CONNECTIVITY IN A MONTANE RIVER BASIN: SALMONID USE OF A MAJOR TRIBUTARY IN THE SMITH RIVER SYSTEM

by

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DEDICATION

I dedicate this thesis to my family. To my parents, Tom and Cathy, who not only raised me properly, but were my first teachers; you lead by example, instruction, and encouragement. To my partner in crime, Christopher, who provides advice and friendship as only a brother can. Words cannot express my gratitude. No matter what path I choose, you provide undying love, support, patience, and confidence that I can succeed. “If you don’t know where you’re going, you might not get there.” (Yogi Berra, “When You Come to the Fork in the Road, Take It!” 2002).

Thanks to you, I’m finally there.

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ABSTRACT

The Smith River is a popular recreational sportfishery in western Montana, but salmonid abundances there are relatively low and limited by high summer water temperatures and low discharges. Smith River tributaries may serve as thermal refuges and also as important spawning and nursery areas. Tributaries unaltered by anthropogenic disturbances may be especially important. If so, maintaining connectivity between the main-stem river and its tributaries would be essential. Moreover, an understanding of salmonid habitat use and management in a stressed system could help identify potential climate change adaptation strategies and tactics. My goal was to determine the roles of a major undisturbed tributary in the life histories and movements of salmonids in a montane river basin. My focus was on Tenderfoot Creek, a remote, unaltered major tributary to the Smith River. A PIT-tag detection network monitored the seasonal movements of rainbow × cutthroat hybrid trout, Mountain Whitefish, Brown Trout, and Brook Trout. Abundances were estimated by electrofishing and snorkeling. Despite thermally stressful conditions in the Smith River, no tagged fish were directly observed using Tenderfoot Creek as a thermal refuge, although such use probably occurred at the confluence within the Smith River. Interchange between Tenderfoot Creek and the Smith River was common for Brown Trout, Mountain Whitefish, and rainbow × cutthroat hybrid trout and consisted mostly of spawning migrations. Some large, presumably dominant Brown Trout appeared to establish permanent territories within Tenderfoot Creek. Spawning effort by Mountain Whitefish and rainbow × cutthroat hybrid trout was high; about 7,568 Mountain Whitefish were observed in spawning aggregations in autumn and estimated abundance of rainbow × cutthroat hybrid trout juveniles ($\hat{N}$ = 25,127) was much higher than that of other taxa. Brown Trout also spawned in Tenderfoot Creek (159 redds counted in 2011 and 2012), and Brook Trout spawned in side channels and tributaries. Tenderfoot Creek is heavily used by Smith River fishes for spawning; maintaining its connectivity and habitat quality is therefore beneficial to recruitment to the Smith River fishery.

INTRODUCTION

Human water management has altered and fragmented riverine ecosystems on a global scale (Nilsson 2005). Over half of the world's major rivers have been affected by dams (Nilsson 2005), and in the United States, 98% of all streams have been physically altered by dams or irrigation diversions (Benke 1990; Pringle 2001). Such fragmentation has been associated not only with the decline of highly migratory fishes, particularly anadromous species such as Chinook Salmon *Oncorhynchus tshawytscha*, steelhead *Oncorhynchus mykiss* (Nehlsen et al. 1991; Kareiva et al. 2000), Green Sturgeon *Acipenser medirostris* (Mora et al. 2009), and American Shad *Alosa sapidissima* (Beasley and Hightower 2000), but also potadromous fishes such as Paddlefish *Polyodon spathula* (Zigler et al. 2004), Colorado Pikeminnow *Ptychocheilus lucius* (Osmundson 2010), and Bull Trout *Salvelinus confluentus* (Rieman et al. 1997). Maintenance and restoration of hydrologic connectivity (the water-mediated transfer of matter, energy, or organisms within or between the elements of the hydrologic cycle; Pringle et al. 2001) in river networks are therefore important to the conservation and management of fishes and fisheries (Van Kirk and Benjamin 2001; Bunn and Arthington 2002; Kondolf et al. 2006).

Many native salmonid species in the Mountain West have become fragmented and isolated as a result of reduced hydrologic connectivity, occupying only portions of their historical ranges (Shepard et al. 2005; Gresswell 2011). Such fragmentation and isolation have increased the susceptibility of these salmonids to human disturbance (Gresswell 2011). Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* occupy only 42% of their historical range (Gresswell 2011), and Westslope Cutthroat Trout

Oncorhynchus clarkii lewisii occupy 60% (Shepard et al. 2005). Bull Trout *Salvelinus confluentus* populations in the Bitterroot River drainage in western Montana that formerly exhibited large-bodied migratory forms now exist primarily as isolated headwater populations, increasing their risk of extirpation (Nelson et al. 2002). Accordingly, connectivity has been associated with predicted occurrence of salmonids (Dunham et al. 1997; Rich et al. 2003) and has therefore been identified as a primary conservation strategy (Gresswell 2011).

Salmonids can be highly mobile; anadromous species are well-known for their lengthy migrations (Nehlsen et al. 1991; Bisson 2009), but potadromous species also exhibit widespread movement and can perform extensive migrations (Gowan and Fausch 1996; Northcote 1997). Such movement was not generally recognized until relatively recently (Gowan et al. 1994; Northcote 1997). Salmonids require multiple habitat types throughout their life histories (Northcote 1997), often migrating great distances upstream from home ranges to spawning areas in small tributaries with specific substrate composition, water quality, and temperatures that maximize the survival of their offspring (Bjornn and Reiser 1991). Loss of connectivity affects access to these spawning areas (Rieman et al. 1997; Isaak et al. 2007) as well as to foraging and juvenile rearing grounds (Northcote 1997).

Areas unaltered by human development are especially important for spawning and rearing because they can provide high quality habitat (Suttle et al. 2004; Kauffman and Hughes 2006). Anthropogenic disturbance in watersheds and riparian zones adversely affects stream functions and processes that influence salmonid recruitment and survival (Kauffman and Hughes 2006; Waco and Taylor 2010; Tomlinson et al. 2011).

Agriculture and logging can increase sedimentation by reducing the effectiveness of riparian vegetation to trap sediment, stabilize banks, and prevent erosion (Kauffman and Hughes 2006). Increased fine sediment reduces the porosity of gravel streambeds, limiting oxygen availability to salmonid eggs in redds and entrapping emerging fry (Chapman 1988). High levels of fine sediment also reduce the growth and survival of juvenile salmonids by causing shifts in available prey (Suttle et al. 2004). Human development of riparian corridors can also alter stream thermal regimes by removing forest cover that blocks solar radiation (Tomlinson et al. 2011). Deforestation and construction of impervious surfaces such as roads and parking lots lower groundwater recharge and ultimately affect stream temperatures by reducing the amount of cool groundwater upwelling in the stream itself (Waco and Taylor 2010). Limiting human development in riverine ecosystems can therefore maintain fishery values (Tomlinson et al. 2011).

Reduction of hydrologic connectivity can also prevent seasonal access to areas of thermally suitable habitat. All salmonids are coldwater species; individuals may attempt to thermoregulate by occupying coolwater refugia when exposed to suboptimal or stressful thermal conditions (Kaeding 1996; Ebersole et al. 2001; Stevens and DuPont 2011). Temperature regimes in river systems vary longitudinally and water temperatures often increase in a downstream direction, generally as elevations decrease and channel widths increase (Vannote et al. 1980). The maximum temperature threshold for a given fish species, particularly a coldwater salmonid, may be located along this longitudinal gradient (McCullough 1999). For example, occurrence of Lahontan Cutthroat Trout in Nevada and Oregon was more likely in stream areas where water temperatures were cooler than 26 °C, and none were found where temperatures exceeded 28.5 °C (Dunham et al. 2003). Hydrologic connectivity ensures that stream-dwelling fish can access thermally suitable habitat

During the twentieth century, mean annual global air temperature increased 0.6 ºC (Solomon et al. 2007) and mean annual air temperature in the Rocky Mountains of the western United States increased by 1 ºC (Saunders et al. 2008). Consequently, the maximum temperature threshold, especially of coldwater species, has progressed upstream, changing and often reducing species distributions and resulting in extirpations (Eaton and Scheller 1996; McCullough et al. 2009; Issak et al. 2012). Average global air temperatures are predicted to increase 1-6 ºC in the next 50-100 years (Solomon et al. 2007) while suitable habitat for all trout is predicted to decrease 47% (Wenger et al. 2011). Maintaining connectivity to areas of thermal refuge such as coolwater tributaries can therefore be important, especially for salmonids in river systems of the U.S. Mountain West (Isaak et al. 2012).

Such concerns prompted Montana Fish, Wildlife and Parks to conduct a basin-wide study to evaluate the importance of maintaining connectivity in the Smith River drainage in western Montana. My study was a part of this larger investigation. Much of the Smith River lies within Smith River State Park, a 95-km river corridor that is accessible only by non-motorized watercraft. Noted for its remote canyon and scenery, Smith River State Park is a popular destination for recreational floaters. Because of its popularity, Montana Fish, Wildlife and Parks instituted a permit system in 1988 to limit the number of floaters. The Smith River is also renowned for its Brown and Rainbow Trout fisheries. However, salmonid abundances there are relatively low and thought to be limited by high summer water temperatures and reduced discharges resulting from water management practices such as irrigation withdrawals. Tributaries of the Smith River provide supplemental flows and may also serve as thermal refuges, spawning and nursery areas, and foraging grounds; Rainbow Trout migrated up to 147 km from the Missouri River upstream into the Smith River and its tributaries to spawn (Grisak et al. 2012). Accessible tributaries unaltered by anthropogenic disturbances may be especially important. Basic fishery inventories and redd counts of the Smith River's major tributaries have occurred in the past, but no comprehensive investigation of the roles that tributaries play in the life histories and movements of Smith River salmonid populations has been conducted. Understanding these roles would enhance management of salmonids in this system and elsewhere and could help identify deficiencies in the main-stem Smith River that could potentially be alleviated through habitat or water management. Furthermore, insights about the management of a thermally stressed and dewatered montane river system could help identify potential climate-change adaptation strategies and tactics.

My goal was to determine the roles of a major undisturbed tributary in the life histories and movements of salmonids in a montane river basin. My focus was on lower Tenderfoot Creek, a major unaltered tributary of the Smith River identified by Montana Fish, Wildlife and Parks as important for supplemental flows and potential salmonid recruitment and thermal refuge. My specific objective was to determine if this tributary was used by salmonids as a thermal refuge, spawning and nursery area, or both. I documented whether Tenderfoot Creek was used by salmonids and to what extent, primarily by monitoring their movements throughout Tenderfoot Creek and between

Tenderfoot Creek and the Smith River. I hypothesized that salmonids would move into Tenderfoot Creek to avoid high water temperatures in the Smith River during summer and to spawn during spring and autumn.

STUDY AREA

Tenderfoot Creek is a major tributary of the Smith River located in the Little Belt mountain range about 140 km north of Bozeman, Montana (Figure 1). Mean annual discharge of the Smith River at the USGS gauging station near Fort Logan, Montana, is 6.7 m^3/s (Figure 2). Tenderfoot Creek is a remote, largely undeveloped major tributary of the Smith River and is located about 26 km downstream of the beginning of Smith River State Park, a river corridor managed by Montana Fish, Wildlife and Parks that extends 95 km from the only put-in at Camp Baker downstream to the only take-out at Eden Bridge (Figure 1). The study area consisted of the lower 13.7 km of Tenderfoot Creek, extending from an impassable barrier to fish movement (Figure 3) at rkm 13.7 downstream to the confluence with the Smith River, with a drainage area of 11,960 ha (Figure 1).

The Tenderfoot Creek watershed is heavily forested, unaltered by agriculture, and largely unaffected by logging practices (Figure 4). Compared to the other major drainages (basin area > 10,000 ha) in the Smith River basin, the Tenderfoot Creek watershed has the highest proportion of forested area and second least proportion of agriculture (Figure 4). Additionally, the Tenderfoot Creek watershed contains the least amount of roads (Figure 5). About 13% of the Tenderfoot Creek watershed is made up by the Tenderfoot Creek Experimental Forest, which is used as a research area for landscape ecology and managed differently than conventional National Forest land; harvest of timber there is done only experimentally in an effort to evaluate sustainable logging practices (Flora and McCaughey 1998). Agriculture, urbanization, logging, and road density are generally negatively associated with fish species richness, salmonid abundance, water quality, and cover complexity, and contribute to high water temperatures and increased siltation, whereas the opposite is true for forested, undeveloped lands (Lenat and Crawford 1994; Pess et al. 2002; Opperman et al. 2005; Kauffman and Hughes 2006). Therefore, I expected Tenderfoot Creek and its watershed to provide high quality salmonid habitat.

A small lead and silver mine was operated intermittently from 1895 to 1903 near Miners Creek, one of the major tributaries of Tenderfoot Creek, (Roby 1950). The mine was abandoned because of low production (Roby 1950). Despite claims made for lead and silver, only copper carbonates and oxides were found when the mine was investigated in 1950 (Roby 1950) and the mine was determined not to be worth evaluating for potential environmental effects by the Montana Bureau of Mines and Geology (Hargrave et al. 2000). Effects of the mine on the Tenderfoot Creek ecosystem were therefore presumed to be negligible.

The geomorphology of Tenderfoot Creek is mostly canyon in its upper reaches and transitions to deep canyon closer to its confluence with the Smith River. The channel splits often from rkm 9.0 upstream to the upper extent of the study area but is primarily single from rkm 9.0 downstream to the confluence. Riffles and bluff pools dominate habitat unit composition, with maximum depths of bluff pools commonly reaching 2 m and occasionally 3 m at base flow. Substrate consists primarily of cobble and gravel and occasionally bedrock, especially in areas of deep canyon. Many side channels of Tenderfoot Creek are influenced by groundwater (cool water temperature and upwelling flow). Most of the tributaries to Tenderfoot Creek are intermittent. Bear and Coyote creeks are intermittent but have subsurface flows. Daisy Creek, Post Creek, Ditch Creek, Miners Creek, and Barrel Coulee are the only perennial tributaries, with all but Post Creek containing fish (Figure 1).

The fish assemblage of Tenderfoot Creek consists of Rocky Mountain Sculpin *Cottus bondi*, Mountain Sucker *Catostomus platyrhynchus*, Mountain Whitefish *Prosopium williamsoni*, Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutt*a, and rainbow × westslope cutthroat hybrid trout *Onchorhynchus mykiss* × *Onchorhynchus clarki lewisi*.

The study area was divided into 78 primary sampling units (length range 81-413 m; average length 179.6 m; Figure 1) based on stream morphology and location of tributaries. These primary sampling units identified where fish were tagged and subsequently relocated, as well as the areas surveyed by snorkeling.

Figures

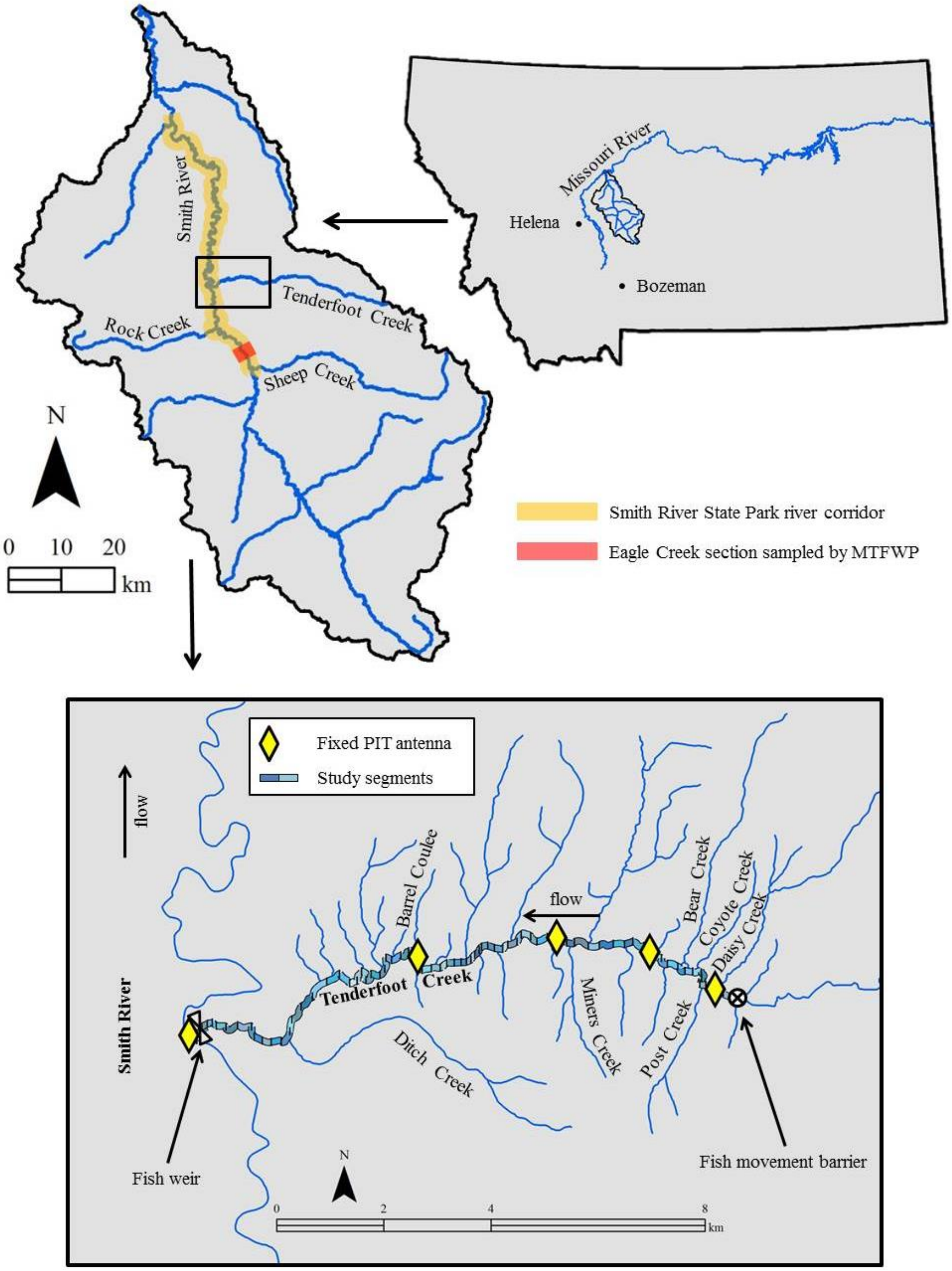

Figure 1. The Smith River, Montana, and its major tributaries and lower Tenderfoot Creek and its major tributaries. Yellow diamonds represent locations of fixed PIT antenna stations. Colors represent individual primary sampling units. Two temperature loggers were installed at each fixed PIT antenna station and two were installed in the Smith River 50 m upstream of the mouth of Tenderfoot Creek.

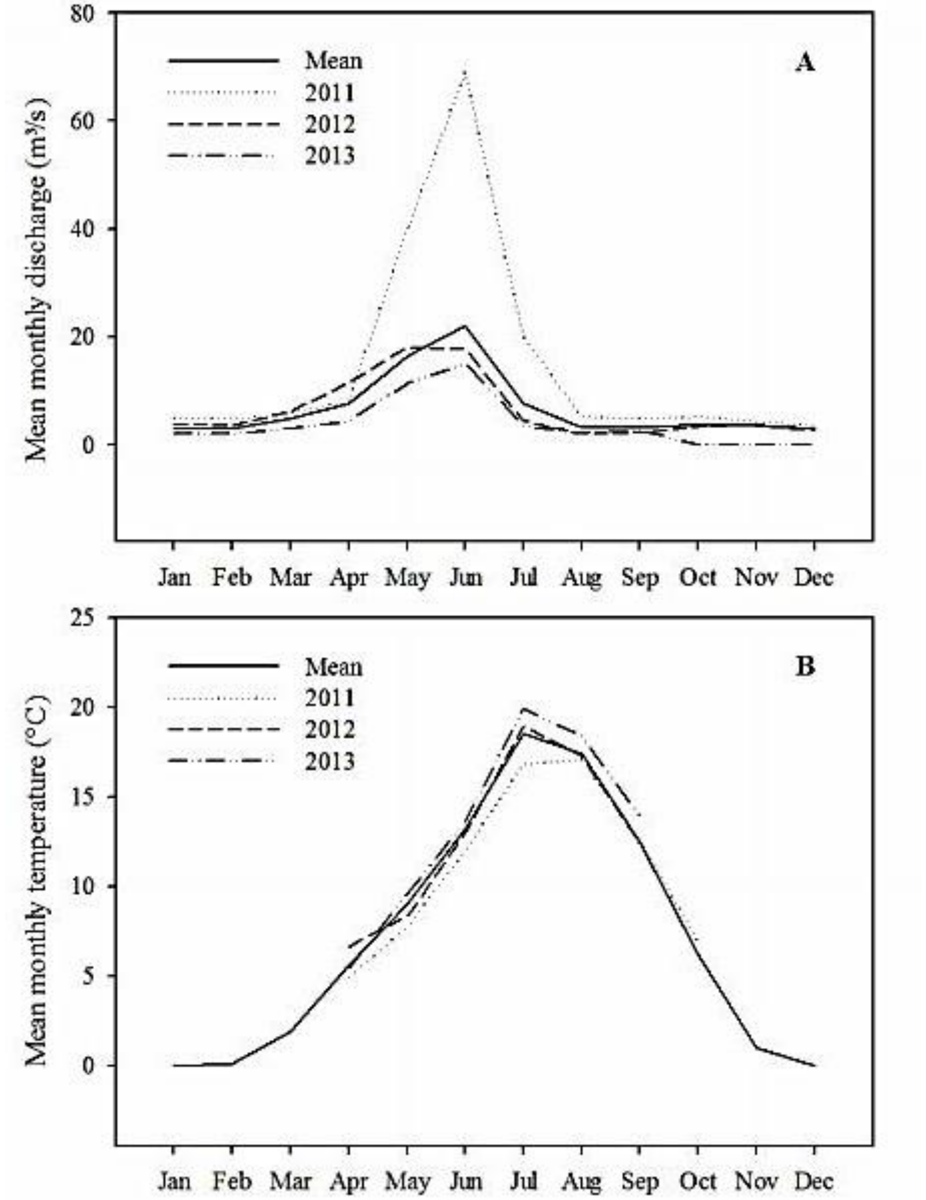

Figure 2. Mean monthly discharges (A) and mean monthly temperatures (B) of the Smith River during 2011, 2012, and 2013 and the overall mean from 1997 to 2013.

