus* nesting islands in Canyon Ferry and Arod Lake (Vivian and Mullen 2018). In the Smith River, all forms of mobile tracking were used to track fish from 2015 to 2017 (Lance 2019). No mobile tracking was conducted from 2018 onward.

Data analysis

The statistical software programs R (v4.0.2; R Core Team 2019) and SigmaPlot 14 (SigmaPlot 2017) were used for analyzing and plotting trends and comparisons in outmigration timing and magnitude. Program R was also used for modeling water temperatures. We used geographic information system (GIS) software (QGIS 2021) for spatial analyses and map construction.

Temperature modeling

Because water temperatures were not available for all tributaries for the full duration of the study, we estimated temperatures using linear regression models where possible, thereby addressing spatial and temporal gaps in stream water temperature data for the Dearborn River, Little Prickly Pear Creek, Lyons Creek, and Wolf Creek. We used water temperature data collected by a network of temperature loggers (Onset Computer Corporation, HOBO Temperature Data Logger, Bourne, Massachusetts) and the U.S. Geological Survey (USGS) gaging station at the Dearborn River (USGS site 06073500; USGS 2019). Daily air temperature measurements collected at the Global Historical Climatology Network (GHCN) weather station in Helena, Montana (Station USR0000MHEL) were available from the National Climatic Data Center (http://www.ncdc.noaa.gov). We considered air temperatures collected in Great Falls, Montana (Stations USW00024143 and USC00243753) as well as near the Sun River, Montana (Station USC00248021), but water temperatures were most strongly correlated with air temperatures collected in Helena, Montana based on preliminary investigations. Discharge data was collected at the Dearborn River (USGS site 06073500; 2019) and Little Prickly Pear Creek (USGS site 06071300; 2019) USGS gage stations. Data for each climate variable were not available for all years; rather, data collection ranged in duration (Table 3.4). For example, water temperature for Lyons Creek was only collected from 2015 to 2017, whereas air temperature was available from 2000 to 2019 (Table 3.4).

We addressed spatial and temporal gaps in stream water temperature data by estimating temperatures using linear regression models. Based on available data collected during the study or previously (Table 3.4), we were able to estimate mean daily water temperatures for the Dearborn River, Little Prickly Pear Creek, Wolf Creek, and Lyons Creek for the months of March through November for the entire duration of the study (from 2009 to 2019). We limited stream temperature modeling to the months of March through November because fish movement data were not collected outside of that timeframe. In addition, the relationship between air temperature and water temperature can become nonlinear during the winter months in waterbodies that experience ice formation (Mohseni and Stefan 1999; Li et al. 2014); using data only during the open water period therefore improved the predictive power of our linear regression models.

We considered air temperature, discharge, and mean daily water temperature of nearby streams as predictors of stream water temperature (Table 3.5). Although models including both air temperature and discharge yielded better predictive power, we ultimately decided to use only air temperature as the predictor for Wolf, Lyons, and Little Prickly Pear creeks because of gaps in discharge and nearby stream temperature data (Table 3.5). Moreover, air temperature explained 83 - 91% of variation in the data (Figure 3.8); adding discharge only marginally improved this (Table 3.5; Figure 3.8). However, we decided to use the model including both air temperature and discharge for estimating mean daily water temperatures of the Dearborn River because of the completeness of Dearborn River discharge data. Furthermore, we used Dearborn River mean daily water temperatures for analysis of outmigration in both Sheep Creek (Missouri River) and the Dearborn River. Air temperature and Dearborn River discharge were not strongly correlated (Figure 3.9).

Timing of outmigration

We considered rainbow and brown trout under 201 mm (7.9”) to be juveniles based on previous work (Leathe et al. 2002; Leathe et al. 2014) and length-frequency histograms created from fish captured during this study. Furthermore, most juvenile trout tagged in upper Missouri River tributaries were likely age-1 fish based on season and length at time of tagging (Leathe et al. 2002). Comparisons made to Leathe et al. 2014 in the discussion are therefore restricted to age-1 trout.

Timing and magnitude of outmigration were assessed using our network of stationary PIT arrays installed near tributary mouths (Figure 3.1). Numbers of outmigrating juvenile rainbow and brown trout were quantified by tributary and species. Outmigration evaluation was limited to 2014 and 2015 which ensured fish detections were of outmigrating individuals and not returning subadults. Fish were deemed to have moved if they were detected at two locations (including tagging location). In the context of this study, outmigration generally consisted of an individual’s initial tagging location and subsequent downstream detection on a tributary antenna. Tagged fish were considered outmigrants if they were tagged in a tributary then detected on a tributary mouth antenna. Date of outmigration was defined as the last detection on a tributary mouth antenna. For example, if an individual was tagged on March 15, then detected on a tributary antenna repeatedly from August 1 to August 10, the date of outmigration was considered August 10. For individuals tagged in Wolf and Lyons creeks, outmigration was defined as entering the mainstem Missouri River (detection on the Little Prickly Pear Creek antenna), but we also examined timing and magnitude of movement into Little Prickly Pear Creek. Because we were interested in outmigration timing, tagged fish that were not detected on a tributary antenna, but were detected elsewhere beyond the tributary antenna, were not considered outmigrants in the context of this analysis even though outmigration ostensibly occurred. Furthermore, to maintain consistency, these individuals were not used in length-frequency analyses of outmigrants. However, the combined totals of outmigrants and individuals detected elsewhere would provide insights into total magnitude of outmigration effort. We therefore also reported total outmigration, which is a combination of number of outmigrants that meet analysis criteria and number of juveniles that were redetected outside of their tagging tributary.

Graphical representations of timing and magnitude of outmigration were accomplished using frequency-histogram plots and cumulative proportions of outmigrants. For each tributary, we used Welch's two-sample t-tests (if data were normally distributed) or Mann-Whitney rank sum tests (if data were not normally distributed) to assess differences in total length at tagging between PIT-tagged fish that outmigrated in 2014, 2015, and those that did not outmigrate. We used one-way analysis of variance (ANOVA) tests to assess differences in mean total length at tagging of PIT-tagged fish among tributaries.

Abiotic factors influencing outmigration

To make direct comparisons with previous studies in the same system, we conducted statistical analyses that replicated those of Leathe et al. (2014) as closely as possible. We investigated the influence of four categorical predictor variables on numbers of outmigrating rainbow trout from Little Prickly Pear Creek and the Dearborn River and brown trout from Little Prickly Pear Creek. Our predictor variables included discharge, water temperature, photoperiod, and lunar phase. We restricted data from March 1 to November 31 when PIT arrays were most reliable and fish movements were highest. We created five categories representing percent change in daily discharge: (1) rapidly decreasing (discharge less than 10% of the previous day, (2) slowly decreasing (discharge less than 1% of the previous day), (3) no change (discharge within 1% of previous day), (4) slowly increasing (discharge greater than 1% of the previous day), and (5) rapidly increasing (discharge greater than 10% of the previous day). Daily mean water temperatures were separated into five ranges: (1) < 7.5 °C, (2) 7.5 to < 10 °C, (3) 10 to < 12.5 °C, (4) 12.5 to < 15 °C, and (5) ≥ 15 °C. Moon phases were separated into four categories: (1) new moon, (2) waxing, (3) full moon, and (4) waning. Photoperiod was divided into three ranges: (1) before the summer solstice: increasing day length, (2) summer solstice to autumn equinox: decreasing day length, and (3) after autumn equinox: increasing night length.

For each site × species combination, we constructed global models including all predictor variables. Therefore, we produced 16 total models for each site × species combination. Models were generalized linear models with a Poisson distribution. We used program R package ‘AER’ to assess overdispersion in global models (Kleiber et al. 2020). If models were overdispersed, we used a negative binomial distribution (function 'glm.nb' in the package 'mass'; Ripley et al. 2013). Overdispersion was only detected for rainbow trout outmigrating from Little Prickly Pear Creek ($P < 0.001$). Despite low variance inflation factors (see paragraph below) and no apparent multicollinearity, we observed high standard errors for the intercept and temperature variable modeling rainbow trout outmigration from Little Prickly Pear Creek. Therefore, we removed the temperature variable from this analysis.

For all global models, we used the ‘dredge’ function in the package ‘MuMIn’ to separately create a set of all possible sub-models and determine the top models for each site × species combination (Bartón 2010). We used an information-theoretic approach using Akaike’s Information Criterion to compare models separately for each site × species combination (AIC;

Burnham and Anderson 2004; Mazerolle 2016). We used AIC corrected for small sample sizes (AIC_C) because number of observations divided by number of parameters was near the suggested lower limits (i.e., $n/K < 40$) and AIC and AIC_C converge at larger sample sizes (Anderson and Burnham 2002; Burnham and Anderson 2004). For model averaging, we included all models within < 4 AIC_C of the top model and weighted estimates according to AIC weight (AIC_W). We report parameter estimates (β), standard errors (SE), adjusted SE, and relative importance of each predictor averaged across top models. We assessed multicollinearity in global and top models for each site × species combination by calculating variance inflation factors (VIFs) with package 'car' (VIFs < 2 are generally acceptable; Fox et al. 2012). To assess the amount of variation explained by models, we calculated R^2 values for global and top models for each site × species combination using the 'rsq' package (Zhang 2018).

Following categorical analyses, we investigated the influence of the same four variables (discharge, water temperature, photoperiod, and lunar phase) on probability of outmigration, but the variables were transformed to be continuous. For probability of outmigration, generalized linear models were fitted with a binomial distribution ("yes" or "no" for outmigration). We investigated probability of outmigration of rainbow trout from Little Prickly Pear Creek, the Dearborn River, Sheep Creek, Lyons Creek, and Wolf Creek into the Missouri River and from Sheep Creek into the Smith River. We also investigated outmigration of brown trout from Little Prickly Pear Creek into the Missouri River. Preliminary univariate models precluded the inclusion of precipitation or barometric pressure (collected by the Automated Surface Observing System and accessed online through the Iowa Environmental Mesonet; https://mesonet.agron.iastate.edu) as predictor variables of outmigration. These variables were not correlated with probability of outmigration. For each site × species combination, we constructed global models including all predictor variables. Therefore, similar to the categorical analyses, 16 total models were produced for each site × species combination. We investigated whether including a quadratic form of discharge improved global model fit using likelihood ratio tests (LRTs; packages 'lmtest'; Hothorn et al. 2019) because we predicted trends in outmigration could mimic trends in discharge (i.e., increase to peak and decrease). We only included the quadratic term and removed the normal term to reduce variance inflation factors in global and top models if the quadratic form of discharge improved model fit. For all combinations, we used multimodel inference to create sets of all possible sub-models, used an information theoretic approach to determine the top model, and averaged across top models (all models within < 4 AIC_C of the top model) according to AIC_W.

Results

Timing and magnitude of outmigration

Upper Missouri River

Rainbow trout

Four hundred thirty-two fish were redetected from 2014 to 2015; however, only 204 were detected as outmigrating individuals (147 in 2014 and 57 in 2015, Table 3.1). One hundred seventy-one individuals ostensibly outmigrated resulting in 375 total outmigrants (Table 3.1). Rainbow trout ranged in length at tagging from 76 to 201 mm (mean = 135 mm, SD ± 28.5; Figure 3.10). Mean tagging length of rainbow trout tagged in Little Prickly Pear Creek was longer than that of rainbow trout tagged in other upper Missouri River tributaries (mean = 150 mm, $P < 0.001$; Figure 3.10). Except for those tagged in Lyons Creek, rainbow trout that outmigrated in 2015 were larger at the time of tagging than in 2014 ($P < 0.075$; Figure 3.11).

Timing of outmigration of rainbow trout into the Missouri River was highly variable and differed among tributaries (Figure 3.12). Pulses of outmigration were generally associated with changes in tributary discharge and occurred both in the spring and autumn, though this second pulse was usually smaller (Little Prickly Pear Creek was an exception). The bulk of outmigrations generally occurred prior to baseflow and maximum summer temperatures. Timing of outmigration out of the Dearborn River was similar to that of Little Prickly Pear Creek but pulse size was smaller (Figure 3.13). Half of Dearborn River outmigrating fish entered the Missouri River by the first of July; 90% entered the Missouri by September 25 (Figure 3.14). Similarly, half of all outmigrating fish tagged in Little Prickly Pear Creek and its tributaries entered the Missouri River by July 7 and 90% entered the Missouri by September 10 (Figure 3.14). However, pulses of outmigration from Little Prickly Pear Creek were more pronounced and corresponded with increases in discharge in May and September (Figure 3.13). Another pulse occurred in July following a modest increase in discharge (Figure 3.13). Outmigration from Sheep Creek occurred earlier; 50% of outmigrating fish entered the mainstem by May 10, and 90% entered the Missouri River by June 24 (Figure 3.14). Outmigration from Sheep Creek was characterized by two early pulses in April and June immediately following increases in discharge and occurring before temperatures reached annual maxima (Figure 3.13). No autumn outmigration was observed in Sheep Creek.

Outmigration of rainbow trout tagged in Lyons Creek and Wolf Creek into Little Prickly Pear Creek was similar in pulse timing and size and corresponded with increases in discharge (Figure 3.15). Half of all fish outmigrating from Lyons Creek and Wolf Creek entered Little

Prickly Pear Creek on June 12 and June 2, respectively. Seventy-five percent of fish outmigrating from Wolf and Lyons creeks entered Little Prickly Pear Creek on June 24 and June 20, respectively (Figure 3.15). However, remaining fish outmigrated later and more gradually from Wolf Creek than Lyons Creek (Figure 3.15). Moreover, fish tagged in Wolf Creek outmigrated from Little Prickly Pear Creek into the Missouri River more gradually than those that were tagged in Lyons Creek (Figure 3.15).

Brown trout

Although 50 brown trout were redetected, only 38 were detected as outmigrating individuals (26 in 2014 and 12 in 2015; Table 3.1). Two individuals ostensibly outmigrated resulting in 40 total outmigrants (Table 3.1). Brown trout length at tagging ranged from 89 to 201 mm (mean = 146 mm, SD ± 27.6; Figure 3.16).

Outmigration of brown trout began earlier than that of rainbow trout but also appeared to be associated with discharge (Figures 3.17 and 3.18). Timing of outmigration of brown trout could only be determined for fish entering the Missouri River from Little Prickly Pear Creek and its tributaries because too few fish were redetected leaving the Dearborn River and Sheep Creek (Table 3.1). Fifty percent of outmigrating brown trout left Little Prickly Pear Creek and entered the Missouri River by June 21 and 90% entered the Missouri River by October 4 (Figure 3.18). Too few fish were redetected to investigate outmigration of brown trout from Lyons and Wolf creeks into Little Prickly Pear Creek (Table 3.1).

Smith River

Rainbow trout

Six hundred and three juvenile rainbow trout were redetected from 2014 to 2015; however, only 45 were categorized as outmigrating individuals (11 in 2014 and 34 in 2015; Table 3.2). Eighty-eight individuals ostensibly outmigrated resulting in 133 total outmigrants (Table 3.2). Rainbow trout ranged in length at tagging from 46 to 201 mm (mean = 144.5 mm, SD ± 32.8; Figure 3.19). Both rainbow and brown trout tagged in Tenderfoot Creek were smaller than those tagged in other Smith River tributaries (mean = 89 mm and mean = 106 mm, respectively; $P < 0.001$; Figure 3.20); however, these fish were tagged using 12 mm tags, which allowed a smaller minimum tagging length.

Because most fish were tagged in late summer and autumn of 2014, more outmigrated in 2015 than in 2014. Too few fish were outmigrated in 2014; the results that follow apply only to fish that were tagged in 2014 and outmigrated the following year in 2015. Outmigrant rainbow trout tagged in Moose and Sheep creeks were combined into one group because too few fish were detected. Too few rainbow and brown trout were detected in tributaries other than Moose and Sheep creeks to provide reliable outmigrating estimates.

Outmigration of juvenile rainbow trout tagged in Moose and Sheep creeks occurred primarily in June, July, and October (Figure 3.21). Outmigration pulses corresponded with increased discharges in June and October as well as increased water temperatures in July (Figure 3.21). Fifty percent of outmigrating rainbow trout entered the Smith River by July 5 and 90% outmigrated by October 20 (Figure 3.22).

Brown trout

Thirty-one brown trout were redetected from 2014 to 2015, but only 18 were detected as outmigrating individuals (6 in 2014 and 12 in 2015; Table 3.2). One individual ostensibly outmigrated resulting in 19 total outmigrants (Table 3.2). Brown trout length at tagging ranged from 76 to 201 mm (mean = 149.0 mm, SD ± 26.1; Figure 3.20).

Outmigration of juvenile brown trout tagged in Hound Creek was characterized by pulses in early spring and autumn (Figure 3.23). Sixty percent of all outmigrants entered the Smith River by April 30 and 90% outmigrated by the end of October (Figure 3.23). The flow regime of the Smith River had little effect on outmigration, but changes in Hound Creek discharge probably did not coincide with the discharge regime of the Smith River. Too few brown trout were detected elsewhere to provide reliable analysis.

Diel timing

Timing of outmigrations in the Missouri and Smith rivers occurred throughout the day but peaked from just after sunset (2000) to midnight and was lowest during the afternoon and early evening (1200 to 1900; Figure 3.24). There were no discernible differences in the diel timing of outmigration among tributaries or species (Figure 3.25).

Abiotic factors influencing outmigration

Upper Missouri River

Rainbow trout

The top categorical models for number of rainbow trout outmigrating from Little Prickly Pear Creek included photoperiod and lunar phase; however, categorical models explained only 2% of the variation in the data (R^2 = 0.02; Table 3.6). Photoperiod category 3 (increasing night length) was the most influential of all predictor variables on the number of outmigrant rainbow trout (*P* = 0.003). Other factors were not statistically significant. The top continuous model included discharge, photoperiod, and temperature (Table 3.7). Continuous models explained 14%

of the variation in the data (Table 3.7). Increasing photoperiod was strongly associated with probability of outmigration and included in seven models (*p* = 0.007; Figure 3.26). Discharge was included in four models whereas temperature and lunar phase were only included in three.

The top categorical model for number of rainbow trout outmigrating from the Dearborn River consisted of the intercept only, but each factor was included in other top models. No variables were correlated with probability of outmigration. The top continuous model included discharge and temperature, but neither were associated with probability of outmigration. Furthermore, this model explained only 3% of the variation in the data (Table 3.7).

In addition to Little Prickly Pear Creek and the Dearborn River, we also investigated continuous models for rainbow trout outmigrating from Sheep, Lyons, and Wolf creeks. The top model for outmigrants in Sheep Creek included both temperature and photoperiod; increasing photoperiod was associated with increased probability of outmigration (*P* = 0.015; Figure 3.26). Top models for Lyons Creek included discharge and photoperiod, and there was marginal evidence (*P* = 0.081) that increasing photoperiod was associated with outmigration (Table 3.7). The top model for Wolf Creek included only photoperiod, and similar to Lyons Creek, photoperiod was positively associated with probability of outmigration (*P* = 0.008; Figure 3.27). Only 4% of the variation in data was explained by models for Lyons and Wolf creek outmigrants and only 6% was explained by models for Sheep Creek.

Brown trout

The top categorical models for number of brown trout outmigrating from Little Prickly Pear Creek included photoperiod and lunar phase, but neither were influential on predicting the number of outmigrants (Table 3.6). Categorical models explained little of the variation in the data (R^2 = 0.01; Table 3.6). The top continuous model included only photoperiod (Table 3.7); no variables were associated with the probability of brown trout outmigration. Similar to categorical models, the top continuous model explained little variation in data (<1%; Table 3.7). Too few brown trout were observed outmigrating from other tributaries to provide reliable estimates (Table 3.1).

Smith River

Rainbow trout

We developed continuous models for outmigration of rainbow trout from only one Smith River tributary, Sheep Creek. The top model included temperature and discharge; temperature was included in all seven top models, whereas discharge was included in four. Increasing temperature was associated with increased probability of outmigration (P = 0.018; Figure 3.27). The top model explained 11% of the variation in data.

Discussion

Patterns in outmigration varied among species and locations and were influenced by a number of different factors. Our analysis implicated some environmental factors as influential on outmigration, but primary drivers in some systems were unclear. Bimodal pulses in outmigration, generally consisting of a large pulse in spring or summer and another smaller pulse in autumn, occurred in every tributary except for Sheep Creek (Missouri River). In addition to reporting similar outmigration timing, Leathe et al. (2014) also observed bimodal pulses in fish outmigrations from Little Prickly Pear Creek and the Dearborn River wherein the autumnal pulse was smaller. However, unlike Leathe et al. (2014), the second pulse occurred immediately following a sudden and unseasonably large increase in discharge in our study. The unseasonable pulse might explain the magnitude of autumnal outmigration observed in Little Prickly Pear Creek. Cumulative proportion analyses illustrated that most outmigration occurred before discharges reached base flows and temperatures reached annual maximums. Therefore, it is possible that most outmigrants leave tributaries before hydrologic and thermal conditions become unfavorable. This was also observed by Leathe et al. (2014), especially for age-1 fish. As fish grow, demand for energy and space increase and resource availability in tributaries becomes less favorable (Chapman 1966). Mainstem river habitat may have been more productive for rearing. The early, rapid outmigration that occurs in Sheep Creek (Missouri River) may indicate that this site has the least favorable conditions for juvenile trout relative to other tributaries in the study.

Results from our models with continuous variables aligned with the findings of Leathe et al. (2014) more than our categorical models; however, none of the variables considered explained much variation. Contrary to our categorical analysis results, models with continuous variables identified increasing photoperiod as the most influential environmental variable affecting outmigration. Although photoperiod was the most prominent factor in categorical models and was positively associated with outmigration in three of our comparisons, increasing night length was identified as most influential. This could be related to the unseasonable pulse in discharge and concomitant pulse in outmigration we observed in autumn when night length increases.

It is difficult to determine how much temperature and discharge influenced outmigration based on our models. Leathe et al. (2014) reported a temperature preference of 7.5–12.5°C for outmigration, which is consistent with numerous other salmonid outmigration studies (Osterdahl 1969; Jonsson and Ruud-hansen 1985; Pavlov et al. 2008), but we did not find strong influences of temperature. Temperature was only influential for rainbow trout migrating from Sheep Creek into the Smith River and outmigration increased when temperatures were 15–20°C, which is much higher than reported elsewhere. Cumulative proportion graphs showed outmigration concomitant with changes in discharge and temperature, but influences of either on models were not consistent among species and tributaries.

Our interpretation of timing of outmigration probably did not influence the effectiveness of our models. Our analysis defined the last detection on these antennas as the outmigration date, but some individuals were detected multiple times over periods of days or weeks on tributary antennas. In contrast, some other studies employing PIT technology to investigate outmigration timing used the initial detection (e.g., Glaid 2017). We therefore performed preliminary analyses investigating the effect of outmigration date (initial detection vs. last detection) on model strength and determined that last detection provided the most reliable analysis.

Our analysis of outmigration, particularly those with categorical variables, were not particularly effective in determining factors influencing outmigration, underscoring the great temporal and spatial variability in environmental influences on outmigration. Such difficulties in identifying relationships between salmonid outmigration and abiotic cues were echoed in Leathe et al. (2014) and in other systems using similar methodologies (Homel and Budy 2008; Pavlov et al. 2008). It is likely that all the variables we included influence outmigration, but levels of influence differ from site to site and even seasonally. For example, emigration of juvenile Bull Trout in the Grande Ronde drainage, Oregon, were correlated with peaks in discharge in spring but falling temperatures in autumn (Bellerud et al. 1997). A PIT telemetry study on Bull Trout outmigration in the Walla Walla River, Oregon, found that seasonal modeling revealed influential factors previously obscured by variability across seasons (Homel and Budy 2008). Including model interactions between environmental variables and seasons to investigate this question would require larger numbers of observations of outmigration than included in this study. Therefore, sub-setting data and modelling within years may be a stronger approach to detect annual or seasonal differences in outmigration cues. Regardless of the individual variable or combination of variables associated with outmigration, this study and Leathe et al. (2014) both documented bimodal pulses of outmigrations in spring and fall that in some cases appeared related to increases in discharge.

Factors leading to differences among outmigrant lengths at tagging were unclear. The larger size of rainbow trout outmigrants in Little Prickly Pear Creek may indicate a productive rearing environment that promotes rapid growth. However, it is also possible that some rainbow trout in this watershed spend their first year in the tributaries of Lyons and Wolf creeks, outmigrating to Little Prickly Pear Creek as age-1 fish before outmigrating to the Missouri River. We are uncertain why more fish with larger size at tagging outmigrated in 2015. It is possible these fish outmigrated in their second year; however, migration checks in the second annulus of scale growth patterns suggested a low proportion (1.5%) of rainbow trout exhibit this strategy in the Missouri River (Munro 2004). It is more likely that these fish outmigrated in 2014 but were not detected and were in fact returning as subadults or spawners. Numerous (N = 87) male rainbow trout with tagging lengths less than 254 mm (10”) were observed with milt. Furthermore, tag detection ranges of fixed PIT arrays were generally lowest during spring discharges, which often coincided with outmigration pulses.

The generally low sample sizes observed in our study could be attributed to a lack of detections by fixed PIT arrays, which were necessary to classify individual outmigrants. Our data set of known outmigrants might have been larger had PIT tag detection ranges been higher during periods of outmigration. We likely underestimated outmigration as detection rates decrease with increased water volume, velocities, and depths (e.g., Zydlewski et al. 2006). Read ranges almost always dropped following spring discharges, frequently to annual lows. Increases in water velocities can rearrange antenna shapes and negatively affect tuning (Zydlewski et al. 2006). Indeed, our antennas frequently required repair and retuning following spring discharges. Nevertheless, we felt that our sample sizes were high enough to proceed with analyses as they were consistent with other PIT telemetry studies of outmigration with similar numbers of fish tagged and issues encountered (Homel and Budy 2008).

Low outmigrant sample sizes might also be a result of a resident life history pattern that was influenced by tagging location. Total numbers of outmigrants comprised relatively low proportions of total numbers of juveniles tagged, but total numbers of juvenile fish redetected on all antennas were high in comparison. Rather than moving past tributary antennas undetected, many fish probably remained in their natal streams and became tributary residents. Location may have biased tagging efforts toward resident fish. For example, most fish in the Sheep Creek watershed in the Smith River were tagged in the upper reaches; had more fish been tagged closer to the confluence, more outmigrants may have been observed.

Our attempt to replicate the analyses of Leathe et al. (2014) may have been limited by our methodology and subsequent sample size. Rotary screw traps employed by Leathe et al. (2014), though time intensive, captured thousands of fish per tributary per sampling season. PIT telemetry allowed us to passively and continuously monitor tagged fish but was limited in numbers of redetected fish. Our highest sample size was 95 for rainbow trout outmigrating from Little Prickly Pear Creek. Even so, continuous models may be more appropriate for outmigration analyses because trends in environmental variables are often continuous in nature. Additionally, results from continuous models may be more informative to fisheries managers making predictions across a wide spectrum of environmental variables in the field.

TABLES

Table 3.1. Number and proportions of juvenile rainbow trout and brown trout (< 201 mm) tagged, redetected, and outmigrated in upper Missouri River tributaries from 2014 to 2015. All fish tagged in 2014. Outmigration is defined as the last detection on the tributary mouth antenna; for fish tagged in Wolf Creek and Lyons Creek, outmigration is defined as the last detection on the Little Prickly Pear Creek antenna.

Tributary	Number tagged	Number/proportion redetected	Number/proportion outmigrated 2014	Number/proportion outmigrated 2015	Total outmigrants
			Rainbow Trout		
Dearborn River	257	52 (0.20)	31 (0.12)	11 (0.04)	44 (0.17)
Sheep Creek	318	66 (0.21)	21 (0.07)	16 (0.05)	39 (0.12)
Little Prickly Pear Creek watershed					
Little Prickly Pear Creek	280	90 (0.32)	39 (0.14)	7 (0.03)	60 (0.21)
Wolf Creek	624	153 (0.25)	38 (0.06)	16 (0.03)	57 (0.09)
Lyons Creek	196	71 (0.36)	18 (0.09)	7 (0.04)	29 (0.15)
Subtotal	1,100	314 (0.29)	95 (0.09)	30 (0.03)	146 (0.13)
Total	1,675	432 (0.26)	147 (0.09)	57 (0.03)	375 (0.22)
			Brown Trout		
Dearborn River	28	1 (0.04)	0	0	0
Sheep Creek	51	5 (0.10)	2 (0.04)	0	3 (0.06)
Little Prickly Pear Creek watershed					
Little Prickly Pear Creek	66	23 (0.35)	15 (0.23)	1 (0.02)	16 (0.24)
Wolf Creek	70	11 (0.16)	1 (0.01)	3 (0.04)	5 (0.07)
Lyons Creek	73	18 (0.25)	8 (0.11)	8 (0.11)	16 (0.22)
Subtotal	209	52 (0.25)	24 (0.11)	12 (0.06)	35 (0.17)
Total	288	58 (0.20)	26 (0.09)	12 (0.04)	40 (0.14)

Table 3.2. Number and proportions of juvenile rainbow trout and brown trout (< 201 mm) tagged, redetected, and outmigrated in Smith River tributaries from 2014 to 2015. All fish were tagged in 2014. Outmigration is defined as the last detection on the tributary mouth antenna; for fish tagged in Moose Creek, outmigration is defined as the last detection on the Lower Sheep Creek antenna.

Tributary	Number tagged	Number/proportion redetected	Number/proportion outmigrated 2014	Number/proportion outmigrated 2015	Total outmigrants
			Rainbow Trout		
Hound Creek	13	2 (0.15)	1 (0.08)	1 (0.08)	2 (0.15)
Tenderfoot Creek	135	17 (0.13)	8 (0.06)	3 (0.02)	19 (0.14)
Sheep Creek watershed					
Sheep Creek	651	244 (0.37)	1 (0.002)	22 (0.03)	52 (0.08)
Moose Creek	759	340 (0.45)	0	8 (0.01)	60 (0.08)
Subtotal	1,410	584 (0.41)	1 (0.001)	30 (0.02)	112 (0.08)
Total	1,558	603 (0.39)	11 (0.01)	34 (0.02)	133 (0.09)
			Brown Trout		
Hound Creek	121	18 (0.15)	2 (0.02)	11 (0.09)	16 (0.13)
Tenderfoot Creek	17	3 (0.18)	1 (0.06)	0	1 (0.06)
Sheep Creek watershed					
Sheep Creek	29	8 (0.28)	0	1 (0.03)	2 (0.07)
Moose Creek	2	2 (1.00)	0	0	0
Subtotal	31	10 (0.32)	0	1 (0.03)	2 (0.06)
Total	169	31 (0.18)	6 (0.04)	12 (0.07)	19 (0.11)

Table 3.3. Locations, average detection ranges (minima and maxima in parentheses), and detection efficiencies of stationary PIT arrays in the upper Missouri River, Sun River, and Smith River subbasins.

Stationary PIT array	GPS coordinates (UTM)	Tag detection distance (inches)	Detection efficiency	Physical location
Missouri River				
Lyons Creek	46.93827, -112.12581	28.5 (6 – 54)	-	Just upstream of confluence with Little Prickly Pear Creek
Wolf Creek	47.00597, -112.08026	29 (6 – 60)	-	Just upstream of confluence with Little Prickly Pear Creek
Little Prickly Pear Creek	47.02251, -112.02018	17 (2 – 42)		Just upstream of confluence with Missouri River
Dearborn River	47.13017, -111.91295	6.3 (2.5 – 9)	-	Just upstream of confluence with Missouri River
Sheep Creek	47.17681, -111.81165	17.7 (4 – 36)	-	Just upstream of confluence with Missouri River
Sun River				
HWY 287	47.54768, -112.36674	8.6 (4.5 – 18)	-	Just upstream of Hwy 287 near Augusta, Montana at rkm 109
Elk Creek	47.51229, -112.33641	30 (4 – 48)	-	rkm 4.5
Durocher	47.54413, -111.57848	7.2 (3 – 18)	-	Upstream of Vaughn, Montana at rkm 32
Smith River				
Big Birch Creek	46.58884, -111.05305	-	0.79	Just upstream of confluence with Smith River
Newlan Creek	46.59094, -111.05070	-	0.79	Just upstream of confluence with Smith River
Canyon Ranch	46.60810, -111.06760	-	0.96	rkm 172
Benton Creek	46.70542, -111.19305	-	0.79	Just upstream of confluence with Smith River
Camas Creek	46.70542, -111.19305	-	0.96	Just upstream of confluence with Smith River
Smith River at Beaver Creek	46.75143, -111.16839	-	1.00	rkm 141
Moose Creek	46.80292, -110.91484	-	0.96	Just upstream of confluence with Sheep Creek
Upper Sheep Creek	46.81047, -110.92272	-	0.71	1 rkm downstream of Moose Creek
Lower Sheep Creek	46.80443, -111.17403	-	0.78	0.9 rkm upstream of confluence with Smith River
Rock Creek	46.86935, -111.27185	-	0.79	Just upstream of confluence with Smith River
Tenderfoot Creek	46.94185, -111.29404	-	0.98	Just upstream of confluence with Smith River
Castle Bar	46.97789, -111.28427	-	0.75	rkm 97
Merganser Bend	47.14734, -111.294	-	0.66	Just downstream of Merganser Bend boat camp
Hound Creek	47.21261, -111.40371	18.5 (4 – 36)	0.96	rkm 2.4
Truly Bridge	47.35658, -111.44140	7.4 (1 – 18)	0.70	rkm 14.6

Table 3.4. Details of climate data used for estimating stream temperatures. No data was collected for Sheep Creek (Missouri River).

Location	Measurement(s)	Method	Years collected
Wolf Creek	Stream temperature	Temperature logger	2015-2017
Lyons Creek	Stream temperature	Temperature logger	2015-2017
	Stream temperature	Temperature logger	1997-2006
Little Prickly Pear Creek	Discharge	USGS gage station	1997-2019
	Stream temperature	USGS gage station	2000-2019
Dearborn River	Discharge	USGS gage station	2000-2019
Helena, Montana	Air temperature	GHCN weather station	2000-2019

Table 3.5. Linear models for predicting mean daily stream temperatures in Little Prickly Pear Creek, Lyons Creek, Wolf Creek, and the Dearborn River, Montana, USA. Data for Little Prickly Pear Creek model is from 2000 to 2003 and 2005 to 2006. Data for the Dearborn River model was collected from 2000 to 2019. Models used are displayed in bold text.

Predictor(s)	P	r^2	*RMSE*
Lyons Creek model			
Air temperature	$\boldsymbol{P < 0.001}$	**0.836**	**1.485**
Little Prickly Pear Creek discharge	$P < 0.001$	0.105	3.416
Air temperature + Little Prickly Pear Creek discharge	$P < 0.001$	0.862	1.345
Wolf Creek model			
Air temperature	$\boldsymbol{P < 0.001}$	**0.892**	**1.285**
Little Prickly Pear Creek discharge	$P < 0.001$	0.102	3.608
Air temperature + Little Prickly Pear Creek discharge	$P < 0.001$	0.915	1.114
Little Prickly Pear Creek model			
Dearborn River water temperature	$P < 0.001$	0.960	1.038
Air temperature	$\boldsymbol{P < 0.001}$	**0.914**	**1.566**
Little Prickly Pear Creek discharge	$P < 0.01$	0.007	5.232
Dearborn River water temperature + discharge	$P < 0.001$	0.964	0.977
Air temperature + Little Prickly Pear Creek discharge	$P < 0.001$	0.918	1.530
Dearborn River model			
Air temperature	$P < 0.001$	0.855	2.043
Dearborn River discharge	$P < 0.001$	0.048	5.210
Air temperature + Dearborn River discharge	$\boldsymbol{P < 0.001}$	**0.890**	**1.782**

Table 3.6. The top-ranked categorical models (of 16 total models each per site × species combination) for number of outmigrants of rainbow and brown trout tagged in Little Prickly Pear Creek and the Dearborn River. Models are sorted by corrected Akaike information criterion (AIC_C) with log likelihood (‘LogLik’), difference in AIC_C from the best supported model (ΔAIC_C), and model weights (AIC_W). Models within < 4 AIC_C of the top model were included in the top model set and multimodel inference. Each model includes an intercept term and ‘intercept only’ denotes when no other predictors were included. Each predictor variable besides the intercept is categorical and includes up to five separate categories. Variance inflation factors are included for top models (‘VIF’) and for global models (‘VIF_G’). R-squared values are also included for top models (‘R^2’) and global models (‘R^2_G’). Within VIF, ‘ND’ indicates that VIFs could not be calculated because < 2 variables were included in that top model.

Species	Num.	Model	df	LogLik	AIC_C	ΔAIC_C	AIC_W	VIF	R^2	VIF_G	R^2_G
		Little Prickly Pear Creek									
Rainbow Trout	1	Photoperiod	4	-189.94	388.04	0.00	0.88	ND	0.02	< 1.9	0.08
	2	Lunar phase + Photoperiod	7	-188.78	391.97	3.94	0.12				
Brown Trout	1	Photoperiod	3	-62.05	130.19	0.00	0.47	ND	0.01	< 2.1	0.03
	2	(Intercept only)	1	-64.32	130.66	0.46	0.37				
	3	Lunar phase + Photoperiod	6	-60.66	133.64	3.45	0.08				
	4	Lunar phase	4	-62.91	133.98	3.79	0.07				
		Dearborn River									
Rainbow Trout	1	(Intercept only)	1	-102.13	206.28	0.00	0.45	ND	0.00	< 3.4	0.07
	2	Photoperiod	3	-100.93	207.95	1.67	0.20				
	3	Temperature	5	-99.10	208.42	2.14	0.16				
	4	Discharge	5	-99.46	209.14	2.86	0.11				
	5	Lunar phase	4	-100.74	209.63	3.35	0.09				

Table 3.7. Top-ranked continuous models for probability of outmigration of rainbow or brown trout from Little Prickly Pear Creek, Dearborn River, and Sheep Creek into the Missouri River. Models are sorted by corrected Akaike information criterion (AIC_C) with log likelihood ('LogLik'), difference in AIC_C from the best supported model (ΔAIC_C), and model weights (AIC_W). Models within < 4 AIC_C of the top model were included in the top model set and multimodel inference. Each model includes an intercept term and 'intercept only' denotes when no other predictors were included. Variance inflation factors are included for top models ('VIF') and for global models ('VIF_G'). R-squared values are also included for top models ('R^2') and global models ('R^2_G'). Within VIF, 'ND' indicates that VIFs could not be calculated because < 2 variables were included in that top model.

Site	Species	Num.	Model	df	LogLik	AIC_C	ΔAIC_C	AIC_W	VIF	VIF_G	R^2	R^2_G
Little Prickly Pear Creek	Rainbow Trout	1	Intercept + Discharge2 + Photoperiod + Temperature	4	-118.49	245.13	0.00	0.36	0.140	< 1.66	0.141	< 1.68
		2	Intercept + Discharge2 + Photoperiod	3	-120.37	246.83	1.70	0.15				
		3	Intercept + Discharge2 + Lunar phase + Photoperiod + Temperature	5	-118.31	246.85	1.72	0.15				
		4	Intercept + Photoperiod	2	-121.55	247.13	2.00	0.13				
		5	Intercept + Photoperiod + Temperature	3	-120.95	247.98	2.85	0.09				
		6	Intercept + Discharge2 + Lunar phase + Photoperiod	4	-120.29	248.74	3.60	0.06				
		7	Intercept + Lunar phase + Photoperiod	3	-121.52	249.12	3.99	0.05				
	Brown Trout	1	Intercept + Photoperiod	2	-62.48	129.01	0.00	0.21	0.007	NA	0.013	< 2.01
		2	Intercept only	1	-63.78	129.58	0.58	0.15				
		3	Intercept + Photoperiod + Temperature	3	-61.76	129.61	0.60	0.15				
		4	Intercept + Lunar phase + Photoperiod	3	-62.38	130.84	1.84	0.08				
		5	Intercept + Discharge^2 + Photoperiod	3	-62.48	131.05	2.04	0.07				
		6	Intercept + Lunar phase	2	-63.67	131.38	2.37	0.06				

		7	Intercept + Discharge^2 + Photoperiod + Temperature	4	-61.63	131.42	2.41	0.06				
		8	Intercept + Discharge^2	2	-63.70	131.44	2.44	0.06				
		9	Intercept + Lunar phase + Photoperiod + Temperature	4	-61.67	131.49	2.49	0.06				
		10	Intercept + Temperature	2	-63.78	131.60	2.60	0.06				
		11	Intercept + Discharge^2 + Lunar phase + Photoperiod	4	-62.38	132.90	3.90	0.03				
Dearborn River	Rainbow Trout	1	Intercept + Discharge + Temperature	3	-80.79	167.67	0.00	0.20	0.031	< 1.09	0.030	< 2.45
		2	Intercept + Photoperiod	2	-82.05	168.13	0.47	0.16				
		3	Intercept + Photoperiod + Temperature	3	-81.37	168.82	1.16	0.11				
		4	Intercept + Discharge + Lunar phase + Temperature	4	-80.36	168.87	1.21	0.11				
		5	Intercept + Temperature	2	-82.71	169.47	1.80	0.08				
		6	Intercept + Discharge + Photoperiod + Temperature	4	-80.70	169.55	1.88	0.08				
		7	Intercept + Lunar phase + Photoperiod	3	-81.86	169.81	2.14	0.07				
		8	Intercept + Discharge + Photoperiod	3	-82.03	170.14	2.47	0.06				
		9	Intercept + Lunar phase + Photoperiod + Temperature	4	-81.17	170.49	2.82	0.05				
		10	Intercept + Discharge + Lunar phase + Photoperiod + Temperature	5	-80.32	170.86	3.20	0.04				
		11	Intercept + Lunar phase + Temperature	3	-82.51	171.10	3.44	0.04				
Sheep Creek	Rainbow Trout	1	Intercept + Temperature + Photoperiod	3	-51.19	108.47	0.00	0.30	0.053	< 1.62	0.059	< 2.78
		2	Intercept + Temperature + Lunar phase + Photoperiod	4	-50.56	109.26	0.79	0.20				
		3	Intercept + Discharge + Temperature + Photoperiod	4	-51.06	110.27	1.80	0.12				
		4	Intercept + Photoperiod	2	-53.21	110.47	2.00	0.11				
		5	Intercept + Lunar phase + Photoperiod	3	-52.49	111.06	2.59	0.08				
		6	Intercept + Discharge + Temperature + Lunar phase + Photoperiod	5	-50.50	111.22	2.75	0.08				
		7	Intercept + Discharge + Photoperiod	3	-52.93	111.96	3.49	0.05				

8	Intercept + Discharge + Lunar phase + Photoperiod	4	-52.03	112.22	3.75	0.05

FIGURES

Figure 3.1. The upper Missouri, Sun, and Smith rivers and their major tributaries. Yellow dots represent USGS gaging stations used in the study. Black diagonals represent dams or diversions. Green diamonds represent fixed PIT antenna arrays. Shaded buffers represent areas where fish movement was monitored by fixed PIT antenna arrays, portable PIT antennas, and physical recapture events.

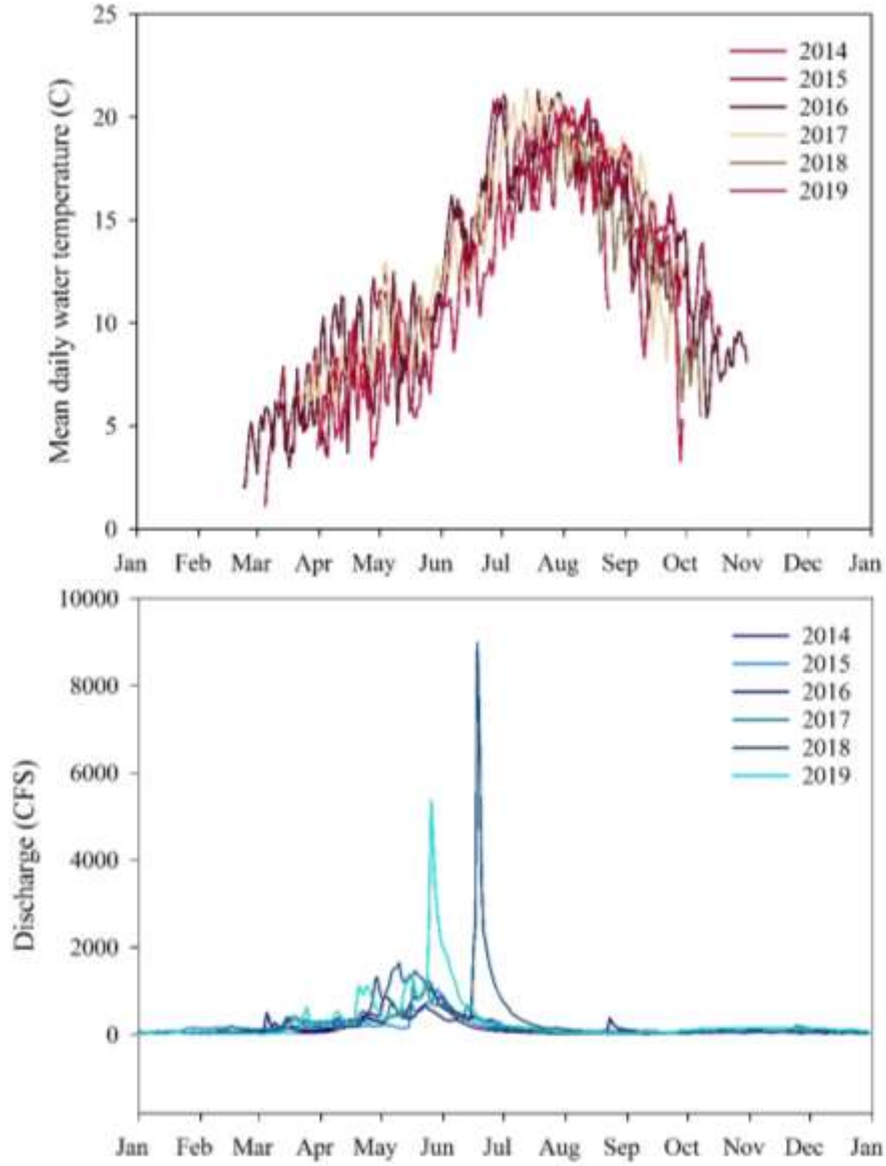


Figure 3.2. Dearborn River hydrograph and thermograph from 2014 to 2019 measured at the USGS gaging station (USGS site 06077200) near Craig, Montana.

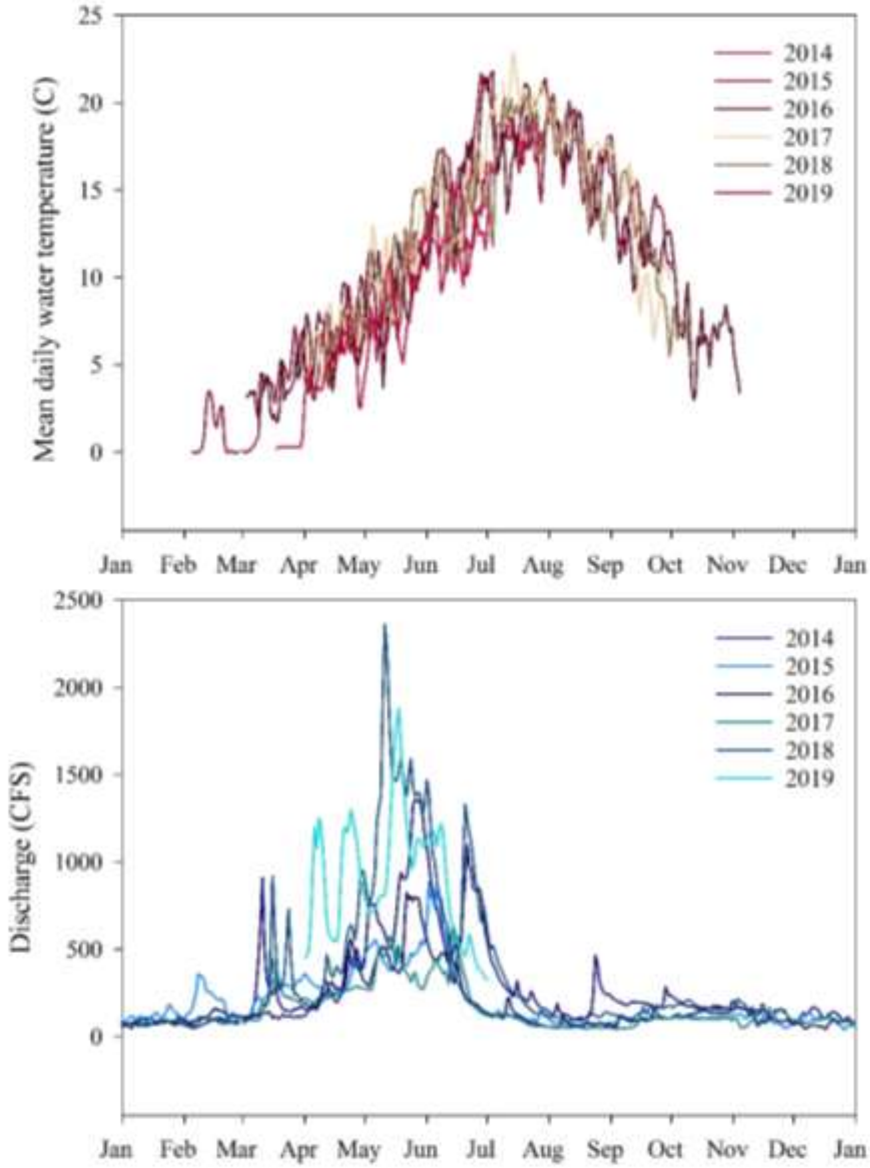


Figure 3.3. Smith River hydrograph and thermograph from 2014 to 2019 measured at the USGS gaging station (USGS site 06077200) near Fort Logan, Montana.

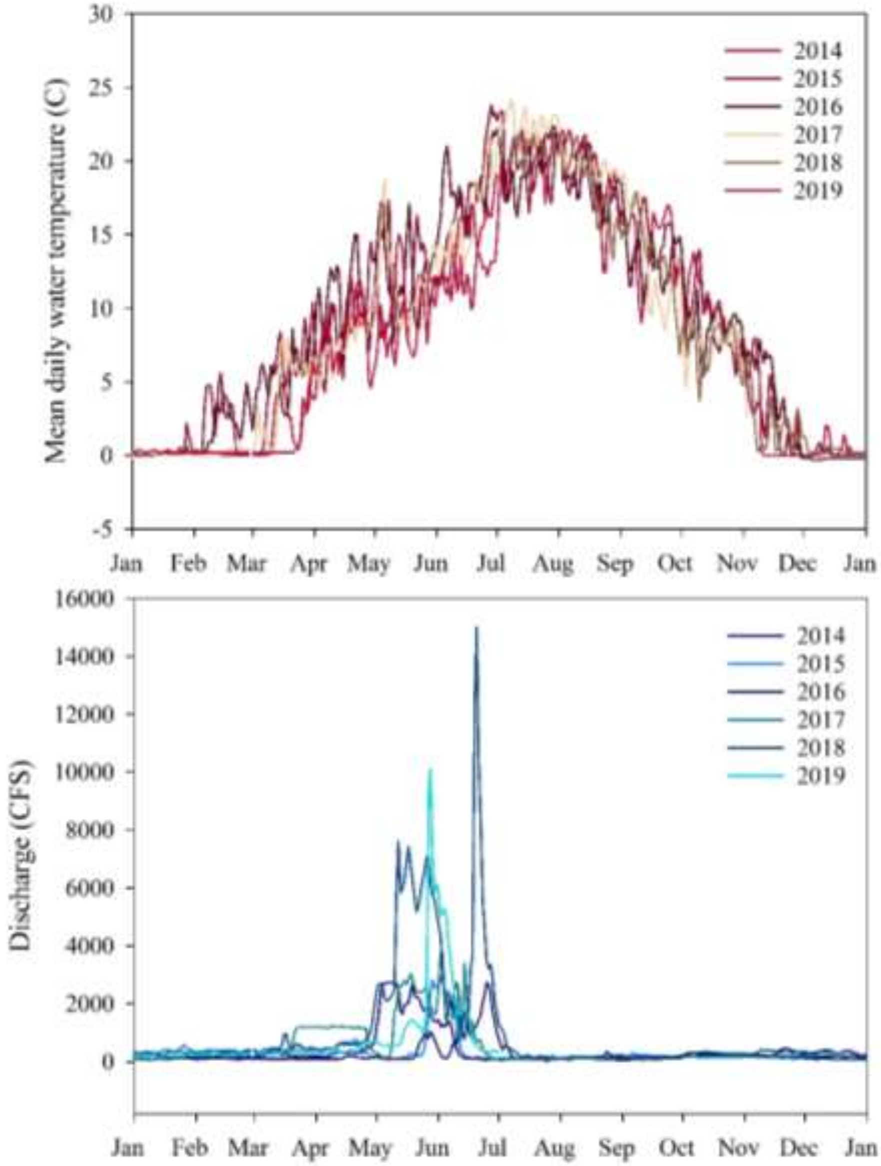


Figure 3.4. Sun River hydrograph and thermograph from 2014 to 2019 measured at the USGS gaging station (USGS site 06077200) near Simms, Montana.

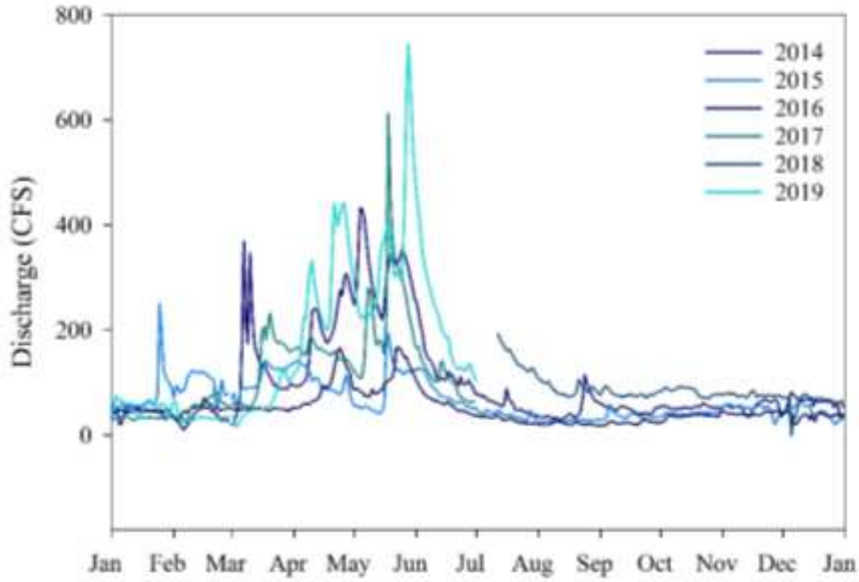


Figure 3.5. Little Prickly Pear Creek hydrograph 2014 to 2019 measured at the USGS gaging station (USGS site 06077200) at the confluence with Wolf Creek.

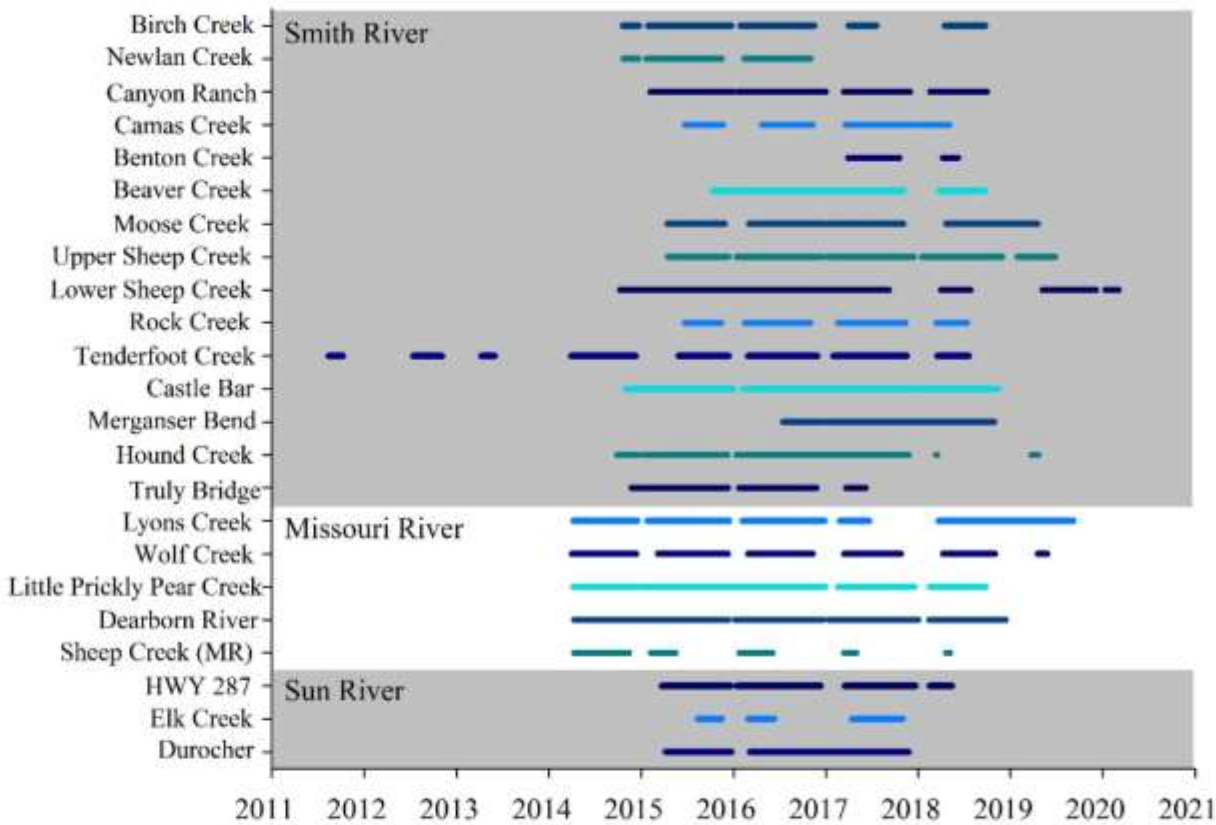
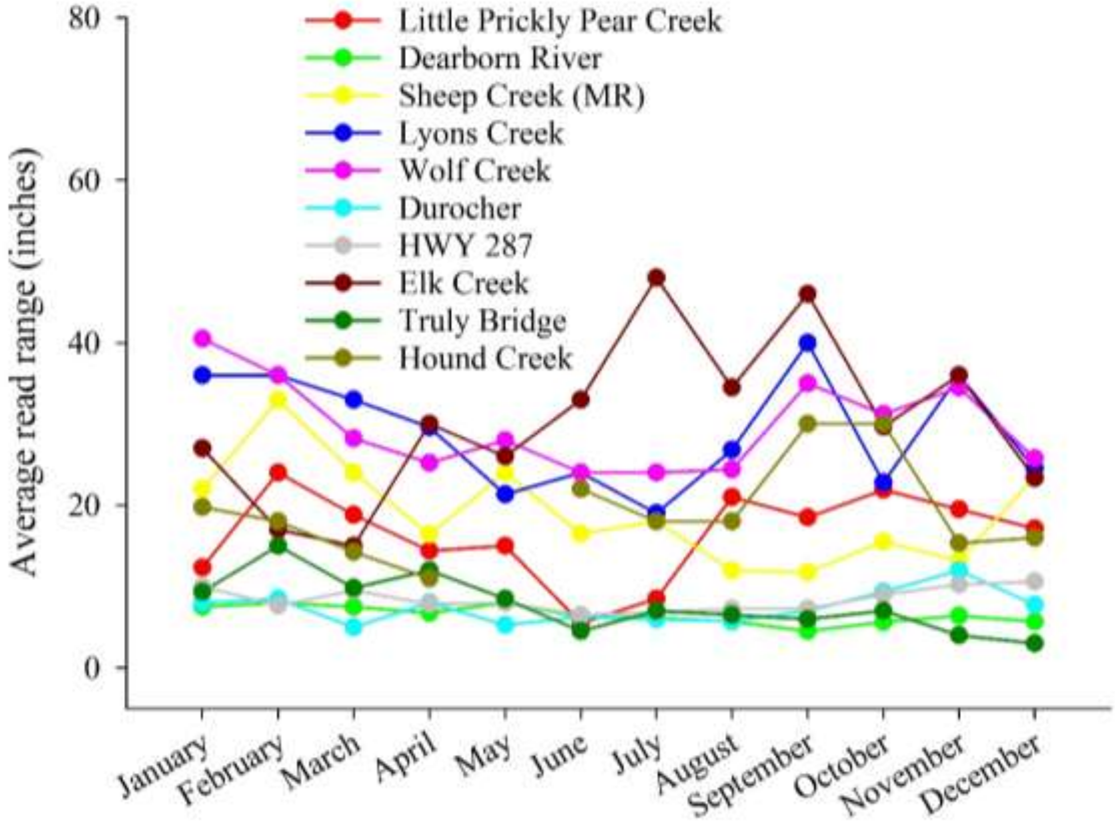


Figure 3.6. Operation timelines of stationary PIT arrays in the Smith, Sun, and upper Missouri River subbasins from 2011 to 2020.



1802

1803 Figure 3.7. Average read ranges of fixed PIT arrays by month from 2015 to 2019.

1804

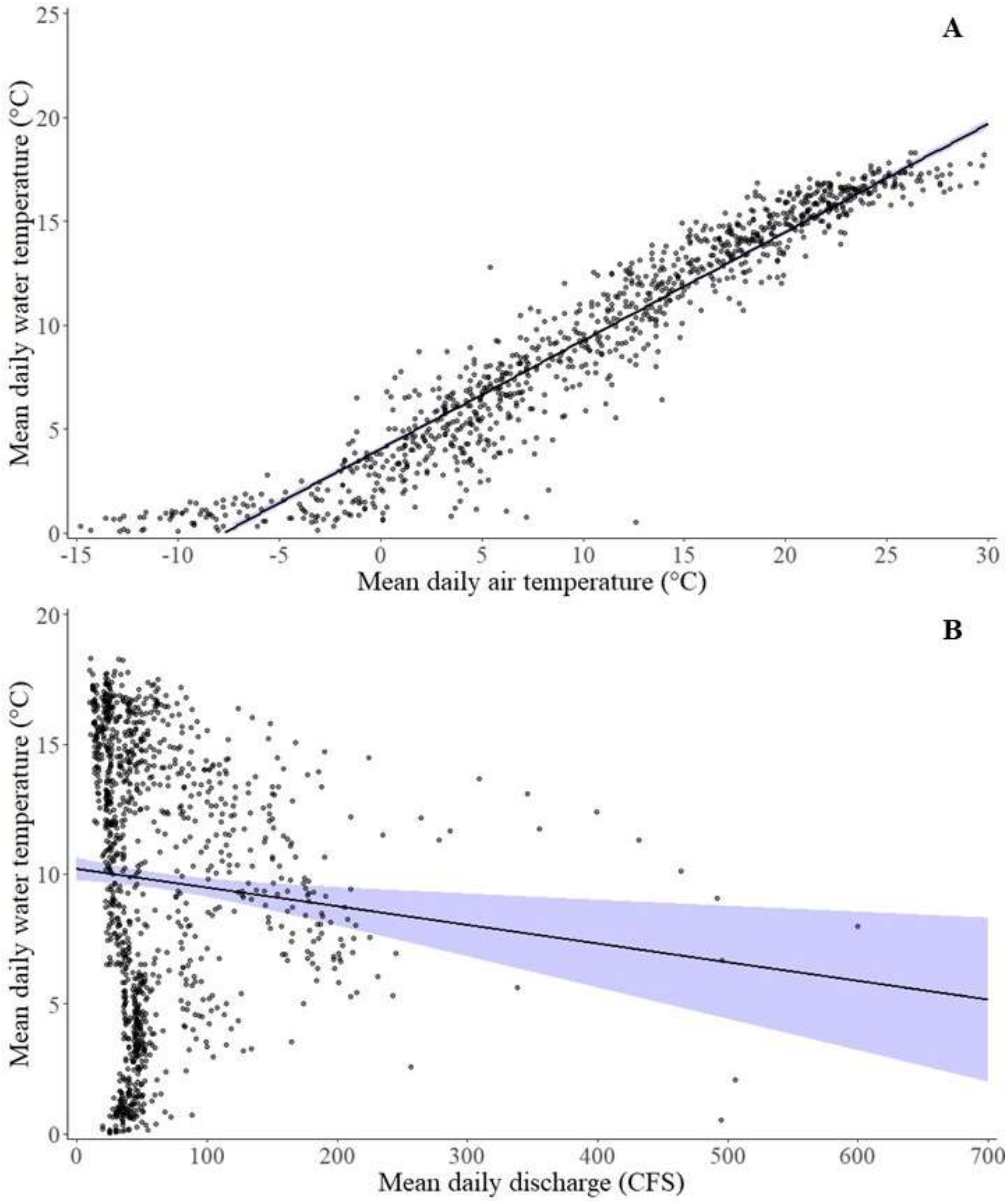


Figure 3.8. Little Prickly Pear Creek stream temperatures as a function of A) air temperatures and B) stream discharges. Data collected from 2000 to 2006; only data from March through November were included for analysis. Solid black lines are linear regression predictions. Gray bands represent 95% confidence intervals of the linear regression models. Black dots represent raw data.