Figure 3. The 6-m high waterfall located at stream kilometer 13.7 of Tenderfoot Creek assumed to be an impassable barrier to fish movement.

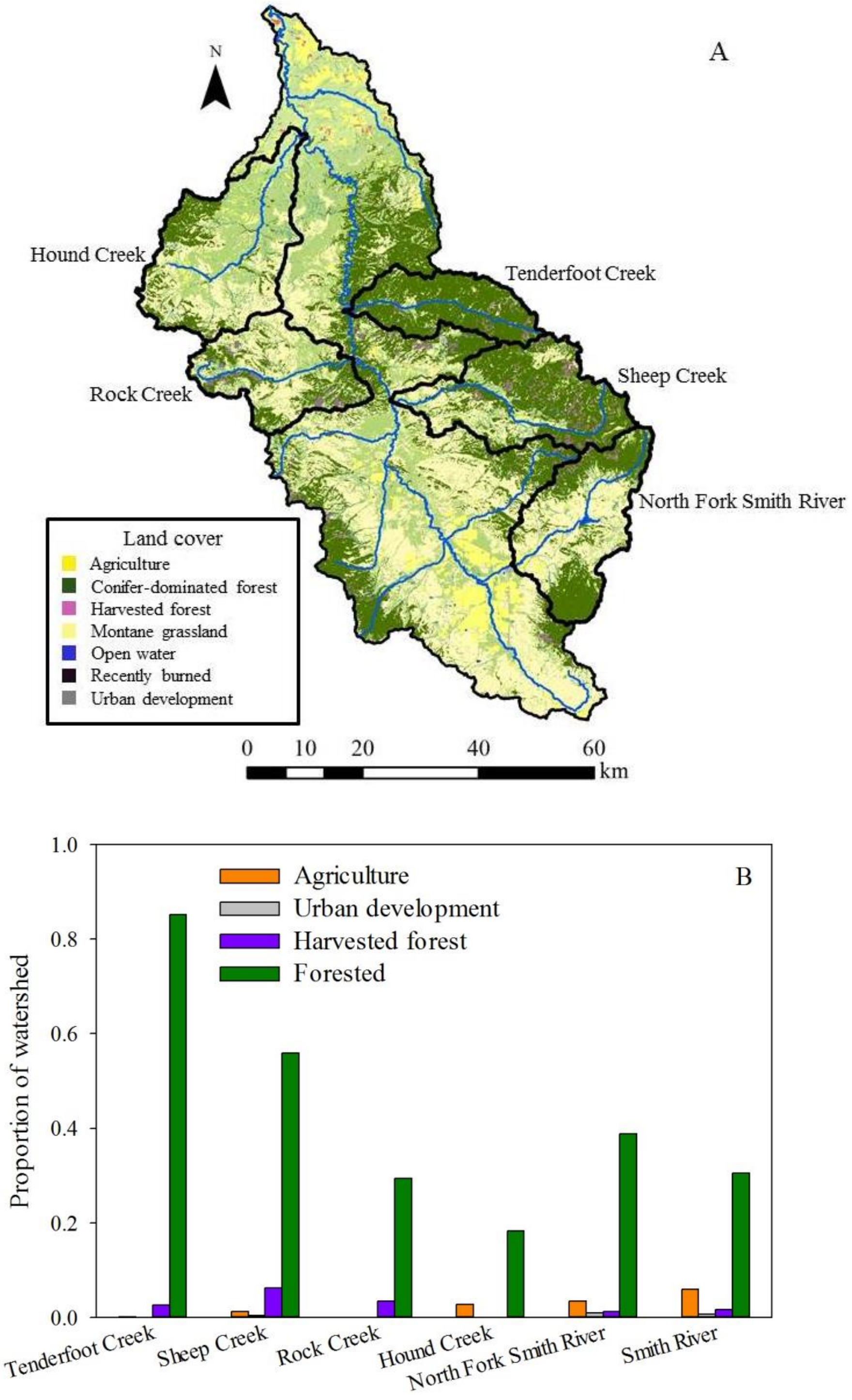

Figure 4. Land cover of the Smith River basin (A) and comparisons of proportions of land cover (B) among the Smith River and its major tributaries.

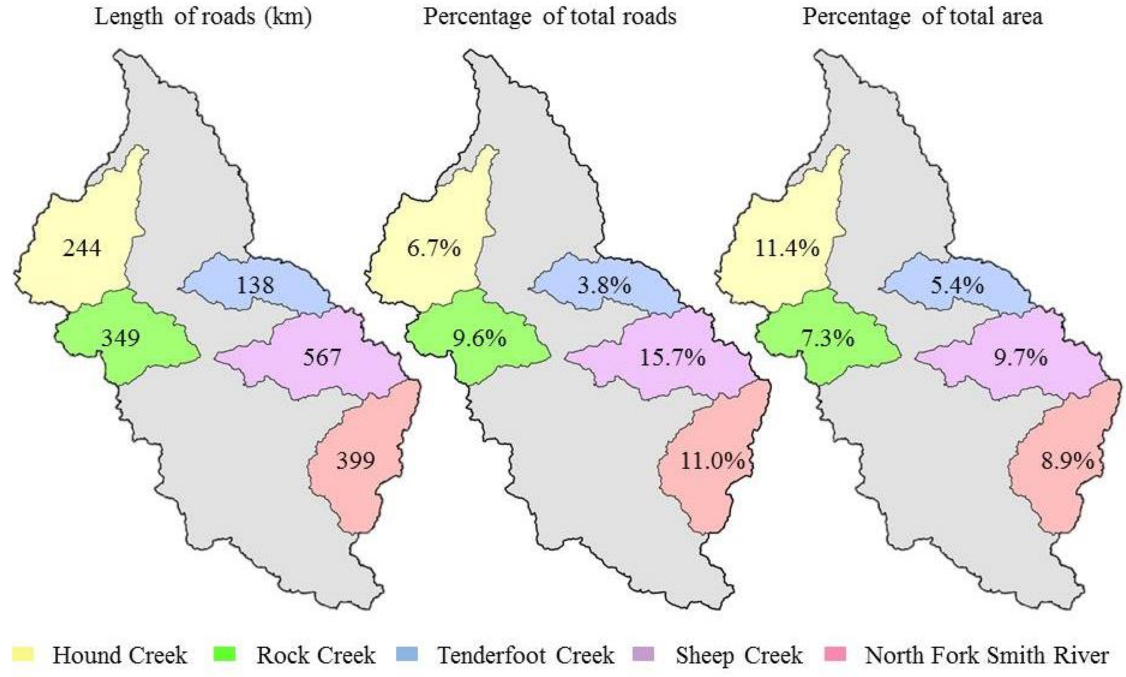

Figure 5. Comparisons of the length of roads (both paved and unpaved), percentage of total road length, and percentage of total area of the drainages of the major tributaries (basin area > 10,000 ha) in the Smith River basin.

METHODS

Lower Tenderfoot Creek (rkm 0.0 to 13.7) is a remote and undeveloped system. Ease and mode of access into the study area changed by season and dictated when field work could occur. Many of the methods proposed before the beginning of the study were modified or rejected later in favor of techniques more applicable to the steep, rugged, and remote terrain of the study area. Determining the most effective methods to accomplish my goals was an iterative process that progressed throughout the course of the study.

Water Temperature

A network of temperature loggers (Onset Computer Corporation, HOBO Pendant Temperature Data Logger, Bourne, Massachusetts) was installed to monitor water temperatures in Tenderfoot Creek and the Smith River. Two redundant loggers were installed at each fixed PIT (passive integrated transponder) antenna station (rkm 0.0, 6.6, 9.9, 11.6, and 13.5 of Tenderfoot Creek) and two loggers were installed in the Smith River 50 m upstream of the mouth of Tenderfoot Creek (Figure 1). Temperature loggers were enclosed in protective PVC cases and affixed to rebar using wire or to boulders using underwater epoxy (Simpson Strong-Tie Company, FX-764, Pleasanton, California). I also used data collected by the United States Geological Survey (USGS) at the gauge station just below Eagle Creek in the Smith River about 20.7 rkm upstream of the mouth of Tenderfoot Creek because deployment of loggers at the confluence (rkm 0.0) did not occur until July 28 in 2011 and July 12 in 2012. Additionally, temperature loggers in the

Smith River were often removed or displaced by recreational floaters, which resulted in the loss of temperature data in 2012.

I characterized the longitudinal distribution of water temperatures in Tenderfoot Creek. Temperature was measured at the upstream end of each of the 78 primary sampling units during snorkel surveys in late August of 2011 and 2012 (described below). A model estimating the water temperature in each of these units at 1900 hours was created for August 25-31 in 2011 using the nearest upstream temperature logger. A longitudinal temperature profile of Tenderfoot Creek at its approximate maximum daily water temperature was created using this model. Sixth-order polynomial regression lines were fitted to daily temperature curves ($r^2 > 0.95$) of HOBO temploggers for August 25-31, 2011. Measurements taken during the snorkel survey were used to adjust the y-intercept of the closest upstream temperature logger and create a daily temperature model for each of the 78 primary sampling units. The temperature at 1900 hours, the approximate time of maximum daily water temperature, was then estimated for each primary sampling unit using these models.

I used two temperature thresholds to identify thermally stressful conditions for salmonids in the Smith River and Tenderfoot Creek: the long-term upper incipient lethal temperature (UILT) and the upper growth limit temperature. I defined the long-term UILT, which is typically referred to as the ultimate upper incipient lethal temperature (UUILT), as the maximum temperature attainable by acclimation at which 50% of the test subjects survive in a laboratory setting for at least 30 days (Fry 1971; Elliott 1981; Kilgour 1985; Selong et al. 2001) (Table 1). The upper growth limit temperature is the maximum temperature at which growth occurs and usually coincides with lethargy and cessation of feeding (Selong et al. 2001; Bear et al. 2007) (Table 1). In general, these values tend to be almost identical (Selong et al. 2001; Bear et al. 2007) (Table 1). I used long-term UILT determinations in favor of more common 7-d UILT estimates because the longer duration of exposure allows for detection of delayed effects that would otherwise be missed in short-term tests (Bear et al. 2007). However, because long-term UILT estimates have not been determined for Brown Trout and Brook Trout, I estimated their long-term UILTs and upper growth limits by subtracting 3 °C from the short-term (7-day) UILT values, as long-term UILTs are 2 to 4 ºC lower than the 7-day values (Selong et al. 2001; Bear et al. 2007) (Table 1).

Snorkel Surveys

Snorkel surveys were performed in August 2011 and 2012 to determine late summer abundance, spatial distribution, and population structure of each salmonid taxon (Brook Trout, Brown Trout, rainbow × cutthroat hybrid trout, and Mountain Whitefish) in Tenderfoot Creek. The size and topography of Tenderfoot Creek made mark-recapture efforts and depletion electrofishing surveys inefficient and unsuccessful. The minimal equipment required for snorkeling (Thurow et al. 2013) made it an ideal sampling technique for the remote sampling locations and terrain of Tenderfoot Creek.

Primary sampling units were sampled beginning at the upper end of the study area (rkm 13.7) and progressing downstream to the confluence (rkm 0.0). Downstream snorkeling within each unit was selected in favor of random or upstream snorkeling because water depths and velocities in pools were too great to allow upstream or lateral movements (snorkelers often could not reach the bottom to maintain position or crawl upstream). Timing of snorkel surveys coincided with low flow and high visibility to ensure snorkeler safety and improve count accuracy. Surveys took place August 25-31 in 2011 and August 3-7 in 2012.

A single snorkeler recorded the number of each species in the following size classes in a single pass of each primary sampling unit on a PVC cuff secured to the snorkeler's arm: 0-100 mm, 100-199 mm, 200-299 mm, 300-399 mm, 400-499 mm, 500-599 mm, and greater than 600 mm (Thurow et al. 2013). Prior to surveying, snorkelers were trained to estimate sizes of objects underwater to adjust to the optical effects of underwater viewing (Thurow et al. 2013). The snorkeler also visually estimated the maximum depth of each primary sampling unit. Water velocity, temperature, and stream width were measured at the upstream end of each unit. Mean unit sampling duration was 16 min.

Two consecutive counts were made in seven randomly selected primary sampling units to evaluate consistency of counts. The mean difference in repeated fish counts was never more than 4 individuals per category (the mean numbers of fish counted in repeated units for < 100, 100-199, 200-299, 300-399, and 400-499 mm size categories were 10.4, 23.7, 29.8, 15.4, and 2.3, respectively) and tended to be higher for the 100-199 and 200-299 mm size classes (Figure 6). Estimated maximum depth profiles were longitudinally consistent between years, although discharge was higher during surveys in 2011 than 2012, which generally resulted in greater estimated maximum depths in 2011 (Figure 7).

PIT Tagging

Seven-hundred and sixty-three fish were tagged with half-duplex 32- or 23-mm PIT tags (Oregon RFID, Portland, Oregon) in Tenderfoot Creek and the Smith River from 2010 to 2012. Taxa tagged were Brook Trout, Brown Trout, rainbow × cutthroat trout hybrids, and Mountain Whitefish (Table 2). Fish were tagged throughout the study area, although topography and access often dictated exactly where fish were tagged (Figure 8). I tagged many fish at the confluence to investigate interchange of fish between Tenderfoot Creek and the Smith River (Figure 8). Fish were collected using a backpack electrofisher (Smith-Root, Inc., Model 12-B, Vancouver, Washington), angling, fish weir, and seine (Table 2) as described below. Fish were placed in perforated holding containers within Tenderfoot Creek following capture. Individual fish were then placed in containers with the anesthetic MS-222 (tricaine methanesulfonate; 50 mg/L) and monitored until locomotion ceased. Fish were measured, weighed, and tagged using a small scalpel coated with antiseptic (10% povidone-iodine solution). Total lengths of all tagged fish (measured to the nearest mm) were recorded as were weights (measured to the nearest g) of 498 tagged fish. Fish that measured at least 300 mm in length were tagged in the dorsal musculature with 32-mm PIT tags to improve retention (Dieterman and Hoxmeier 2009) (Figure 9). Fish 140 to 300 mm long were tagged in the peritoneal cavity with 32-mm PIT tags; fish 100 to 140 mm long were tagged in the peritoneal cavity with 23-mm PIT tags. Fish less than 100 mm long were not tagged and were released immediately to reduce stress; their counts, lengths, and numbers were not recorded. Incisions were small enough that slight resistance was felt when inserting the tags; incisions were not sutured to reduce handling time (Gries and Letcher 2002). PIT tags were soaked in antiseptic prior to insertion to prevent infection of the incision site. Following tagging, fish were placed in perforated recovery containers within Tenderfoot Creek and monitored until locomotion was restored. All tagged fish were additionally marked by trimming the adipose fin to identify them as tagged individuals (Figure 10). Trimming was preferred over clipping the entire fin to encourage regeneration of the fin (Thompson and Blankenship 1997). Additionally, complete removal of the fin is detrimental to swimming efficiency in turbulent water, as it may serve as a flow sensor (Buckland-Nicks et al. 2011).

Backpack Electrofishing

I tried to sample throughout the study area, but the size and depth of Tenderfoot Creek limited where electrofishing could be used efficiently and safely; pools deeper than 2 m could not be electrofished. Some primary sampling units were sampled more than once. The crew consisted of an electrofisher operator and a single netter. I tried to cover the entire reach using a zig-zag pattern but focused on good habitat, often electrofishing such areas more than once to maximize catch. The netter attempted to capture all salmonids longer than 100 mm. Electrofishing was discontinued if water temperatures reached 18 ºC to reduce stress on fish. Water conductivity ranged from 164 to 334 µs/cm. Electrofishing power ranged from 400 to 500 V, frequency ranged from 20 to 25 Hz, and the pulse width was 3 ms.

Angling

Much of the study area consisted of bluff pools in deep canyons. Angling was used to sample these deep canyon pools in Tenderfoot Creek and in the Smith River. The minimal equipment needed for fly-fishing makes it an ideal technique for sampling remote areas where access is limited. Angling crews consisted of two or three flyfishers. Flyfishers used 4- to 7-weight fly rods and were free to use any fly pattern. Barbs on hooks were pinched down to reduce physical injury to fish. We limited the playing time of hooked fish to reduce stress. Captured fish were held in perforated containers within the stream before being anesthetized, measured, and tagged. Angling was discontinued when water temperatures exceeded 18 ºC.

Confluence Fish Weir

An upstream-downstream fish weir located about 350 m upstream of the confluence with the Smith River was used to catch fish to be tagged and to determine seasonal movements of fish, particularly interchange between Tenderfoot Creek and the Smith River. The weir captured fish as they left the Smith River and entered Tenderfoot Creek, especially during the upstream spawning migrations of Mountain Whitefish and Brown Trout (Table 2). Commercial-grade snow fence was secured using T-posts anchored in the substrate in an X-shape (Figure 11). This configuration funneled fish as they moved upstream or downstream into steel box traps (Figure 12). The fish weir was operated for 4-7 days each month from July to October in 2011 and 2012 (Figure 11). The box traps were checked every 3 h during operation of the weir. The number of each species moving upstream or downstream was recorded. Captured fish were placed in holding containers prior to anesthesia, measurement, and tagging. Fish were released after recovery in the direction inferred by their capture at least 50 m from the trap in an effort to prevent immediate recapture.

Seining

A seine (6.1 m long × 1.8 m high with 0.6-cm mesh) was used to sample large schools of Mountain Whitefish that occupied deep pools in the lower 3 km of Tenderfoot Creek in autumn of 2011. Entire pools were seined, beginning at the upstream end and ending at the downstream end. Pool lengths and therefore seine hauls never exceeded 40 m. Care was taken to keep the lead line on the bottom and the ends close to the banks to prevent fish from escaping under or around the seine. Captured fish were placed in perforated holding containers within Tenderfoot Creek before being anesthetized, measured, and tagged

Fixed Antenna Stations

A network of five fixed antenna stations was constructed throughout the lower 13.7 km of Tenderfoot Creek at rkm 0.0, 6.6, 9.9, 11.6, and 13.5 to monitor the large-scale seasonal movements of PIT-tagged fish (Figure 1). I tried to distribute stations evenly throughout the study area, but access and topography often dictated the final location of each fixed station, particularly in the lower half of the study area (rkm 0.0 to 6.6) where deep canyons limited sunlight necessary to charge station batteries.

Antenna stations consisted of a PIT-tag reader (Oregon RFID, multi-antenna HDX reader, Portland Oregon), two stream-width antennas, and a tuning board for each antenna (Oregon RFID, standard remote tuner board, Portland, Oregon). Each station was powered by one or two 12-V deep-cycle batteries. Batteries were charged by two or three solar panels ranging from 30 to 65 W. Maximum-efficiency solar controllers (Morningstar Corp., Sunsaver MPPT 15, Newtown, Pennsylvania) were used to optimize the limited available sunlight in the deep canyon of Tenderfoot Creek. A pair of stream-width antennas was positioned at each site about 3 m apart to infer direction from sequential detections (Armstrong et al. 1996; Connolly et al. 2008; Lucas et al. 1999; Zydlewski et al. 2006). Antennas were oriented flat on the bottom of the stream in areas of shallow depth and high velocity, such as riffles, where fish were unlikely to hold for long periods of time (Armstrong et al. 1996). A flat-bed orientation was selected in favor of a vertical, circular placement for ease of installation and to withstand high flow events (Armstrong et al. 1996; Johnston et al. 2009). Antenna wire (fine-stranded power cable or speaker wire, Raptor Wire, 8-10 AWG, Holly Hill, Florida) was buried 5-10 cm beneath the surface of the substrate to avoid displacement (Johnston et al. 2009). Antennas were tuned for optimal tag detection range by measuring inductance and adjusting tuning capacitors on the tuner boards accordingly. Antennas were considered sufficiently tuned when tag detection range exceeded water depth at base flow, or about 0.3 m. Recorded detections were uploaded every 2 weeks to a laptop computer. Tag detection range was evaluated during each upload and adjusted if necessary.

The stations operated in some combination from 2010 to 2013, primarily during summer when sunlight was most abundant (Figure 13), which allowed complete monitoring of any movement related to thermoregulation. Additionally, the station at rkm 9.9 was maintained by snowmobile and operated from January 8 to April 1 of 2012 and

January 25 to February 9 of 2013, providing some insight into winter movement or lack thereof (Figure 13). Two stations (rkm 0.0 and 9.9) were operated during the spring of 2013 from April 4 to May 31 (Figure 13), which allowed monitoring of spawning migrations of rainbow × cutthroat hybrid trout.

Portable Antenna Surveys

Portable antenna surveys were conducted to complement the network of fixed antenna stations. Fixed antenna stations passively monitored large-scale seasonal movements but did not detect presence elsewhere or movement on a finer scale. Portable antenna surveys allowed me to actively relocate fish between stations and monitor fine-scale movements. Relocations were recorded by primary sampling unit. Two portable antenna designs were used: a two-handed rectangular antenna operated by a wader (Figure 14), and a completely submersible unit operated by a snorkeler (Figure 15). Existing antenna designs (Hill et al. 2006) were too small for the topography and size of Tenderfoot Creek; most were designed for small, headwater streams (Hill et al. 2006). A two-person design described for use on a bigger system, the Big Hole River, Montana (S. Vatland, Montana State University, personal communication), was considered but ultimately not used because the canyon walls and deep bluff pools that characterize most of Tenderfoot Creek would have made operation inefficient. Unique antennas appropriate for the terrain of the study system were therefore constructed to improve effectiveness of portable surveys.