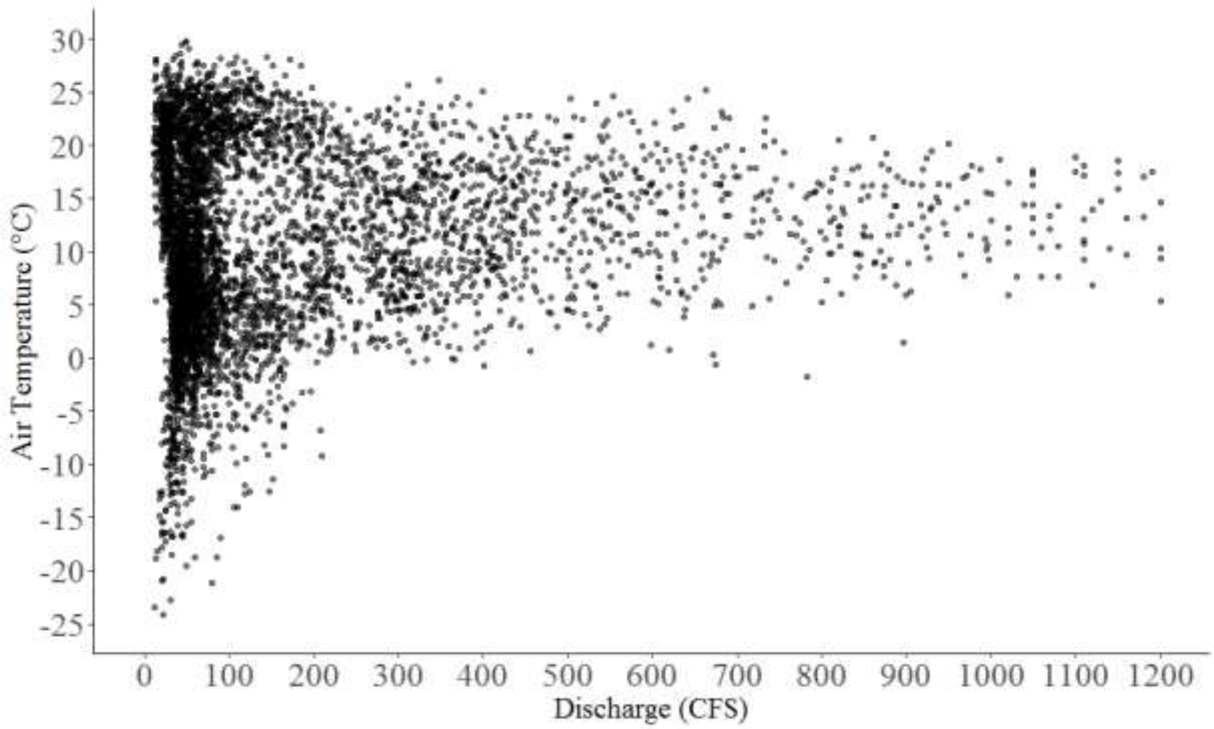


Figure 3.9. The relationship between Dearborn River discharge (USGS site 06073500; USGS 2019) and Helena, Montana mean daily air temperature.

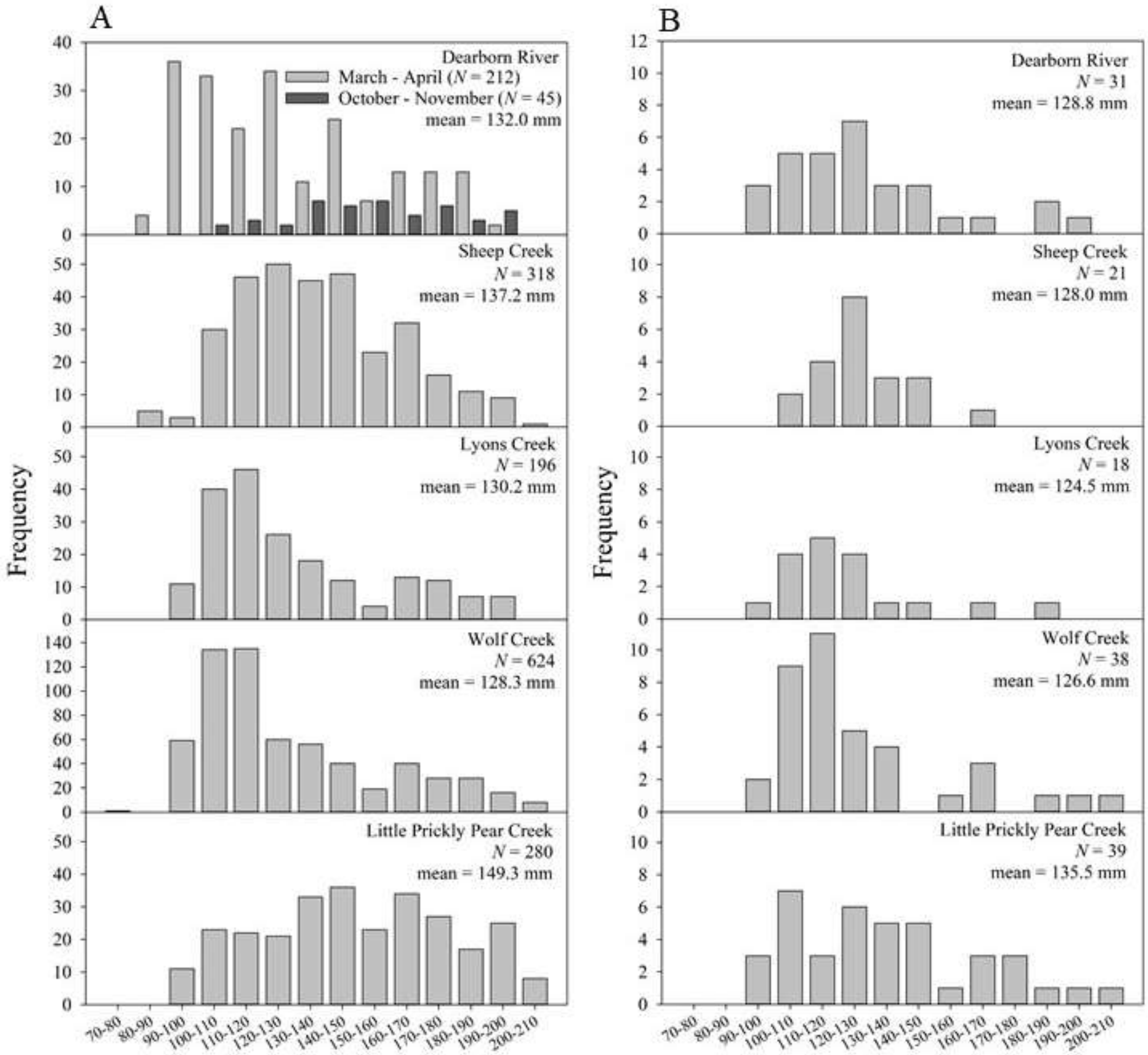


Figure 3.10. Length-frequency distributions of juvenile rainbow trout (TL < 201 mm) tagged in (A) and outmigrated from (B) upper Missouri River tributaries in 2014. Except for 45 individuals tagged in the Dearborn River, all juvenile rainbow trout were tagged from March to May of 2014.

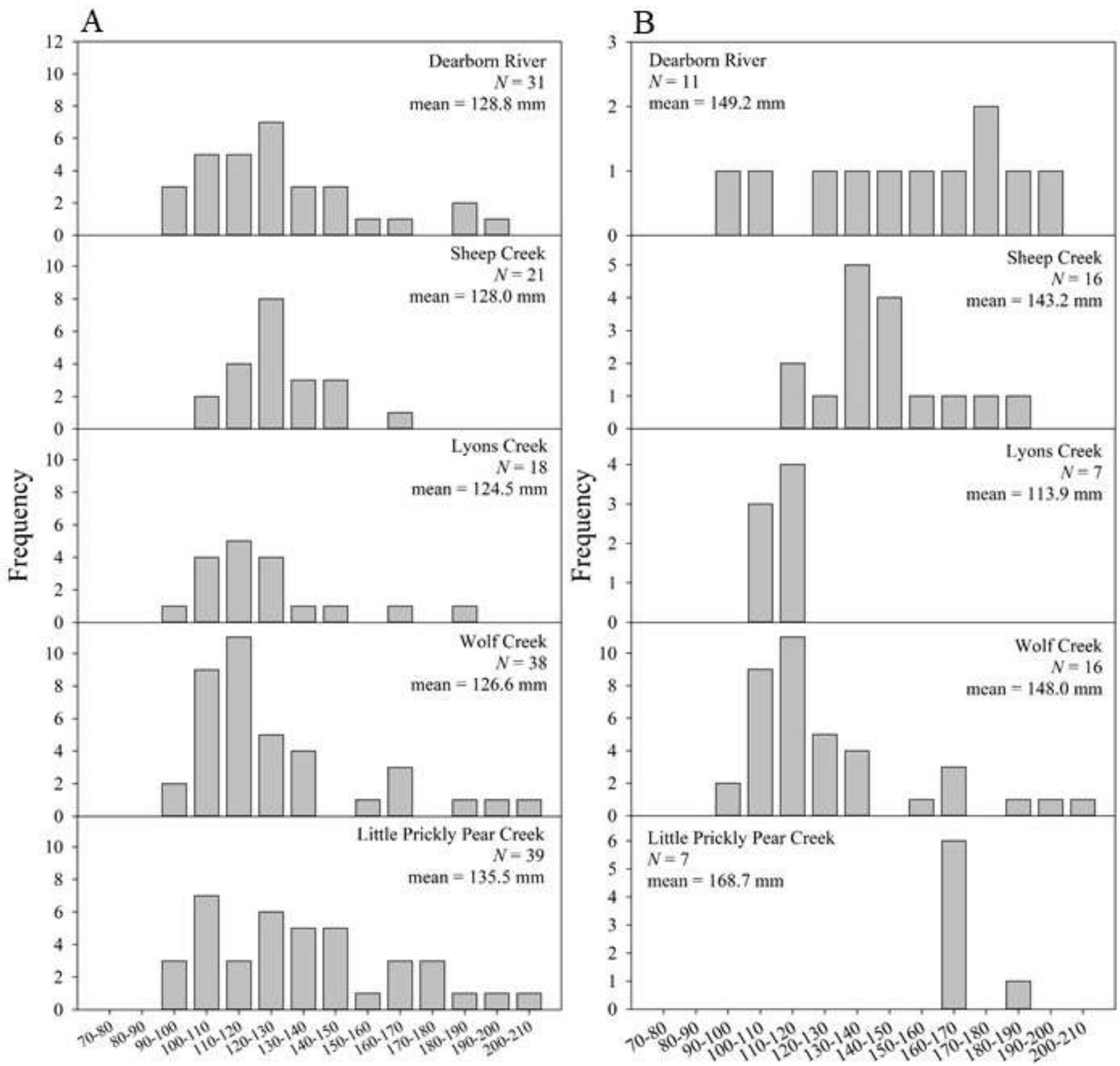


Figure 3.11. Length-frequency distributions of juvenile rainbow trout documented outmigrating from upper Missouri River tributaries in 2014 (A) and 2015 (B).

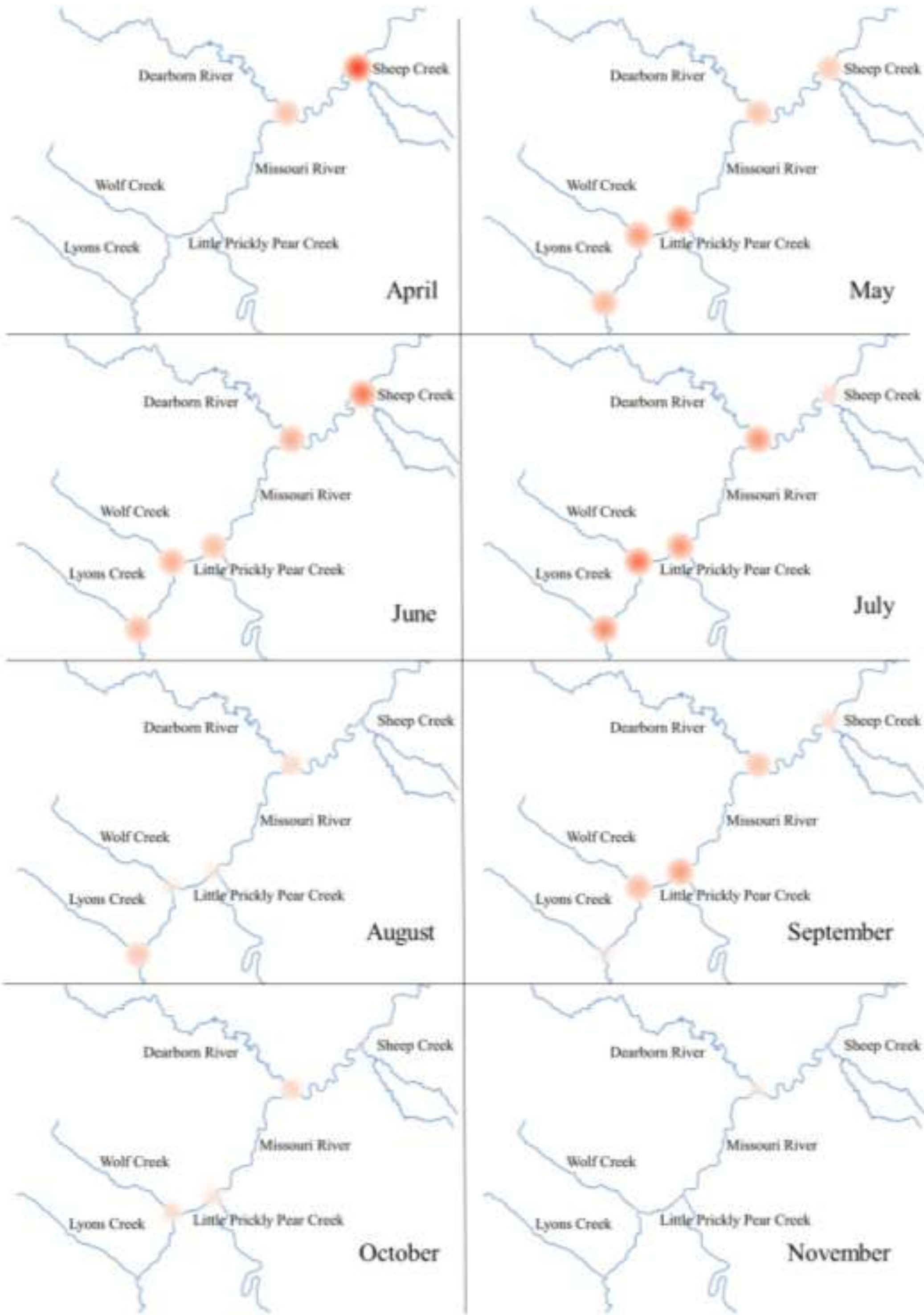


Figure 3.12. Outmigration pulses of tagged juvenile rainbow trout by month out of upper Missouri River tributaries in 2014. Red dots represent the proportion of fish that outmigrated that month for each tributary. The darker the gradient, the higher the proportion.

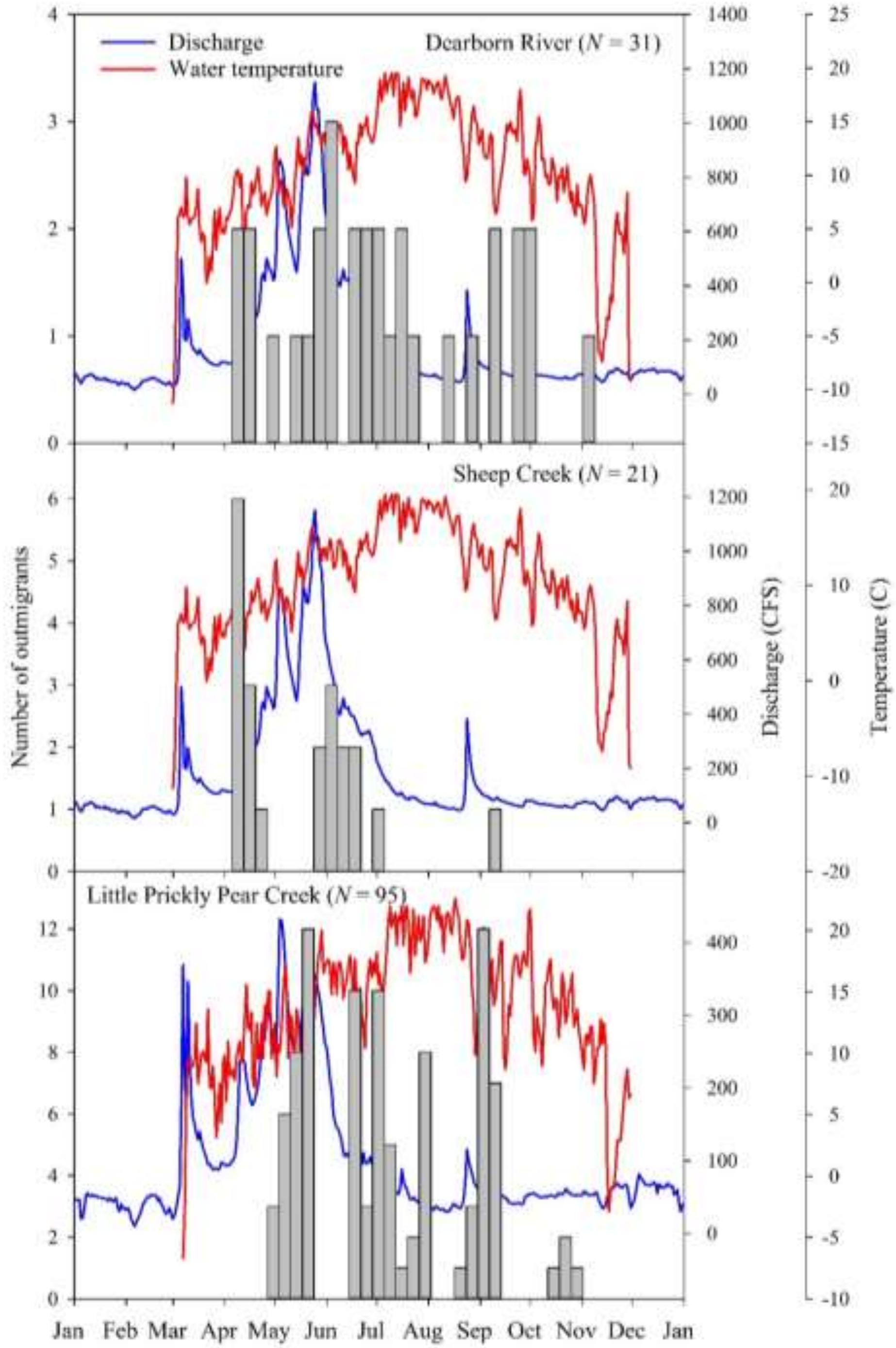


Figure 3.13. Weekly outmigration of tagged juvenile rainbow trout out of the Dearborn River, Sheep Creek, and Little Prickly Pear Creek in 2014. Number of outmigrants out of Little Prickly Pear Creek include all fish tagged upstream in Lyons Creek, Wolf Creek, and Little Prickly Pear Creek. The solid blue line represents daily discharge collected at USGS gaging stations at Little Prickly Pear Creek (USGS site 06071300; 2019) and the Dearborn River (USGS site 06073500; 2019). The red lines represent estimated Dearborn River and Little Prickly Pear Creek water temperatures. Discharge and temperature data for the Dearborn River were used as surrogates for Sheep Creek because data were not available.

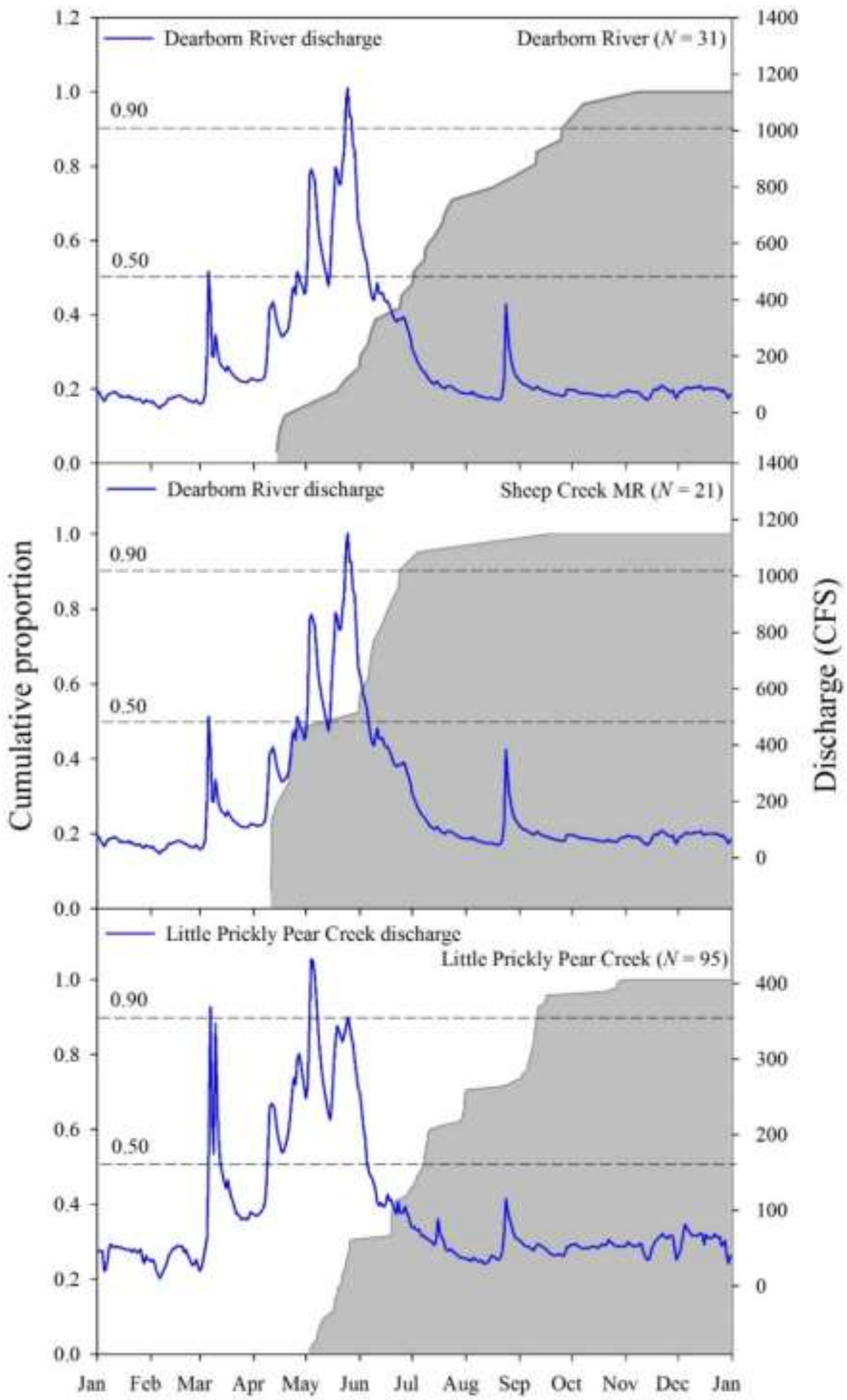


Figure 3.14. Cumulative proportion of all juvenile rainbow trout that outmigrated into the Missouri River after being tagged in the Dearborn River, Sheep Creek, and Little Prickly Pear Creek and its tributaries Lyons Creek and Wolf Creek in 2014. The solid blue line represents daily discharge collected at USGS gaging stations at Little Prickly Pear Creek (USGS site 06071300; 2019) and the Dearborn River (USGS site 06073500; 2019).

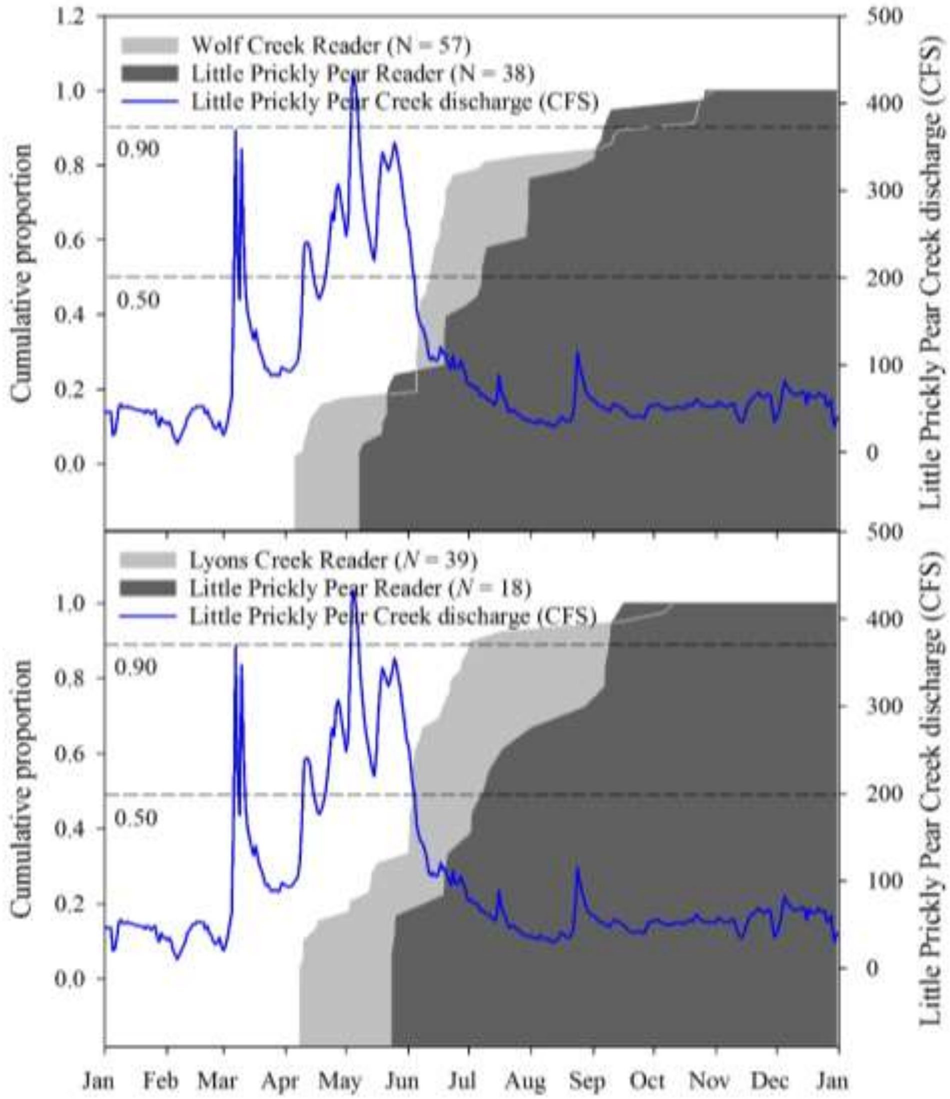


Figure 3.15. Cumulative proportion of all juvenile rainbow trout that outmigrated from Wolf Creek and Lyons Creek into Little Prickly Pear Creek and then entered the Missouri River. Gray areas represent the cumulative proportion of fish outmigrating from either Wolf Creek or Lyons Creek and dark areas represent the cumulative proportion of those same fish outmigrating from Little Prickly Pear Creek into the Missouri River. The solid blue line represents daily discharge collected at the USGS gaging station on Little Prickly Pear Creek (USGS site 06071300; 2019).

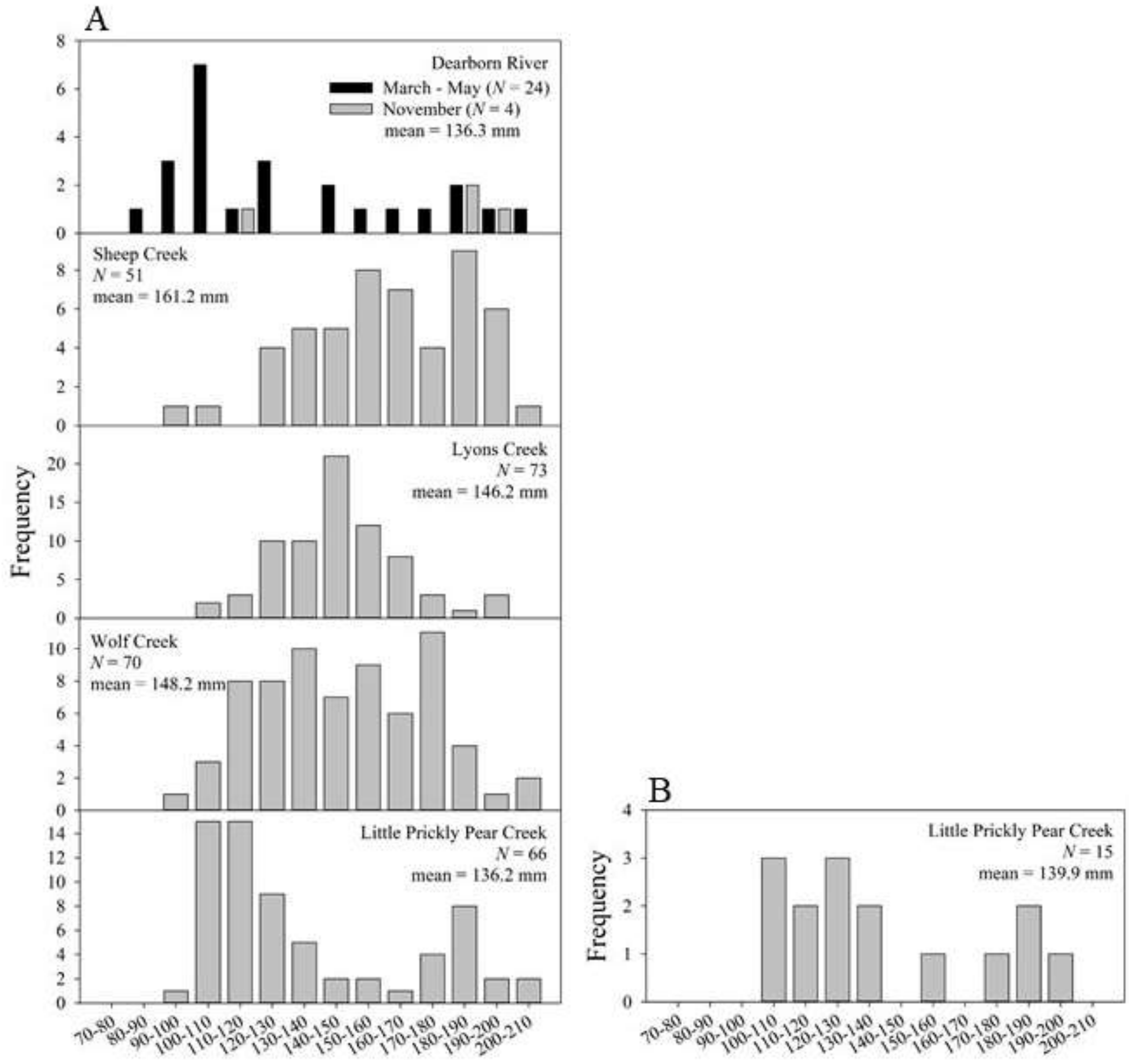


Figure 3.16. Length-frequencies distributions of juvenile brown trout (TL < 201 mm) tagged in (A) and outmigrated from (B) upper Missouri River tributaries in 2014. Except for 4 individuals tagged in the Dearborn River, all juvenile brown trout were tagged from March to May of 2014. Too few brown trout were documented outmigrating from the Dearborn River, Sheep Creek, Lyons Creek, and Wolf Creek to display length-frequency distributions.

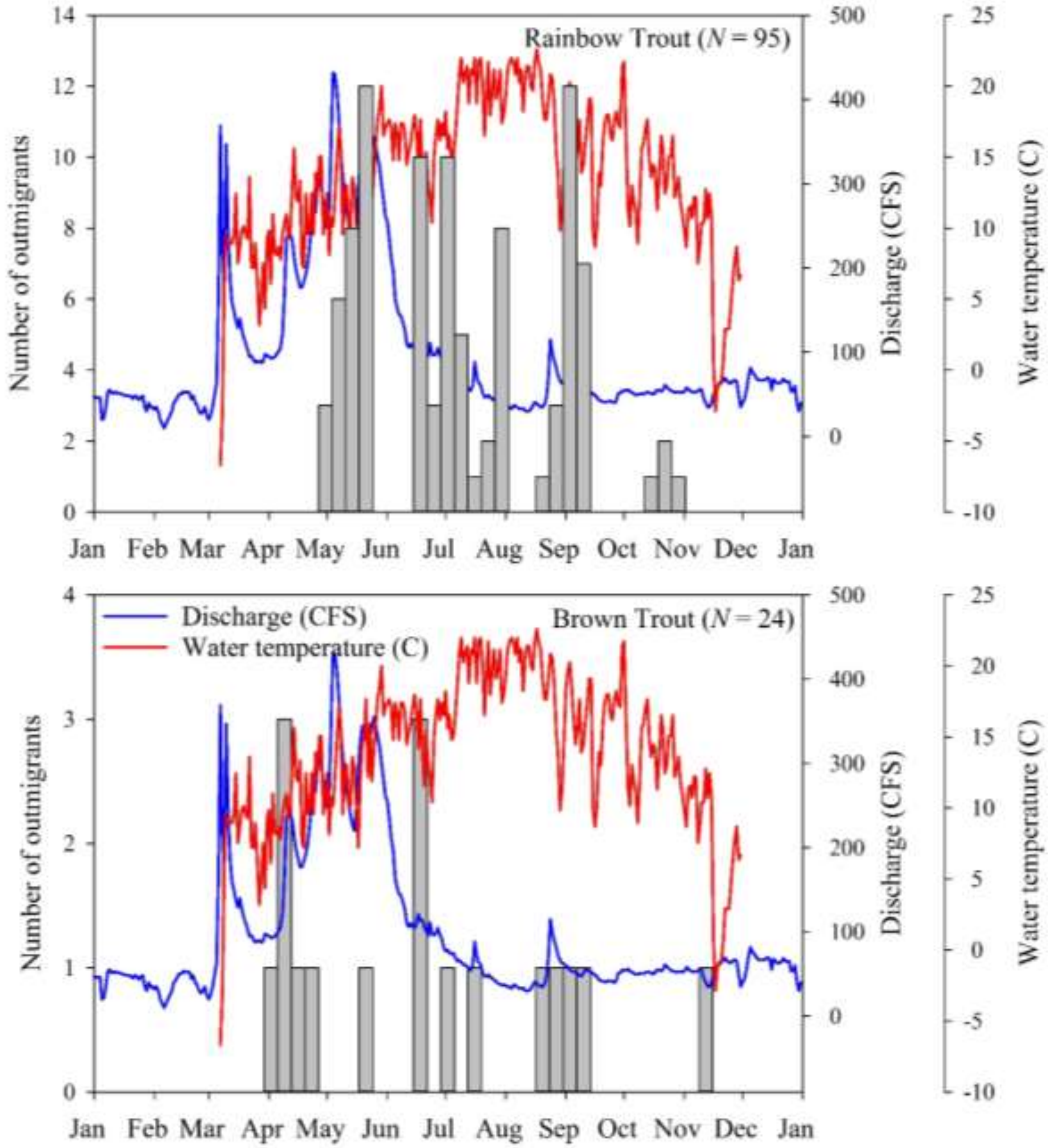


Figure 3.17. Weekly outmigration of rainbow trout and brown trout tagged in Little Prickly Pear Creek and its tributaries Lyons Creek and Wolf Creek into the Missouri River in 2014. The solid blue line represents daily discharge collected at the USGS gaging station on Little Prickly Pear Creek (USGS site 06071300; 2019). The red line represents estimated Little Prickly Pear Creek water temperatures.

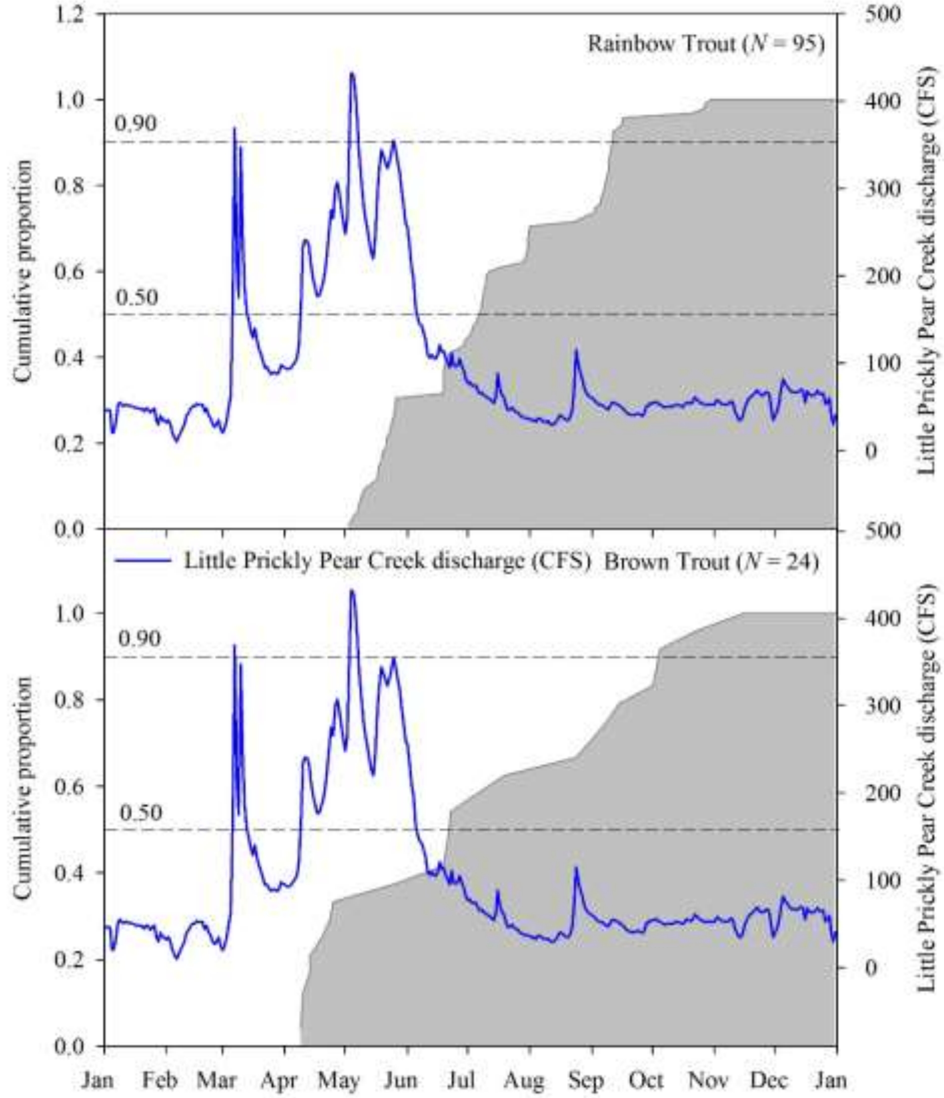


Figure 3.18. Cumulative proportion of juvenile rainbow trout and brown trout that outmigrated from Little Prickly Pear Creek and its tributaries into the Missouri River. The solid blue line represents daily discharge collected at the USGS gaging station on Little Prickly Pear Creek (USGS site 06071300; 2019).

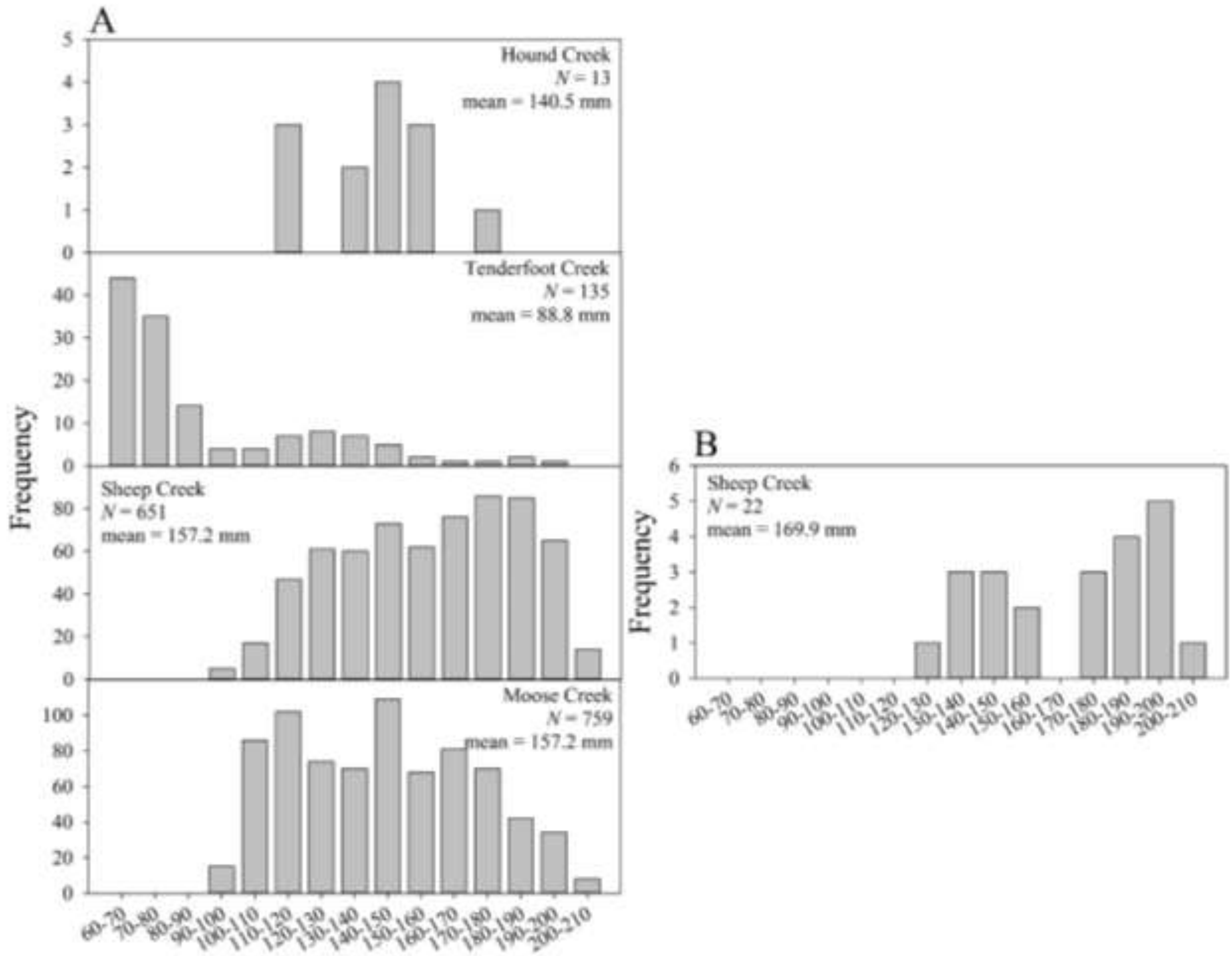


Figure 3.19. Length-frequency distributions of juvenile rainbow trout (TL < 201 mm) tagged in Smith River tributaries in 2014 (A) and outmigrated from Smith River tributaries in 2015 (B). Too few fish were detected outmigrating from Hound, Tenderfoot, and Moose creeks in 2015 to provide length-frequency distributions.

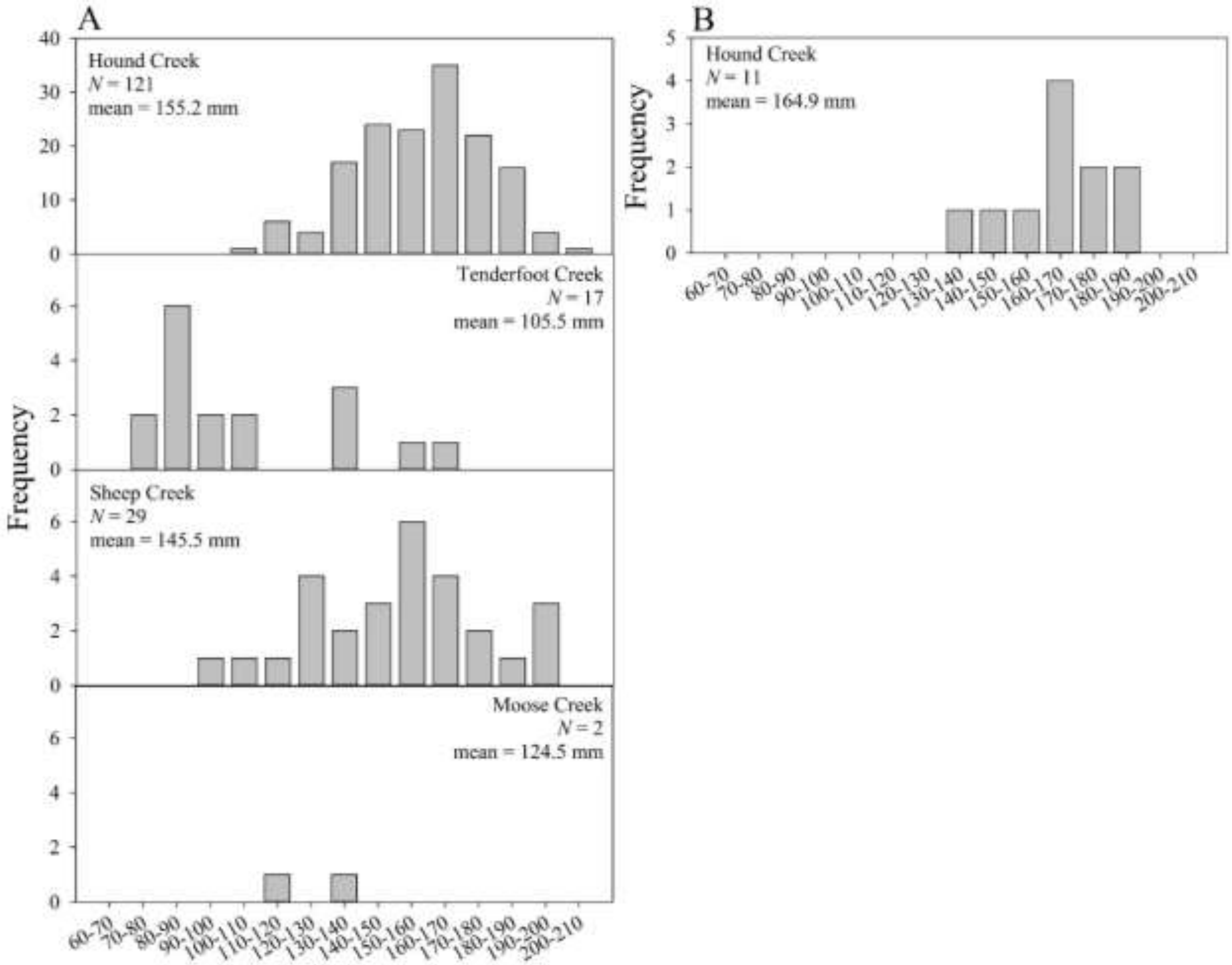


Figure 3.20. Length-frequency distributions of juvenile brown trout (TL < 201 mm) tagged in Smith River tributaries in 2014 (A) and outmigrated from Smith River tributaries in 2015 (B). Too few fish were detected outmigrating from Tenderfoot, Sheep, and Moose creeks in 2015 to provide length-frequency distributions.

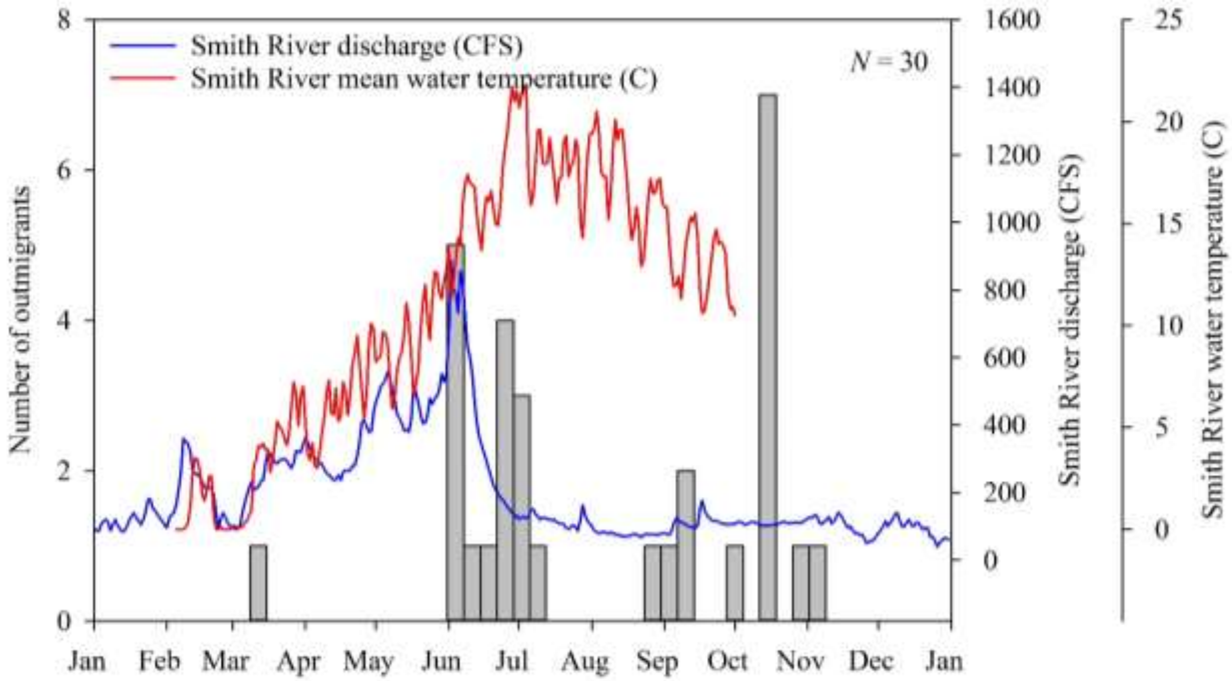


Figure 3.21. Weekly outmigration in 2015 of juvenile rainbow trout tagged in Moose and Sheep creeks in 2014. The solid red line represents mean daily water temperature of the Smith River whereas the solid blue line represents daily discharge. Water temperature and discharge data was collected at the USGS gaging station just below Eagle Creek (USGS site 06077200; 2019).

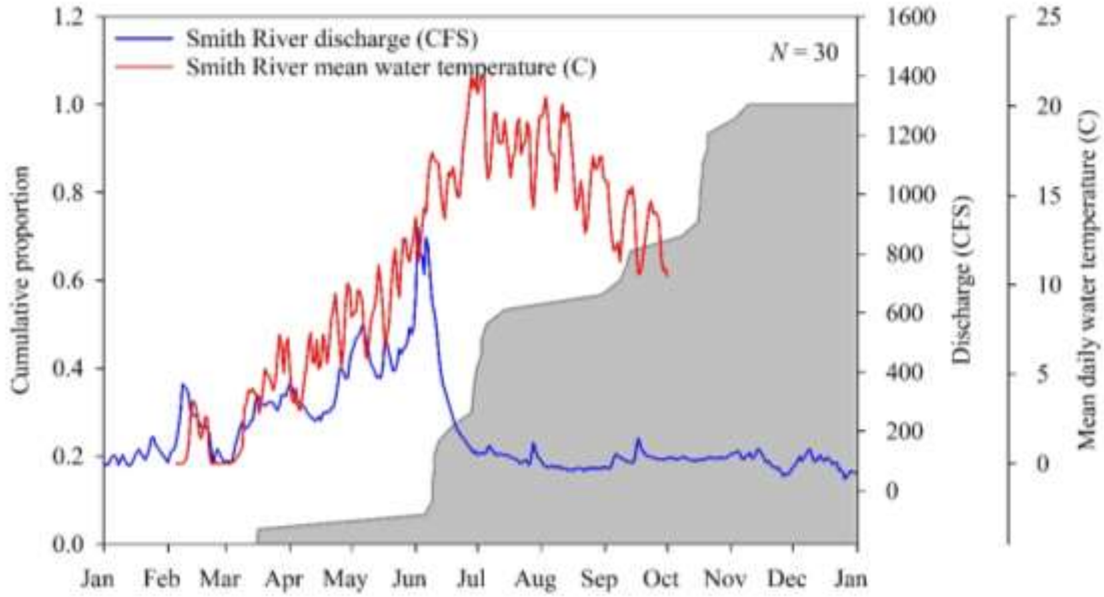


Figure 3.22. Cumulative proportion of juvenile rainbow trout that outmigrated from Moose and Sheep creeks into the Smith River in 2015. The solid red line represents mean daily water temperature of the Smith River whereas the solid blue line represents daily discharge. Water temperature and discharge data was collected at the USGS gaging station just below Eagle Creek (USGS site 06077200; 2019).

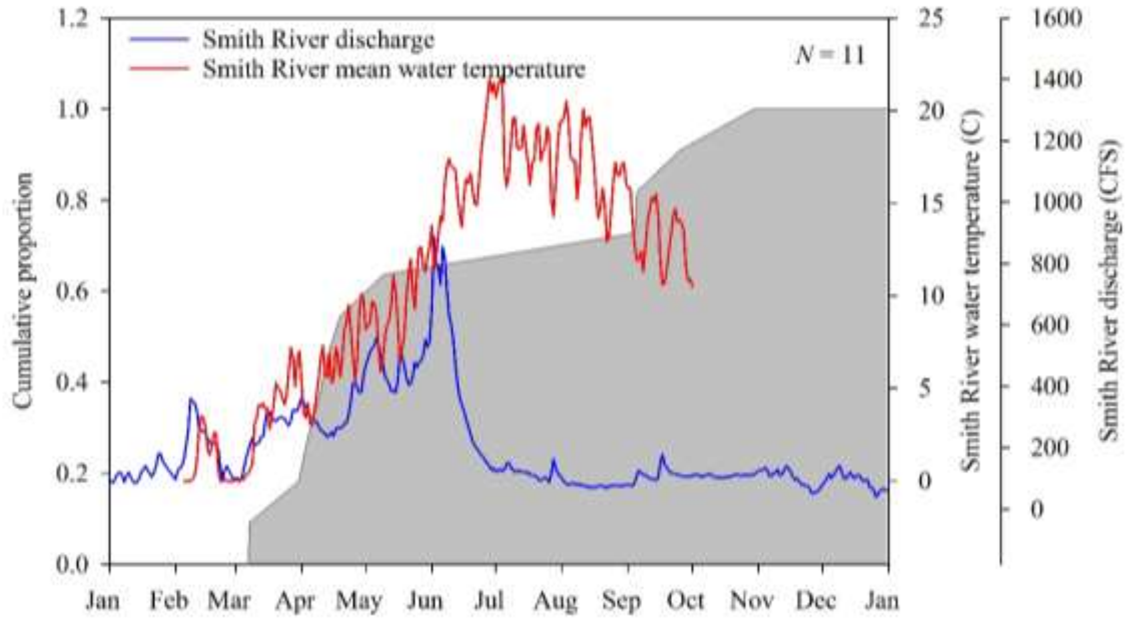


Figure 3.23. Cumulative proportion of juvenile brown trout that outmigrated from Hound Creek into the Smith River in 2015. The solid red line represents mean daily water temperature of the Smith River whereas the solid blue line represents daily discharge. Water temperature and discharge data was collected at the USGS gaging station on the Smith River near Eden, Montana (USGS site 06077500; 2019).

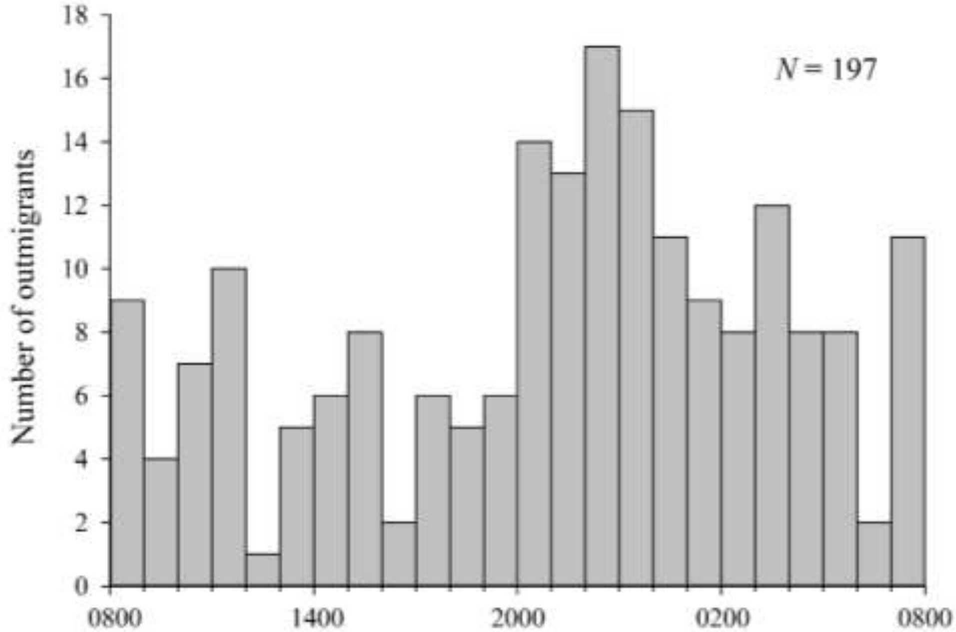


Figure 3.24. Diel timing of outmigration of brown trout and rainbow trout from tributaries in the upper Missouri River subbasin (Dearborn River, Little Prickly Pear Creek, Lyons Creek, Wolf Creek, and Sheep Creek) in 2014 and Smith River subbasin (Sheep Creek, Moose Creek, and Hound Creek) in 2015.

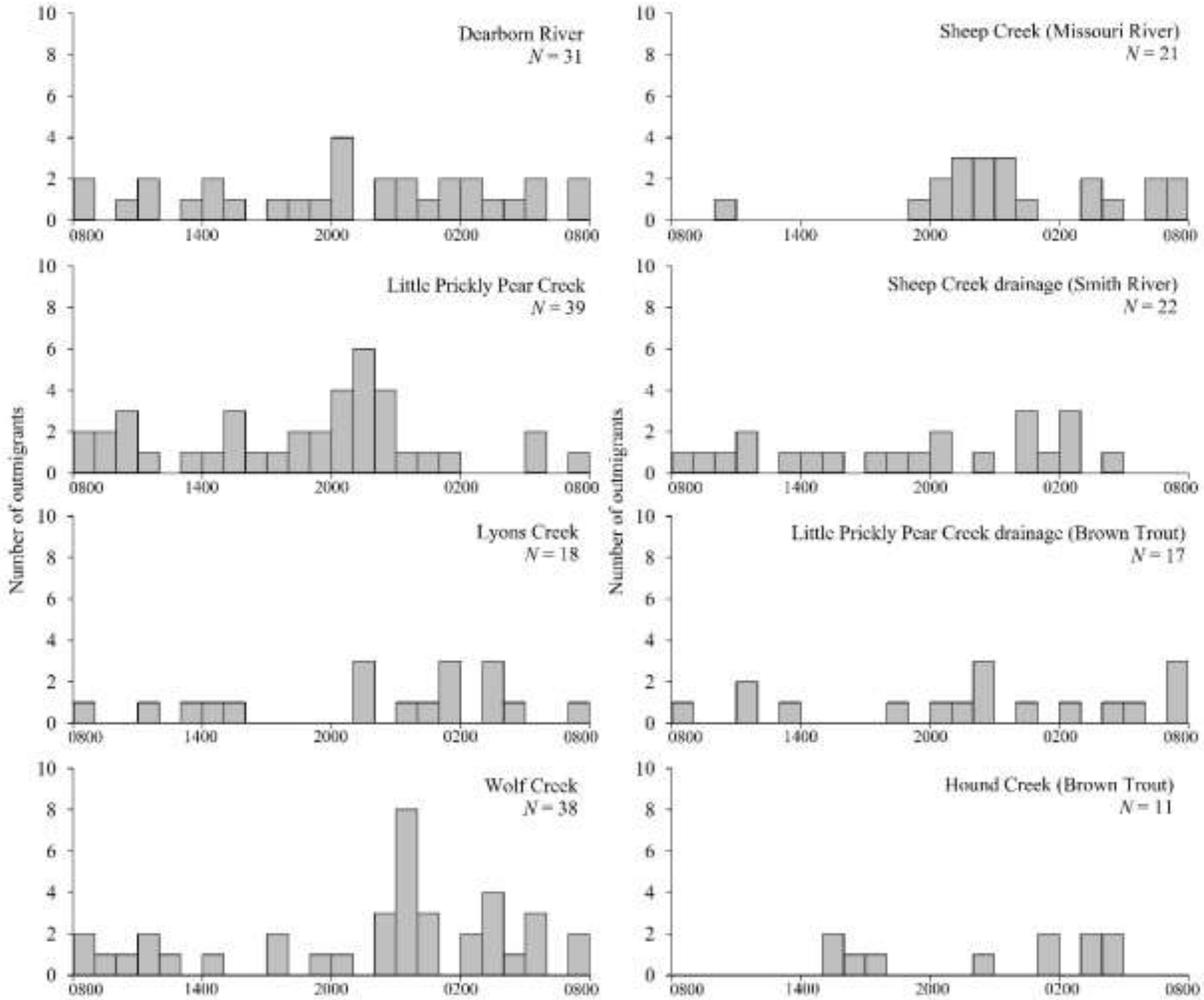


Figure 3.25. Diel timing of rainbow trout and brown trout in each Missouri River tributary in 2014 and each Smith River tributary in 2015. Graphs depict outmigration of rainbow trout unless otherwise specified.

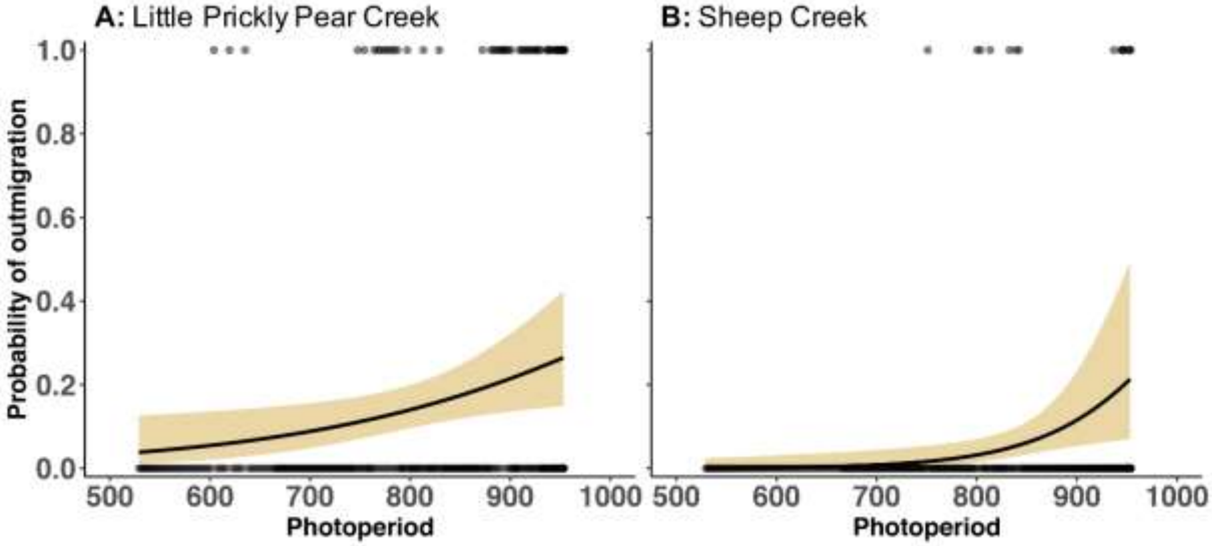


Figure 3.26. Influence of photoperiod on the probability of outmigration of rainbow trout out of Little Prickly Pear Creek (A) and Sheep Creek (B).

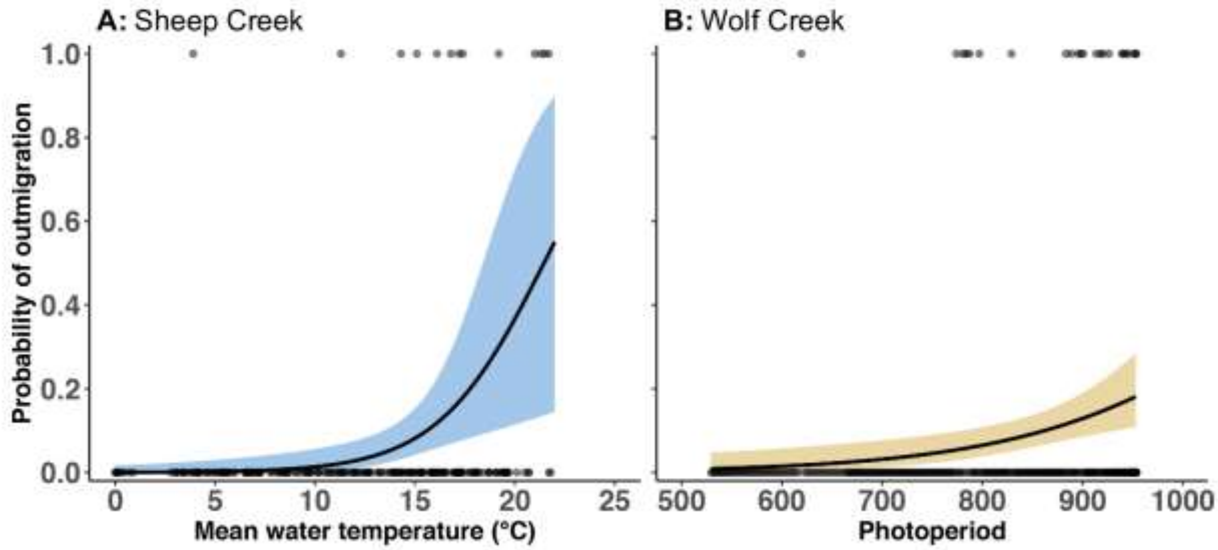


Figure 3.27. Influence of mean water temperature on probability of rainbow trout outmigrating from Sheep Creek, Smith River (A) and influence of photoperiod on probability of rainbow trout outmigrating from Wolf Creek, Missouri River (B).