Wading Antenna Design

A modified single-operator, hand-held antenna (Hill et al. 2006) was used in 2011 to track PIT-tagged fish in Tenderfoot Creek. The antenna consisted of a PIT-tag reader (Oregon RFID, HDX backpack reader, Portland, Oregon), antenna wire within a handheld PVC frame, and a single tuning board (Oregon RFID, standard remote tuner board, Portland, Oregon) mounted in a watertight housing (Pelican-Case, MicroCase 1050, San Antonio, Texas) (Figure 14). Power was provided by a 14.7-V lithium polymer battery. Fine-stranded speaker wire (Raptor Wire, 8-10 AWG, Holly Hill, Florida) was housed in a handheld rectangular PVC frame measuring 1.5 m × 0.6 m. This configuration produced a detection range of 1.0 to 1.5 m for 32-mm PIT tags. The operator waded downstream in a zigzag pattern in an attempt to cover as much area as possible. Particular emphasis was placed on areas of cover where fish might hold (e.g., undercut banks, overhead cover), especially in deep pools. The entire study area was surveyed in 2011 on September 20-21 and October 17-18. The lower half of the study area (rkm 0.0 to 6.6) was surveyed in 2012 on August 16-17.

Snorkel Antenna Design

A completely submersible portable antenna was used in 2013. Conventional portable antennas generally consist of a handheld antenna worn by a single operator that wades through the study area in an effort to cover as much water as possible (Hill et al. 2006). The antenna itself is submersible but the PIT-tag reader and power supply must be kept dry. Although the wading antenna design was used with some success, fish evaded the detection field by swimming at depths the antenna could not reach. A completely submersible portable antenna, worn by a snorkeler, allowed better coverage of deep pools.

The antenna consisted of a PIT-tag reader (Oregon RFID, HDX backpack reader, Portland, Oregon) within a watertight housing (Pelican-Case, Case 1400, San Antonio, Texas), antenna wire within a handheld, circular frame, and a single tuner board (Oregon RFID, standard remote tuner board, Portland, Oregon) within a separate watertight housing (Pelican-Case, MicroCase 1050, San Antonio, Texas) (Figure 15). Power was provided by a 14.7-V lithium-polymer battery housed with the PIT-tag reader. The watertight housing containing both the PIT-tag reader and power supply was worn as a backpack by the snorkeler. Twinax networking cable connecting the tuner board to the PIT-tag reader was housed in high-pressure automotive hose (Aeroquip Performance, FC300, Dublin) and connected to both watertight housings using high pressure AN-6 swivel fittings, allowing the entire unit to be submerged and the networking cable to twist freely. Fine-stranded speaker wire (Raptor Wire, 8-10 AWG, Holly Hill, Florida) was housed in a circular PVC frame with a diameter of about 0.5 m. This configuration produced a tag detection range of 0.8 to 1.0 m for 32-mm PIT tags. The operator progressed downstream walking in shallow water and snorkeling in deep pools. Areas between pools with cover (undercut banks, large woody debris) were surveyed. The operator attempted to expose all fish to the antenna detection field in each pool, making multiple passes if necessary. Particular emphasis was placed on diving deep to expose large fish that tended to occupy deep water to the detection field. The entire study area was surveyed in 2013 on July 15-16.

Redd Counts

Redd counts were performed in October of 2010, 2011, and 2012 to estimate spawning effort of Brown Trout in Tenderfoot Creek. Redd counts of rainbow × cutthroat hybrid trout were not possible because of limited water clarity and access into the study area during their spawning period in April and May (spring runoff). Redds are excavations in the substrate made by spawning trout for egg deposition and have a characteristic pit and downstream tailspill (Crisp and Carling 1989) (Figure 16). When newly constructed, the pit will be mostly void of periphyton (Crisp and Carling 1989). Depressions without corresponding tailspills were not considered redds. Two surveyors progressed upstream or downstream, taking care not to step on redds. Location of each redd was recorded in UTM using a handheld GPS unit (Garmin International, Inc., eTrex Venture, Olathe, Kansas) and marked on a satellite photo. Lateral location within the stream (facing downstream: left, middle, or right) of each redd was recorded. The temperature of the tailspill of every fifth redd was taken at a gravel depth of 5 cm (Grost et al. 1991) to the nearest 0.01 ºC using a high-precision digital thermometer (ERTCO, Model T2011-45, Dubuque, Iowa) to estimate egg-location temperature. Water velocity of every fifth redd was recorded to the nearest 0.01 m/s using a portable flowmeter (Marsh McBirney Inc., Flo-mate Model 2000, Frederick, Maryland) and depth of the pit of every fifth redd was also recorded to the nearest 0.1 m.

The entire study area (rkm 0.0 to 13.7) was never surveyed for redds within a single year because the periods between the beginning of spawning activity and the onset of inclement weather that precluded access were short. Inclement weather began during the third week of October in all three years (October 25, 2010, October 24, 2011, and October 23, 2012). The upper half of the study area (rkm 6.6 to 13.7) was surveyed in October of 2010 and the lower half of the study area (rkm 0.0 to 6.6) was surveyed in October of 2011 and 2012. I started with the lower half in 2011 and 2012 because no redds were found in the upper half in 2010.

Brook Trout Spawning Surveys

Brook Trout spawning areas were recorded in UTM using a handheld GPS unit (Garmin International, Inc., eTrex Venture, Olathe, Kansas). Brook Trout spawning took place largely in heavily vegetated tributaries and side channels, making observation of redds difficult. Locations of actively spawning Brook Trout were recorded in favor of redd counts in an effort to devote more time to Brown Trout redd counts in the main stem of Tenderfoot Creek. Brook Trout redds were identified and recorded when confirmed by the presence of Brook Trout.

Mountain Whitefish Video Surveys

Pole-mounted video cameras (GoPro, Hero 2, San Mateo, California) were used to estimate the number of Mountain Whitefish spawning in the lower 3 km of Tenderfoot Creek in October of 2012. Estimating Mountain Whitefish spawning effort is difficult because they do not construct redds (Brown 1952; Stalnaker and Gresswell 1974; Thompson and Davies 1976). Although several hundred Mountain Whitefish were captured in the confluence fish weir during autumn spawning migrations, I observed thousands in nearby deep pools. The number of Mountain Whitefish observed in

Tenderfoot Creek was higher than the number captured in the weir because I operated the weir only four to seven days each month.

A camera operator performed a single pass by walking slowly upstream on the shallow side of each pool deeper than 1.0 m (N = 21). The camera was submerged using a pole 2.0 m in length and angled to capture the most fish per frame of video. The operator moved cautiously and maintained a distance of at least 3 m between the camera and the aggregated fish to avoid alarming them. A video file was created for each pool surveyed, resulting in 21 individual videos. Frame captures of each video were created using image-editing software (VideoLAN, VLC Media Player, Paris, and Adobe Systems, Photoshop 7.0, San Jose, California). Frame captures allowed for more accurate counts by providing still images rather than motion pictures. The video was viewed frame by frame until fish in the previous frame capture were out of view, at which time the next frame capture was viewed. This was continued until the entire pool was viewed. A grid was superimposed on each frame capture to assist in counting all individuals and to prevent counting individuals twice. The numbers of fish in all frame captures from a pool were summed to get a total count. The total number of fish in each of the 21 pools was summed to estimate the minimum number of spawning Mountain Whitefish in the lower 3 km of Tenderfoot Creek.

Juvenile Surveys

Three-pass depletion backpack electrofishing was conducted in September and October of 2012 to estimate abundances of juvenile fish in Tenderfoot Creek to evaluate its use as a nursery area. Additionally, because redd counts of rainbow × cutthroat hybrid trout were not possible, abundances of juvenile rainbow × cutthroat hybrid trout provided insight into the role of Tenderfoot Creek as a spawning area.

Primary sampling units were categorized into 12 contiguous groups based on stream morphology and tributary location (group 1, primary units 1-7; 2, 8-11; 3, 12-16; 4, 17-20; 5, 21-27; 6, 28-32; 7, 33-40; 8, 41-18; 9, 49-56; 10, 57-62; 11, 63-67; 12, 68-78). Two of these primary sampling units in each of the 12 groups were randomly selected (1: 6 and 7; 2: 9 and 10; 3: 12 and 16; 4: 17 and 20; 5: 25 and 27; 6: 28 and 29; 7: 33 and 38; 8: 42 and 46; 9: 53 and 56; 10: 59 and 60; 11: 64 and 67; 12: 74 and 75). I then randomly selected one 10-m long secondary sampling unit (measured longitudinally) within each selected primary sampling unit to sample by electrofishing. Pools greater than 1.0 m in depth were excluded because of low electrofishing efficiency and safety concerns. Such sections did contain juveniles, especially in backwater areas, based on snorkel survey observations. Juveniles that favored these backwater areas, such as brown trout (Hayes and Baird 1994), were therefore not collected, which may have resulted in underestimated abundances for some species. When secondary sampling units with deep pools were encountered, surveyors progressed upstream to the next 10-m section that was shallow enough to survey. Block nets were placed at the upstream and downstream boundaries of each secondary sampling unit to prevent escape of fish. The electrofisher operator walked in a zigzag pattern, beginning downstream and progressing upstream, in an effort to cover as much area as possible. A single netter attempted to capture all juveniles. After each pass, fish were placed in perforated holding containers within the stream before anesthetizing, measuring, and counting them. Twenty-five haphazardly selected individuals of each species were measured after all passes were completed. Fish were held in perforated containers after each pass a safe distance away from the survey area to prevent re-exposure to the electrofishing field. The average duration of each pass was about 10 min. Water velocity, temperature, and stream width were recorded for each secondary sampling unit. A total of 24 secondary sampling units was surveyed.

Unfortunately, I did not achieve depletion often enough to calculate abundance estimates using removal methods. I therefore used the total numbers caught in the secondary sampling units to estimate the minimum number of juveniles in each primary sampling unit. I used a two-stage cluster sampling approach to estimate the total number of juveniles in each sampling group (Lohr 2010). I then added the group estimates to determine a minimum total abundance estimate of juveniles of each taxon in Tenderfoot Creek. Calculation of variation was not possible because only two primary sampling units were selected and only one secondary sampling unit was selected (Lohr 2010). The estimates are useful for comparisons, especially among taxa in this study, but should be considered with caution.

Tables

Table 1. Summary of short- and long-term upper incipient lethal temperatures (UILTs) and upper growth limit temperatures of juvenile salmonids. Long-term and upper growth limit values marked with an asterisk were estimated by subtracting 3.0 ºC from short-term UILT estimates for that particular species (Selong et al. 2001; Bear et al. 2007).

Species	Short-term UILT (C º)	Long-term UILT (C º)	Upper growth limit (C º)	Reference
Brown Trout	24.7 (7 d)			Elliott 1981
		21.7*		
			19.5	Elliott et al. 1995
Westslope Cutthroat Trout	24.1 (7 d)	19.6 (60 d)	20.0	Bear et al. 2007
Rainbow Trout	26.0 (7 d)	24.3 (60 d)	24.0	Bear et al. 2007
Brook Trout	24.5 (7 d)			McCormick et al. 1972
		21.5*	21.5*	
Mountain Whitefish	23.6 (7 d)	22.6 (33 d)	22.2	Brinkman et al. 2013

Table 2. Numbers and proportions of Brown Trout, rainbow × cutthroat hybrid trout, Brook Trout, and Mountain Whitefish tagged, by method, in Tenderfoot Creek and the Smith River from June through November, 2010 to 2013. *N* = number of individuals of a taxon tagged and *P* = proportion of individuals of a taxon tagged.

Taxon	Number tagged	Electrofishing		Confluence fish weir		Angling		Seine	
		N	*P*	*N*	*P*	*N*	*P*	*N*	*P*
Brown Trout	66	39	0.59	20	0.30	7	0.11	0	0
Rainbow × cutthroat trout	355	186	0.52	29	0.08	139	0.39	1	0.01
Brook Trout	55	51	0.93	0	0	4	0.07	0	0
Mountain Whitefish	287	109	0.38	115	0.40	50	0.17	13	0.05
Total	763	385	0.50	164	0.21	200	0.26	14	0.02

Figures

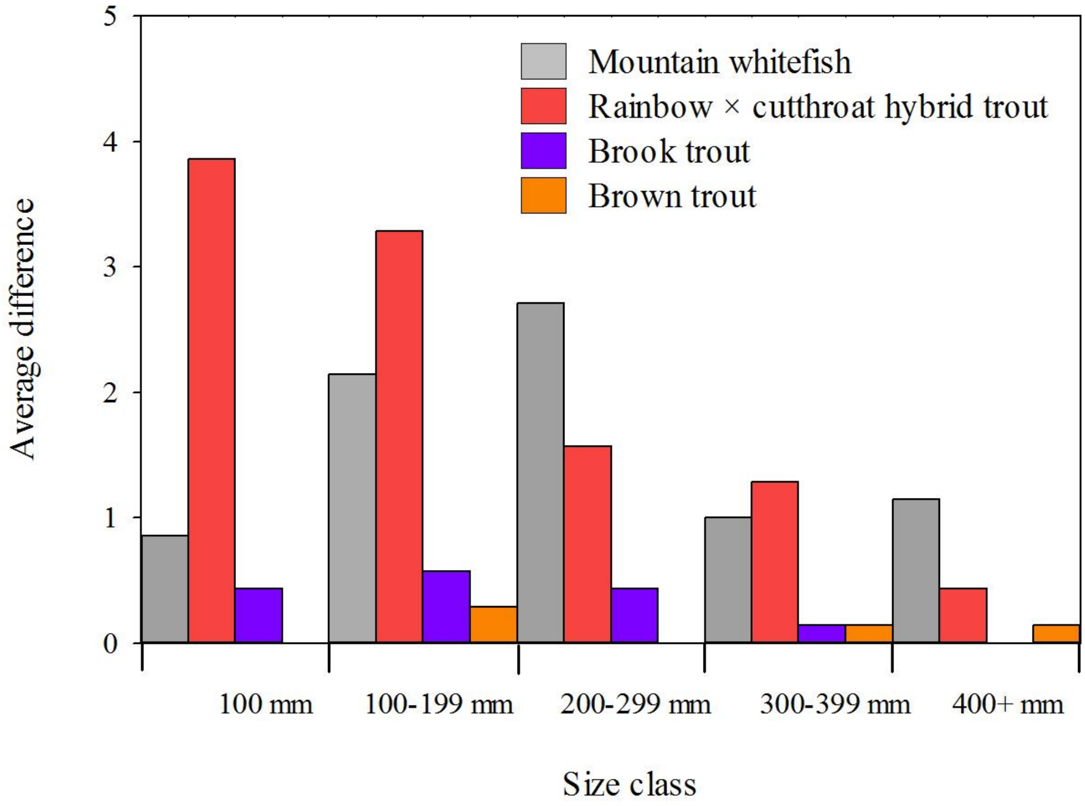

Figure 6. The mean differences in numbers of fish counted by size class in repeated snorkel surveys of 7 primary sampling units randomly selected to determine the consistency of counts.

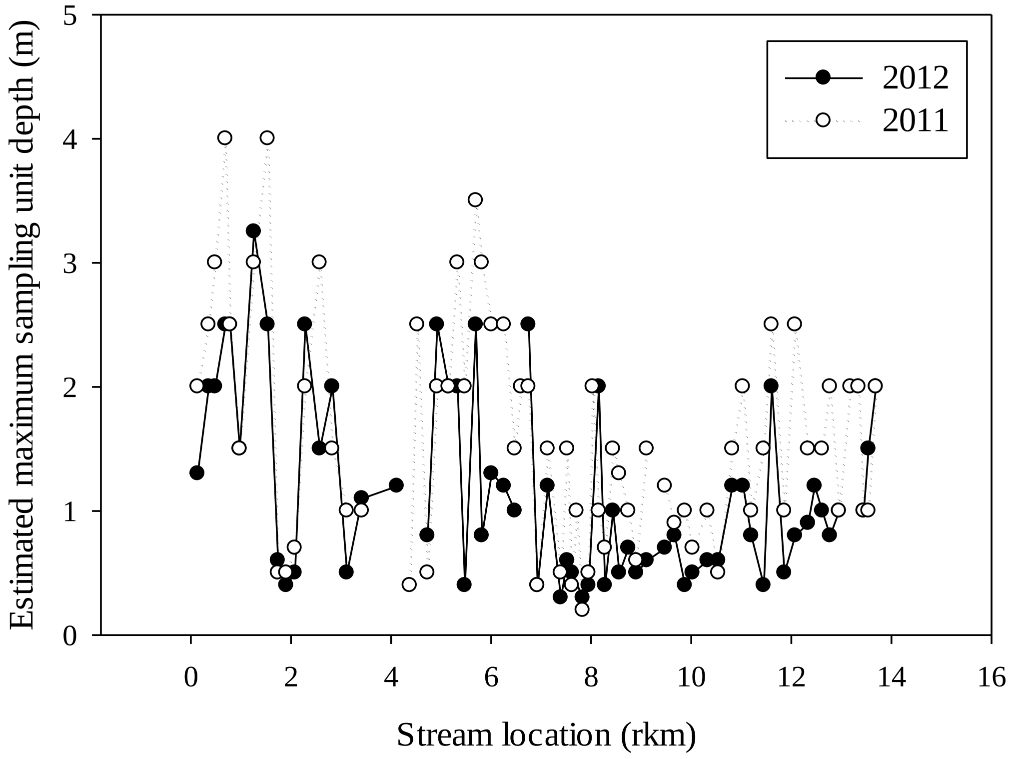

Figure 7. Maximum primary sampling unit depths estimated during snorkel surveys in late August of 2011 and 2012.

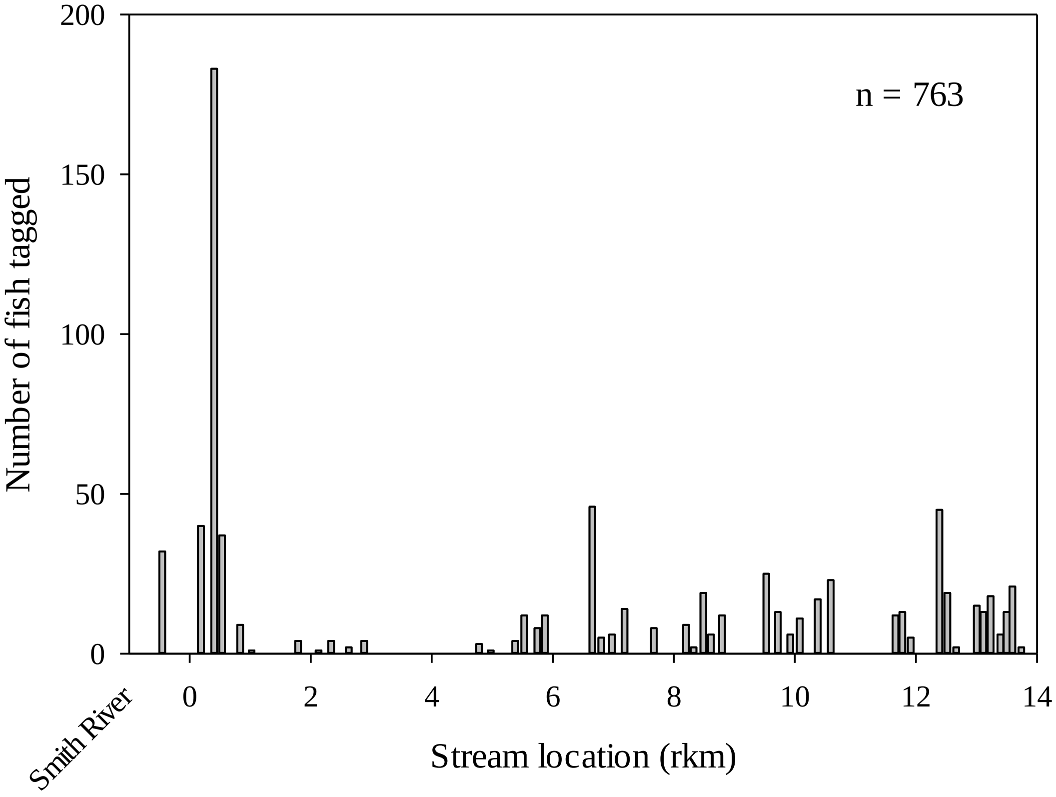

Figure 8. Distribution of tagging locations of fish tagged in Tenderfoot Creek and the Smith River from 2010 to 2012. Fish were collected by electrofishing, fish weir, seine, and angling. Stream location is the distance from the confluence with the Smith River.

Figure 9. Insertion of a PIT tag into the dorsal musculature of a rainbow × cutthroat hybrid trout.

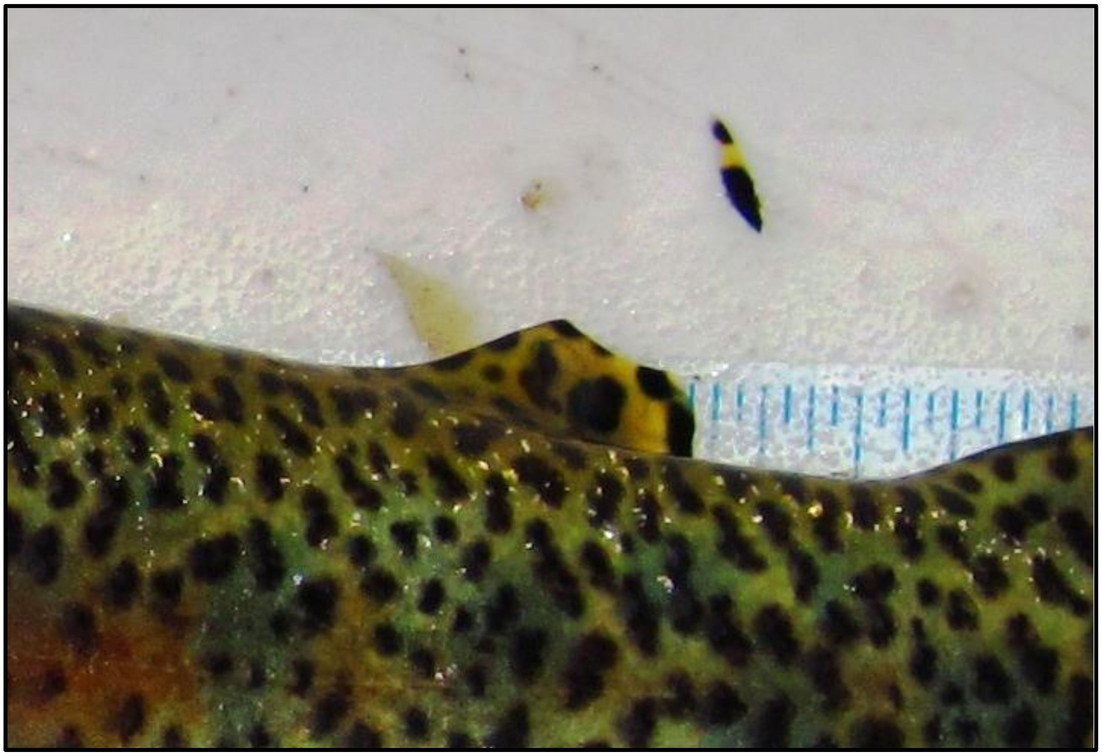

Figure 10. Trimmed adipose fin of a rainbow × cutthroat hybrid trout.

Figure 11. The upstream and downstream fish weir operated about 350 m upstream of the confluence of Tenderfoot Creek with the Smith River. The weir was operated 4-7 days every month from July to October in 2011 and 2012.

Figure 12. The inside of the upstream-direction steel box trap of the confluence fish weir on October 22, 2012. About 111 Mountain Whitefish had entered the trap within 3 h.

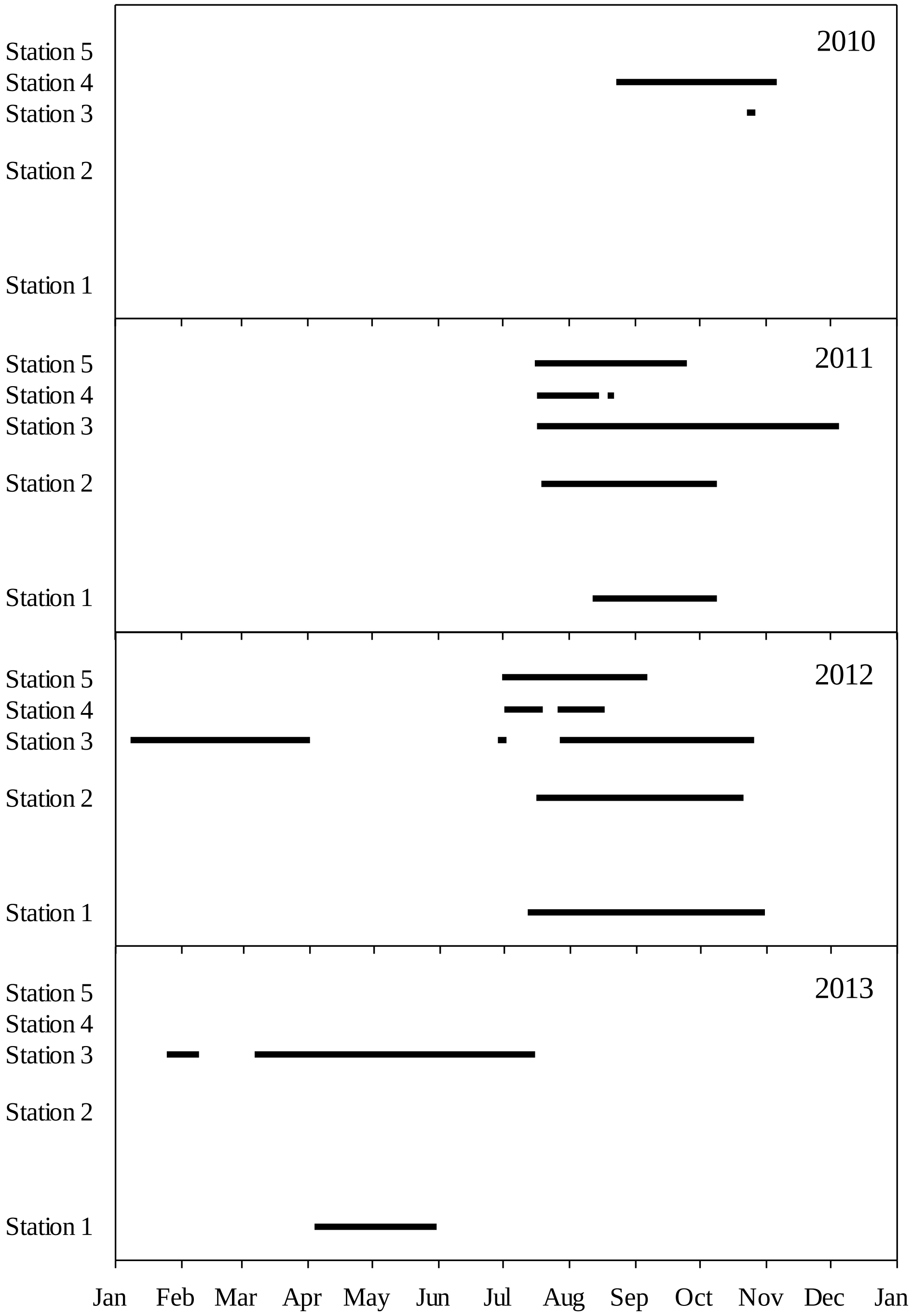

Figure 13. Operation times of fixed PIT antenna stations in Tenderfoot Creek from 2010 to 2013. Station labels on the y-axis are spaced vertically to represent actual spacing of stations in the study area. Station 1 is the confluence station and Station 5 is the uppermost station.

Figure 14. Wading antenna being used during a portable antenna survey in Tenderfoot Creek in October of 2011.

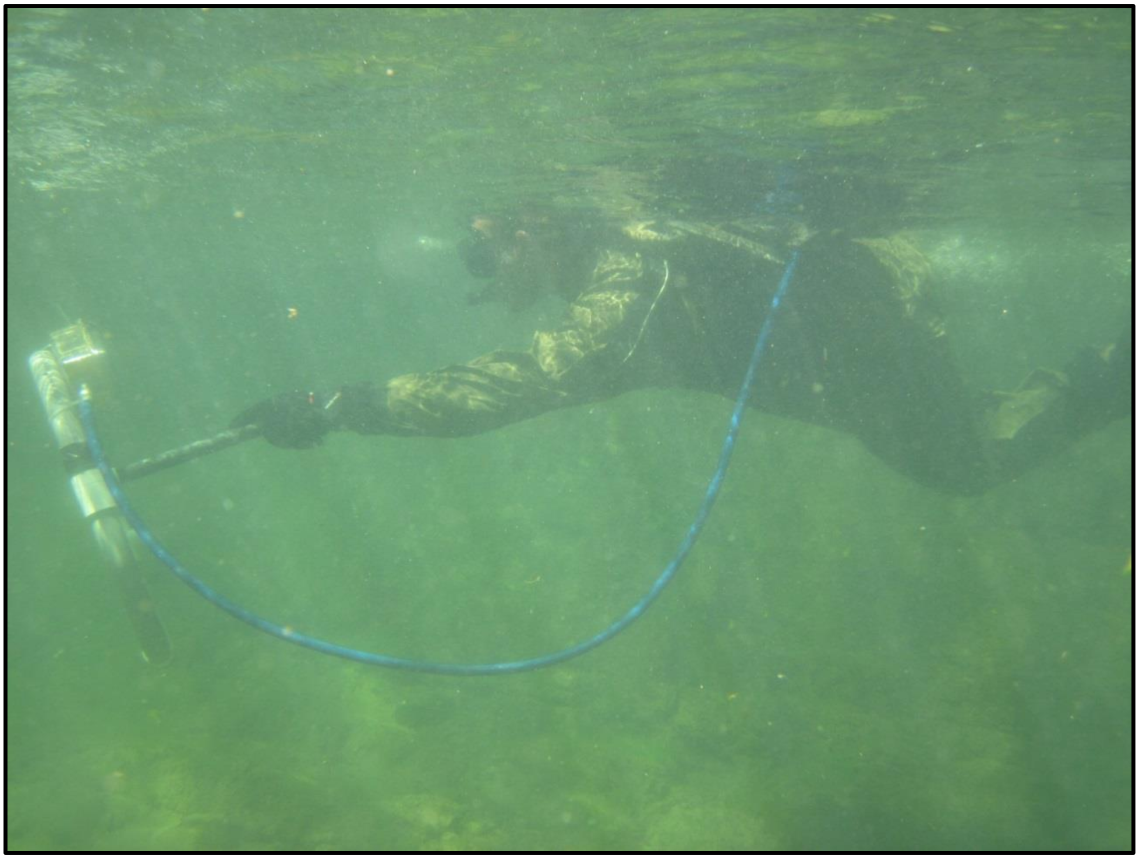

Figure 15. Snorkel antenna being used during a portable antenna survey in July of 2013.

Figure 16. A fresh Brown Trout redd, Tenderfoot Creek, October 20, 2011.

ANALYSIS

I used four unique ways to present movements of tagged fish: observed movement, activity, net direction, and inferred spatial distribution. All four analyses were based on a single data set of relocations but involved methods and assumptions unique to each. I filtered fixed-station and portable-antenna data until a relocation could be defined as one detection per fish per day (i.e., multiple relocations of a unique individual on the same day were considered a single relocation). Tag numbers detected on fixed stations and portable antennas were linked to corresponding data collected for each fish during tagging using a database management system. The resulting dataset was the basis for all analyses presented herein. Analyses were applied selectively to each taxon depending on the characteristics of the data on each.

Observed Movement

Observed movement of tagged fish was a graphical representation of relocations collected by all sampling methods (fixed stations, portable antennas, angling, fish weir, and electrofishing). This was the simplest presentation of relocation data and advantageous because no assumptions are necessary, other than tag relocations represent fish relocations (i.e., the PIT tag is in a live fish and the tag was not shed). Observed movement of Mountain Whitefish, rainbow × cutthroat hybrid trout, and Brook Trout is presented below.

Activity

Activity of tagged fish was approximated by the number of individuals relocated on fixed stations (or a specific fixed station) per day and did not include relocations recorded by other sampling methods. Days when a high number of individuals were relocated were considered periods of high activity, and vice versa. This presentation assumed that all tagged fish had an equal chance of being relocated. Activity of Brown Trout and Mountain Whitefish is presented below.

Net Direction

This analysis was specific to a single fixed station and used sequential relocations on the station’s two antennas to determine the net direction of movement of a group of individuals. For example, if 2 individuals were determined to have moved downstream and 1 individual was determined to have moved upstream, the net direction would be -1. Detection efficiency of both antennas was assumed to be equal and 100%; that is, a tagged fish had an equal chance of being detected on antenna 1 as on antenna 2 and a tagged fish moving past either antenna was detected 100% of the time. Net direction of rainbow × cutthroat hybrid trout on the confluence station is presented below.

Inferred Spatial Distribution

Inferred spatial distribution allowed me to show the location of tagged fish in space and time using a single graphical representation. This was the most complicated analysis and also required the most assumptions. I divided the study area into six locations (Smith River, Tenderfoot Creek rkm 0.0 to 6.6, rkm 6.6 to 9.9, rkm 9.9 to 11.6, rkm 11.6 to 13.5, and rkm 13.5 to 13.7) based on the presence of fixed stations. An encounter history for each tagged fish was constructed using relocations collected by all sampling methods. Using this encounter history, I created a spatio-temporal data set that inferred fish location by day based on relocations and fixed station operation. However, not all fixed stations ran continuously or at the same time. To account for this, location of an individual fish was represented as a fraction when more than one location could not be ruled out. For example, if a tagged fish was relocated on the fixed station at rkm 0.0 on July 5 and relocated again on the fixed station at rkm 9.9 on July 8, but the fixed station between these two stations (at rkm 6.6) was not operational during that time frame, the location of that individual would be represented by 0.5 between rkm 0.0 and rkm 6.6 and 0.5 between rkm 6.6 and rkm 9.9 on July 6 and 7. In other words, either location of that fish could not be ruled out because the station at rkm 6.6 was not operational. Presence in both locations is therefore represented by equal fractions (in this case 0.5). Inferred spatial distribution is represented by a gradient of fish-days, or the number of days spent in each location per fish. Additionally, when the first relocation of an individual in a given year was recorded moving upstream on the fixed station at rkm 0.0, I assumed that individual was located in the Smith River prior to the date of that relocation. This analysis also assumes that tagged fish did not die or shed their tags (100% retention of tags) and that fixed stations had detection efficiencies of 100%. Inferred spatial distribution of Brown Trout is presented below.

RESULTS

Temperature Regimes

Estimated water temperatures of primary sampling units in Tenderfoot Creek at 1900 hours from August 25-31 in 2011 generally increased as the location of units progressed downstream but decreased at rkm 2.4 and 8.5 (Figure 17). A large, in-channel spring at rkm 8.6 caused a sharp decrease in temperature that persisted about 1.0 rkm downstream (Figure 17). Additionally, the second-largest tributary of Tenderfoot Creek, Ditch Creek (rkm 2.6), caused a decline in temperature that persisted about 0.8 rkm downstream (Figure 17).This temperature drop began upstream of the confluence of Ditch Creek and Tenderfoot Creek, probably because of hyporheic groundwater flows associated with Ditch Creek.

Mean daily water temperatures measured at the USGS gauge station in the Smith River 20.7 rkm upstream of the mouth of Tenderfoot Creek were slightly warmer than those measured by the HOBO temperature logger 50 m upstream of the mouth of Tenderfoot Creek in 2011 (Figure 18). The mean difference was 0.38 ºC and ranged from -0.41 to 0.84 ºC (Figure 18). The calculated differences in temperatures between Tenderfoot Creek and the Smith River in 2012 are therefore slightly greater than they would have been had temperatures measured 50 m upstream of the Tenderfoot Creek confluence been used.

Tenderfoot Creek was cooler than the Smith River during summer months, but the difference in temperature ranged widely and was largest when water temperatures were high (Figure 19). The mean difference between the mean daily water temperature of

Tenderfoot Creek at the confluence (rkm 0.0) and the mean daily water temperature of the Smith River (measured 50 m upstream of the mouth of Tenderfoot Creek) from July 28 to August 31 of 2011 was 1.90 ºC and ranged from 0.69 to 2.67 ºC (Figure 19). The mean difference between the mean daily water temperature of Tenderfoot Creek at the confluence (rkm 0.0) and the mean daily water temperature of the Smith River 20.7 rkm upstream of the mouth of Tenderfoot Creek from July 12 to August 31 of 2012 was 2.10 ºC and ranged from 0.20 to 3.59 ºC (Figure 19).

Maximum water temperatures in the Smith River frequently exceeded upper incipient lethal temperatures and upper growth limit temperatures of Brown Trout, Mountain Whitefish, Rainbow Trout, and Brook Trout in 2012 but never in 2011 (Figure 19). Maximum water temperatures in the Smith River in 2012 exceeded the long-term UILTs of Brown Trout on 34 days, of Mountain Whitefish on 20 days, of Rainbow Trout on 3 days, and of Brook Trout on 34 days (Figure 19). Maximum water temperature in the Smith River exceeded the upper growth limits of Brown Trout on 31 days in 2011 and 58 days in 2012, of Mountain Whitefish on no days in 2011 and 21 days in 2012, of Rainbow Trout on 22 days in 2011 and 56 days in 2012, and of Brook Trout on no days in 2011 and 34 days in 2012 (Figure 19). However, such exposures were not continuous; diel temperature fluctuations in the Smith River were commonly 7.0 to 9.0 ºC such that water temperatures were thermally stressful for only a few hours daily. On July 31, 2012, when the maximum annual temperature was recorded, water temperatures exceeded the long-term UILTs of Brown Trout, Mountain Whitefish, Rainbow Trout, and Brook Trout for 9, 6, 2, and 9 hours (Figure 20). The upper growth limit temperatures of Brown Trout, Mountain Whitefish, Rainbow Trout, and Brook Trout were surpassed on this day for 13, 7, 13, and 9 hours. The minimum water temperature recorded on this day was well below the long-term UILTs and upper growth limit temperatures. Additionally, the number of hours when temperatures were below stressful levels exceeded the number of hours when temperatures surpassed them (i.e., the period of stress was shorter than the period of recovery). Days when the mean temperature was above the long-term UILTs and upper growth limits were therefore the most stressful to fish because the period of stress exceeded the period of recovery. However, this only applied to the upper growth limit of Brown Trout in 2012, when 10 such days occurred (Figure 19). Nevertheless, conditions in the Smith River were at times at thermally stressful levels that fish would be expected to avoid if possible.

Brown Trout

Movement

Observed Brown Trout movement was rare and mostly restricted to autumn spawning migrations, but a large proportion of tagged individuals was relocated (32 of 66; Table 4), which allowed me to identify two distinct movement patterns (Figure 21). Eleven individuals were classified as “Smith River migrants” and were consistently relocated at the confluence station or in the Smith River and relocated only within Tenderfoot Creek during autumn spawning periods (Figure 22). Eighteen individuals were classified as “Tenderfoot Creek residents” and were consistently relocated in the same or proximal primary sampling units within Tenderfoot Creek among years and never relocated at the confluence station (Figure 23). Three individuals were not relocated enough to be categorized with confidence, but they were relocated at the confluence fish weir only, suggesting they were probably Smith River migrants.

Among-station movement of Brown Trout was mostly restricted to upstream spawning migrations by Smith River migrants (Figure 22). Two Smith River migrants (one in 2011 and one in 2012) made upstream spawning migrations to at least rkm 9.9. Only one individual (a Smith River migrant) was detected on three separate fixed stations. Smith River migrants did not enter Tenderfoot Creek until August 31 in 2011 and remained below Station 3 (rkm 9.9), at least until station shutdown on December 5, 2011. Smith River migrants entered Tenderfoot Creek on September 21 in 2012 and remained there at least until station shutdown on October 30, 2012, with the highest concentration of fish being between Station 1 and 2 (rkm 0.0-6.6). Tenderfoot Creek residents exhibited a much smaller range of movement than Smith River fish. Movement of Tenderfoot Creek residents among stations was rare in all years. Downstream movement among stations was not documented in any year by individuals in either group, though relocations among years suggested it occurred when stations were not operating, in winter or early spring.

Brown Trout did not appear to use Tenderfoot Creek as a thermal refuge. No Brown Trout were observed moving out of the Smith River and upstream into Tenderfoot Creek when water temperatures in the Smith River were high. Eleven Brown Trout were assumed to be in the Smith River when water temperatures were high based on sequential relocations, but none of these individuals were detected on the confluence station in July or August of 2011 or 2012.

Brown Trout activity was highest in late summer and autumn and ceased completely following sharp decreases in water temperature. The number of detections of all Brown Trout at fixed stations was high in the beginning of August in 2011 and in late July in 2012, although no movement among stations occurred, suggesting increased localized activity only (Figure 24). All Brown Trout activity ceased for several weeks following large decreases in water temperature associated with major precipitation events (beginning September 3, 2011, and August 26, 2012) but started again in mid-September and continued until at least late October in 2011 and 2012 (Figure 24).

Population Characteristics

Tenderfoot Creek residents tended to be larger than Smith River migrants. Mean length of tagged Tenderfoot Creek residents was 457 mm with a range of 319 to 533 mm; mean length of tagged Smith River migrants was 435 mm with a range of 348 to 531 mm (Figure 25). Mean relative weight of all tagged Brown Trout was 92.1 (Table 3). Snorkel surveys of residents produced a similar size distribution to that of the tagged residents, although the proportion of individuals between 300 mm and 400 mm was higher in snorkel surveys than among tagged fish (Figure 25).

Spatial distributions of resident Brown Trout in Tenderfoot Creek were similar in 2011 and 2012 (Figure 26) but more Brown Trout were observed during snorkel surveys in 2012 (N = 124) than in 2011 (N = 48) despite identical sampling efforts. Only two Brown Trout less than 100 mm were observed during snorkel survey in 2011 and 2012. The numbers of Brown Trout in Tenderfoot Creek greater than 200 mm in 2011 (3.4/rkm) and 2012 (8.3/rkm) were much lower than in the Smith River in 2011

(155/rkm; Figure 27). Densities of Brown Trout were higher in primary sampling units with deep pools than in shallower units (Figure 28).

Spawning

Brown Trout spawning was observed only in the lower 6.6 rkm of Tenderfoot Creek and was higher in 2012 than in 2011. No Brown Trout redds were found in the upper half of the study area (rkm 6.6 to 13.7) in 2010. A total of 159 Brown Trout redds was counted during 2011 ($N = 69$) and 2012 ($N = 90$) in the lower half of the study area (Figure 29). Eleven redds inventoried in 2012 were found at the same locations of those in 2011. Mean (± 95%) water velocity at redds was higher in 2012 (0.52 ± 0.07 m/s) than in 2011 (0.41 ± 0.03 m/s) ($t = 2.912$, df = 43, $P = 0.006$). Mean water depth and temperature at redds were lower in 2012 (0.17 ± 0.01 m; 6.7 ± 0.27 ºC) than in 2011 (0.26 ± 0.02 m; 9.3 ± 0.13°C) (Mann-Whitney Rank Sum Test: $U = 22$, $P = <0.001$; $t = -18.320$, df = 42, $P = < 0.001$). Age-0 Brown Trout were not observed above primary sampling unit 8.6 (rkm 8.2-8.3), and the highest density of age-0 Brown Trout was found in primary sampling unit 1.5 (rkm 0.6-0.7). A total of 24 age-0 Brown Trout was sampled, much fewer than age-0 rainbow × cutthroat hybrid trout (503) but higher than Brook Trout (15) and Mountain Whitefish (7). I expanded this count to estimate a minimum abundance of 1,162 age-0 Brown Trout in Tenderfoot Creek.