CHAPTER FOUR

GROWTH RATES AND AGE STRUCTURES OF SALMONIDS IN THE UPPER MISSOURI RIVER, SUN RIVER, AND SMITH RIVER

Introduction

Understanding age structure and growth patterns in salmonid populations is necessary for making sound management decisions but difficult when diverse life history patterns are present (Al-Chokachy and Budy 2008; Homel and Budy 2008). In the upper Missouri River, annual trout age studies were conducted for a 30-year period from 1981 to 2012 to evaluate and predict year-class strengths using scale patterns (Grisak et al. 2015). However, variability in life history aspects, particularly outmigration, may have produced variation in scale annulus formation and inconsistent results (Grisak et al. 2015).

Known-age fish would provide a standard to evaluate historical studies and insights into current population structures. We used a combination of PIT telemetry and physical recaptures to determine growth rates and age structures of rainbow trout, brown trout, and mountain whitefish in the upper Missouri, Sun, and Smith rivers. Our objective was to compare growth rates and age structures among upper Missouri River, Sun River, and Smith River salmonid populations, and evaluate accuracy of previous age and growth methodologies.

Methods

PIT-tagging

A total of 11,936 fish was tagged in the upper Missouri River basin from 2010 to 2019; 3,572 in the upper Missouri River subbasin (Table 4.1), 739 in the Sun River subbasin (Table 4.2), and 7,625 in the Smith River subbasin (Table 4.3). From 2010 to 2012, 777 fish were tagged as part of a Montana State University graduate study investigating Tenderfoot Creek, a major tributary of the Smith River (Ritter 2015). Most of these fish were likely not present from 2014 to 2019; however, some fish tagged in 2012 were active until at least 2018 (Mullen and Vivian 2019).

Fish were collected with boat, barge, and backpack electrofishers, and fyke nets, anesthesized with Aqui-S 20E (Aqui-S New Zealand Ltd.; 10 to 20 mg/L) or MS-222 (tricaine methanesulfonate; 50 mg/L), and implanted with HDX PIT tags. Location, species, and total length (TL) were recorded for each fish at the time of tagging; 20% (2,389 of 11,936) were also weighed. The date when a fish was collected and tagged was recorded as the first observation for each individual. PIT tags were surgically implanted into the abdominal cavity through small incisions made by a small scalpel coated with antiseptic. Most fish were tagged with 23 or 32-mm HDX PIT tags; a small number of fish (217 of 11,936) were tagged with 12-mm HDX PIT tags. Lengths and weights of recaptured fish were also recorded to investigate age and growth.

<u>Monitoring fish movement</u>

A network of 23 stationary PIT arrays monitored the movements of PIT-tagged fish throughout the upper Missouri River basin (Table 4.4 and Figure 4.1). Five arrays were installed in the upper Missouri River subbasins in the spring of 2014, three arrays were installed in the Sun River subbasin in the spring of 2015, and 15 arrays were installed in the Smith River subbasin from 2014 to 2016 (Table 4.4 and Figure 4.1). These monitoring stations ran in some combination from 2010 to 2019 (Figure 4.2). The Dearborn River, Little Prickly Pear Creek, Truly Bridge, and Hound Creek arrays were damaged by flows in the spring and early summer of 2018. All but Truly Bridge were repaired and reinstalled. Five stations were operated in Tenderfoot Creek from 2010 to 2014, but only one array installed at the mouth of Tenderfoot Creek was maintained after 2013 (Table 4.4 and Figure 4.1; Ritter 2015). Age and growth analyses used data collected prior to 2014 and afterward, but all other analyses were restricted to data collected after 2013.

Antenna stations consisted of a PIT-tag reader (Oregon RFID, multi-antenna HDX reader and long-range HDX reader, Portland, Oregon), one to two stream-width antennas, and a tuning board for each antenna (Oregon RFID, standard remote tuner board and long-range tuner board, Portland, Oregon). Antenna arrays were powered by 12-V DC supplied by either solar panels or 120-V AC converters. Antennas were placed in areas where fish would unlikely stay for long periods of time (e.g., riffles and shallow water habitat) to prevent many consecutive detections and to monitor interchange between mainstem river and tributaries (rather than localized use near the antennas). All antennas were oriented flat on the bottom (swim over or flat-bed design; Armstrong et al. 1996) and tuned to best possible vertical read ranges for tags oriented perpendicularly to the antennas.

Mobile PIT arrays were used to actively monitor fish movements and complement the network of fixed monitoring stations. Mobile tracking was conducted using raft, kayak, and pole-mounted antennas (Hill et al. 2006; McKinstry and Mackinnon 2011); methods are explained in detail by Lance 2019. In the upper Missouri Sun rivers, mobile tracking by raft and kayak was conducted in 2015 and 2016 but discontinued thereafter because of low detection range. A pole-mounted antenna was used in 2016 to scan tributaries and islands of the upper Missouri River and American white pelican *Pelecanus erythrorhynchus* nesting islands in Canyon Ferry and Arod Lake (Vivian and Mullen 2018). In the Smith River, all forms of mobile tracking were used to track fish from 2015 to 2017 (Lance 2019). No mobile tracking was conducted from 2018 onward.

<u>Data analysis</u>

In addition to physical recapture events, we used detection intervals to investigate longevity of rainbow trout, brown trout, and mountain whitefish in all subbasins. Detection intervals were calculated using the initial date of detection and final date of detection collected by fixed PIT array, mobile tracking, or physical recapture events. We also plotted distributions of length at tagging and detection interval associations to estimate observed longevities. For example, an individual detected after 4 years with an initial tagging length of 300 mm was likely older than an individual with the same detection interval but initial tagging length of 100 mm.

Growth rates of salmonids vary seasonally and by age, so comparisons should be interpreted with caution. Intervals between capture events varied and often exceeded one year, frequently encompassing differing numbers of growing seasons. Moreover, in the upper Missouri River subbasin, our yearly means were calculated over an average of 3.5 years and probably not representative of age-specific yearly growth. For example, rainbow trout captured in the Dog Creek subwatershed (Montana Fish, Wildlife & Parks Cascade sampling section) by Grisak et al. (2015) exhibited mean yearly growth from age-1 to age-2 of 99 mm (3.9”), whereas mean yearly growth from age-3 to age-4 was 48 mm (1.9”). Even so, some comparisons were made by calculating yearly growth rates over similar intervals using those determined by Grisak et al. (2015).

We used box and whisker plots and growth curves as graphical representations of growth rate comparisons. We used t-tests to compare annual growth rates within species between subbasins and Kruskal-Wallis one-way ANOVAs to compare growth rates of brown trout among subbasins and growth rates of all species combined among subbasins. Unfortunately, too few individuals were collected for reliable comparisons of growth rates between fish tagged in the mainstem and tributaries so lengths at tagging were compared by location instead. Outliers (negative values and values exceeding 200 mm annually), presumably a result of discrepancies in field measurements or data entry, were excluded from both analyses and graphical representations. The statistical software programs R (v4.0.2; R Core Team 2019) and SigmaPlot 14 (SigmaPlot 2017) were used for analyzing and plotting trends and comparisons in outmigration timing and magnitude.

Results

Upper Missouri River subbasin

All species of fish tagged in the mainstem were larger than those tagged in tributaries ($p = 0.001$).

Rainbow trout

Most rainbow trout tagged in the upper Missouri River and its tributaries were smaller than 240 mm (9.5”); mean length was 177 mm (7.0”; Figure 4.3). Tagging lengths ranged from

76 mm (3.0”) to 511 mm (20.1”; Figure 4.3). Mean relative weight of the five fish captured and weighed was 95.7 (Table 4.5).

The mean time interval between the date tagged and date of last detection of the 713 redetected rainbow trout was 1.4 years and reached 5.2 years (Figure 4.4). All rainbow trout redetected for at least 3 years had a tagging length less than 300 mm (11.8”; Figure 4.5). However, there were five rainbow trout redetected after 2.5 years that had tagging lengths greater than 400 mm (15.7”; Figure 4.5).

Seven rainbow trout tagged in the upper Missouri River subbasin were recaptured, measured, and weighed (Table 4.6). Intervals between initial tagging date and date of recapture ranged from 3.4 to 4.5 years. Rainbow trout collected by Grisak et al. (2015) in the Dog Creek subwatershed had an average yearly growth of 87 mm (3.4”) from age-0 to age-3 over the 30-year study period, whereas we observed an average yearly growth rate of 71 mm (2.8”) over an average interval of 3.5 years and ranged from 43 mm/year (1.7 inches/year) to 102 mm/year (4.0 inches/year; Table 4.6 and Figure 4.6). Mean yearly growth rate of brown trout from age-1 to age-4 determined by Grisak et al. (2015) was higher than what we observed (99 mm/year compared to 88 mm/year, respectively). Yearly and overall growth rates appeared higher in the Missouri River than those observed in the Smith River (Figures 4.6 and 4.7), but differences in yearly growth rates were not statistically significant (P = 0.15).

Brown trout

Most brown trout tagged in the upper Missouri River and its tributaries were smaller than 240 mm (9.5”); mean length was 205 mm (8.1”; Figure 4.3). Tagging lengths ranged from 76 mm (3.0”) to 508 mm (20.”; Figure 4.3). Mean relative weight of the 11 fish captured and weighed was 96.3 (Table 4.5).

The mean time interval between the date tagged and date of last detection of the 124 redetected brown trout was 1.7 years and reached 6.0 years (Figure 4.4). Two brown trout redetected after at least 5 years had tagging lengths greater than 240 mm (9.4”; Figure 4.5). A brown trout measuring 107 mm (4.2”) at tagging had the longest interval between tagging and last detection (6.0 years) of any fish of any species tagged in the upper Missouri River (Figure 4.5). The last detection of this fish was a recapture during annual population sampling (rather than a detection on a fixed PIT antenna).

Six brown trout tagged in the upper Missouri River subbasin were recaptured, measured, and weighed (Table 4.6). Three individuals were recaptured twice and one individual was recaptured three times (Table 4.6). Intervals between initial tagging date and date of recapture ranged from 0.8 to 4.0 years (Table 4.6). Yearly growth had a mean of 54 mm/year (2.1 inches/year) and ranged from 7 mm/year (0.3 inches/year) to 104 mm/year (4.1 inches/year; Table 4.6 and Figure 4.6). Mean yearly growth of initial recaptures was 88 mm/year (3.5”/year) and ranged from 69 mm/year (2.7”/year) to 104 mm/year (4.1”/year). Yearly and overall growth rates appeared higher in the Missouri River than those observed in the Sun and Smith rivers (Figures 4.6 and 4.7), but differences in yearly growth rates were not statistically significant (P = 0.111).

Mountain whitefish

Most mountain whitefish tagged in the upper Missouri River and its tributaries were larger than 300 mm (11.8”); mean length was 377 mm (14.8”; Figure 4.3). Tagging lengths ranged from 127 mm (5.0”) to 506 mm (19.9”; Figure 4.3). No mountain whitefish were captured and weighed in the upper Missouri River.

The time interval between the date tagged and date of last detection of the 81 redetected mountain whitefish had a mean of 1.4 years and maximum of 4.1 years (Figure 4.4). Only one mountain whitefish was redetected after four years, but this individual had a tagging length of 363 mm (14.3”; Figure 4.5). Half of the eight mountain whitefish were redetected after at least three years and had tagging lengths greater than 400 mm (15.7”; Figure 4.5). All but four mountain whitefish redetected in the upper Missouri River had tagging lengths greater than 300 mm (11.8”; Figure 4.5).

Sun River

Combined yearly growth rates of all species were lower than those of the upper Missouri and Smith River subbasins ($p = 0.005$).

Rainbow trout

The size distribution of rainbow trout tagged in the Sun River was mostly normal; mean length was 315 mm (12.4”; Figure 4.8). Tagging lengths ranged from 135 mm (5.3”) to 541 mm (21.3”; Figure 4.8). No rainbow trout were captured and weighed in the Sun River.

The mean time interval between the date tagged and date of last detection of the 31 redetected rainbow trout was 0.6 years and reached 3.0 years (Figure 4.4). Only one individual was redetected after 3 years and had a tagging length of 333 mm (13.1”; Figure 4.5). Only three rainbow trout were redetected after at least two years, but all had tagging lengths greater than 300 mm (11.8”; Figure 4.5).

Brown trout

Most brown trout tagged in the Sun River were larger than 300 mm (11.8”); mean length was 340 mm (13.4”; Figure 4.8). Tagging lengths ranged from 125 mm (4.9”) to 528 mm (20.8”; Figure 4.8). Mean relative weight of the five fish captured and weighed was 88.0 (Table 4.5).

The time interval between the date tagged and date of last detection of the 72 redetected brown trout had a mean of 1.3 years and maximum of 5.1 years (Figure 4.4). Most brown trout were redetected after 3.2 years or less; the five brown trout redetected after at least four years were recaptured during annual population sampling (rather than detected on PIT antennas). These individuals had tagging lengths ranging from 259 mm (10.2”) to 447 mm (17.3”) and were the only fish measured and weighed (Table 4.6). Yearly growth rates had a mean of 23.4 mm/year (0.9 inches/year) and ranged from 11 mm/year (0.4 inches/year) to 46 mm/year (1.8 inches/year; Table 4.6 and Figure 4.6). Yearly growth rates appeared lower than those observed in the upper Missouri River and Smith River (Figure 4.6). Overall growth rates of brown trout with similar tagging lengths also appeared lower than those observed in the other subbasins (Figure 4.7).

Mountain whitefish

The size distribution of mountain whitefish tagged in the Sun River was mostly normal; mean length was 318 mm (12.5”; Figure 4.8). Tagging lengths ranged from 165 mm (6.5”) to 472 mm (18.6”; Figure 4.8). Mean relative weight of the three fish captured and weighed was 99.5 (Table 4.5).

The time interval between the date tagged and date of last detection of the 49 redetected mountain whitefish had a mean of 1.2 years and maximum of 4.1 years (Figure 4.4). Five mountain whitefish were redetected after at least 3 years and all had tagging lengths greater than 280 mm (11”). Two mountain whitefish were redetected after at least four years and had tagging lengths of 345 mm (13.6”) and 368 mm (14.5”; Table 4.6). Both individuals were recaptured during annual population sampling.

Three mountain whitefish tagged in the Sun River were recaptured, measured, and weighed (Table 4.6). Intervals between initial tagging date and date of recapture were 3.1, 4.0, and 4.1 years (Table 4.6). Yearly growths were 9 mm/year (0.4 inches/year), 11 mm/year (0.4 inches/year), and 16 mm/year (0.6 inches/year; Table 4.6 and Figure 4.6). Yearly and overall growth rates appeared similar to those observed in the Smith River (Figures 4.6 and 4.7; $P = 0.457$).

Smith River

Rainbow trout

Most rainbow trout tagged in Smith River tributaries were smaller than 240 mm (9.5”), whereas the opposite was true for fish tagged in the mainstem river (Figure 4.9). Mean length of all tagged rainbow trout was 210 mm (8.3”; Figure 4.9). Tagging lengths ranged from 46 mm (1.8”) to 511 mm (20.1”; Figure 4.9). Mean relative weight of the 606 fish captured and weighed was 91.6 (Table 4.5). Relative weight was highest in the South Fork Smith River watershed and was generally higher in upper (southernmost) watersheds (Figure 4.10).

The time interval between the date tagged and date of last detection of the 1,584 redetected rainbow trout had a mean of 1.6 years and maximum of 6.7 years (Figure 4.4). Three rainbow trout were redetected after at least 6 years (Figure 4.5). Of the ten rainbow trout redetected after at least five years, all but three had tagging lengths greater than 200 mm (Figure 4.5), and all were tagged in either 2010 or 2011 during the Tenderfoot Creek graduate study (Table 4.6).

One hundred and five rainbow trout tagged in the Smith River were recaptured, measured, and weighed (Table 4.6). Ten individuals were recaptured twice (Table 4.6). Intervals between initial tagging date and date of recapture had a mean of 1.2 years and ranged from 0.8 to 4.0 years (Table 4.6). Mean yearly growth was 55 mm/year (2.1 inches/year) and ranged from 0 mm/year (0.3 inches/year) to 217 mm/year (8.5 inches/year; Table 4.6 and Figure 4.6). Yearly growth rates appeared lower than those observed in the Missouri River (Figure 4.6).

Brown trout

Size distributions of brown trout tagged in tributaries and mainstem of the Smith River were mostly normal, although there were more brown trout less than 200 mm (7.9”) tagged in tributaries (Figure 4.9). Mean length of all tagged brown trout was 318 mm (12.5”; Figure 4.9). Tagging lengths ranged from 61 mm (2.4”) to 660 mm (26.0”; Figure 4.9). Mean relative weight of the 437 fish captured and weighed was 95.0 (Table 4.5). Relative weight was highest in the South Fork Smith River watershed and tended to be higher in upper (southernmost) watersheds (Figure 4.11).

The time interval between the date tagged and date of last detection of the 552 redetected brown trout had a mean of 1.3 years and maximum of 6.6 years (Figure 4.4). Four brown trout were redetected after at least five years; three of these individuals had tagging lengths greater than 400 mm (15.7”; Figure 4.5). One of these individuals was tagged in 2014, the other three were tagged in either 2010 or 2011 (Table 4.6).

Twenty-eight brown trout tagged in the Smith River were recaptured, measured, and weighed (Table 4.6). Four individuals were recaptured twice (Table 4.6). Intervals between initial tagging date and date of recapture had a mean of 1.2 years and ranged from 0.1 to 3.0 years (Table 4.6). Mean yearly growth was 82 mm/year (3.2 inches/year) and ranged from 0 mm/year to 191 mm/year (7.5 inches/year; Table 4.6 and Figure 4.6). Yearly growth rates appeared lower than those observed in the Missouri River (Figure 4.6).

Mountain whitefish

Size distributions of mountain whitefish tagged in tributaries and the mainstem of the Smith River were mostly normal, although there were more individuals less than 300 mm (11.8”) tagged in tributaries (Figure 4.9). Mean length of all tagged mountain whitefish was 300 mm (11.8”; Figure 4.9). Tagging lengths ranged from 76 mm (3.0”) to 597 mm (23.5”; Figure 4.9). Mean relative weight of the 1,132 fish captured and weighed was 99.1 (Table 4.5). Relative weight was highest in the Newlan Creek watershed and tended to be higher in upper (southernmost) watersheds (Figure 4.12).

The time interval between the date tagged and date of last detection of the 1,447 redetected mountain whitefish had a mean of 1.7 years and maximum of 7.3 years (Figure 4.9). Eight mountain whitefish were redetected after at least six years; all of these individuals had tagging lengths greater than 200 mm (7.9”) and were tagged in 2011 or 2012 (Figure 4.5). Two individuals were redetected after more than seven years; these fish had tagging lengths of 236 mm (9.3”) and 308 mm (12.1”) and were tagged in Tenderfoot Creek in 2012 (Table 4.6).

Twenty-one mountain whitefish tagged in the Smith River were recaptured, measured, and weighed (Table 4.6). One individual was recaptured twice (Table 4.6). Intervals between initial tagging date and date of recapture had a mean of 1.1 years and ranged from 0.1 to 2.5 years (Table 4.6). Mean yearly growth was 20 mm/year (0.8 inches/year) and ranged from 0 mm/year to 78 mm/year (3.1 inches/year; Table 4.6 and Figure 4.6). Yearly growth rates appeared lower than those observed in the Sun River (Figure 4.6).

Discussion and comparisons to previous studies

Calculation of growth rates and assessment of age structures were difficult because of variability in location data and intervals between physical recaptures and detections. Reported growth rates and ages are rough estimates without full knowledge of the life history of each recaptured and detected individual. We make comparisons to previous studies, but proper evaluation of the methodologies used therein was not possible.

Growth rates observed by Grisak et al. (2015) were generally higher than what we observed, potentially because fish were collected in the productive mainstem Missouri River whereas we initially captured some individuals in tributaries. Even though eventual recaptures occurred in the mainstem Missouri River, the duration of time individuals spent in tributaries may have slowed growth rates. Evidence of the continued annual increases in age at length of rainbow trout observed by Grisak et al. (2015) was difficult to distinguish because of low sample size and inconsistent intervals between captures.

Growth rates among all species in the upper Missouri River were higher than those observed in the Sun and Smith rivers even though sample sizes of physical recaptures in the

Missouri and Sun rivers generally precluded statistically significant results. Indeed, the tailwater fishery below Holter Dam in the Missouri River is generally accepted as one of the most productive in Montana (Grisak et al. 2012b). High summer water temperatures and low discharges resulting from irrigation withdrawals may be limiting factors of growth rate in the Sun and Smith rivers (Ritter 2015; Vivian and Mullen 2017; Ritter et al. 2020).

Rainbow trout ages based on detection intervals and lengths at tagging were consistent with that observed by Grisak et al. (2015) in the Cascade sampling section (Dog Creek subwatershed). Estimated ages of physical recaptures also supported Grisak et al. (2015); age-4 fish ranged from 432 mm (17.0”) to 465 mm (18.3”). Detection intervals suggested brown trout reached at least seven to eight years of age; one seven-year old fish that was recaptured measured 521 mm (20.5”), which was slightly less than the mean (but still within ranges) reported by Grisak et al. (2015) for brown trout captured in the Cascade sampling section.

Fish in the Smith River were the longest-lived compared to the Sun and upper Missouri rivers. Although PIT arrays monitored detected fish in the Smith River for the longest duration (2011 to 2020), redetected fish also tended to have the highest combination of detection interval and length at tagging. Two rainbow trout tagged around 140 mm (5.5”) in length were redetected after 6.7 years, suggesting these fish were approaching seven to eight years of age. Several brown trout with tagging lengths greater than 400 mm (15.7”) were redetected after five to 6.5 year intervals, suggesting these fish could have been approaching eight to ten years of age. Furthermore, physical recaptures showed a much slower growth rate than that observed in the Missouri River, which is not surprising based on direct growth rate comparisons.

Longevity in the Sun River was more difficult to determine because duration of PIT array operation was limited. Rainbow trout probably reached five to seven years of age; one individual with a tagging length of 333 mm (13”) was detected after an interval of three years. Observed lifespans of brown trout may have been seven to nine years old; one individual with a tagging length of 389 mm (15.3”) was detected after an interval of 5 years.

Mountain whitefish exhibited the highest propensity to reach old ages in all subbasins, especially the Smith River. The longest detection intervals in the study were two mountain whitefish at 7.3 years. Furthermore, these fish were several years old at the time of initial capture; tagging lengths were 304 mm (12”) and 236 mm (9.3”), suggesting these fish were at least nine to ten years old. This longevity is well-documented in other systems; 90% of populations surveyed in Idaho showed individuals reaching at least ten years old (Meyer et al. 2011). Unsurprisingly, mountain whitefish exhibited the highest survival probability among species in the Smith River subbasin (Lance 2019).

Relative weights in the Smith River appeared highest in upstream watersheds for all species but may have been affected by low sample sizes for rainbow and brown trout. Lance (2019) identified these watersheds (Camas Creek, Newlan Creek, North Fork Smith River, and South Fork Smith River watersheds) as the headwaters geomorphic region. Characterized by an unconstrained agricultural valley (Lance 2019), the nutrient input from land management practices and agricultural operations may have increased productivity and subsequent body condition of individual fish, even though survival probabilities were highest in the canyon geomorphic region (Deep Creek, Tenderfoot Creek, Rock Creek, Eagle Creek, and Sheep Creek watersheds; Lance 2019).

TABLES

Table 4.1. Number of fish tagged by species and subwatershed in the Missouri River subbasin from 2014 to 2016. Superscripts represent subwatersheds that include locations of annual population sampling. Miscellaneous species include Mountain Sucker, Yellow Perch, and Walleye.

	Species								
Subwatershed	rainbow trout	Brown Trout	Mountain Whitefish	Brook Trout	Burbot	White Sucker	Longnose Sucker	Misc	Total
Tributary									
Dearborn River	390	131	46	-	-	40	46	2	655
Sheep Creek	424	72	-	-	-	2	-	-	498
Little Prickly Pear Creek watershed									
Little Prickly Pear Creek	521	86	1	-	-	9	2	-	619
Wolf Creek	760	94	-	-	-	-	-	-	853
Lyons Creek	263	114	-	-	-	1	-	-	377
Subtotal	2,358	495	47	-	-	52	48	2	3,002
Mainstem									
City of Great Falls	3	6	7	-	1	2	1	1	21
Dog Creek[1]	66	68	4	-	-	23	1	-	162
Finigan Creek[2]	8	4	-	-	-	-	-	-	12
Log Gulch	37	59	114	-	1	-	-	-	211
Prewett Creek	10	-	105	-	-	26	1	1	143
Wilson Butte	4	1	-	-	15	-	1	-	22
Subtotal	128	138	230	-	17	51	4	2	570
Total	2,487	633	277	-	17	103	52	4	**3,572**

[1] Craig annual population sampling section.
[2] Cascade annual population sampling section.

Table 4.2. Number of fish tagged by species and subwatershed in the Sun River subbasin from 2015 to 2016. Superscripts represent subwatersheds that include locations of annual population sampling. Miscellaneous species include Mountain Sucker, Yellow Perch, and Walleye.

	Species							
Subwatershed	Rainbow Trout	Brown Trout	Mountain Whitefish	Brook Trout	Burbot	White Sucker	Longnose Sucker	Total
Tributary								
Elk Creek	9	125	46	3	-	2	-	142
Mainstem								
City of Simms[1]	96	128	145	-	-	5	-	374
Cutting Shed Coulee	48	100	76	-	-	-	-	223
Subtotal	144	228	221	-	-	5	-	597
Total	153	353	223	3	-	8	-	**739**

[1] Simms annual population sampling section.

Table 4.3. Number of fish tagged by species and subwatershed in the Smith River subbasin from 2010 to 2017. Superscripts represent subwatersheds that include locations of annual population sampling.

	Species								
Subwatershed	Rainbow Trout	Brown Trout	Mountain Whitefish	Brook Trout	Burbot	White Sucker	Longnose Sucker	Mountain Sucker	Total
Tributary									
Big Birch Creek	8	56	10	11	-	3	-	-	88
Hound Creek	24	367	11	-	-	48	19	-	469
Newlan Creek	1	21	5	33	8	46	-	-	114
Sheep Creek watershed									
Lower Sheep	51	26	120	1	-	9	1	-	208
Middle Sheep	689	77	52	13	-	2	-	-	833
Upper Sheep	284	40	40	4	-	2	-	-	370
Moose Creek	908	6	271	21	-	-	-	-	1,204
Rock Creek	13	68	17	-	-	-	-	-	98
Tenderfoot Creek	483	85	460	94	-	-	-	-	1,122
Subtotal	2,455	706	986	166	8	110	20	-	4,451
Mainstem									
Bear Gulch	42*	48	59	-	-	-	2	-	151
Blacktail Creek[1]	376	172	258	-	6	5	7	-	824
Boston Coulee	18*	38	129	-	-	8	7	-	200
Cottonwood Creek[2]	56*	93	211	7	3	6	6	-	381
Rock Springs Creek	38*	178	235	8	2	23	-	-	484
Rocky Coulee	56	47	113	-	-	3	2	-	221
Two Creek	277*	187	356	-	13	12	12	1	858
Subtotal	864	763	1,360	15	24	57	36	-	3,119
Total	3,323	1,510	2,346	192	32	167	56	1	**7,625**

[1] Eagle Creek annual population sampling section.
[*] Includes one Westslope Cutthroat Trout. A total of five was tagged in the Smith River subbasin.

Table 4.4. Locations, average detection ranges, and detection efficiencies of stationary PIT arrays in the upper Missouri River, Sun River, and Smith River subbasins.

Stationary PIT array	GPS coordinates (UTM)	Tag detection distance (inches)	Detection efficiency	Physical location
		Missouri River		
Lyons Creek	46.93827, -112.12581	28.5 (6 – 54)	-	Just upstream of confluence with Little Prickly Pear Creek
Wolf Creek	47.00597, -112.08026	29 (6 – 60)	-	Just upstream of confluence with Little Prickly Pear Creek
Little Prickly Pear Creek	47.02251, -112.02018	17 (2 – 42)		Just upstream of confluence with Missouri River
Dearborn River	47.13017, -111.91295	6.3 (2.5 – 9)	-	Just upstream of confluence with Missouri River
Sheep Creek	47.17681, -111.81165	17.7 (4 – 36)	-	Just upstream of confluence with Missouri River
		Sun River		
HWY 287	47.54768, -112.36674	8.6 (4.5 – 18)	-	Just upstream of Hwy 287 near Augusta, Montana at rkm 109
Elk Creek	47.51229, -112.33641	30 (4 – 48)	-	rkm 4.5
Durocher	47.54413, -111.57848	7.2 (3 – 18)	-	Upstream of Vaughn, Montana at rkm 32
		Smith River		
Big Birch Creek	46.58884, -111.05305	-	0.79	Just upstream of confluence with Smith River
Newlan Creek	46.59094, -111.05070	-	0.79	Just upstream of confluence with Smith River
Canyon Ranch	46.60810, -111.06760	-	0.96	rkm 172
Benton Creek	46.70542, -111.19305	-	0.79	Just upstream of confluence with Smith River
Camas Creek	46.70542, -111.19305	-	0.96	Just upstream of confluence with Smith River
Smith River at Beaver Creek	46.75143, -111.16839	-	1.00	rkm 141
Moose Creek	46.80292, -110.91484	-	0.96	Just upstream of confluence with Sheep Creek
Upper Sheep Creek	46.81047, -110.92272	-	0.71	1 rkm downstream of Moose Creek
Lower Sheep Creek	46.80443, -111.17403	-	0.78	0.9 rkm upstream of confluence with Smith River
Rock Creek	46.86935, -111.27185	-	0.79	Just upstream of confluence with Smith River
Tenderfoot Creek	46.94185, -111.29404	-	0.98	Just upstream of confluence with Smith River
Castle Bar	46.97789, -111.28427	-	0.75	rkm 97
Merganser Bend	47.14734, -111.294	-	0.66	Just downstream of Merganser Bend boat camp
Hound Creek	47.21261, -111.40371	18.5 (4 – 36)	0.96	rkm 2.4
Truly Bridge	47.35658, -111.44140	7.4 (1 – 18)	0.70	rkm 14.6

Table 4.5. Means and ranges of relative weights of rainbow trout, brown trout, and mountain whitefish measured, weighed, and tagged in the upper Missouri River, Sun River, and Smith River subbasins.

Taxon	*N*	Mean	Minimum	Maximum
Missouri River				
Rainbow Trout	5	95.7	87.3	104.5
Brown Trout	11	96.3	80.3	132.0
Mountain Whitefish	-	-	-	-
Sun River				
Rainbow Trout	-	-	-	-
Brown Trout	5	88.0	83.4	95.6
Mountain Whitefish	3	99.5	93.3	108.2
Smith River				
Rainbow Trout	606	91.6	53.2	187.1
Brown Trout	437	95.0	47.1	131.1
Mountain Whitefish	1,132	99.1	50.0	179.2

Table 4.6. Summary of tagged fish recaptured in the upper Missouri River, Sun River, and Smith River subbasins from 2014 to 2020.