Mountain Whitefish

Movement

Observed movement of Mountain Whitefish was common; I relocated a large proportion of tagged individuals (181 of 287, of which 173 were relocated in 2012; Table 4), which allowed me to identify at least two distinct movement groups based on interchange patterns between Tenderfoot Creek and the Smith River: summer residents and spring visitors (Figure 30). Summer residents remained in Tenderfoot Creek throughout the sampling season and migrated downstream to spawning areas in lower reaches in October (Figure 30). Spring visitors exited Tenderfoot Creek in July and returned to spawn in October, though relocations suggested they did not move far upstream then (Figure 30). A potential third group, autumn spawners, may have contributed to the large aggregations numbering thousands of individuals in October and November of 2011 and 2012. However, I did not observe this pattern among tagged fish; every individual relocated in the autumn was tagged in the spring, suggesting that these large aggregations may have been spring visitors that were not observed because of high, turbid water resulting from spring run-off.

No Mountain Whitefish were observed moving into Tenderfoot Creek when water temperatures in the Smith River were high. Only 8 of 113 individuals assumed to be in the Smith River when water temperatures were high were detected at the confluence station in July or August of 2012. However, these eight individuals briefly left Tenderfoot Creek at the same time as spring visitors and entered the Smith River, but immediately returned to Tenderfoot Creek and remained through October. Ninety-seven

Mountain Whitefish were relocated at the confluence station in July when maximum water temperature in the Smith River exceeded 20 °C, but 89 of these individuals were spring visitors leaving Tenderfoot Creek (Figures 30 and 31).

Observed movements of tagged Mountain Whitefish consisted mostly of downstream migration in July by spring visitors (July 12-29), downstream migration in October by summer residents (October 2-30), and upstream migration by spring visitors in autumn (October 4-30). Fifty-six individuals were relocated at the confluence station (rkm 0.0) moving into Tenderfoot Creek in September, October, and November of 2012. Nineteen of the sixty-nine individuals still in Tenderfoot Creek at station shutdown were relocated moving upstream by the confluence station in spring of 2013, suggesting these individuals overwintered in the Smith River. An upstream migration of 24 individuals was observed from April 14 to May 22, 2013 that preceded an increase in Smith River discharge and followed an upstream spawning migration by rainbow × cutthroat hybrid trout (Figure 32).

Population Characteristics

Mean length of tagged Mountain Whitefish was 310 mm with a range of 146 to 453 mm (Figure 33); mean relative weight of tagged Mountain Whitefish was 92.5 (Table 3). Length-frequency distributions derived from snorkel surveys differed greatly from 2011 to 2012; more fish were observed in the less-than-100 mm, 100-200 mm, and 300-400 mm size classes in 2012 (Figure 33). Length-frequency distributions of tagged Mountain Whitefish also differed greatly between 2011 and 2012, although only 48 fish were tagged in 2011.

More Mountain Whitefish were observed during snorkel surveys in 2012 (*N* = 4,442) than in 2011 (*N* = 1,724), despite identical effort (Figure 34). Spatial distributions of Mountain Whitefish in Tenderfoot Creek were similar in 2011 and 2012 (Figure 34). Mountain Whitefish tended to occupy the deep canyon pools in the lower primary sampling units of Tenderfoot Creek close to the confluence with the Smith River. Abundance of Mountain Whitefish was highest within 3 rkm of the confluence with the Smith River (Figure 34). Density of Mountain Whitefish was higher in primary sampling units with deep pools than in shallower units (Figure 35).

Spawning

Mountain Whitefish used Tenderfoot Creek heavily for spawning. Large aggregations of spawning whitefish were observed in early November of 2011 (Figure 36), and about 7,568 whitefish were counted in spawning aggregations during video surveys in the lowermost 3 km of Tenderfoot Creek on October 24, 2012 (Figure 37). In addition, 426 Mountain Whitefish were captured in the confluence fish weir in October 2011 (*N* = 15) and 2012 (*N* = 411); many showed physiological characteristics (tubercles, milt, or eggs) associated with spawning. Only 7 age-0 Mountain Whitefish were captured during juvenile surveys—fewer than Brook Trout (15) and Brown Trout (24) and many fewer than rainbow × cutthroat hybrid trout (503). I expanded this count to estimate a total number of 809 juvenile Mountain Whitefish in Tenderfoot Creek. About 704 age-1 Mountain Whitefish less than 100 mm were observed during snorkel surveys in 2012 (Figure 33)—many more than in 2011 (*N* = 2), despite identical effort. The large number of spawning adults coupled with the low number of juvenile Mountain Whitefish observed in Tenderfoot Creek suggests most young Mountain Whitefish emigrate to the Smith River to mature.

Rainbow × Cutthroat Hybrid Trout

Movement

Observed movements of rainbow × cutthroat hybrid trout within Tenderfoot Creek and interchange between Tenderfoot Creek and the Smith River were extensive; 118 of 355 tagged rainbow × cutthroat hybrid trout were relocated from 2010 to 2013 (Table 4). Observed movements of rainbow × cutthroat hybrid trout consisted of downstream migrations within Tenderfoot Creek in July and August of 2011 and 2012 after high discharges in Tenderfoot Creek had subsided (Smith River discharges had also peaked and decreased to base flow; Figure 38), and upstream migration from April 11 to May 29 of 2013 (Figure 32). Among-station movement of rainbow × cutthroat hybrid trout was common; 26 individuals were relocated on at least two fixed stations, 8 on three fixed stations, and 2 on four fixed stations. Interchange of tagged rainbow × cutthroat hybrid trout between Tenderfoot Creek and the Smith River was also common; 49 of the 118 relocated individuals were relocated at the confluence station.

Among-station movement of rainbow × cutthroat hybrid trout was predominantly spawning-related. An upstream spawning migration by 10 individuals was observed in April and May of 2013 that preceded an increase in Smith River discharge and an upstream migration by Mountain Whitefish (Figure 32). Additionally, 21 of the individuals that moved downstream within Tenderfoot Creek in July and August of 2011 and 2012 left Tenderfoot Creek (Figure 38), suggesting that they were out-migrating spawners.

Movements of rainbow × cutthroat hybrid trout were made by large, presumably mature individuals; small individuals moved less, suggesting they remained within Tenderfoot Creek until reaching a mature size. Mean length of relocated individuals was significantly longer (258 mm) than that of individuals not relocated (233 mm) (Mann-Whitney Rank Sum Test: $U = 11{,}251$, $P = 0.003$).

Rainbow × cutthroat hybrid trout did not use Tenderfoot Creek as a thermal refuge. No rainbow × cutthroat hybrid trout were directly observed moving into Tenderfoot Creek and no rainbow × cutthroat hybrid trout assumed to be in the Smith River (based on relocations) in 2011 were detected on the confluence station when water temperature in the Smith River was high. In 2012, 3 of the 19 individuals assumed to be in the Smith River were detected at the confluence station when water temperature was high. However, these individuals tended to be in the Smith River when water temperature was highest (Figure 39) and were repeatedly detected at the confluence station throughout both summer and autumn, suggesting their home ranges included the confluence (Figure 39).

Population Characteristics

Mean length of tagged rainbow × cutthroat hybrid trout was 241 mm with a range of 103 to 449 mm (Figure 40); mean relative weight of tagged rainbow × cutthroat hybrid trout was 89.5 (Table 3). Snorkel surveys produced a similar size distribution; length-frequency distributions produced by snorkel surveys were similar in 2011 and 2012 (Figure 40).

Spatial distributions of rainbow × cutthroat hybrid trout in Tenderfoot Creek were similar in 2011 and 2012 but more rainbow × cutthroat hybrid trout were observed during snorkel surveys in 2012 ($N = 4{,}661$) than in 2011 ($N = 2{,}601$), despite identical effort (Figure 41). The numbers of rainbow × cutthroat hybrid trout greater than 200 mm in Tenderfoot Creek in 2011 (56/rkm) and 2012 (112/rkm) were fewer than the number of Rainbow Trout greater than 200 mm in the Smith River in 2011 (155/rkm; Figure 27). Abundance of rainbow × cutthroat hybrid trout was highest within 2 km of the waterfall at the upper extent of the study area (Figure 41). I found no association between maximum estimated unit depth and density of rainbow × cutthroat hybrid trout. Additionally, I could not find an explanation for the high abundance of rainbow × cutthroat hybrid trout from rkm 4.9 to 6.6 or at rkm 12.8.

Spawning

Although redd counts were not possible during the rainbow × cutthroat hybrid trout spawning period in Tenderfoot Creek, evidence existed that spawning occurred. Sixteen rainbow × cutthroat hybrid trout were captured in the downstream confluence weir in July of 2011 and 2012. All were mature fish (average length of these individuals was 359 mm with a range of 293 mm to 438 mm) and showed physiological signs associated with post-spawning condition (low body mass and vibrant colors; Figure 42). The mean relative weight of these individuals was much lower (78.8) than that of all tagged rainbow × cutthroat hybrid trout (90.3) (Mann-Whitney Rank Sum Test: U = 469.5, $P < 0.001$).

Tenderfoot Creek was used extensively by rainbow × cutthroat hybrid trout as a nursery area; 503 age-0 rainbow × cutthroat hybrid trout were captured during juvenile surveys, many more than Brown Trout (24), Brook Trout (15) and Mountain Whitefish (7). I expanded this count to estimate a total of 25,127 juvenile rainbow × cutthroat hybrid trout in Tenderfoot Creek. More age-1 rainbow × cutthroat hybrid trout less than 100 mm long were observed during snorkel surveys in 2012 (N = 1,192) than in 2011 (N = 651), despite identical effort.

Brook Trout

Movement

Brook Trout moved little and none moved between Tenderfoot Creek and the Smith River. Five of fifty-five tagged Brook Trout were relocated from 2010 to 2013 (Table 4). Among-station movement was rare (Figure 43). Only one individual was relocated in more than one year (Figure 43). None were relocated at the confluence fixed station (Figure 43). No upstream movement was observed at any time while stations were running (Figure 43).

Population Characteristics

Mean length of tagged Brook Trout was 173 mm with a range of 124 to 307 mm (Figure 44); mean relative weight of tagged Brook Trout was 96.8 (Table 3). Snorkel surveys produced a similar size distribution of fish longer than 100 mm (Figure 44);

comparison of fish under 100 mm was not possible because they were not tagged or measured.

Spatial distribution of Brook Trout was similar in 2011 and 2012 (Figure 43). Opposite of the temporal trend for the other taxa, fewer Brook Trout were observed during snorkel surveys in 2012 (*N* = 342) than in 2011 (*N* = 445), despite identical effort (Figure 45). Moreover, the numbers of age-0 (less than 100 mm) Brook Trout observed were similar in 2011 (130) and 2012 (115).

Brook Trout occupied shallow areas influenced by tributary and groundwater inflows. Densities of Brook Trout tended to decrease as distances to tributaries or springs increased (Figure 46). Densities of age-0 Brook Trout tended to be higher in primary sampling units close to tributaries in both 2011 and 2012 but especially in 2011 when no age-0 Brook Trout were observed more than 1,000 m from a tributary (Figure 47). I found no association between estimated maximum sampling unit depth and density of Brook Trout.

Spawning

Brook Trout spawning was restricted to six areas, mostly in side channels and Daisy, Lobley, and Miners creeks and Barrel Coulee (Figure 48). Only three Brook Trout redds were observed in the main stem of Tenderfoot Creek during Brown Trout spawning surveys conducted in autumn from 2010 to 2012.

Based on densities of age-0 Brook Trout observed during snorkel surveys, rearing habitat was proximal to tributaries, suggesting that abundances of age-0 Brook Trout were higher than the juvenile electrofishing surveys indicated. A total of 15 age-0 Brook

Trout was sampled during juvenile surveys—fewer than age-0 rainbow × cutthroat hybrid trout (503) and Brown Trout (24), but more than Mountain Whitefish (7). I used this count to estimate a total of 405 juvenile Brook Trout in Tenderfoot Creek, which however, is probably an underestimate as none of the primary sampling units sampled during juvenile surveys were near tributaries where abundances of age-0 Brook Trout were high.

Tables

Table 3. Means and ranges of relative weights of Brown Trout, rainbow × cutthroat hybrid trout, Brook Trout, and Mountain Whitefish measured, weighed, and tagged in Tenderfoot Creek and the Smith River, 2010 to 2012. Proportion weighed was calculated as the number weighed out of the total number tagged of that species.

Taxon	Mean	Minimum	Maximum	Number weighed	Proportion weighed
Brown Trout	92.1	75.2	111.5	15	0.23
Rainbow × cutthroat trout	89.5	68.7	120.1	199	0.56
Brook Trout	96.8	68.9	113.3	19	0.35
Mountain Whitefish	92.5	68.9	111.1	265	0.92

Table 4. Relocations of Brown Trout, rainbow × cutthroat hybrid trout, Brook Trout, and Mountain Whitefish tagged in Tenderfoot Creek and the Smith River by fixed station antennas, portable antennas, fish weir, electrofishing, and angling from June through November, 2010 to 2013. *N* = number of fish relocated and *P* = proportion of fish relocated. Sixteen individuals were relocated by multiple methods. These occurrences were counted only once when calculating total proportions.

		Fixed station		Portable antenna		Confluence fish weir		Angling		Electro-fishing		Total	
Taxon	Number tagged	*N*	*P*	*N*	*P*	*N*	*P*	*N*	*P*	*N*	*P*	*N*	*P*
Brown Trout	66	25	0.38	4	0.06	3	0.05	1	0.02	1	0.02	32	0.49
Rainbow × cutthroat trout	355	108	0.30	16	0.05	0	0	2	0.01	0	0	117	0.33
Brook Trout	55	4	0.07	1	0.02	0	0	0	0	0	0	5	0.09
Mountain Whitefish	287	166	0.58	17	0.06	5	0.02	0	0	0	0	181	0.63
Total	763	303	0.40	38	0.05	8	0.01	3	0.01	1	0.01	335	0.44

Figures

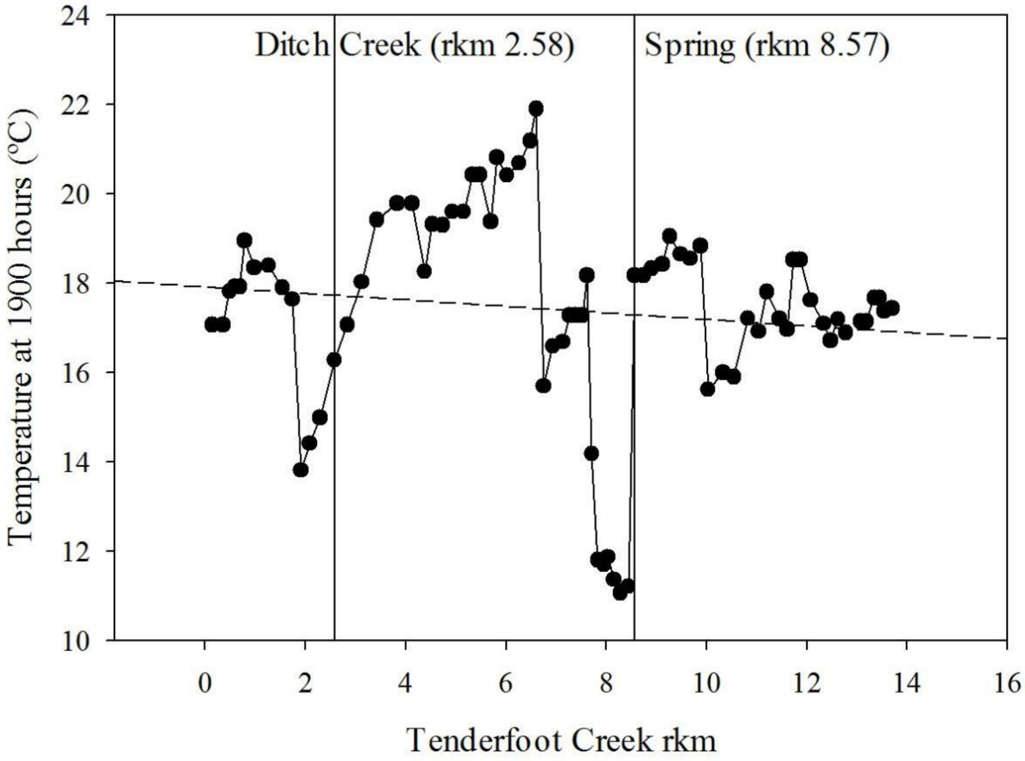

Figure 17. Estimated water temperatures August 25-31, 2011, at 1900 hours at each of the 78 primary sampling units in lower Tenderfoot Creek. The dotted line represents the overall trend (regression line) of unit water temperatures. Solid vertical lines show the point locations of two major influences on temperature, Ditch Creek and a large in-channel spring.

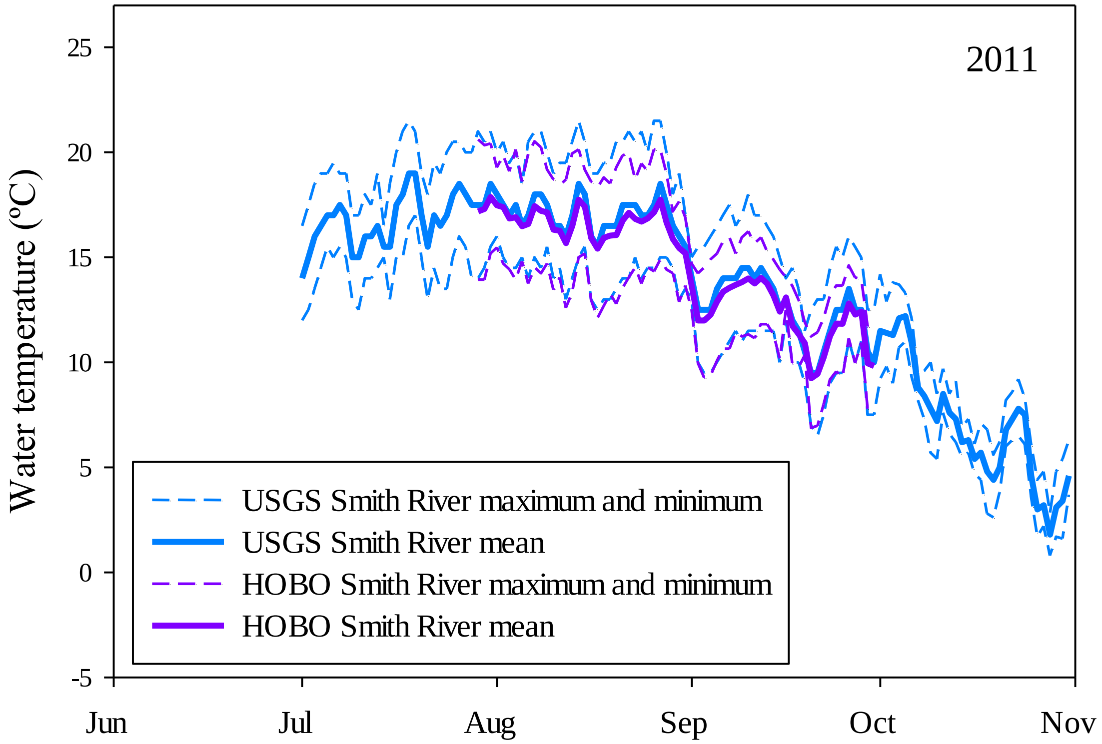

Figure 18. Comparison of water temperatures recorded at the USGS gauge station 20.7 rkm upstream of the mouth of Tenderfoot Creek and 50 m upstream of the mouth of Tenderfoot Creek recorded with a HOBO temperature logger in 2011.

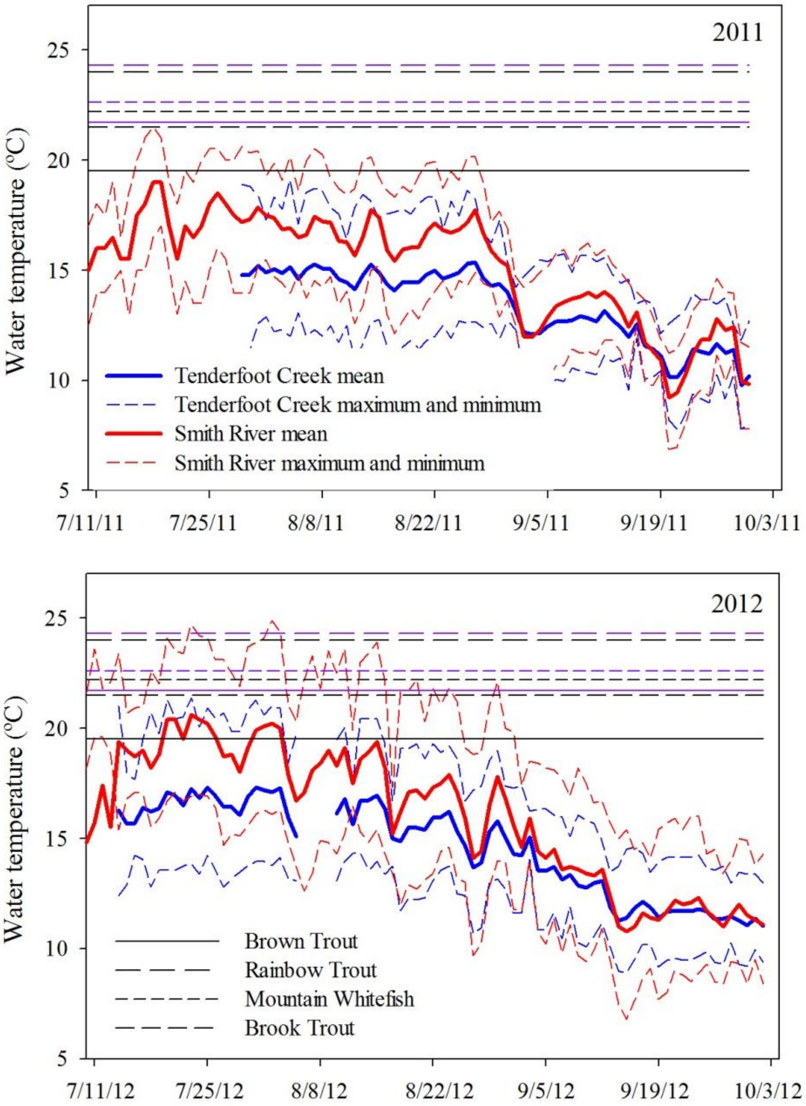

Figure 19. Maximum, mean, and minimum daily water temperatures recorded in Tenderfoot Creek at rkm 0.0 and in the Smith River. Smith River water temperatures were recorded by a temperature logger 50 m upstream of the mouth of Tenderfoot Creek in 2011 and by the USGS station below Eagle Creek 20.7 rkm upstream of the mouth of Tenderfoot Creek in 2012. UILTs are long-term estimates (> 30 d) as determined by other studies or estimated from existing short-term UILTs (7 d) and are represented by purple lines. Upper growth limit temperatures are represented by black lines. Brook Trout long-term UILT and upper growth limit temperatures were estimated from an existing short-term UILT as the same value (21.5 ºC).