PIT	Date tagged	Subwatershed tagged	Tagging length, weight (mm, kg)	Date recaptured	Subwatershed recaptured	Recapture length, weight (mm, kg)	Time to recapture (years)	Growth (mm)	Growth rate (mm/year)
Missouri River									
				Rainbow Trout					
384.3515DD8A5A	3/12/2014	Wolf Creek	102	9/28/2017	Log Gulch	465, 1.0	3.55	363	102
384.3515DD8CC0	4/2/2014	Sheep Creek	119	10/10/2017	Log Gulch	460, 1.1	3.53	340	96
384.3515DD8DEF	3/28/2014	Little Prickly Pear Creek	140	9/27/2017	Log Gulch	432, 0.8	3.51	292	83
384.3515DD8FAE	3/20/2014	Little Prickly Pear Creek	196	10/1/2018	Log Gulch	445	4.54	249	55
384.3515DDF963	4/28/2014	Dog Creek	254	9/27/2017	Log Gulch	406, 0.7	3.42	152	45
384.3515DDF9A2	4/29/2014	Dog Creek	282	10/11/2017	Log Gulch	432, 0.9	3.46	150	43
384.3515DDF9F1	5/6/2014	Dog Creek	211	10/10/2017	Log Gulch	483	3.43	272	79
				Brown Trout					
384.3515DD91A8	3/11/2014	Wolf Creek	170	5/3/2017	Log Gulch	432, 0.8	3.15	262	83
				4/24/2018	Log Gulch	442, 0.7	0.97	10	10
384.3515DDF960	4/28/2014	Dog Creek	244	5/3/2017	Log Gulch	452, 1.3	3.02	208	69
				4/24/2018	Log Gulch	470, 1.3	0.97	18	18
				4/29/2020	Dog Creek	488, 1.2	2.02	18	9
384.3515DDF96E	4/28/2014	Dog Creek	107	4/23/2018	Log Gulch	505, 1.2	3.99	399	100
				5/13/2020	Dog Creek	521, 1.2	2.06	15	7
384.3515DDF9BF	5/5/2014	Dog Creek	180	5/3/2017	Log Gulch	450, 0.9	3.00	269	90
				4/23/2018	Log Gulch	467, 0.9	0.97	18	18
384.3515DDFBCE	5/5/2014	Log Gulch	168	4/23/2018	Log Gulch	493, 1.2	3.97	325	82
384.3515DDFC27	5/7/2014	Log Gulch	234	5/3/2017	Log Gulch	546, 1.7	2.99	312	104
Sun River									
				Brown Trout					
384.3515DE9C23	3/19/2015	City of Simms	259	4/15/2019	Cutting Shed Coulee	447, 0.9	4.08	188	46
384.358D11A6A8	3/23/2015	Cutting Shed Coulee	389	3/30/2020	Cutting Shed Coulee	460, 0.9	5.02	71	14
384.358D11A6D8	3/23/2015	Cutting Shed Coulee	434	4/4/2019	Cutting Shed Coulee	478, 1.0	4.03	43	11
384.358D11A7B2	3/23/2015	Cutting Shed Coulee	447	9/4/2019	Cutting Shed Coulee	533, 1.5	4.45	86	19
384.358D11A7D0	3/19/2015	City of Simms	315	4/8/2020	Fourmile Creek	452, 0.8	5.06	137	27
				Mountain Whitefish					
384.3515DCBA9C	3/30/2015	Cutting Shed Coulee	368	4/15/2019	Cutting Shed Coulee	409, 0.7	4.05	41	10
384.358D11A7D1	3/19/2015	City of Simms	290	4/9/2018	City of Simms	338, 0.4	3.06	48	16
384.358D11A7FF	3/23/2015	Cutting Shed Coulee	345	4/5/2019	Cutting Shed Coulee	384, 0.5	4.04	38	9
Smith River									
				Rainbow Trout					
384.3515DC408E	10/7/2014	Upper Sheep Creek	183	5/24/2016	Upper Sheep Creek	272, 0.2	1.63	89	55
384.3515DC40B0	10/7/2014	Upper Sheep Creek	180	7/7/2016	Upper Sheep Creek	254	1.75	74	42

Table 24 – continued

PIT	Date tagged	Subwatershed tagged	Tagging length, weight (mm, kg)	Date recaptured	Subwatershed recaptured	Recapture length, weight (mm, kg)	Time to recapture (years)	Growth (mm)	Growth rate (mm/year)
384.3515DC40B5	10/7/2014	Upper Sheep Creek	201	5/24/2016	Upper Sheep Creek	287, 0.2	1.63	86	53
				7/7/2016	Upper Sheep Creek	295	0.12	8	63
384.3515DC40E3	10/7/2014	Upper Sheep Creek	132	7/7/2016	Upper Sheep Creek	185	1.75	53	30
384.3515DC415B	9/18/2014	Blacktail Creek	427	9/24/2015	Blacktail Creek	437, 0.7	1.02	10	10
384.3515DC4173	9/18/2014	Blacktail Creek	414	9/24/2015	Blacktail Creek	417, 0.8	1.02	3	2
384.3515DC418A	9/18/2014	Blacktail Creek	356	9/24/2015	Blacktail Creek	401, 0.6	1.02	46	45
384.3515DC4191	9/18/2014	Blacktail Creek	246	9/24/2015	Blacktail Creek	310, 0.3	1.02	64	62
				9/13/2016	Blacktail Creek	345, 0.4	0.97	36	37
384.3515DC4194	9/18/2014	Blacktail Creek	257	9/24/2015	Blacktail Creek	300, 0.2	1.02	43	42
384.3515DC4195	9/18/2014	Blacktail Creek	279	9/24/2015	Blacktail Creek	368, 0.5	1.02	89	87
384.3515DC41BB	9/18/2014	Blacktail Creek	297	9/24/2015	Blacktail Creek	358, 0.4	1.02	61	60
384.3515DC41D2	9/18/2014	Blacktail Creek	249	9/24/2015	Blacktail Creek	318, 0.3	1.02	69	67
				9/13/2016	Blacktail Creek	356, 0.5	0.97	38	39
384.3515DC41DD	9/9/2014	Blacktail Creek	236	9/13/2016	Blacktail Creek	376, 0.6	2.01	140	69
384.3515DC41E2	9/9/2014	Blacktail Creek	328	9/13/2016	Blacktail Creek	419, 0.8	2.01	91	45
384.3515DC41F0	9/17/2014	Blacktail Creek	264	9/24/2015	Blacktail Creek	318, 0.4	1.02	53	52
384.3515DC41FB	9/9/2014	Blacktail Creek	343	9/24/2015	Blacktail Creek	371, 0.5	1.04	28	27
384.3515DC420F	9/17/2014	Blacktail Creek	373	9/17/2018	Blacktail Creek	422, 0.7	4.00	48	12
384.3515DC421F	9/9/2014	Blacktail Creek	183	9/24/2015	Blacktail Creek	297, 0.3	1.04	114	110
384.3515DC4229	9/17/2014	Blacktail Creek	287	9/24/2015	Blacktail Creek	335, 0.4	1.02	48	47
384.3515DC422D	9/17/2014	Blacktail Creek	335	9/24/2015	Blacktail Creek	348, 0.5	1.02	13	12
384.3515DC4237	9/17/2014	Blacktail Creek	185	9/24/2015	Blacktail Creek	262, 0.2	1.02	76	75
384.3515DC4238	9/17/2014	Blacktail Creek	287	9/24/2015	Blacktail Creek	363, 0.5	1.02	76	75
384.3515DDFA09	9/8/2014	Blacktail Creek	295	9/13/2016	Blacktail Creek	391, 0.6	2.02	97	48
384.3515DDFA0C	9/9/2014	Blacktail Creek	272	9/24/2015	Blacktail Creek	330, 0.4	1.04	58	56
384.3515DDFA14	9/8/2014	Blacktail Creek	198	9/24/2015	Blacktail Creek	323, 0.3	1.04	124	119
384.3515DDFA16	9/17/2014	Blacktail Creek	290	9/24/2015	Blacktail Creek	310	1.02	20	20

Table 24 – continued

PIT	Date tagged	Subwatershed tagged	Tagging length, weight (mm, kg)	Date recaptured	Subwatershed recaptured	Recapture length, weight (mm, kg)	Time to recapture (years)	Growth (mm)	Growth rate (mm/year)
384.3515DDFA26	9/8/2014	Blacktail Creek	323	9/24/2015	Blacktail Creek	373, 0.6	1.04	51	49
					Blacktail Creek	368, 0.4	0.97	-5	-5
384.3515DDFA27	9/8/2014	Blacktail Creek	302	9/24/2015	Blacktail Creek	368, 0.6	1.04	66	63
384.3515DDFA2B	9/8/2014	Blacktail Creek	231	9/13/2016	Blacktail Creek	318, 0.4	2.02	86	43
384.3515DDFA32	9/8/2014	Blacktail Creek	236	9/24/2015	Blacktail Creek	330, 0.4	1.04	94	90
384.3515DDFA40	9/8/2014	Blacktail Creek	218	9/24/2015	Blacktail Creek	318, 0.3	1.04	99	95
384.3515DDFA43	9/8/2014	Blacktail Creek	229	9/24/2015	Blacktail Creek	310, 0.3	1.04	81	78
384.3515DDFA48	9/8/2014	Blacktail Creek	188	9/24/2015	Blacktail Creek	269, 0.2	1.04	81	78
384.3515DDFA4A	9/8/2014	Blacktail Creek	257	9/24/2015	Blacktail Creek	307, 0.3	1.04	51	49
384.3515DDFA4E	9/8/2014	Blacktail Creek	259	9/24/2015	Blacktail Creek	330, 0.4	1.04	71	68
384.3515DDFA54	9/17/2014	Blacktail Creek	330	9/24/2015	Blacktail Creek	378, 0.6	1.02	48	47
384.3515DDFA5D	9/8/2014	Blacktail Creek	290	9/24/2015	Blacktail Creek	312, 0.3	1.04	23	22
384.3515DDFA74	9/8/2014	Blacktail Creek	175	9/24/2015	Blacktail Creek	279, 0.2	1.04	104	100
				9/13/2016	Blacktail Creek	338, 0.4	0.97	58	60
384.3515DDFA7C	9/8/2014	Blacktail Creek	417	9/24/2015	Blacktail Creek	439, 0.9	1.04	23	22
384.3515DDFA81	9/8/2014	Blacktail Creek	259	9/24/2015	Blacktail Creek	320, 0.3	1.04	61	58
384.3515DDFA83	9/17/2014	Blacktail Creek	257	9/24/2015	Blacktail Creek	333, 0.4	1.02	76	75
384.3515DDFA86	9/8/2014	Blacktail Creek	185	9/24/2015	Blacktail Creek	411, 0.7	1.04	226	217
384.3515DDFA87	9/9/2014	Blacktail Creek	254	9/24/2015	Blacktail Creek	353, 0.4	1.04	99	95
384.3515DDFA9A	9/8/2014	Blacktail Creek	234	9/24/2015	Blacktail Creek	287, 0.3	1.04	53	51
384.3515DDFA9B	9/9/2014	Blacktail Creek	297	9/13/2016	Blacktail Creek	356, 0.4	2.01	58	29
384.3515DDFAA4	9/17/2014	Blacktail Creek	305	9/24/2015	Blacktail Creek	406	1.02	102	100
384.3515DDFAA6	9/8/2014	Blacktail Creek	213	9/24/2015	Blacktail Creek	315, 0.4	1.04	102	97
384.3515DDFAAA	9/9/2014	Blacktail Creek	229	9/24/2015	Blacktail Creek	302, 0.3	1.04	74	71
				9/13/2016	Blacktail Creek	325, 0.3	0.97	23	24
384.3515DDFAAE	9/9/2014	Blacktail Creek	224	9/13/2016	Blacktail Creek	373, 0.6	2.01	150	74
384.3515DDFABB	9/17/2014	Blacktail Creek	414	9/24/2015	Blacktail Creek	424, 0.7	1.02	10	10

Table 24 – continued

PIT	Date tagged	Subwatershed tagged	Tagging length, weight (mm, kg)	Date recaptured	Subwatershed recaptured	Recapture length, weight (mm, kg)	Time to recapture (years)	Growth (mm)	Growth rate (mm/year)
384.3515DE2A33	9/10/2014	Middle Sheep Creek	183	7/7/2016	Upper Sheep Creek	241	1.82	58	32
384.3515DE2A40	9/10/2014	Middle Sheep Creek	155	4/14/2017	Blacktail Creek	315	2.59	160	62
384.3515DE2A49	9/10/2014	Middle Sheep Creek	213	7/7/2016	Upper Sheep Creek	254	1.82	41	22
384.3515DE2A61	9/10/2014	Middle Sheep Creek	145	7/7/2016	Upper Sheep Creek	246	1.82	102	56
384.3515DE2A9C	9/10/2014	Middle Sheep Creek	272	7/7/2016	Upper Sheep Creek	292	1.82	20	11
384.3515DE2AB7	9/11/2014	Middle Sheep Creek	142	9/13/2016	Blacktail Creek	330, 0.3	2.01	188	94
384.3515DE2BB0	9/17/2014	Middle Sheep Creek	165	7/7/2016	Upper Sheep Creek	282	1.81	117	65
				3/23/2017	Cottonwood Creek	279	0.71	-3	-4
384.3515DE2BE9	9/17/2014	Middle Sheep Creek	142	5/24/2016	Upper Sheep Creek	254, 0.2	1.68	112	66
384.3515DE2C13	9/17/2014	Middle Sheep Creek	185	7/7/2016	Upper Sheep Creek	277	1.81	91	51
384.3515DE9796	10/15/2014	Moose Creek	152	8/29/2015	Moose Creek	196, 0.1	0.87	43	50
384.3515DE97C7	10/15/2014	Moose Creek	130	7/7/2016	Upper Sheep Creek	262	1.73	132	76
384.3515DE9804	10/15/2014	Moose Creek	236	9/24/2015	Blacktail Creek	267, 0.2	0.94	30	32
384.3515DE9812	10/15/2014	Moose Creek	175	7/7/2016	Upper Sheep Creek	249	1.73	74	43
384.3515DE9841	10/15/2014	Moose Creek	234	8/29/2015	Moose Creek	244, 0.1	0.87	10	12
384.3515DE9A62	10/9/2014	Middle Sheep Creek	117	8/29/2015	Middle Sheep Creek	201, 0.1	0.89	84	94
384.3515DE9B95	10/13/2014	Rock Springs Creek	234	3/22/2017	Rock Springs Creek	386, 0.2	2.44	152	62
384.3515DE9C29	10/15/2014	Moose Creek	175	3/23/2017	Cottonwood Creek	269, 0.2	2.44	94	39
384.3515DE9CC6	10/15/2014	Moose Creek	150	8/29/2015	Moose Creek	196, 0.1	0.87	46	52
384.3515DE9CE6	10/15/2014	Moose Creek	102	9/13/2016	Blacktail Creek	274, 0.2	1.92	173	90
384.3515DE9EAD	10/20/2014	Moose Creek	175	10/24/2016	Two Creek	297, 0.3	2.01	122	61
384.3515DE9ED1	10/29/2014	Moose Creek	137	8/29/2015	Moose Creek	183	0.83	46	55
384.358D11A8C9	10/21/2014	Lower Sheep Creek	211	9/24/2015	Blacktail Creek	257, 0.2	0.93	46	49
384.358D11A9E8	10/29/2014	Moose Creek	183	8/29/2015	Moose Creek	211, 0.1	0.83	28	34
384.358D11A9F1	10/29/2014	Moose Creek	155	10/24/2016	Two Creek	290, 0.2	1.99	135	68
384.358D11AA24	10/29/2014	Moose Creek	163	8/29/2015	Moose Creek	203, 0.1	0.83	41	49
384.358D11AA39	10/29/2014	Moose Creek	221	7/7/2016	Upper Sheep Creek	272	1.69	51	30
3D6.0017F7A28A	10/15/2015	Two Creek	361, 0.6	10/24/2016	Two Creek	373, 0.5	1.03	13	12
3D6.0017F7A28B	10/15/2015	Two Creek	333	10/17/2016	Two Creek	368, 0.5	1.01	36	35
3D6.0017F7A364	10/15/2015	Two Creek	338	10/24/2016	Two Creek	404, 0.7	1.03	66	64
3D6.0017F7A37D	10/15/2015	Two Creek	274	10/17/2016	Two Creek	338, 0.4	1.01	64	63
3D6.00182C0410	10/15/2015	Two Creek	315	10/18/2016	Two Creek	361, 0.6	1.01	46	45
3D6.00182C0420	10/15/2015	Two Creek	218	10/18/2016	Two Creek	305, 0.3	1.01	86	85
3D6.00182C0423	10/15/2015	Two Creek	226	10/17/2016	Two Creek	338, 0.4	1.01	112	111
3D6.00182C042B	10/15/2015	Two Creek	305	10/17/2016	Two Creek	351, 0.4	1.01	46	45
3D6.00182C0458	10/15/2015	Two Creek	330	10/25/2016	Two Creek	391, 0.6	1.03	61	59

Table 24 – continued

PIT	Date tagged	Subwatershed tagged	Tagging length, weight (mm, kg)	Date recaptured	Subwatershed recaptured	Recapture length, weight (mm, kg)	Time to recapture (years)	Growth (mm)	Growth rate (mm/year)
3D6.00182C045E	10/15/2015	Two Creek	307	10/17/2016	Two Creek	338, 0.4	1.01	30	30
3D6.00182C0463	10/15/2015	Two Creek	330	10/17/2016	Two Creek	323, 0.3	1.01	-8	-8
3D6.00182C0470	10/15/2015	Two Creek	239	10/17/2016	Two Creek	305, 0.3	1.01	66	66
3D6.00182C047C	10/15/2015	Two Creek	231	10/17/2016	Two Creek	323, 0.3	1.01	91	91
3D6.00182C0490	10/15/2015	Two Creek	213	10/25/2016	Two Creek	287, 0.3	1.03	74	72
3D6.00182C04A3	10/15/2015	Two Creek	368	10/17/2016	Two Creek	384, 0.5	1.01	15	15
3D6.00182C04A7	10/15/2015	Two Creek	345	10/18/2016	Two Creek	409, 0.8	1.01	64	63
3D6.00182C04AF	10/15/2015	Two Creek	361	10/17/2016	Two Creek	371, 0.6	1.01	10	10
3D6.00182C051C	5/24/2016	Upper Sheep Creek	236, 0.1	3/23/2017	Cottonwood Creek	264, 0.2	0.83	28	34
3D6.00182C053F	5/24/2016	Upper Sheep Creek	193, 0.1	7/7/2016	Upper Sheep Creek	211	0.12	18	147
3D6.00182C0544	5/24/2016	Upper Sheep Creek	211, 0.1	3/23/2017	Cottonwood Creek	221, 0.1	0.83	10	12
3D6.00182C0553	5/25/2016	Cottonwood Creek	391, 0.6	3/23/2017	Cottonwood Creek	452, 0.9	0.83	61	74
3D6.00182C056D	5/25/2016	Cottonwood Creek	363, 0.5	6/23/2016	Cottonwood Creek	373, 0.6	0.08	10	128
				3/23/2017	Cottonwood Creek	399	0.75	25	34
3D6.00182C05A5	10/15/2015	Two Creek	358	10/18/2016	Two Creek	399, 0.6	1.01	41	40
3D6.00182C05F8	10/15/2015	Two Creek	206	10/17/2016	Two Creek	310, 0.3	1.03	104	103
3D6.00182C0609	10/15/2015	Two Creek	249	10/24/2016	Two Creek	318, 0.3	1.03	69	67
3D6.00182C0624	10/15/2015	Two Creek	315	10/24/2016	Two Creek	361, 0.5	1.03	46	45
3D6.00182C062D	10/15/2015	Two Creek	208	10/24/2016	Two Creek	312, 0.3	1.03	104	101
3D6.00182C0635	10/15/2015	Two Creek	226	10/17/2016	Two Creek	318, 0.3	1.01	91	91
				6/7/2017	Two Creek	343	0.67	25	38
3D6.00183A1BE5	6/23/2016	Cottonwood Creek	419, 0.9	8/19/2016	Blacktail Creek	419	0.16	0	0
				3/23/2017	Cottonwood Creek	429, 0.8	0.59	10	17
				Brown Trout					
384.3515DC4163	9/18/2014	Blacktail Creek	315	9/24/2015	Blacktail Creek	404, 0.7	1.02	89	88
384.3515DC4202	9/17/2014	Blacktail Creek	307	9/24/2015	Blacktail Creek	386, 0.8	1.02	79	77
384.3515DDFA50	9/8/2014	Blacktail Creek	315	9/24/2015	Blacktail Creek	381, 0.6	1.04	66	63
				3/24/2016	Blacktail Creek	399, 0.8	0.50	18	36
384.3515DE9A00	10/13/2014	Rock Springs Creek	361	3/22/2017	Rock Springs Creek	462, 0.9	2.44	102	42
384.3515DE9EBA	10/21/2014	Lower Sheep Creek	330	3/24/2016	Blacktail Creek	424, 0.8	1.42	94	66
3D6.0017F7A226	10/15/2015	Two Creek	386	10/17/2016	Two Creek	404, 0.6	1.01	18	18
3D6.0017F7A24F	10/15/2015	Two Creek	249	10/17/2016	Two Creek	330, 0.4	1.01	81	81
3D6.0017F7A39D	10/15/2015	Two Creek	305	10/17/2016	Two Creek	366, 0.5	1.01	61	60
3D6.0017F7A407	10/15/2015	Two Creek	302	10/17/2016	Two Creek	348, 0.5	1.01	46	45
3D6.001808A869	5/25/2016	Cottonwood Creek	178, 0.1	6/23/2016	Cottonwood Creek	213, 0.1	0.08	36	448
3D6.00181F2B53	10/15/2015	Two Creek	455	10/9/2018	Two Creek	465, 1.0	2.99	10	3
3D6.00182C03DF	10/22/2015	Two Creek	257	10/10/2018	Two Creek	411, 0.7	2.97	155	52
3D6.00182C03E7	3/24/2016	Blacktail Creek	368, 0.5	9/13/2016	Blacktail Creek	386, 0.6	0.47	18	38
3D6.00182C0406	10/15/2015	Two Creek	445	10/17/2016	Two Creek	460, 0.8	1.01	15	15

Table 24 – continued

PIT	Date tagged	Subwatershed tagged	Tagging length, weight (mm, kg)	Date recaptured	Subwatershed recaptured	Recapture length, weight (mm, kg)	Time to recapture (years)	Growth (mm)	Growth rate (mm/year)
3D6.00182C0421	10/15/2015	Two Creek	254	10/17/2016	Two Creek	320, 0.3	1.01	66	66
3D6.00182C0444	10/15/2015	Two Creek	254	9/28/2018	Two Creek	483, 1.2	2.96	229	77
3D6.00182C045A	10/15/2015	Two Creek	236	10/17/2016	Two Creek	345, 0.4	1.01	109	108
3D6.00182C0492	10/15/2015	Two Creek	439	10/18/2016	Two Creek	478, 1.3	1.01	38	38
3D6.00182C0496	10/15/2015	Two Creek	343	10/17/2016	Two Creek	417, 0.7	1.01	74	73
3D6.00182C0498	10/15/2015	Two Creek	251	10/24/2016	Two Creek	345, 0.5	1.03	94	91
3D6.00182C049A	10/15/2015	Two Creek	211	10/17/2016	Two Creek	325, 0.4	1.01	114	113
3D6.00182C04A6	10/15/2015	Two Creek	399	10/17/2016	Two Creek	419, 0.9	1.01	20	20
				10/9/2018	Two Creek	452, 1.1	1.98	33	17
3D6.00182C04AB	10/15/2015	Two Creek	363	10/17/2016	Two Creek	406, 0.8	1.01	43	43
3D6.00182C0529	5/25/2016	Cottonwood Creek	429, 0.8	6/23/2016	Cottonwood Creek	452, 1.0	0.08	23	288
				3/23/2017	Cottonwood Creek	480, 1.1	0.75	28	37
3D6.00182C0540	5/24/2016	Upper Sheep Creek	249, 0.1	7/7/2016	Upper Sheep Creek	272	0.12	23	190
				3/23/2017	Cottonwood Creek	269, 0.2	0.71	-3	-4
3D6.00182C054F	5/25/2016	Cottonwood Creek	457, 0.9	6/23/2016	Cottonwood Creek	462, 1.0	0.08	5	64
3D6.00182C056E	5/25/2016	Cottonwood Creek	424, 0.8	6/23/2016	Cottonwood Creek	439, 1.0	0.08	15	192
3D6.00182C05CA	10/15/2015	Two Creek	267	6/17/2017	Two Creek	401	1.67	135	80
				Mountain Whitefish					
384.3515DE9BC5	10/14/2014	Cottonwood Creek	257	3/24/2016	Blacktail Creek	312, 0.3	1.44	46	39
384.3515DE9D3E	10/15/2014	Moose Creek	297	4/14/2017	Blacktail Creek	305, 0.3	2.50	8	3
384.3515DE9D57	10/15/2014	Moose Creek	259	4/13/2017	Blacktail Creek	305, 0.3	2.50	46	18
384.358D117C6F	8/9/2014	Two Creek	333	10/17/2016	Two Creek	366, 0.5	2.19	33	15
3D6.0017F7A2B0	10/15/2015	Two Creek	315	10/18/2016	Two Creek	328, 0.4	1.01	13	13
3D6.0017F7A2CD	10/15/2015	Two Creek	358	10/25/2016	Two Creek	368, 0.5	1.03	10	10
3D6.0017F7A2F6	10/15/2015	Two Creek	307	10/24/2016	Two Creek	330, 0.4	1.03	23	22
3D6.0017F7A390	10/15/2015	Two Creek	323	10/18/2016	Two Creek	338, 0.4	1.01	15	15
3D6.001807A418	9/24/2015	Blacktail Creek	124	9/13/2016	Blacktail Creek	201, 0.1	0.97	76	78
3D6.001808A87A	5/25/2016	Cottonwood Creek	163	3/23/2017	Cottonwood Creek	211, 0.1	0.83	48	58
3D6.00181F2B2A	9/24/2015	Blacktail Creek	284	9/13/2016	Blacktail Creek	295, 0.3	0.97	10	10
3D6.00182C040B	10/15/2015	Two Creek	310	10/18/2016	Two Creek	330, 0.3	1.01	20	20
3D6.00182C052C	5/25/2016	Cottonwood Creek	396, 0.7	3/23/2017	Cottonwood Creek	406, 0.7	0.83	10	12
3D6.00182C053E	5/24/2016	Upper Sheep Creek	284, 0.2	7/7/2016	Upper Sheep Creek	292	0.12	8	63
				4/13/2017	Blacktail Creek	290, 0.2	0.77	-3	-3
3D6.00182C0575	5/24/2016	Upper Sheep Creek	302, 0.2	4/13/2017	Blacktail Creek	306, 0.2	0.89	4	4
3D6.00182C0593	10/15/2015	Two Creek	343	10/17/2016	Two Creek	348	1.01	5	5
3D6.00182C0594	10/15/2015	Two Creek	335	10/17/2016	Two Creek	348	1.01	13	13
3D6.00182C059D	10/15/2015	Two Creek	343	10/18/2016	Two Creek	361, 0.4	1.01	18	18
3D6.00182C059F	10/15/2015	Two Creek	414	10/17/2016	Two Creek	422, 0.7	1.01	8	8

Table 24 – continued

PIT	Date tagged	Subwatershed tagged	Tagging length, weight (mm, kg)	Date recaptured	Subwatershed recaptured	Recapture length, weight (mm, kg)	Time to recapture (years)	Growth (mm)	Growth rate (mm/year)
3D6.00182C05C0	10/15/2015	Two Creek	315	10/18/2016	Two Creek	325, 0.3	1.01	10	10
3D6.00182C05C7	10/15/2015	Two Creek	384	10/17/2016	Two Creek	396, 0.6	1.01	13	13
Brook Trout									
3D6.00182C056C	5/25/2016	Cottonwood Creek	239, 0.1	6/23/2016	Cottonwood Creek	264, 0.2	0.08	25	320
Burbot									
384.3515DC4184	9/18/2014	Blacktail Creek	483	9/13/2016	Blacktail Creek	536, 1.0	1.99	53	27
3D6.00182C04A8	10/15/2015	Two Creek	615	10/17/2016	Two Creek	660, 2.4	1.01	46	45
3D6.00182C055C	3/24/2016	Blacktail Creek	584, 1.2	9/13/2016	Blacktail Creek	584, 1.2	0.47	0	0
White Sucker									
3D6.00182C04AA	10/15/2015	Two Creek	414	10/18/2016	Two Creek	419, 1.0	1.01	5	5

FIGURES

Figure 4.1. The upper Missouri, Sun, and Smith rivers and their major tributaries. Yellow dots represent USGS gaging stations used in the study. Black diagonals represent dams or diversions. Green diamonds represent fixed PIT antenna arrays. Shaded buffers represent areas where fish

movement was monitored by fixed PIT antenna arrays, portable PIT antennas, and physical recapture events.

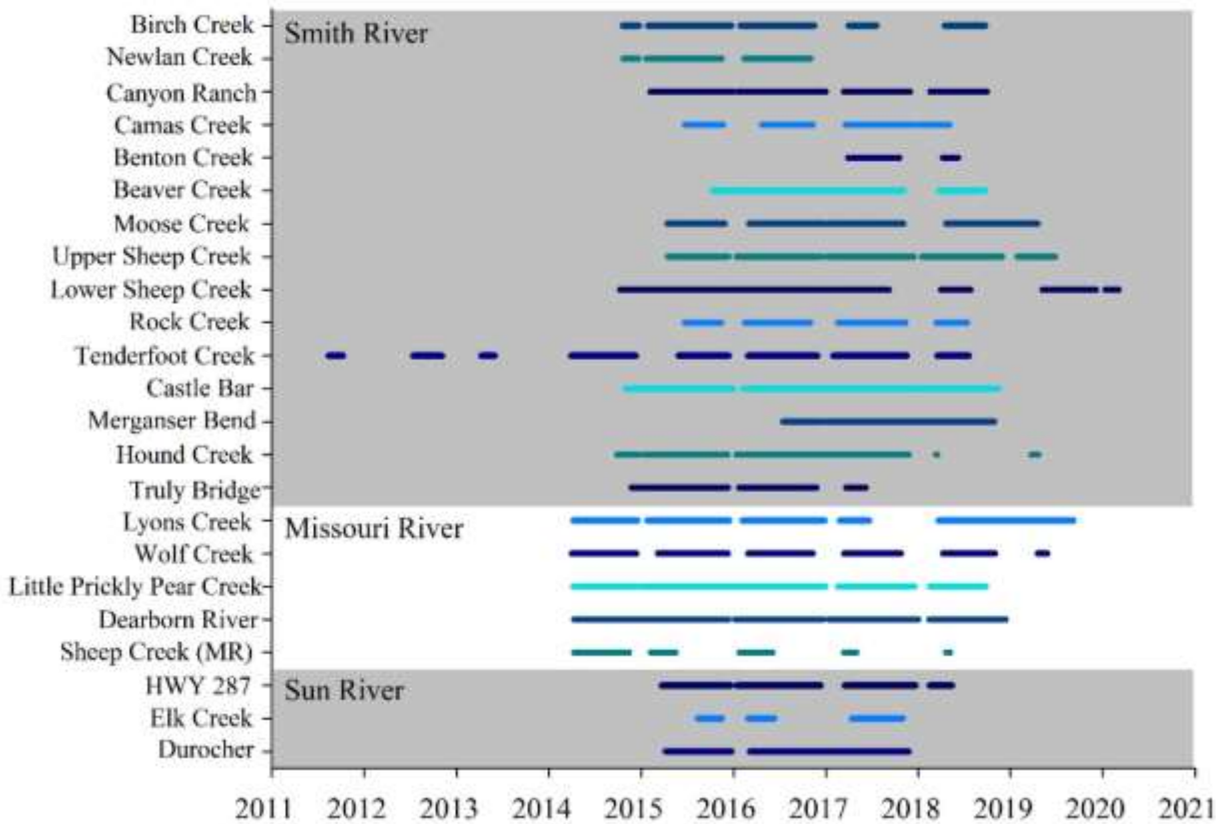


Figure 4.2. Operation timelines of stationary PIT arrays in the Smith, Sun, and upper Missouri River subbasins from 2011 to 2020.

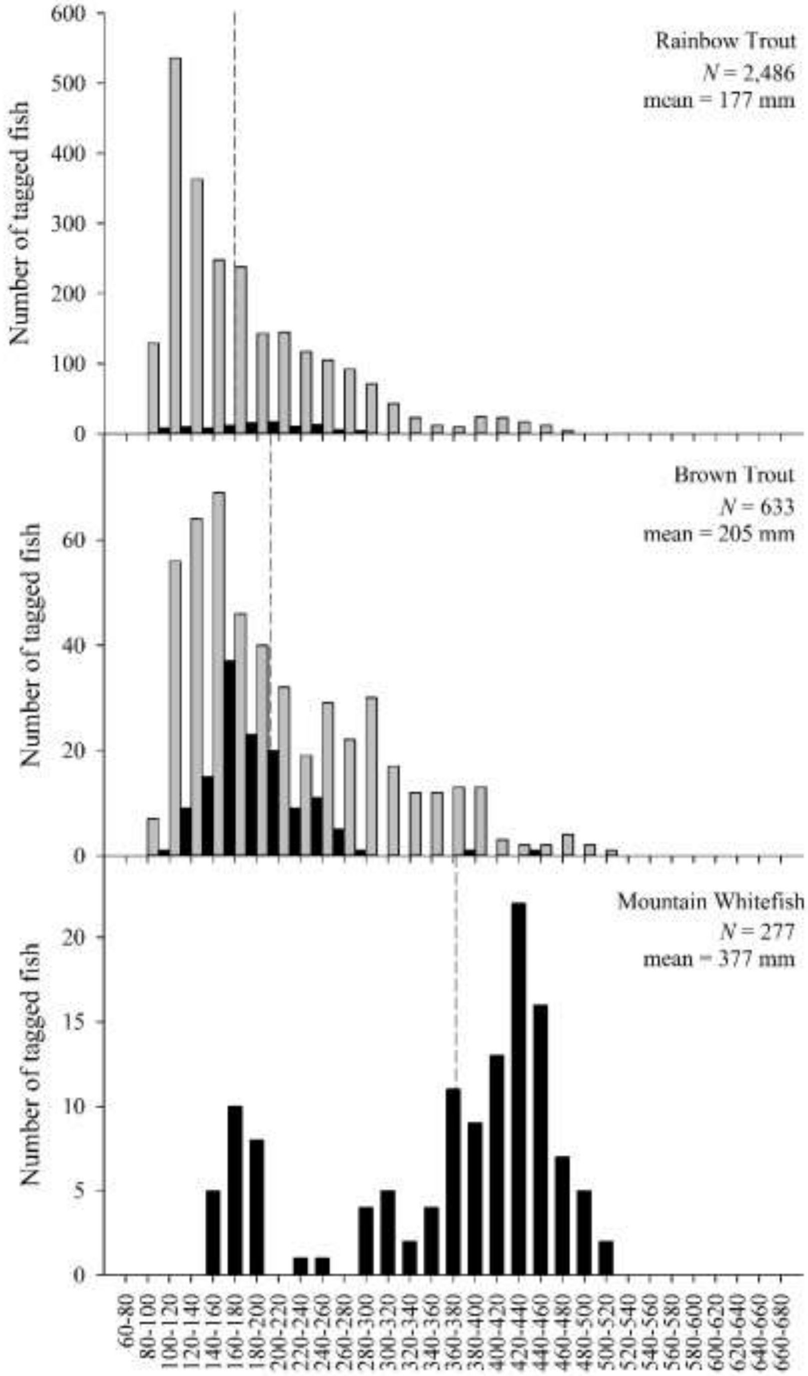


Figure 4.3. Length-frequency distributions of rainbow trout, brown trout, and mountain whitefish captured and tagged in the upper Missouri River and its tributaries from 2014 to 2016. Gray bars represent fish tagged in tributaries whereas black bars represent fish tagged in the mainstem river.

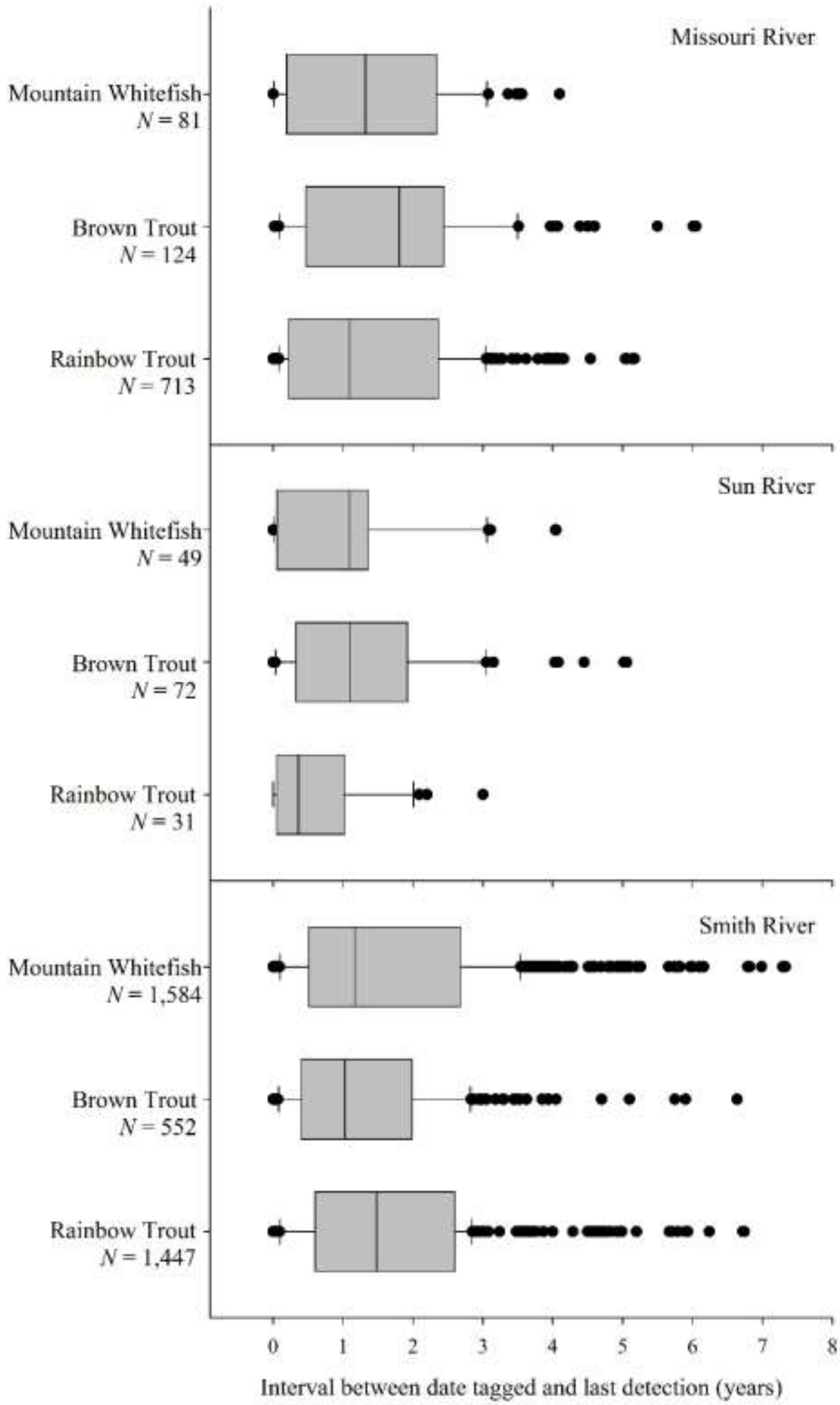


Figure 4.4. Distributions of time intervals between date tagged and date of last detection of rainbow trout, brown trout, and mountain whitefish tagged and redetected in the upper Missouri River, Sun River, and Smith River from 2010 to 2020.

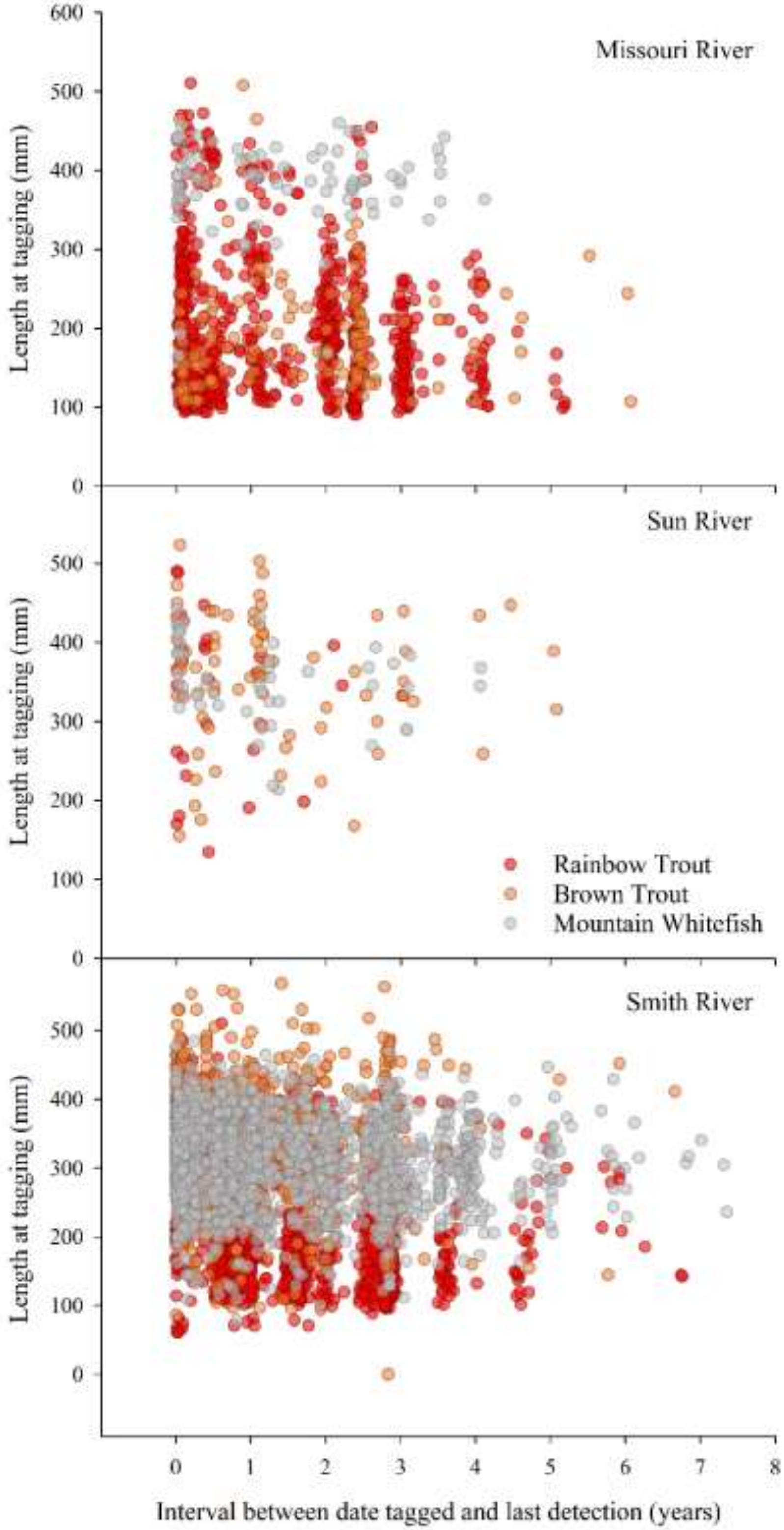


Figure 4.5. Length at tagging and time interval between date tagged and date of last detection of rainbow trout, brown trout, and mountain whitefish redetected in the upper Missouri River, Sun River, and Smith River from 2010 to 2020.

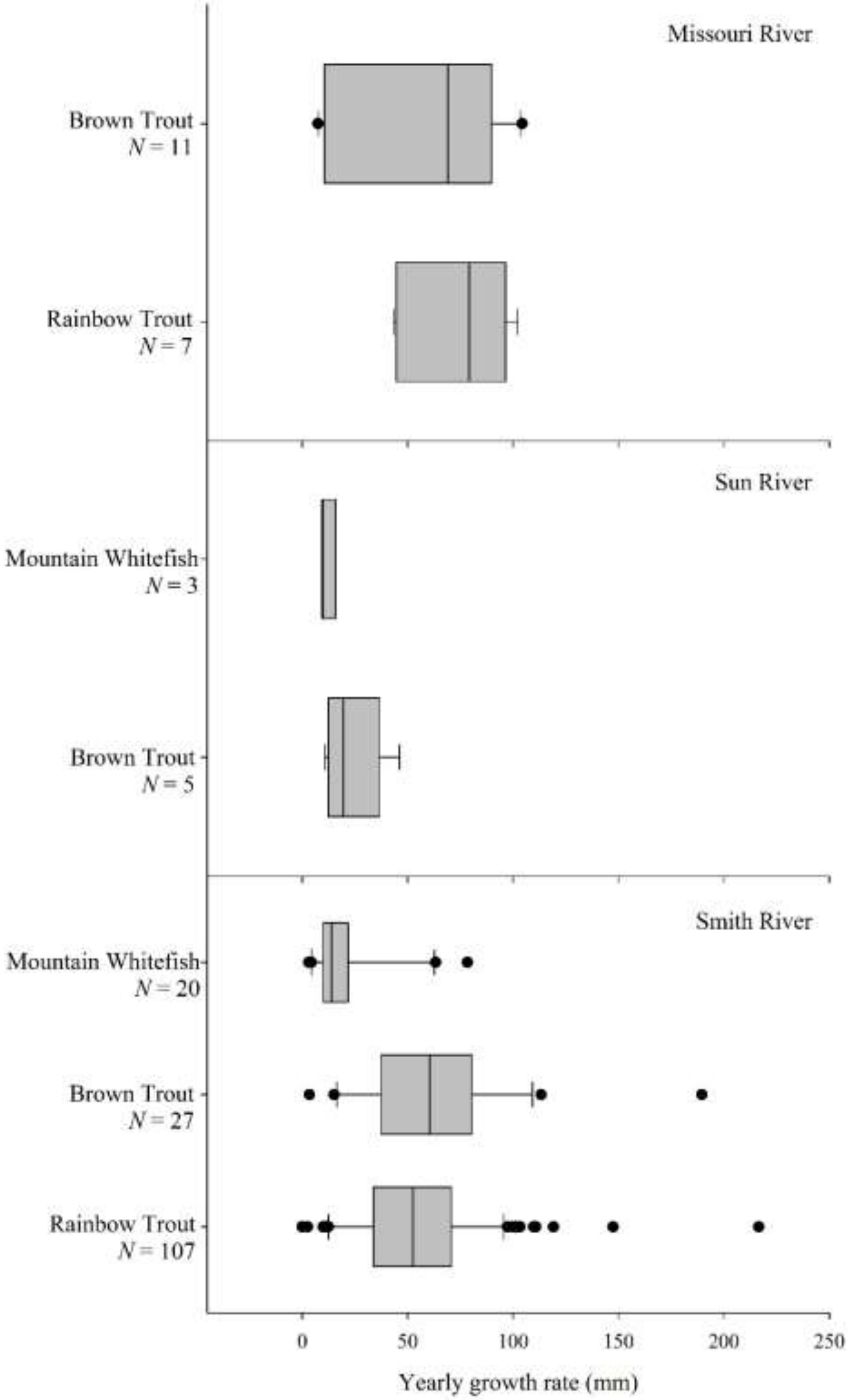


Figure 4.6. Yearly growth rates of rainbow trout, brown trout, and mountain whitefish recaptured, measured, and weighed in the upper Missouri River, Sun River, and Smith River from 2014 to 2020.

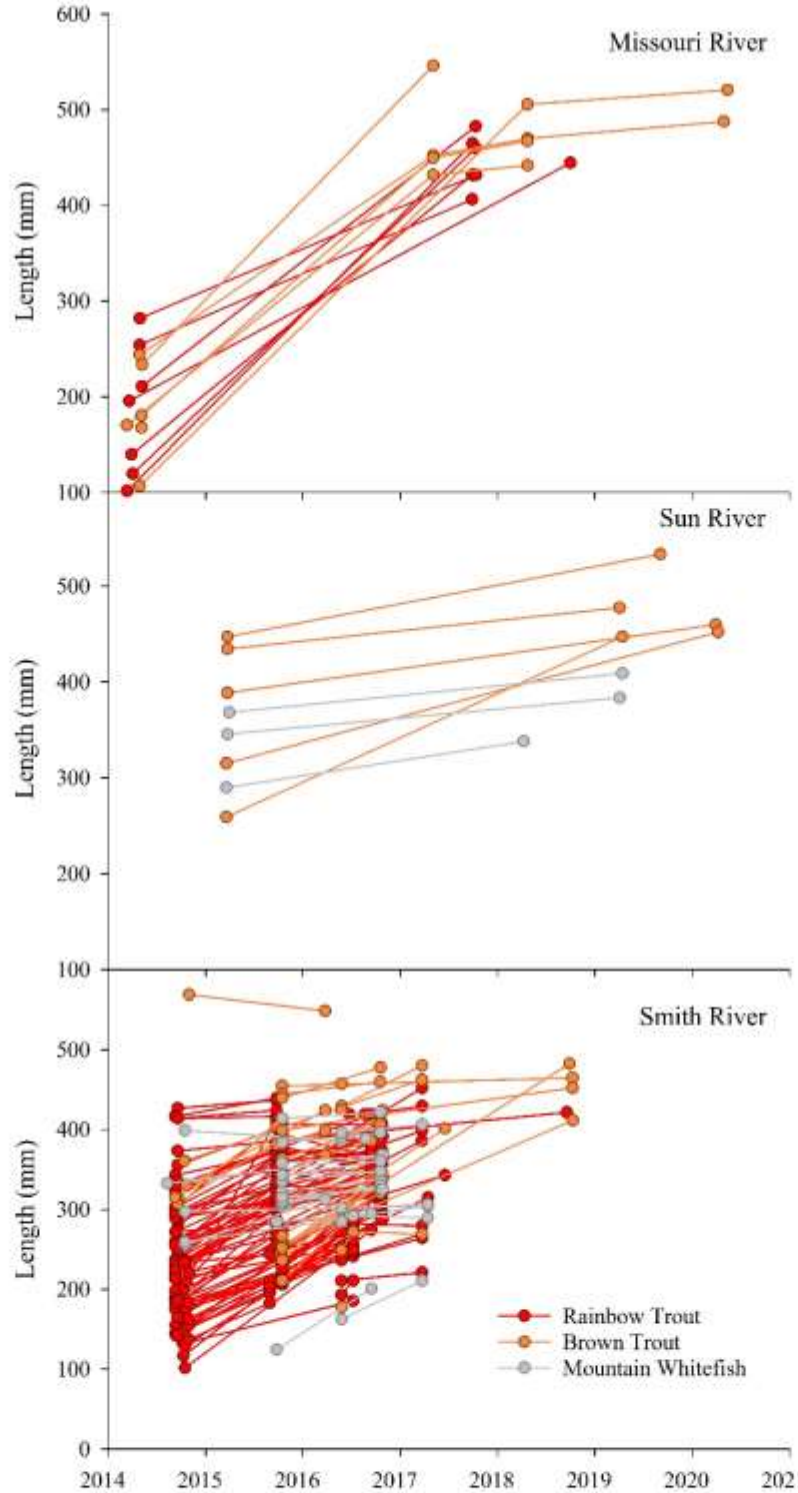


Figure 4.7. Growth curves of rainbow trout, brown trout, and mountain whitefish recaptured, measured, and weighed in the upper Missouri River, Sun River, and Smith River from 2014 to 2020 from initial tagging date to date of final recapture.

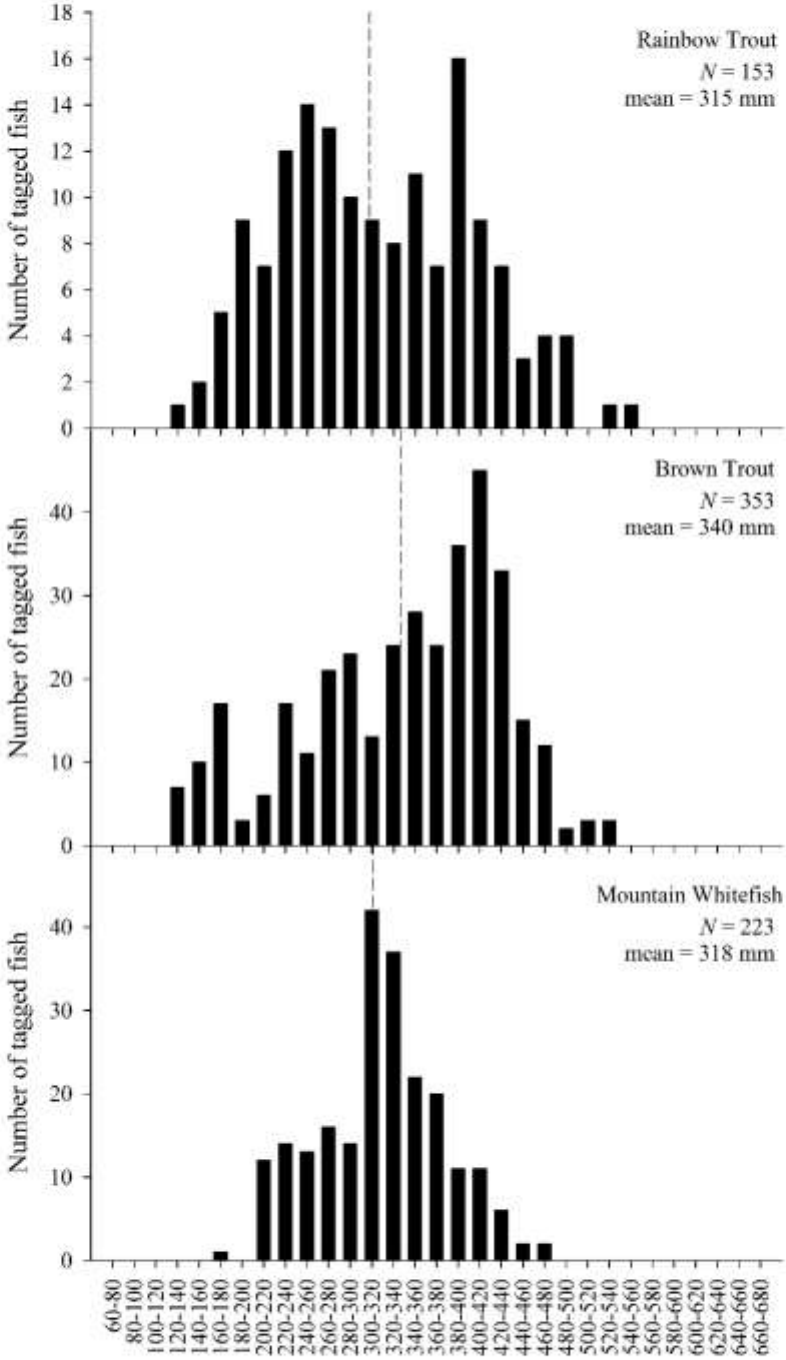


Figure 4.8. Length-frequency distributions of rainbow trout, brown trout, and mountain whitefish captured and tagged in the Sun River in 2015.

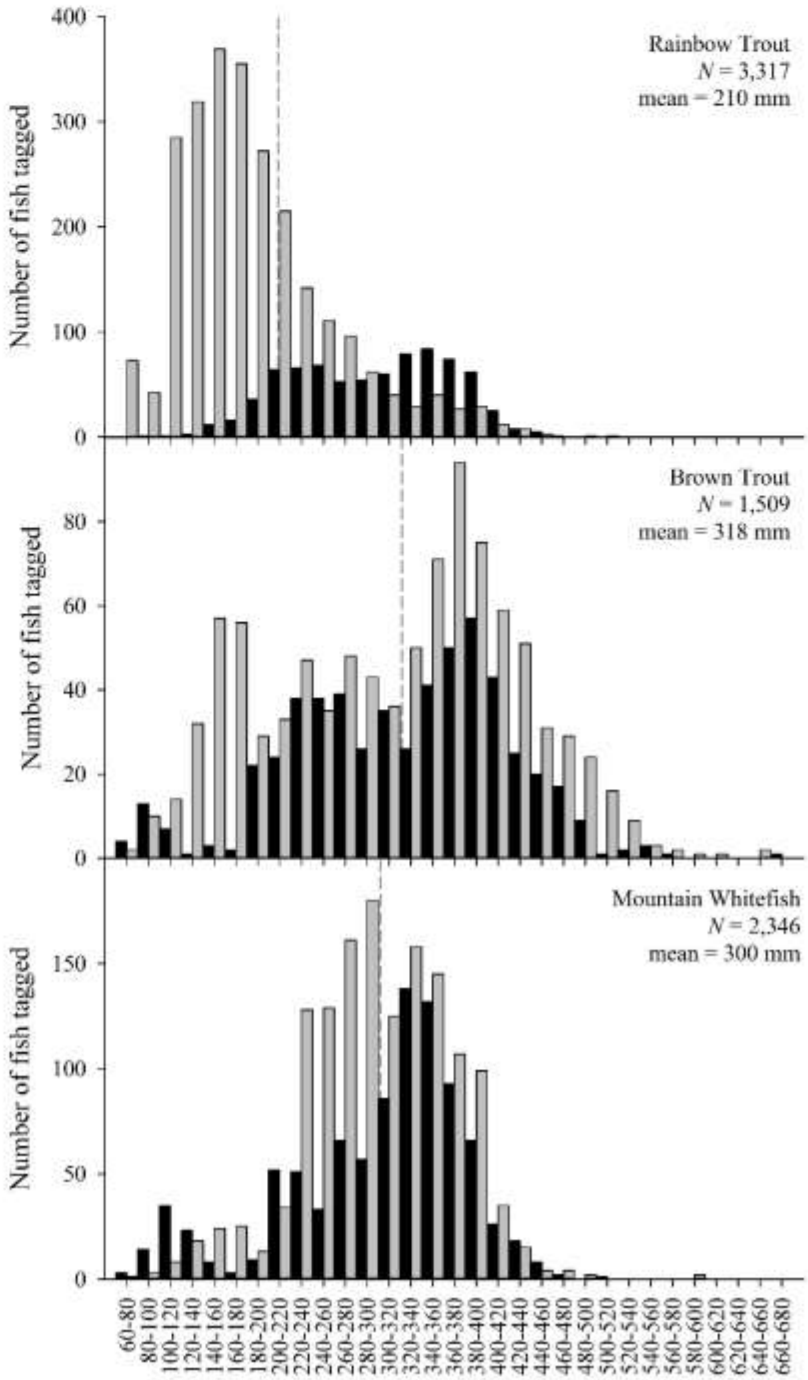


Figure 4.9. Length-frequency distributions of rainbow trout, brown trout, and mountain whitefish captured and tagged in the Smith River and its tributaries from 2010 to 2017. Gray bars represent fish tagged in tributaries whereas black bars represent fish tagged in the mainstem river.

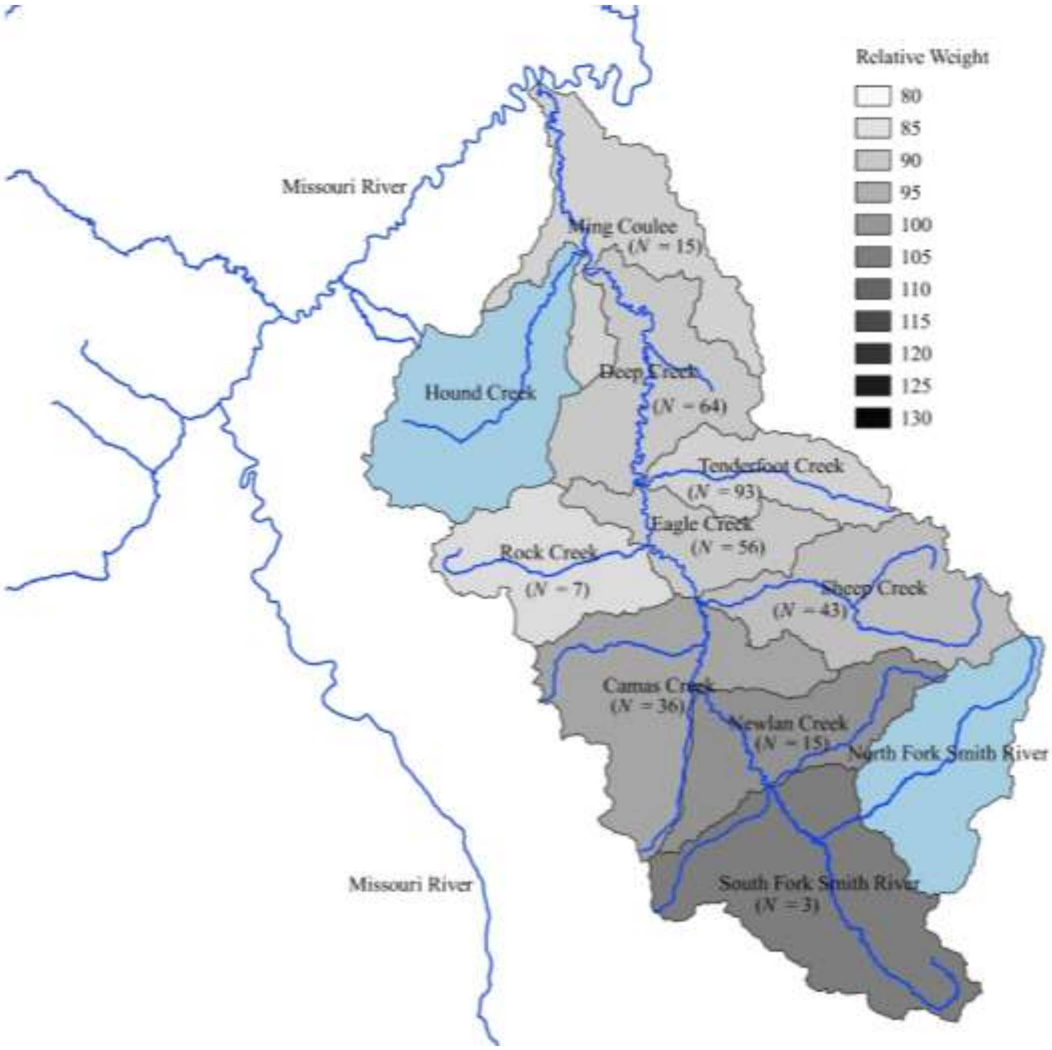


Figure 4.10. Relative weights of rainbow trout captured, measured, and weighed by tagging location (watershed) from 2010 to 2018 in the Smith River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

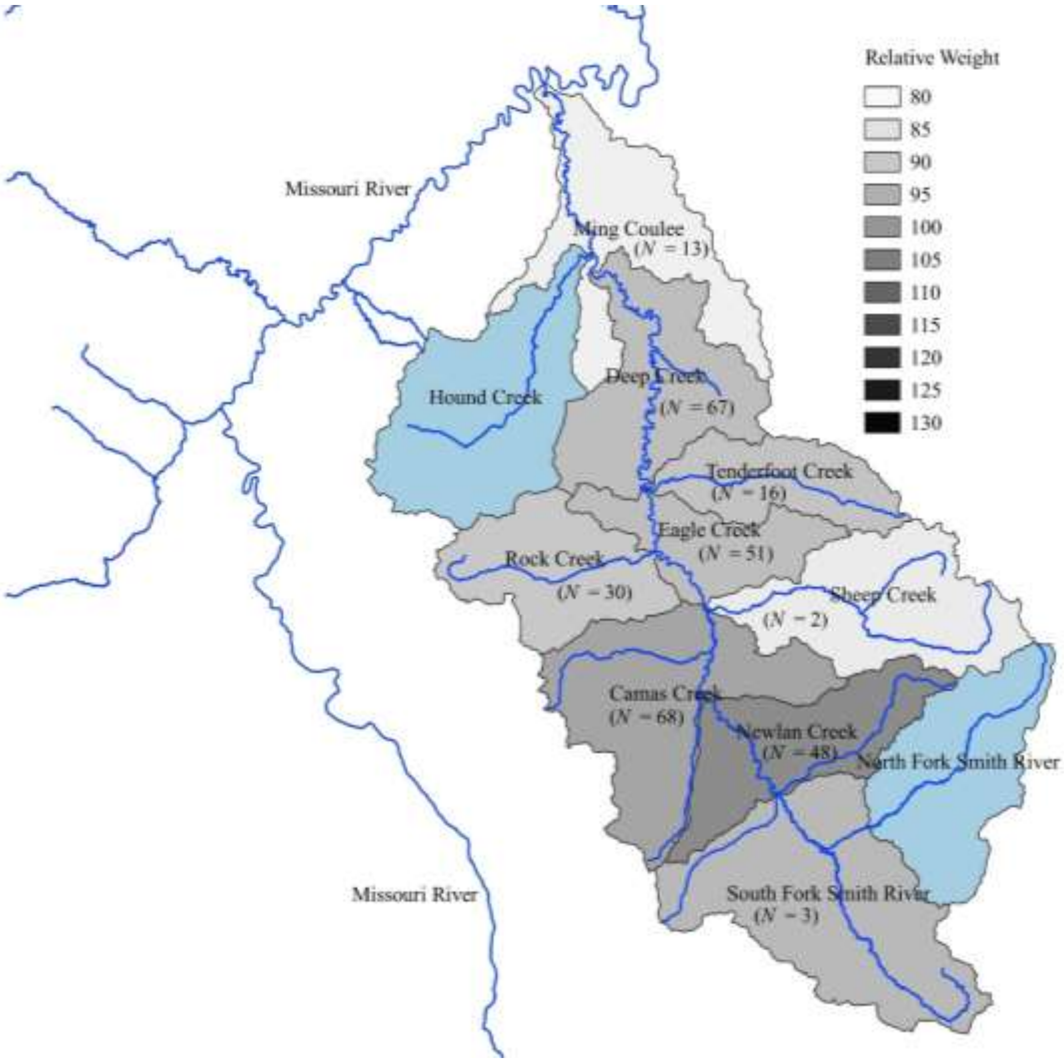


Figure 4.11. Relative weights of brown trout captured, measured, and weighed by tagging location (watershed) from 2011 to 2018 in the Smith River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

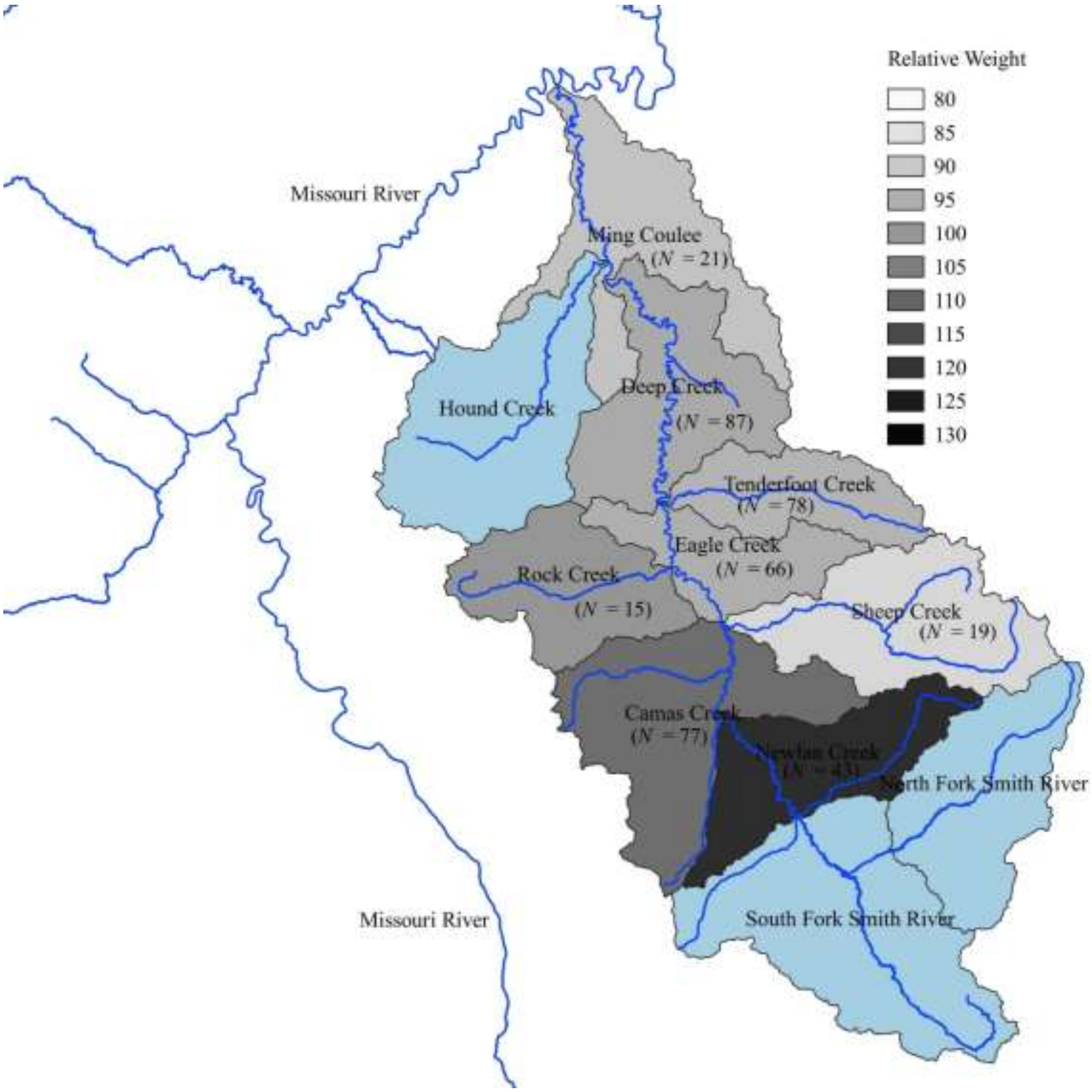


Figure 4.12. Relative weights of mountain whitefish captured, measured, and weighed by tagging location (watershed) from 2010 to 2017 in the Smith River subbasin. Proportion is represented by the gray gradient, with darker shades indicating a higher percentage. Light blue areas represent watersheds that were not part of the analysis.