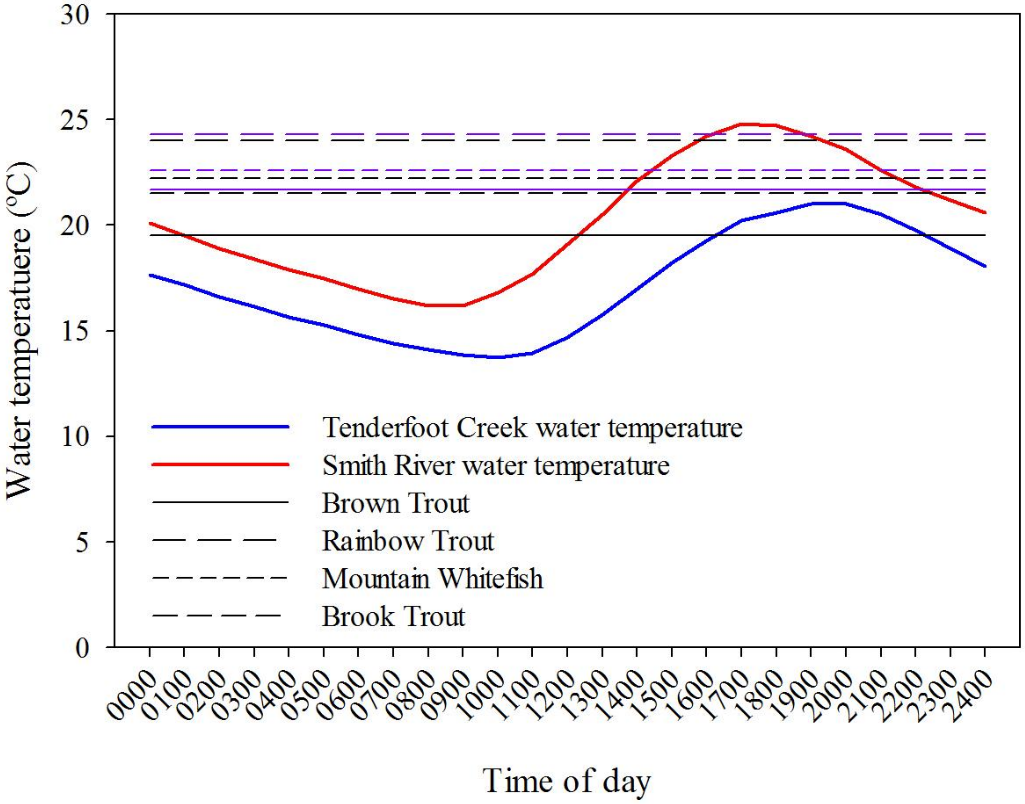

Figure 20. Diel temperature cycles of Tenderfoot Creek and the Smith River on July 31, 2012, when the highest temperature during the study was recorded (24.9 ºC, in the Smith River). Tenderfoot Creek water temperature was measured with a HOBO temperature logger at the confluence with the Smith River, and Smith River water temperature was measured at the USGS gauge station 20.7 rkm upstream of the mouth of Tenderfoot Creek. UILTs are long-term estimates (> 30 d) as determined by other studies or estimated from existing short-term UILTs (7 d) and are represented by purple lines. Upper growth limit temperatures are represented by black lines. Brook Trout long-term UILT and upper growth limit temperature were estimated from an existing short-term UILT as the same value (21.5 ºC).

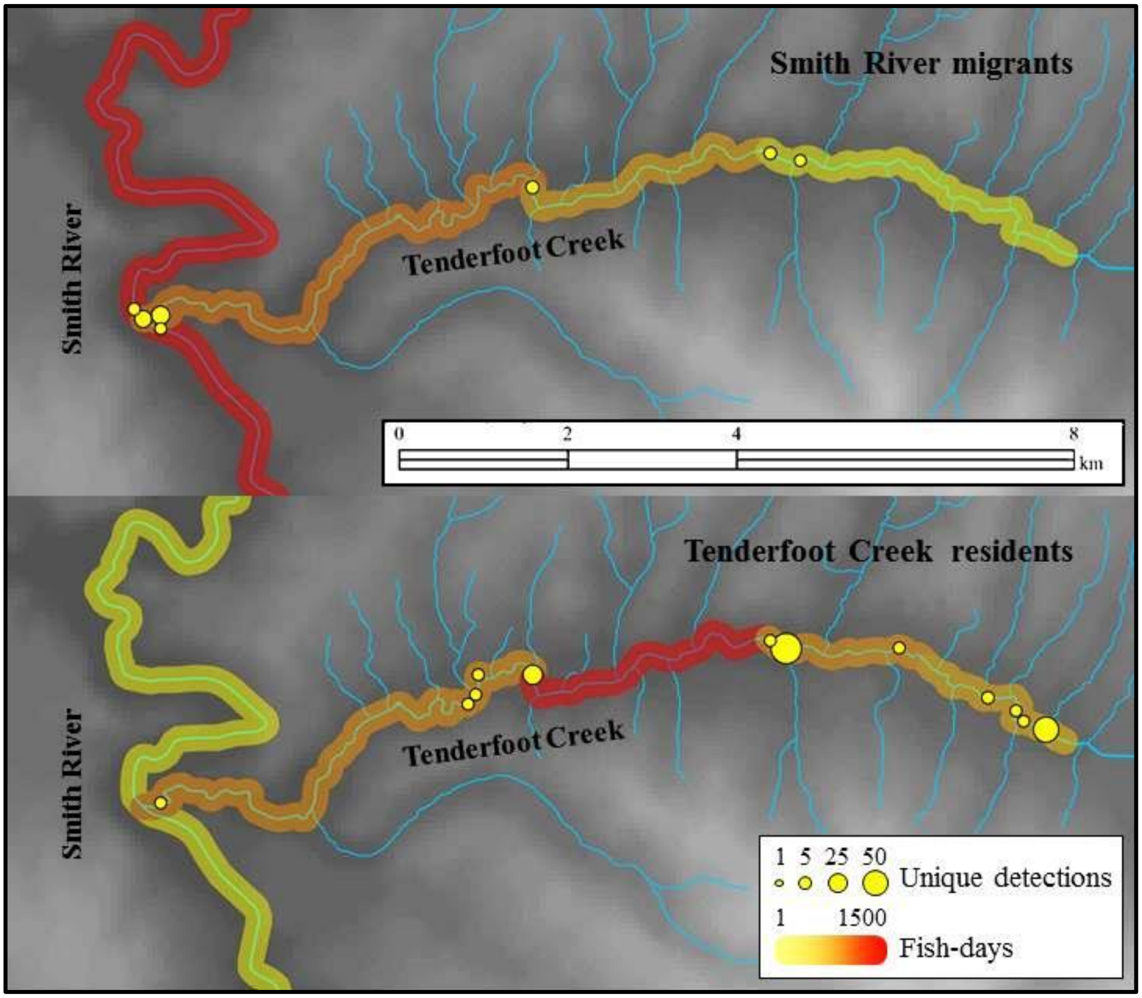

Figure 21. Inferred spatial distribution and number of unique detections of Brown Trout of both movement groups in Tenderfoot Creek and the Smith River in both 2011 and 2012. Inferred spatial distribution is shown as a gradient of fish-days. Fish-days are defined as the number of days per fish spent in the Smith River and between fixed stations in Tenderfoot Creek. Light yellow indicates a low number of fish-days whereas dark red indicates a higher number of fish-days. Unique detections are defined as one detection per day per individual fish and are represented by the yellow circles. Circle size increases as the number of unique detections increases at the same location. Indication of location in the Smith River by Tenderfoot Creek residents may be a result of fewer stations running and subsequent loss of resolution. In other words, the possibility that an individual could be in the Smith River could not be ruled out.

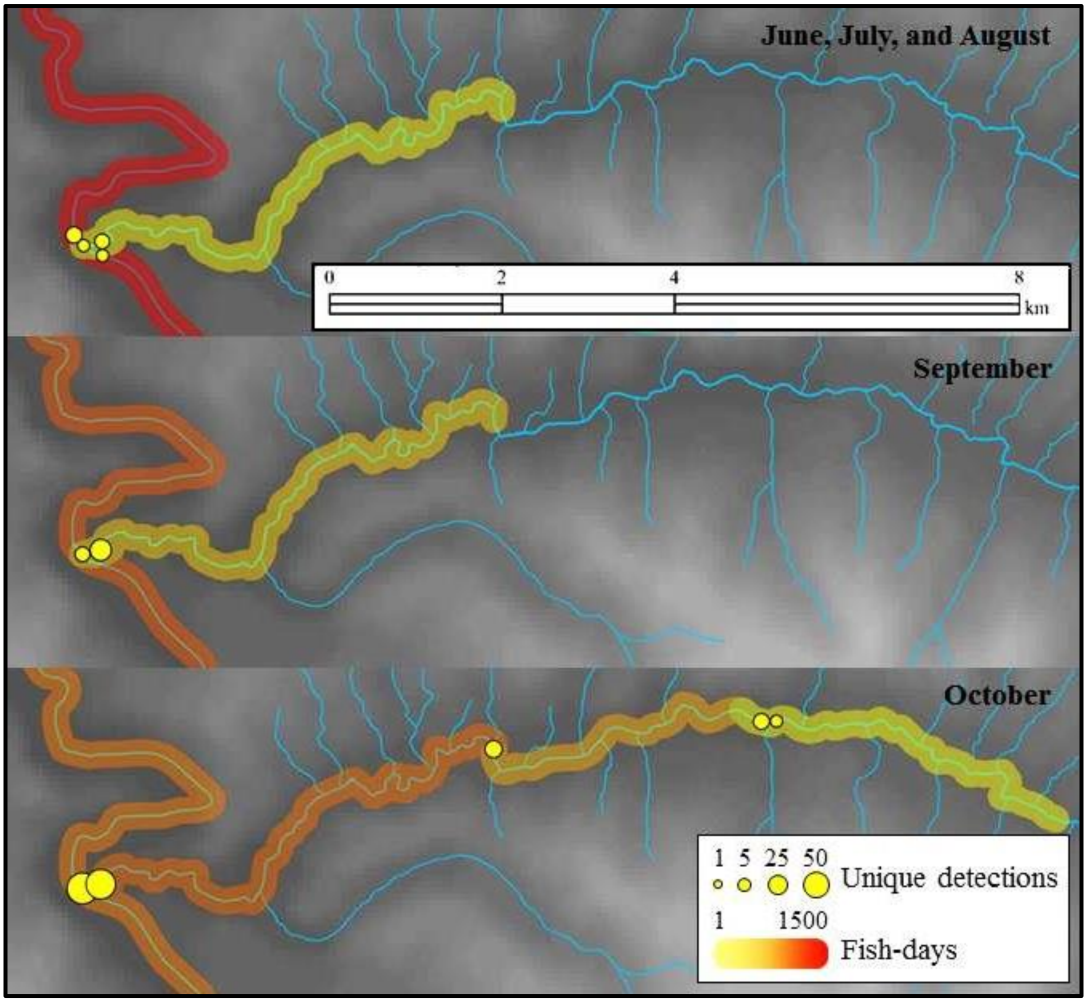

Figure 22. Inferred spatial distribution and number of unique detections of Smith River migrant Brown Trout by month in Tenderfoot Creek and the Smith River in 2011 and 2012. Inferred spatial distribution is shown as a gradient of fish-days. Fish-days are defined as the number of days per fish spent in the Smith River and between fixed stations in Tenderfoot Creek. No color indicates no time spent at that location. Light yellow indicates a low number of fish-days, whereas dark red indicates a higher number of fish-days. Unique detections are defined as one detection per day per individual fish and are represented by the yellow circles. Circle size increases as the number of unique detections increases at the same location.

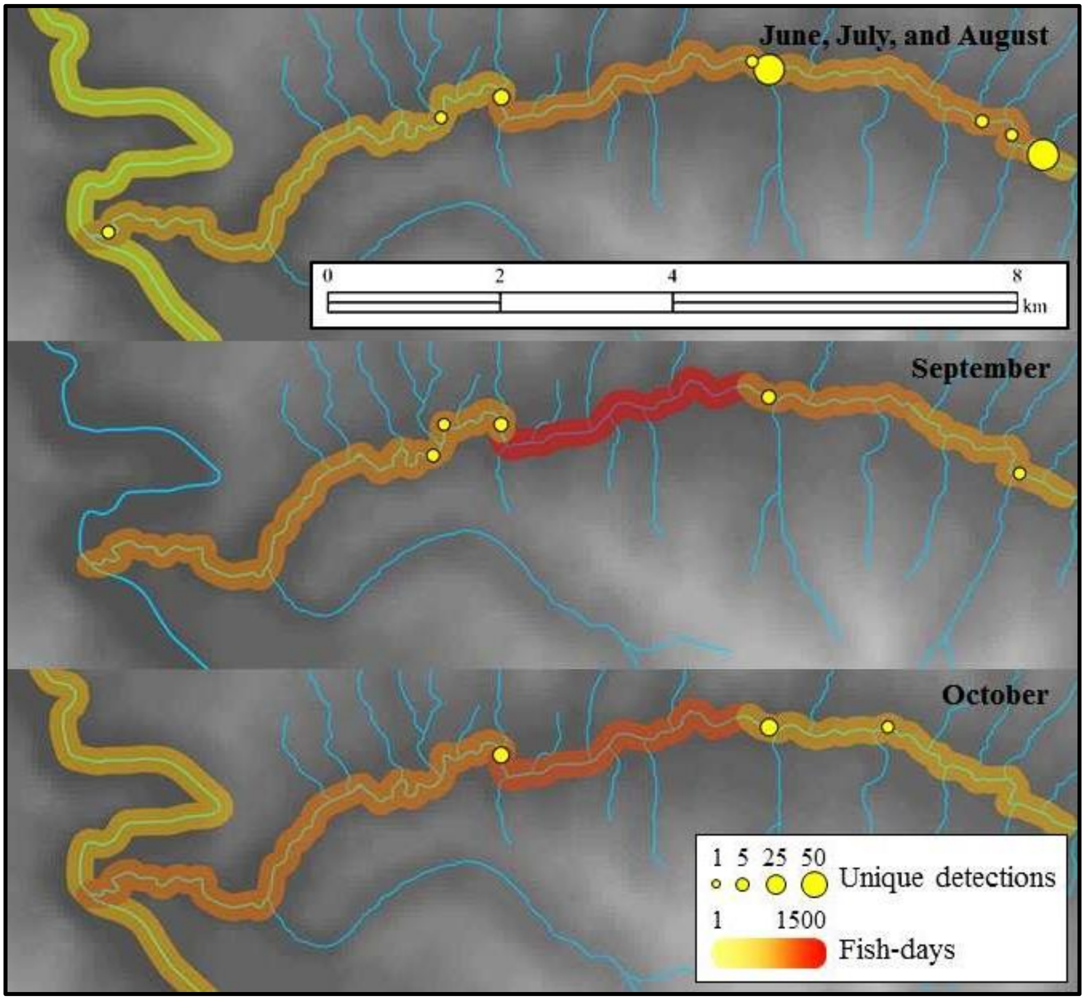

Figure 23. Inferred spatial distribution and number of unique detections of Tenderfoot Creek resident Brown Trout by month in Tenderfoot Creek and the Smith River in 2011 and 2012. Inferred spatial distribution is shown as a gradient of fish-days. Fish-days are defined as the number of days per fish spent in the Smith River and between fixed stations in Tenderfoot Creek. No color indicates no time spent at that location. Light yellow indicates a low number of fish-days, whereas dark red indicates a higher number of fish-days. Unique detections are defined as one detection per day per individual fish and are represented by the yellow circles. Circle size increases as the number of unique detections increases at the same location.

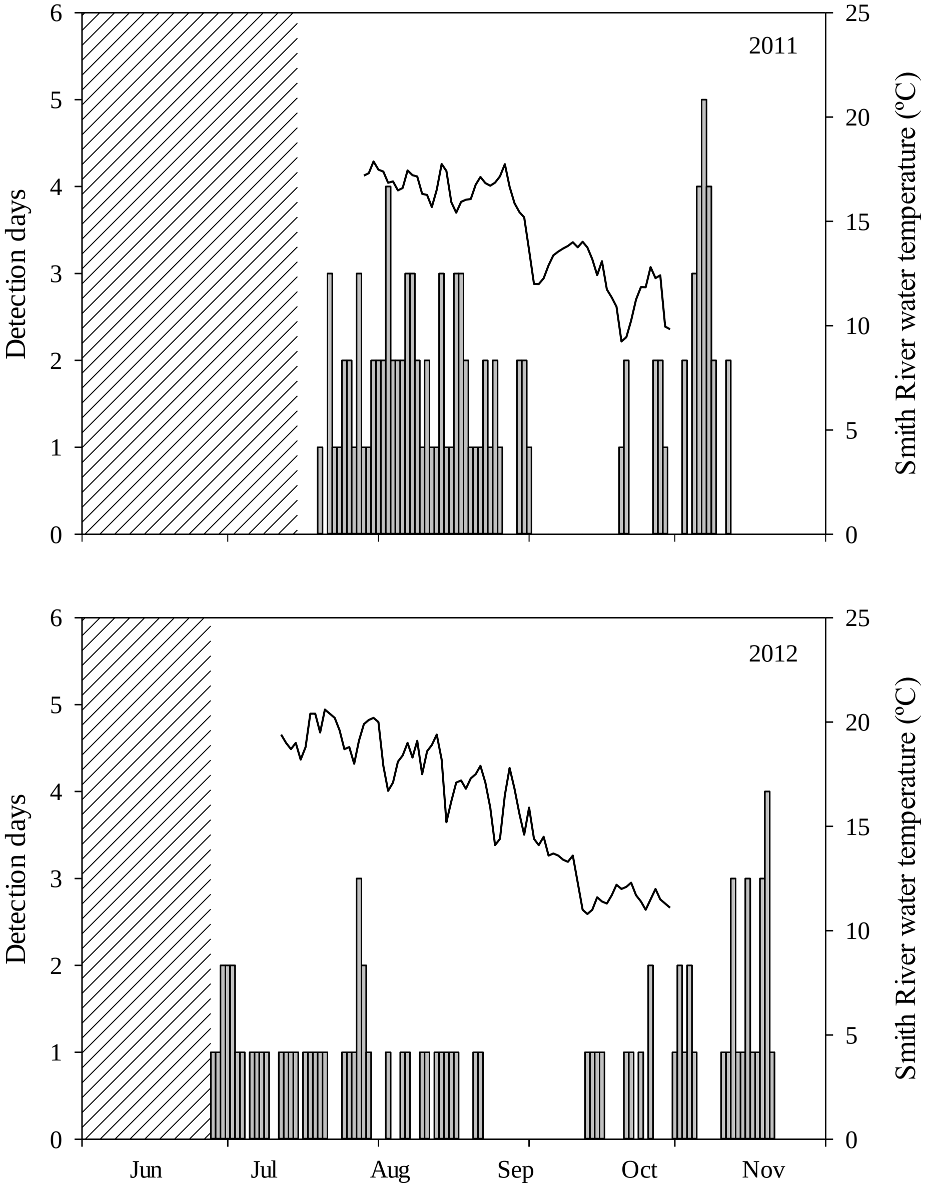

Figure 24. Fixed station detections of tagged Brown Trout in 2011 and 2012. Detection days are defined as one detection per day per individual and are represented by bars. The continuous line represents Smith River water temperature. The first major drops in water temperature in autumn were associated with weather systems that produced precipitation in both years. Cross-hatched areas indicate when fixed stations were not operating.

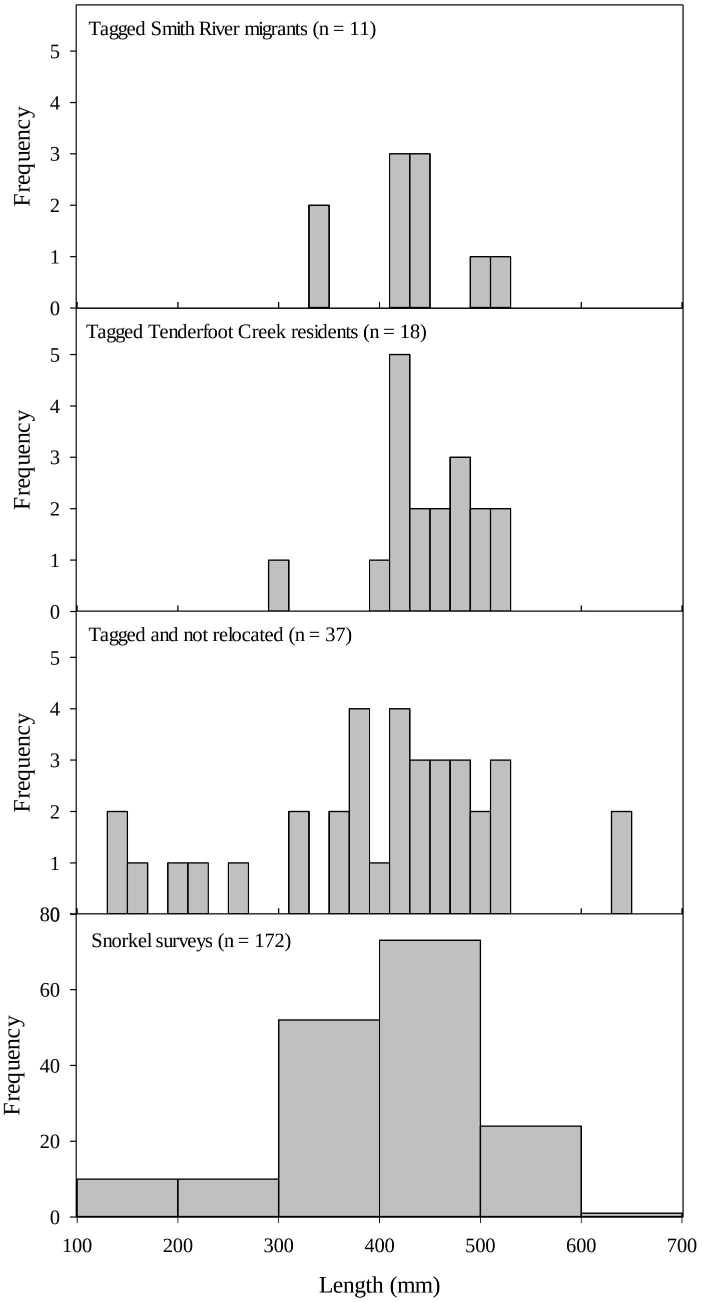

Figure 25. Length–frequency distributions of Brown Trout groups tagged in the Smith River and Tenderfoot Creek and Brown Trout observed during snorkel surveys in Tenderfoot Creek in August of 2011 and 2012.