CHAPTER FIVE

CONCLUSIONS

Life history patterns of salmonid populations in the upper Missouri River basin are diverse and vary among subbasins, watersheds, species, years, and seasons. This study provides further insights into such patterns, but a comprehensive understanding requires comparisons to complementary studies implementing an assortment of methodologies. Outmigration is influenced by a variety of abiotic factors that themselves vary considerably as components of a dynamic river system. Similar to previous studies on Missouri River tributaries, a bimodal outmigration pattern was observed in most streams and the outmigration often appeared related to changes in discharge. Outmigration occurred the earliest in the smallest streams, which may be an adaptive response to reduced habitat availability with a decrease in discharge in smaller streams. Although straying rates are lower than expected, spawning patterns are potentially more diverse than previously thought and suggest multiple life history patterns. This is further supported by the low incidence of outmigration movements. Minimum homing rates were generally greater than straying rates, but many fish could not be categorized or were unaccounted for and could have been tributary residents, mortalities, or undetected. Mainstem spawning patterns are probably more complex than those of tributary spawners, but sample sizes and the ability to monitor fish in the mainstem limits the ability to make conclusions. Growth rates in the upper Missouri River subbasin remain high, but longevity in the Smith River is highest relative to the upper Missouri River and Sun River. Inter-subbasin connectivity among fish populations does exist and likely contributes to an already diverse genetic composition, though the full extents of either are still unknown. The complexity in life history patterns of salmonids in the upper Missouri River basin probably contributes to the persistence and productivity of the fishery in the presence of highly variable environmental disturbances, including whirling disease. Maintaining and promoting this complexity requires management that facilitates connectivity at both spatial and temporal scales. Temporal variation in life histories suggests future studies would benefit from simultaneous application of multiple methodologies.

LITERTURE CITED

Al-Chokhachy, R., and P. Budy. 2008. Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709-1722. doi: 10.1577/t07-247.1

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66:912–918.

Armstrong, J., V. Braithwaite, and P. Rycroft. 1996. A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish. Journal of Fish Biology 48:539-541.

Armstrong, J. D., and N. A. Herbert. 1997. Homing movements of displaced stream-dwelling brown trout. Journal of Fish Biology 50:445-449.

Bartón, K. 2010. MuMIn: multi-model inference, 2010. R package version 1.

Baxter, C. V. 2002. Fish movement and assemblage dynamics in a Pacific Northwest riverscape. Doctoral dissertation. Oregon State University, Corvallis, Oregon.

Bellerud, B. L., S. Gunkel, A. R. Hemmingsen, D. V. Buchannan, and P. J. Howell. 1997. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon: 1996 annual report. Bonneville Power Administration, Portland, Oregon.

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

Bennett, S., R. Al-Chokhachy, B. B. Roper, and P. Budy. 2014. Annual variation of spawning cutthroat trout in a small western USA stream: a case study with implications for the conservation of potamodromous trout life history diversity. North American Journal of Fisheries Management 00:1-14.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference - understanding AIC and BIC in model selection. Sociological Methods & Research 33:261–304.

Chapman D. W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345-357.

Downs, C. C., Horan D., Morgan-Harris E., and R. Jakubowski. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management 26:190-200.

Dunham, J., and B. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications **9**:642-655.

Fox, J., and coauthors. 2012. Package ‘car’. Vienna: R Foundation for Statistical Computing.

Glaid, J. R. 2017. Subadult bull trout out-migration in the Thompson River drainage, Montana. Master’s thesis, Montana State University, Bozeman, Montana.

Gresswell, R. E.,W. J. Liss, and G. L. Larson. 1994. Life-history organization of Yellowstone Cutthroat Trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 51:298–309.

Grisak, G. G. 1999. Missouri River rainbow trout spawning study, Missouri River young of the year trout investigations II and Montana statewide whirling disease investigations. Progress report. Montana Fish, Wildlife & Parks, Bozeman, Montana.

Grisak, G. 2012. An evaluation of trout movements in the upper Smith River basin. Montana Fish, Wildlife & Parks, Great Falls, Montana.

Grisak, G., A. Strainer, and B. Tribby. 2012a. Rainbow trout and brown trout movements between the Missouri River, Sun River, and Smith River, Montana. Montana Fish, Wildlife & Parks, Helena, Montana.

Grisak, G., A. Strainer, and B. Tribby. 2012b. Rainbow trout spawning characteristics and relation to the parasite *Myxobolus cerebralis* in the Missouri River, Montana. Intermountain Journal of Science 18:6-19.

Grisak G., B. Tribby, T. Elam, and G. Madel. 2015. Missouri River – Holter Dam tailwater trout ageing. Montana Fish, Wildlife & Parks, Great Falls, Montana.

Hamann EJ, Kennedy BP (2012) Juvenile dispersal affects straying behaviors of adults in a migratory population. Ecology 93:733–740

Harcup, M. F., R. Williams, and D. M. Ellis. 1984. Movements of brown trout, *Salmo trutta* L., in the River Gwyddon, South Wales. Journal of Fish Biology 24:415-426.

Hilderbrand, R. H., and J. L. Kershner. 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho-Utah. Transactions of the American Fisheries Society 129:5.

Hogen D.M. & Scarnecchia D.L. 2006: Distinct fluvial and adfluvial migration patterns of a relict charr, *Salvelinus confluentus*, stock in a mountainous watershed, Idaho, USA. Ecology of Freshwater Fish. 15: 376–387.

Hollander, J., M. Verzijden, E. Svensson, and C. Brönmark. 2014. Dispersal and phenotypic plasticity. Pages 110-125 *in* L. A. Hansson and S. Åkesson, editors. Animal movement across scales, 1 edition. Oxford University Press, New York.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in northeastern Oregon. Transactions of the American Fisheries Society 137:869-880.

Jonsson B. & Ruud-Hansen J. 1985: Water temperature as a primary influence of timing of seaward migrations of Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 42:593–595.

Keefer, M. L., and C. C. Caudill. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24:333-368.

Kershner, J. L., J. E. Williams, R. E. Gresswell, and J. Lobon-Cervia, editors. 2019. Trout and char of the world. American Fisheries Society, Bethesda, Maryland.

Kleiber, C., A. Zeileis, and M. A. Zeileis. 2020. Package ‘AER’. R package version 1.2 4.

Lance, M. J. 2019. Spatial and temporal variability in movements and vital rates of sympatric salmonids in an unfragmented, inland watershed. Master’s thesis. Montana State University, Bozeman.

Leathe, S. A. 2001. An evaluation of juvenile trout production of Little Prickly Pear Creek and Dearborn River, Montana, using rotary screw traps. Montana Fish, Wildlife & Parks, Great Falls.

Leathe, S. A., D. L. Scarnecchia, and Y. Lim. 2014. Emigration patterns of age 0 and age 1 potamodromous rainbow trout Oncorhynchus mykiss and brown trout Salmo trutta from two Missouri River tributaries, Montana, USA. Journal of Vertebrate Biology 63:137-150.

Li, H., X. Deng, D.-Y. Kim, and E. P. Smith. 2014. Modeling maximum daily temperature using a varying coefficient regression model. Water Resources Research 50:3073-3087.

Mazerolle, M. J. 2016. Model Selection and Multimodel Inference Based on (Q)AIC(c). Documentation for R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Meka, J. M., E. E. Knudsen, D. C. Douglas, and R. B. Benter. 2003. Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. Transactions of the American Fisheries Society 132:717-732.

Meyer, K. A., D. J. Schill, F. S. Elle, and J. A. Lamansky. 2003. Reproductive demographics and factors that influence length at sexual maturity of Yellowstone cutthroat trout in Idaho. Transactions of the American Fisheries Society 132:183-195.

Meyer, K. A., F. S. Elle, and J. A. Lamansky. 2011a. Environmental factors related to the distribution, abundance, and life history characteristics of mountain whitefish in Idaho. North American Journal of Fisheries Management 29:753-767. doi: 10.1577/m08-015.1

Mohseni, O. and H. G. Stefan. 1999. Stream temperature/air temperature relationship: a physical interpretation. Journal of Hydrology 218:128-141.

Montana Fish, Wildlife & Parks. 2015. Statewide Angling Pressure Estimates for Waterbodies by Region and Drainage Sorted Alphabetically. Montana Fish, Wildlife & Parks, Helena, Montana.

Mullen, J., K. Vivian, and G. Grisak. 2017. Status report for Northwestern Energy FERC Project 2188. Montana Fish, Wildlife, & Parks, Great Falls, Montana.

Mullen, J., K. Vivian, and G. Grisak. 2018. Status report for Northwestern Energy FERC Project 2188. Montana Fish, Wildlife, & Parks, Great Falls, Montana.

Mullen, J., and K. Vivian. 2019. Status report for Northwestern Energy FERC Project 2188. Montana Fish, Wildlife & Parks, Great Falls, Montana.

Munro, A. R. 2004. Identification of life history variation in salmonids using otolith microchemistry and scale patterns: implications for illegal introductions and for whirling disease in Missouri River rainbow trout. Doctoral dissertation. Montana State University, Bozeman.

Nehring, B.R. and P.G. Walker. 1996. Whirling disease in the wild: the new reality in the Intermountain West. Fisheries 21(6):28-30.

Österdahl L. 1969: The smolt run of a small Swedish river. In: Northcote T.G. (ed.), Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver, Canada: 205–215.

Pavlov, D. S., E. A. Kirillova, and P. I. Kirillov. 2008. Patterns and some mechanisms of downstream migration of juvenile salmonids (with reference to the Utkholok and Kalkaveyem Rivers in northwestern Kamchatka). Journal of Ichthyology 48(11):937-980.

Pettit, S. W., and R. L. Wallace. 1975. Age, growth, and movement of mountain whitefish, *Prosopium williamsoni* (Girard), in the North Fork Clearwater River, Idaho. Transactions of the American Fisheries Society 104(1):68-76.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ripley, B., and coauthors. 2013. Package ‘mass’. Cran R 538.

Ritter, T. D. 2015. Connectivity in a montane river basin: salmonid use of a major tributary in the Smith River system. Master's Thesis. Montana State University, Bozeman, Montana.

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

Thompson, G. E., and R. W. Davies. 1976. Observations on the age, growth, reproduction, and feeding of mountain whitefish (Prosopium williamsoni) in the Sheep River, Alberta. Transactions of the American Fisheries Society 105(2):208-219.

Vincent, E. R. 1996. Whirling disease and wild trout: the Montana experience. Fisheries 21(6):32–33.

Vivian, K., and J. Mullen. 2017. 2015 Sun river drainage water temperature. Montana Fish, Wildlife, & Parks. Great Falls, Montana.

Vivian, K., and J. Mullen. 2018. American white pelican predation of upper Smith River fisheries. FERC Project 2188: Project 2017-20, Montana Department of Fish Wildlife and Parks, Great Falls, Montana.

Watschke, D. A. 2006. Assessment of tributary potential for wild rainbow trout recruitment in Hebgen Reservoir, Montana. Master's Thesis. Montana State University, Bozmean, Montana.

Zhang, D. 2018. rsq: R-squared and related measures. R package version 1.

Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492-502.

APPENDIX

Table A1. Summary statistics for top-ranked models for number of outmigrants of rainbow and Brown trout in Little Prickly Pear Creek and Dearborn River. Numbers in parentheses next to variables denote the categorical level within each variable. 'Num. mods' indicates how many of the top models and 'Importance' indicates the proportion of models each variable was included in. 'SE' is standard error and 'Adj. SE' is adjusted standard error.

Site	Species	Variable	Num. mod.	Importance	β	SE	Adj. SE	z	p
Little Prickly Pear	Rainbow Trout	Intercept	2	1.0	-1.10	0.26	0.26	4.15	< 0.001
		Photoperiod(2)	2	1.0	0.51	0.33	0.33	1.53	0.126
		Photoperiod(3)	2	1.0	-1.79	0.59	0.59	3.00	0.003
		Lunar phase(2)	1	0.5	0.03	0.18	0.18	0.18	0.861
		Lunar phase(3)	1	0.5	0.01	0.14	0.14	0.04	0.966
		Lunar phase(4)	1	0.5	0.08	0.27	0.27	0.30	0.763
	Brown Trout	Intercept	4	1.0	-2.70	0.39	0.39	6.847	< 0.001
		Photoperiod(2)	2	0.5	-0.02	0.38	0.38	0.063	0.949
		Photoperiod(3)	2	0.5	-0.95	1.16	1.16	0.820	0.412
		Lunar phase(2)	2	0.5	0.10	0.36	0.36	0.273	0.785
		Lunar phase(3)	2	0.5	0.01	0.28	0.28	0.048	0.961
		Lunar phase(4)	2	0.5	0.15	0.44	0.44	0.344	0.731
Dearborn	Rainbow Trout	Intercept	5	1.0	-2.16	0.45	0.45	4.749	< 0.001
		Photoperiod(2)	1	0.2	0.07	0.23	0.23	0.313	0.754
		Photoperiod(3)	1	0.2	-0.08	0.28	0.28	0.274	0.784
		Temperature(2)	1	0.2	0.04	0.27	0.27	0.138	0.890
		Temperature(3)	1	0.2	-0.02	0.28	0.28	0.075	0.940
		Temperature(4)	1	0.2	0.10	0.33	0.33	0.312	0.755
		Temperature(5)	1	0.2	0.15	0.41	0.41	0.376	0.707
		Discharge(2)	1	0.2	-0.12	0.38	0.38	0.316	0.752
		Discharge(3)	1	0.2	-0.08	0.30	0.30	0.260	0.795
		Discharge(4)	1	0.2	-0.11	0.38	0.38	0.290	0.772
		Discharge(5)	1	0.2	-0.16	0.54	0.54	0.301	0.763
		Lunar phase(2)	1	0.2	-0.06	0.26	0.26	0.210	0.834
		Lunar phase(3)	1	0.2	0.02	0.14	0.14	0.170	0.865
		Lunar phase(4)	1	0.2	-0.02	0.18	0.18	0.108	0.914

Table A2. Summary statistics testing for dispersion for each site × species combination. Bold *P*-values indicate when a negative binomial was used instead of a poisson distribution. ‘Dispersion’ is the estimate of dispersion for each global model.

Site	Species	Dispersion	*z*	*P*
Little Prickly Pear Creek	Rainbow Trout	1.75	3.41	< **0.001**
	Brown Trout	0.94	-2.16	0.985
Dearborn River	Rainbow Trout	1.13	1.12	0.131

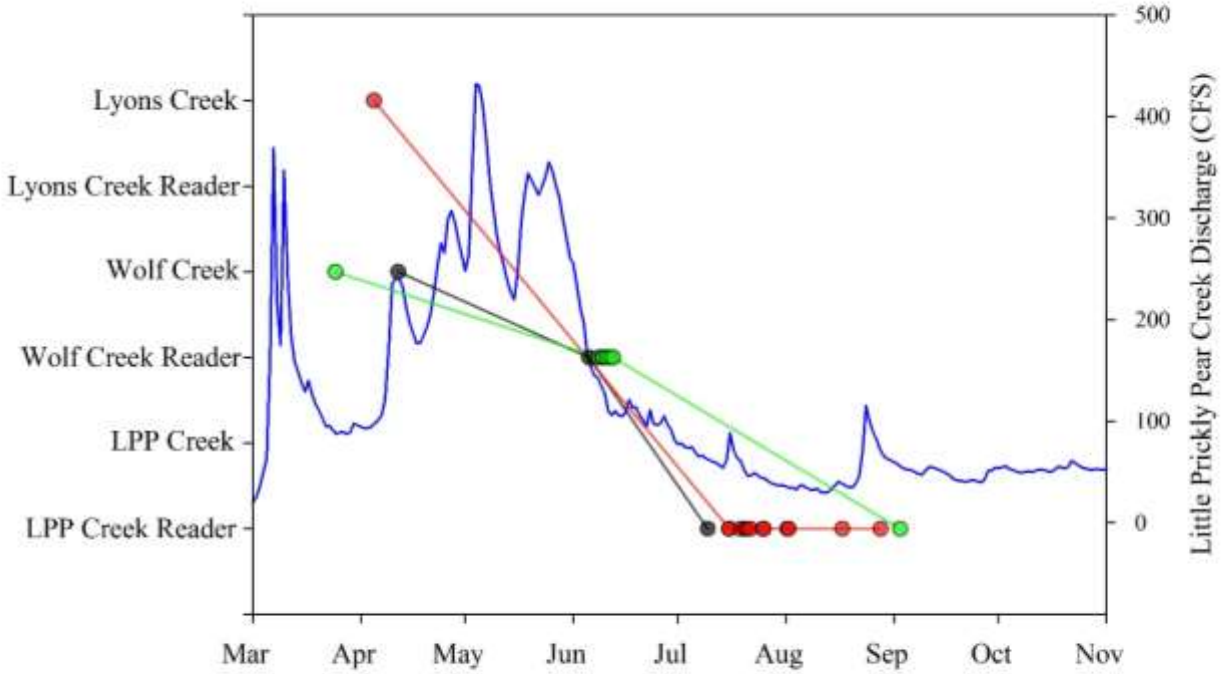


Figure A1. Common patterns of outmigration observed in rainbow trout tagged in Lyons and Wolf creeks in 2014. Black lines represent the most frequent outmigration pattern characterized by a relatively fast rate of migration. Green lines represent individuals that exited Wolf or Lyons Creek first, then remained in Little Prickly Pear Creek for some time before migrating to the Missouri River. Red lines represent individuals that were repeatedly detected on the Little Prickly Pear Creek antenna array at the confluence with the Missouri River before finally entering the main stem river. Blue lines represent discharge of Little Prickly Pear Creek at the USGS gaging station.

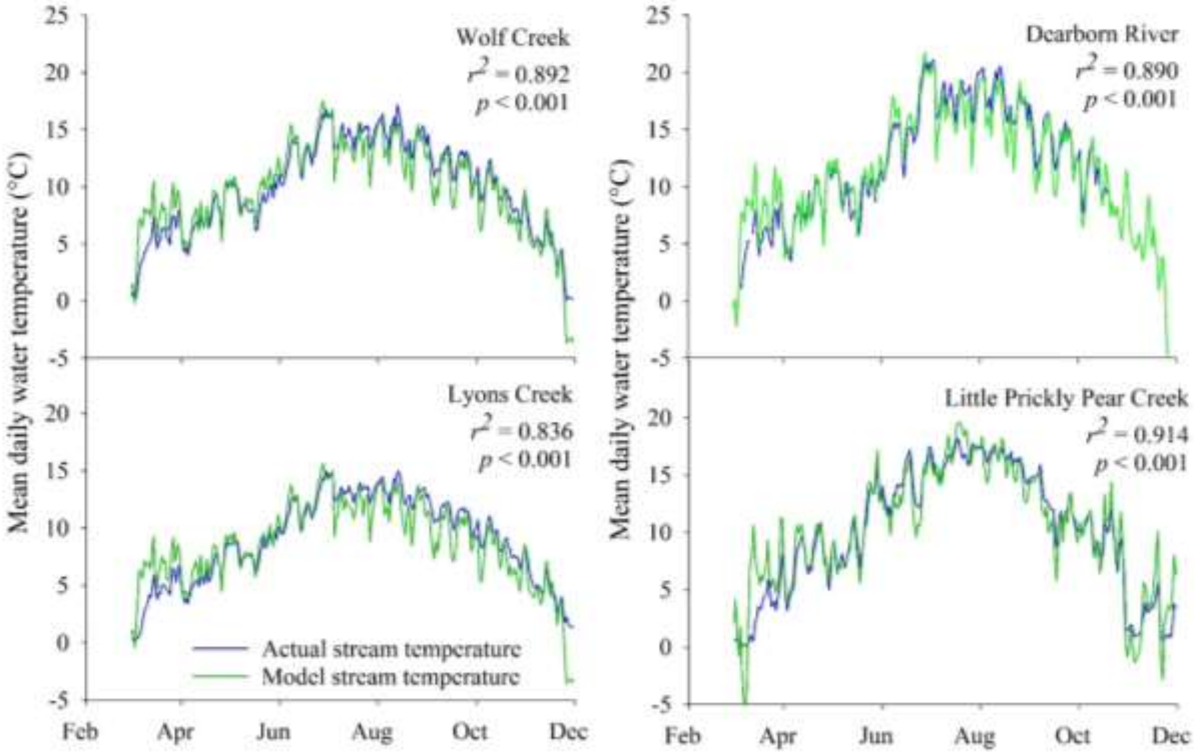


Figure A2. Comparisons of measured mean daily water temperatures and estimated mean daily water temperatures for Wolf and Lyons creeks and the Dearborn River from March 1 to November 30, 2015 and for Little Prickly Pear Creek from March 1 to November 30, 2003. Solid blue lines represent measured mean daily water temperatures whereas solid green lines represent estimated mean daily water temperatures.

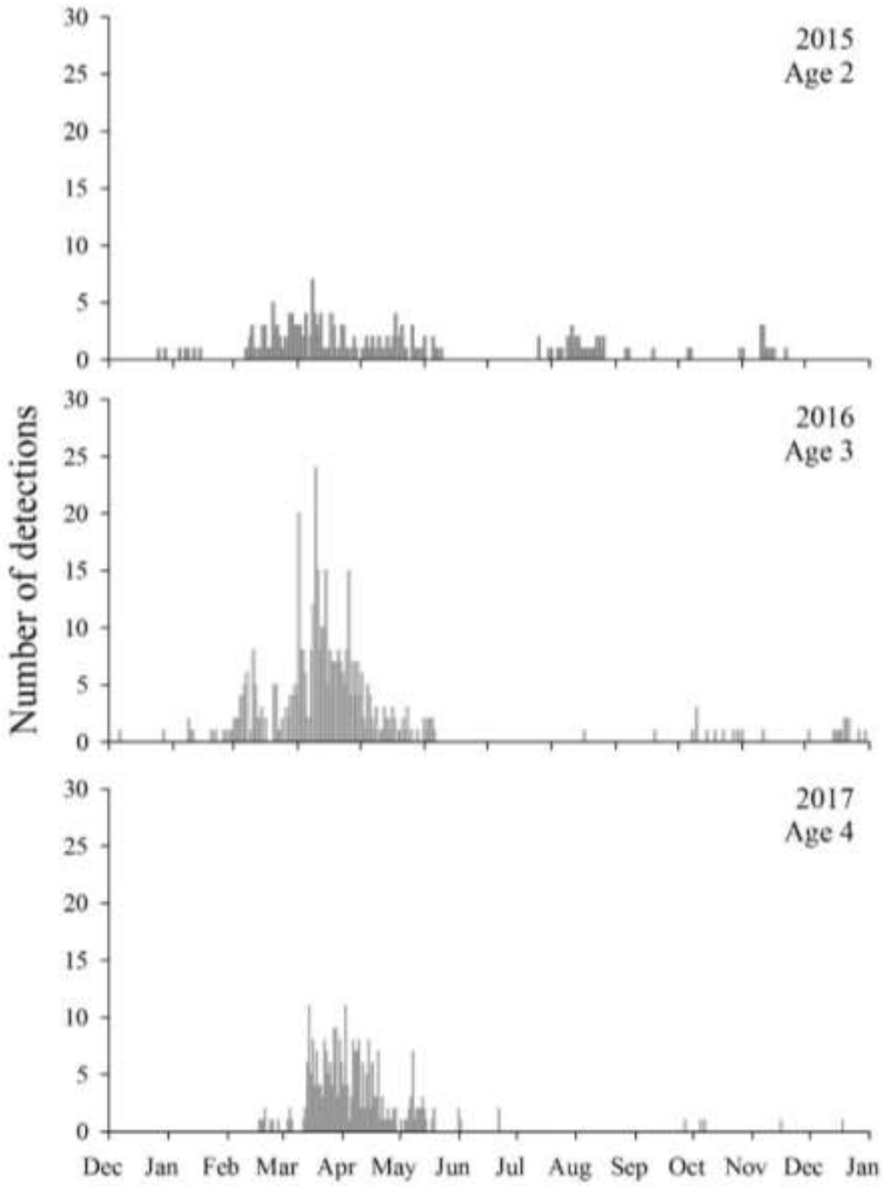


Figure A3. Detections of PIT-tagged rainbow trout tagged in Upper Missouri River tributaries in 2014 on all upper Missouri River PIT antennas. Individuals that were classified as outmigrants in 2015 were excluded from the 2015 graph.

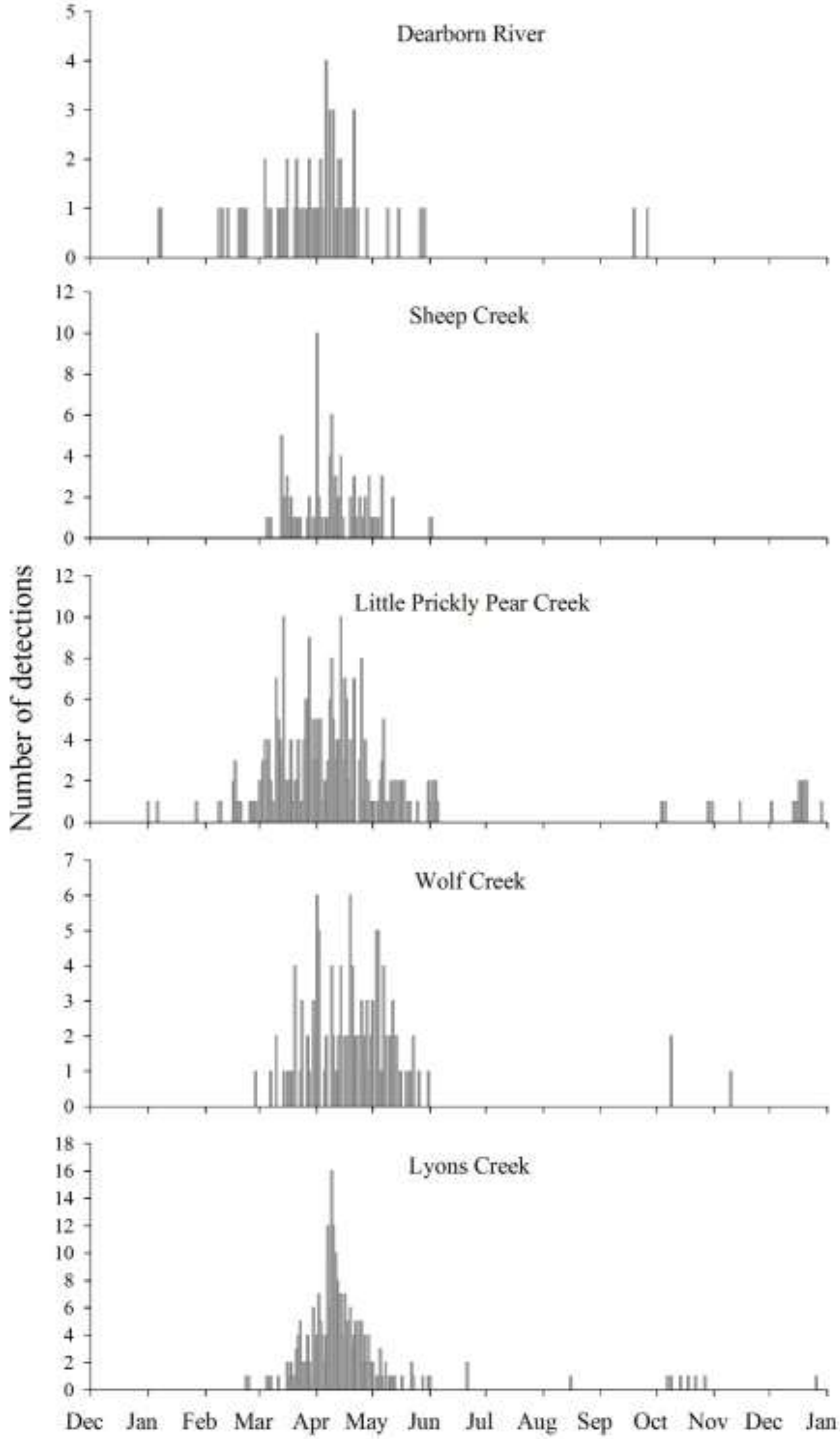


Figure A4. Detections of mature rainbow trout (age 3+, >300 mm at tagging) on upper Missouri River tributary PIT antennas from 2016 to 2018.