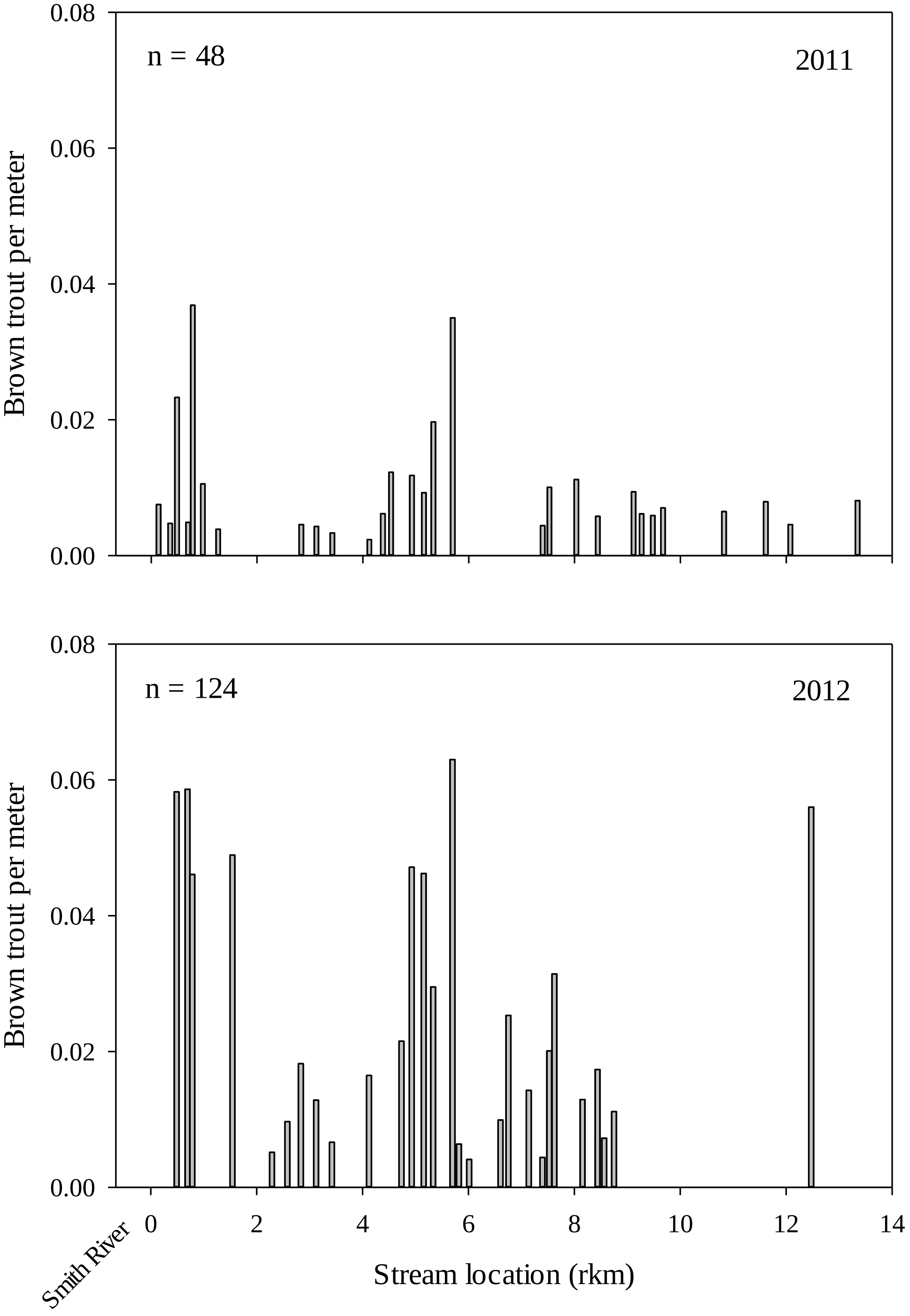

Figure 26. Distributions of Brown Trout determined by snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012. Bars represent the numbers of Brown Trout observed per linear meter of stream.

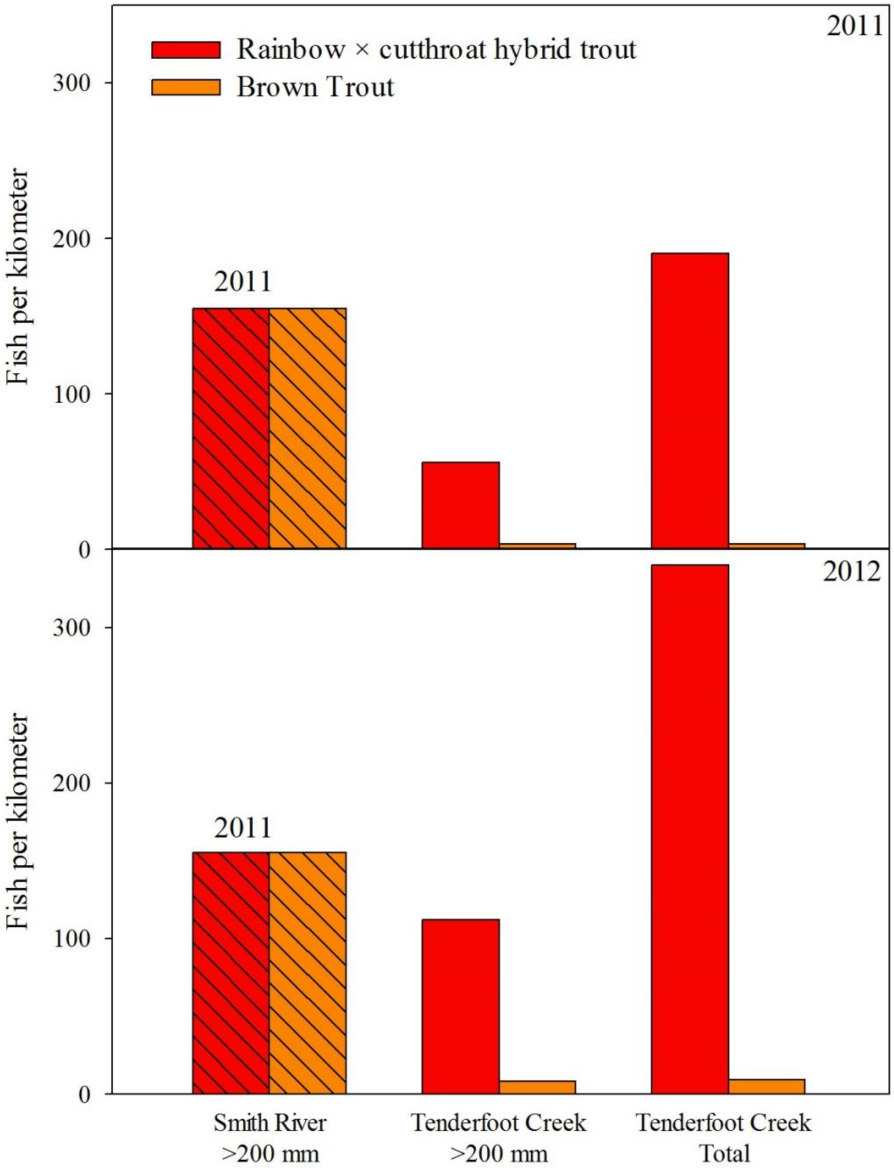

Figure 27. Comparisons of the numbers of fish per km in the Smith River in 2011 and Tenderfoot Creek in 2011 and 2012. The numbers of fish per km in the Smith River were calculated by Montana Fish, Wildlife and Parks using the Petersen mark-recapture estimator on boat electrofishing data collected in the Eagle Creek section. The numbers of fish per km in Tenderfoot Creek were determined from counts made during snorkel surveys.

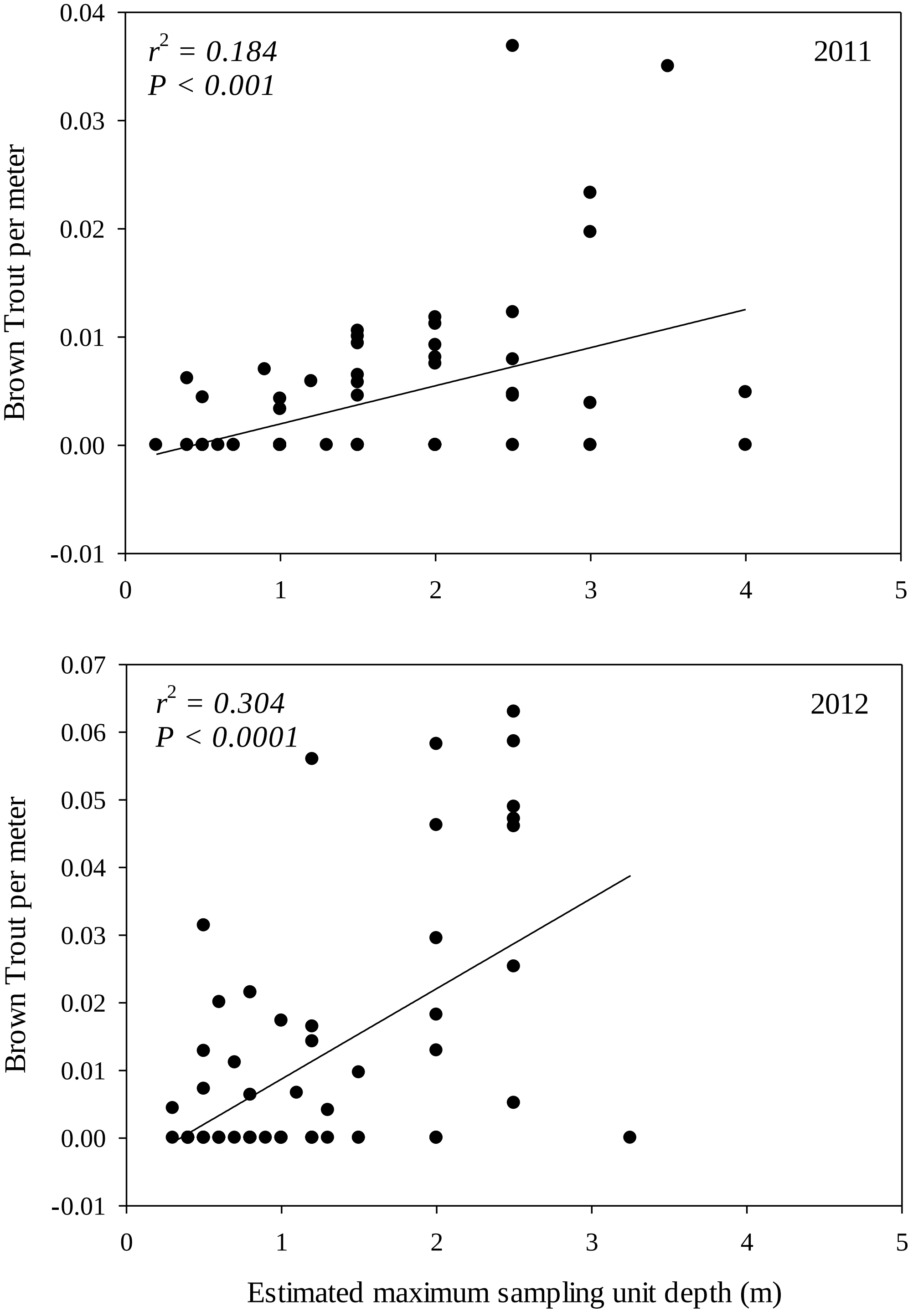

Figure 28. Densities of Brown Trout and maximum depths of primary sampling units estimated during snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012.

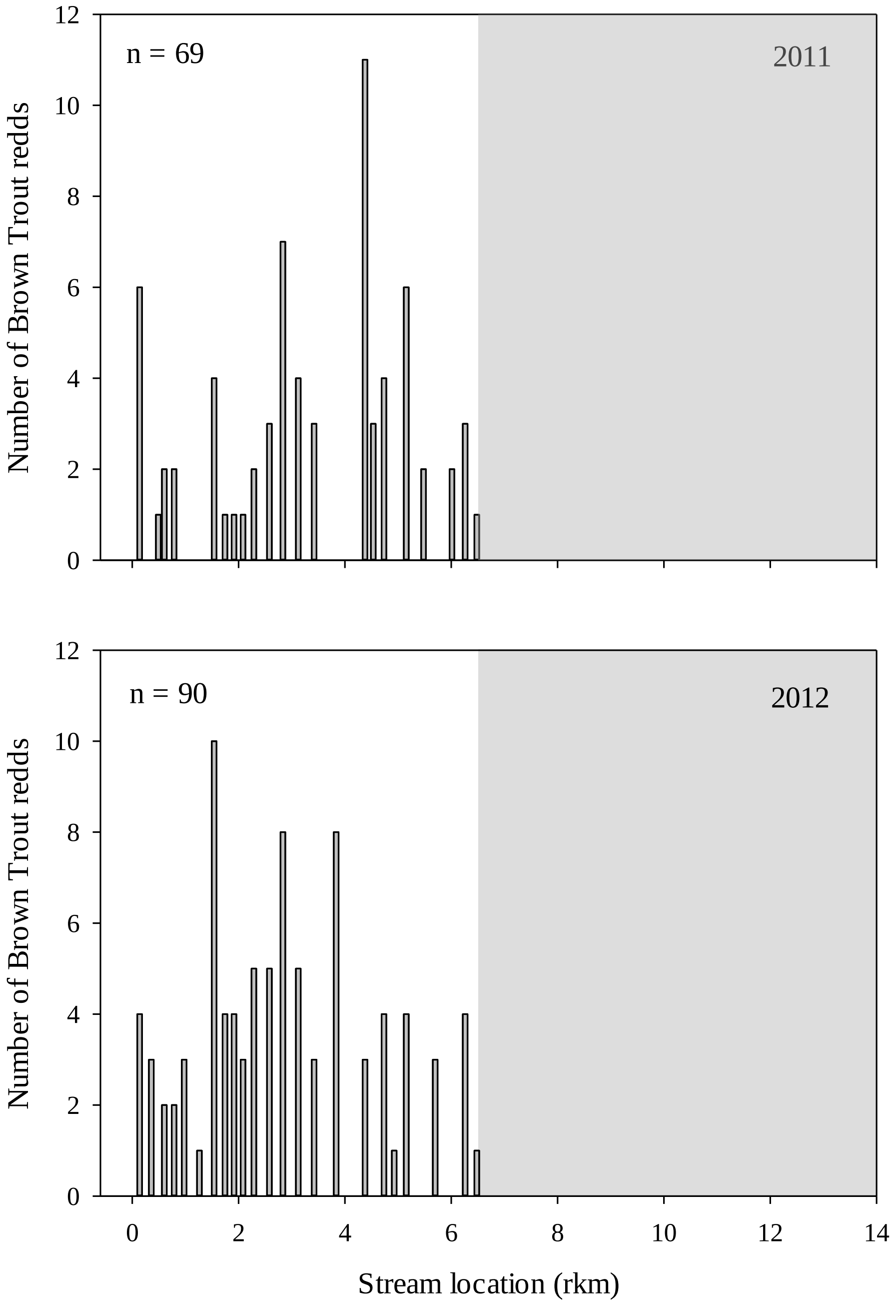

Figure 29. Distributions of Brown Trout redds determined by surveys of the first 6.6 km of Tenderfoot Creek from the confluence with the Smith River in late October of 2011 and 2012. Translucent gray areas indicate where spawning surveys were conducted only in 2010 (not in 2011 and 2012). No redds were observed in surveys conducted above rkm 6.6 in 2010.

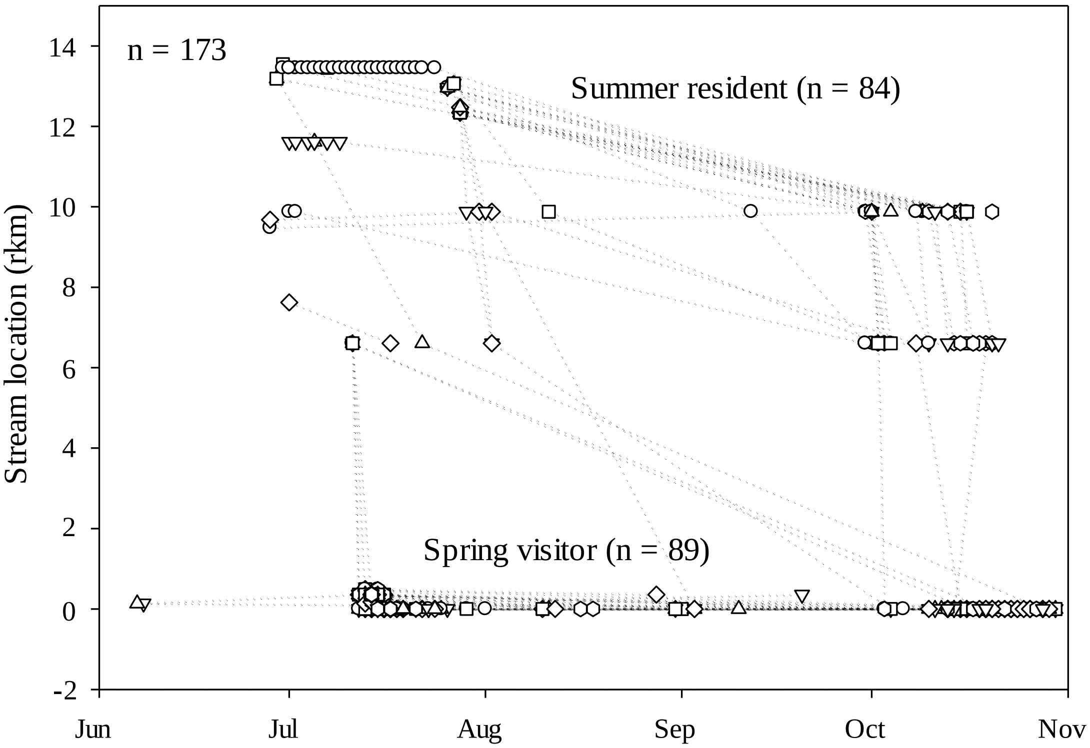

Figure 30. Observed movements of all relocated Mountain Whitefish in 2012. Symbols represent individual fish and lines represent movements (or lack thereof) of those individuals. Stream location is the distance from the confluence with the Smith River.

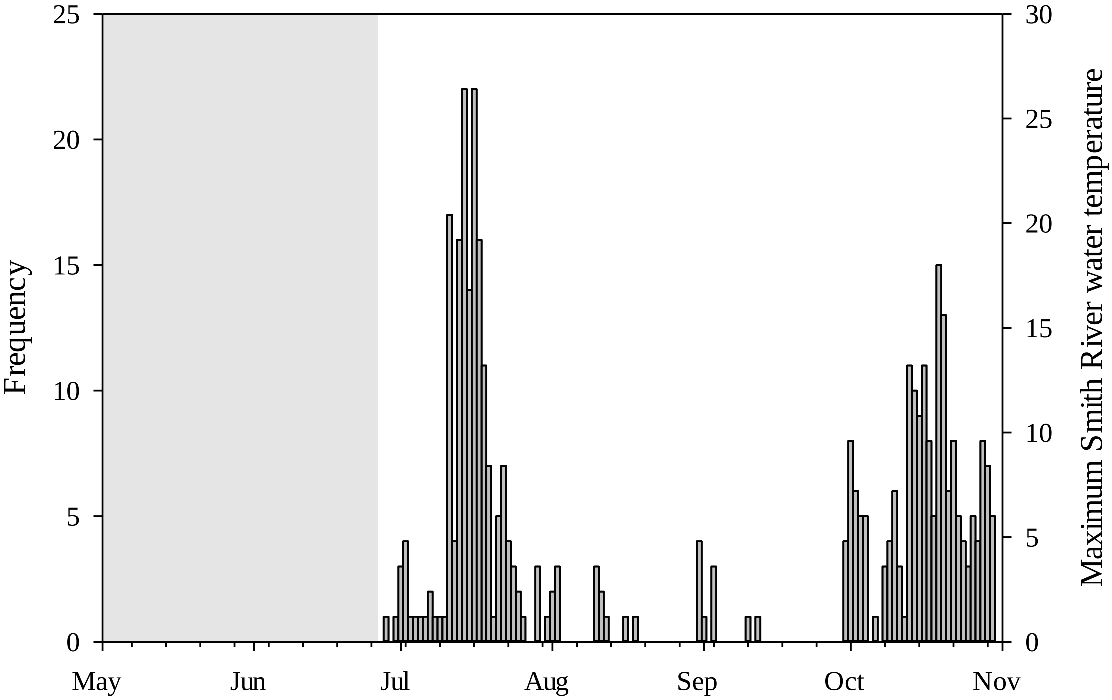

Figure 31. Unique detections of Mountain Whitefish on Station 1 at the confluence of Tenderfoot Creek with the Smith River in 2012. Unique detections are defined as one detection per day per individual and are represented by bars. The continuous line represents maximum daily Smith River water temperatures. The shaded area indicates when the station was not operating.

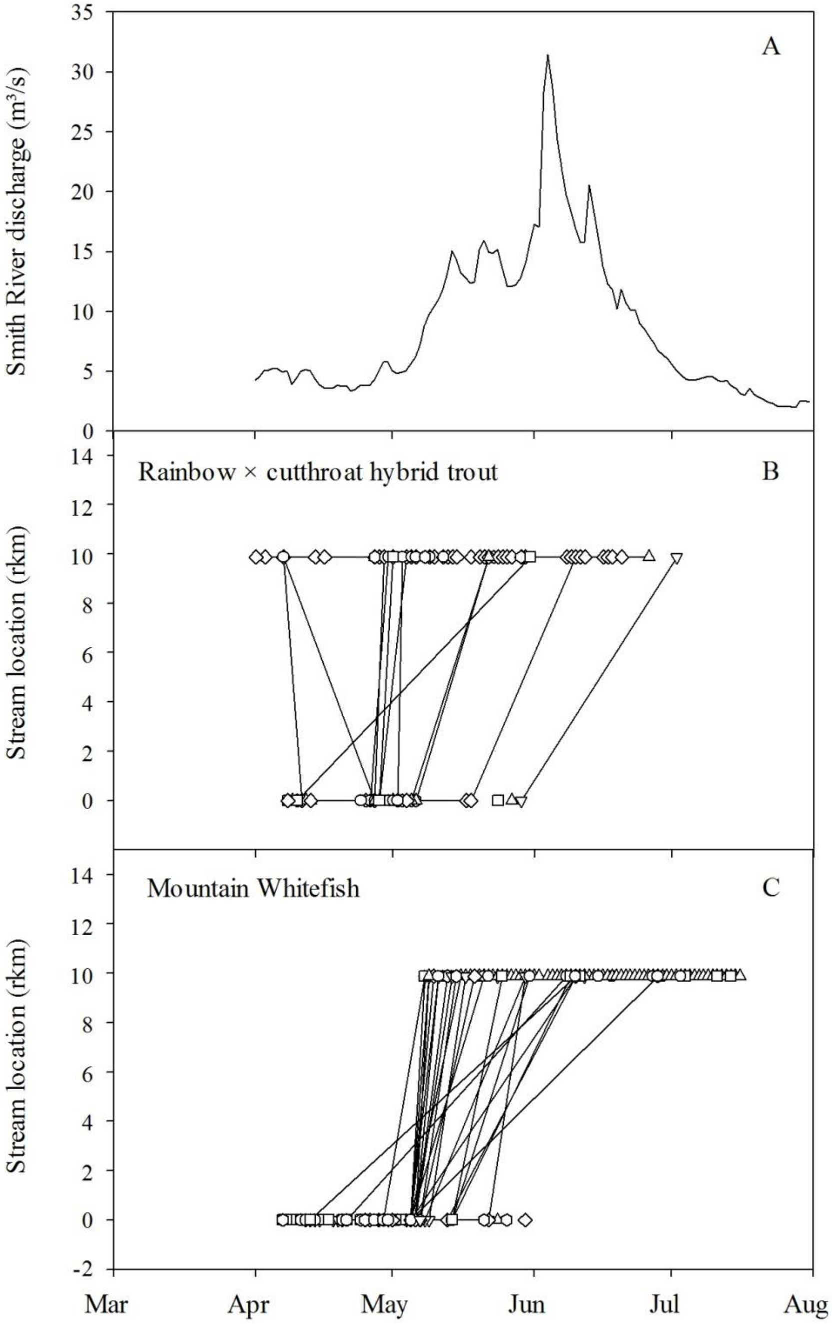

Figure 32. (A) Daily Smith River discharge and observed movements of (B) rainbow × cutthroat hybrid trout and (C) Mountain Whitefish in spring of 2013. Symbols represent individual fish and lines represent movements (or lack thereof) of those individuals. Stream location is the distance from the confluence with the Smith River.

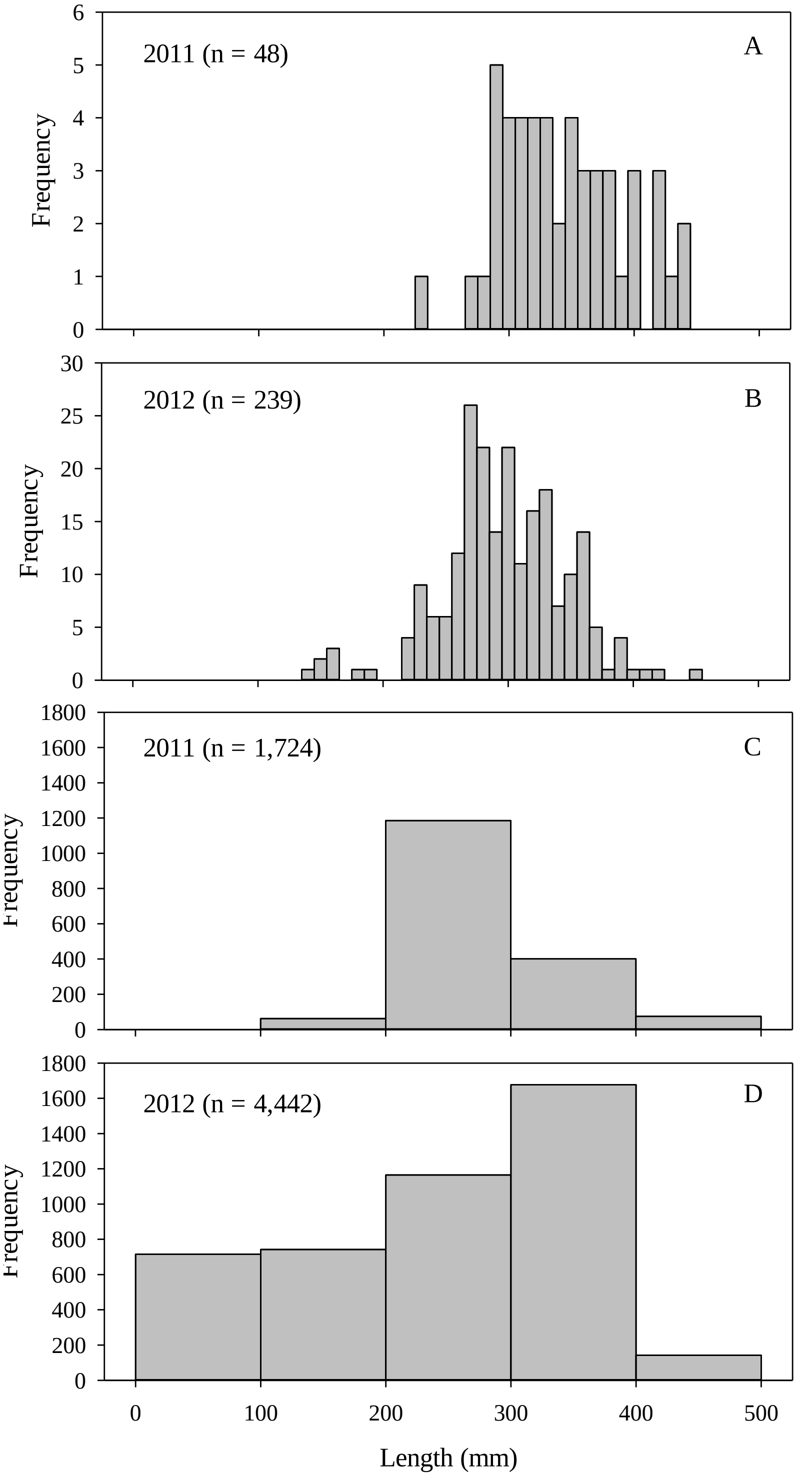

Figure 33. Length-frequency distributions of Mountain Whitefish tagged in (A) 2011 and (B) 2012 and Mountain Whitefish observed during snorkel surveys in (C) August of 2011 and (D) 2012 in Tenderfoot Creek.

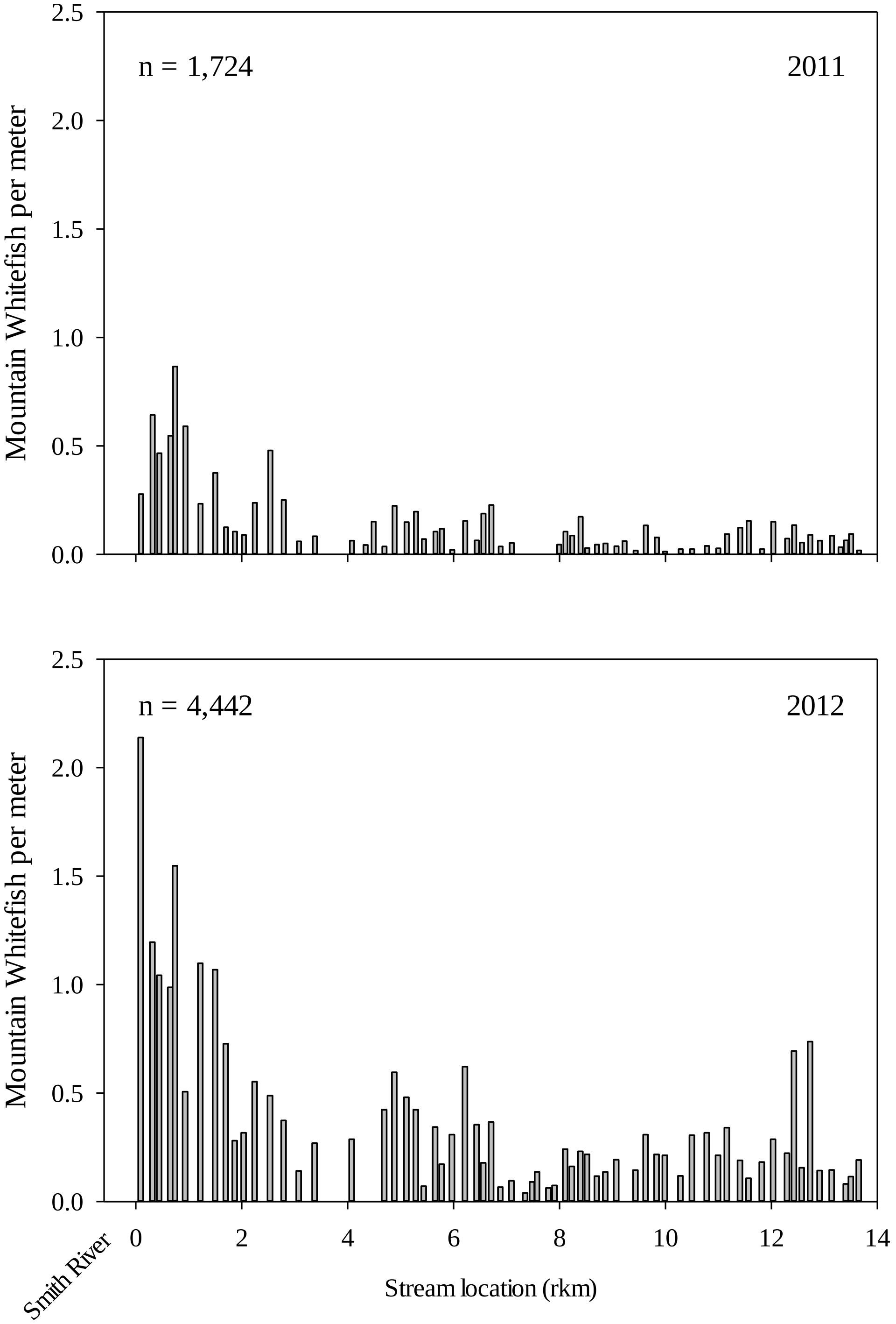

Figure 34. Distributions of Mountain Whitefish determined by snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012. Bars represent the numbers of Mountain Whitefish observed per linear meter of stream.

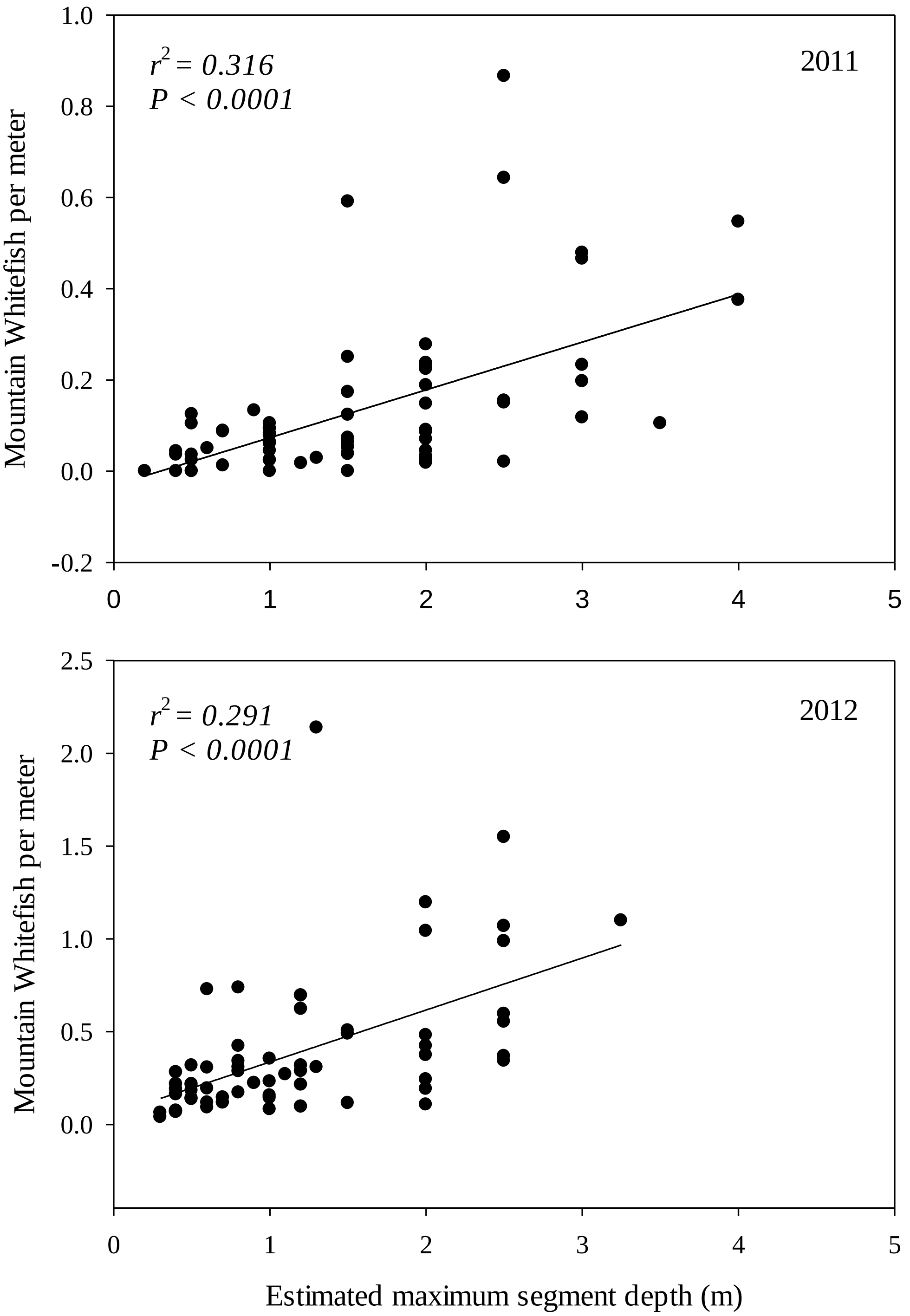

Figure 35. Densities of Mountain Whitefish and maximum depths of primary sampling units estimated during snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012.

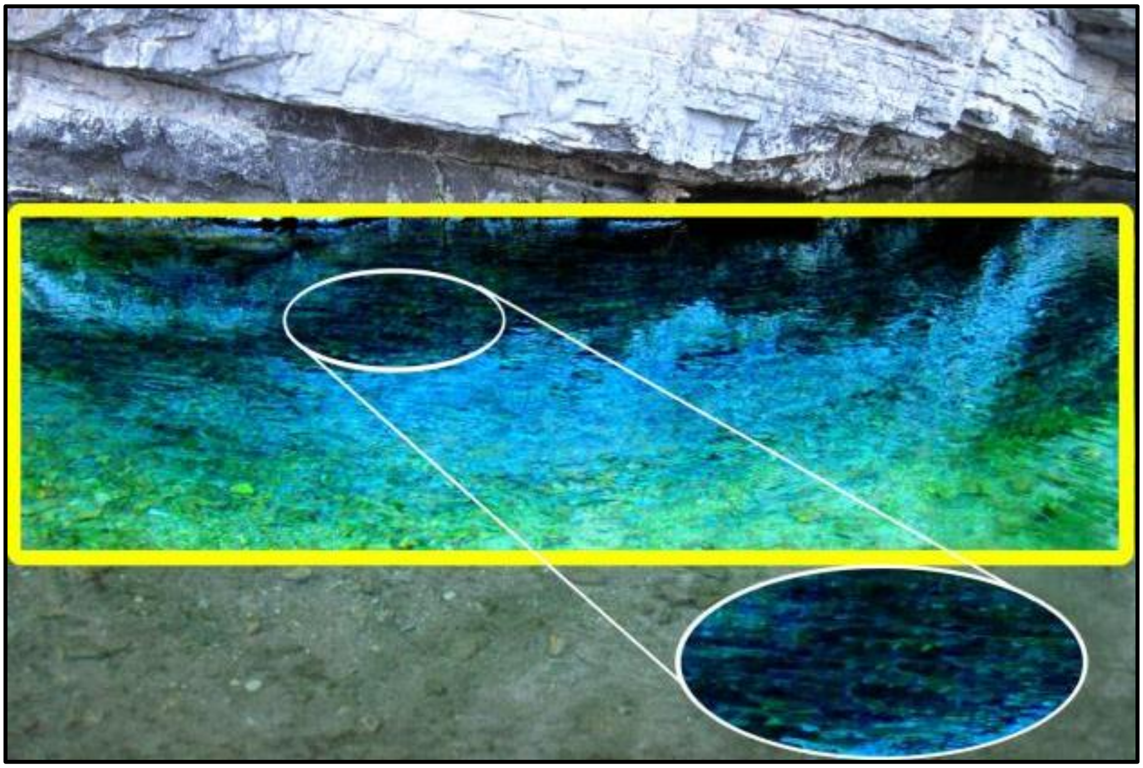

Figure 36. A large aggregation of Mountain Whitefish in primary sampling unit 1.2 (rkm 0.1-0.4) on November 3, 2011. Photograph is digitally-enhanced within the yellow box to highlight individual fish.

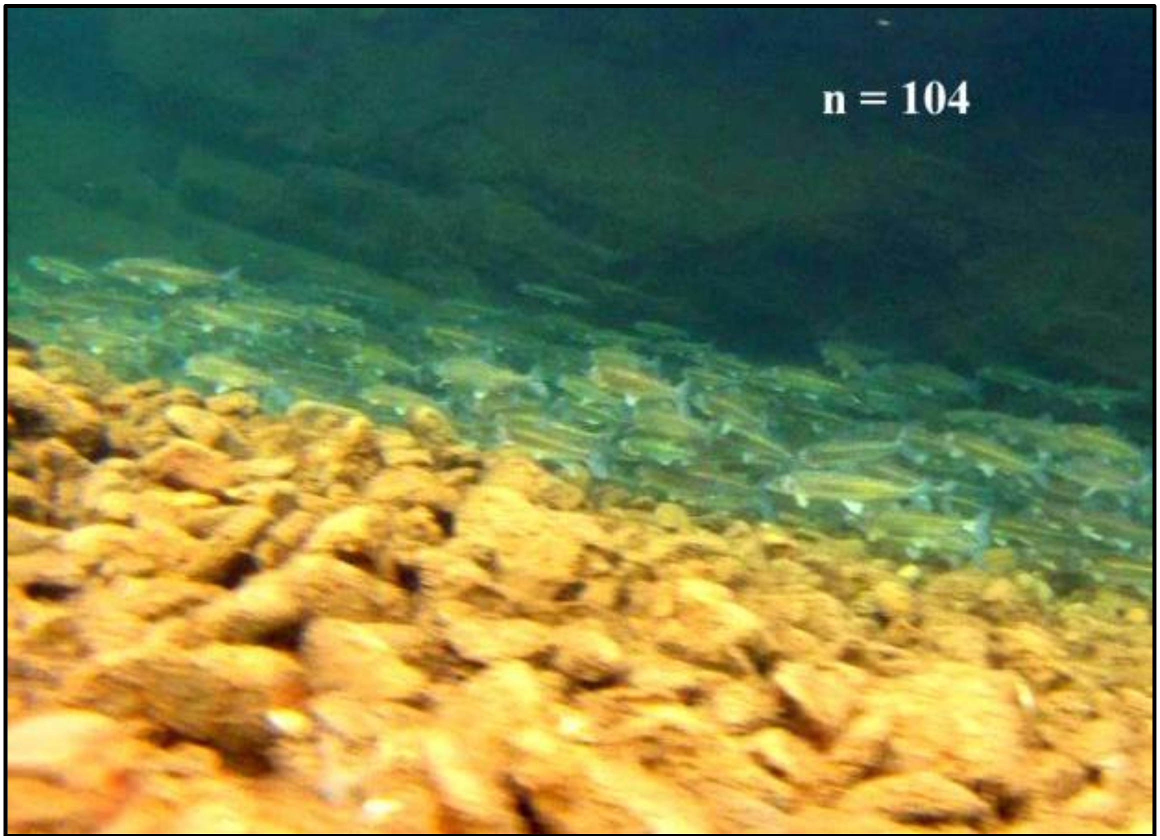

Figure 37. Screenshot from a video survey of a spawning aggregation of about 104 Mountain Whitefish in primary sampling unit 1.2 (0.1-0.4) performed on October 24, 2012. About 515 individuals were counted in this 12 × 30 m pool.

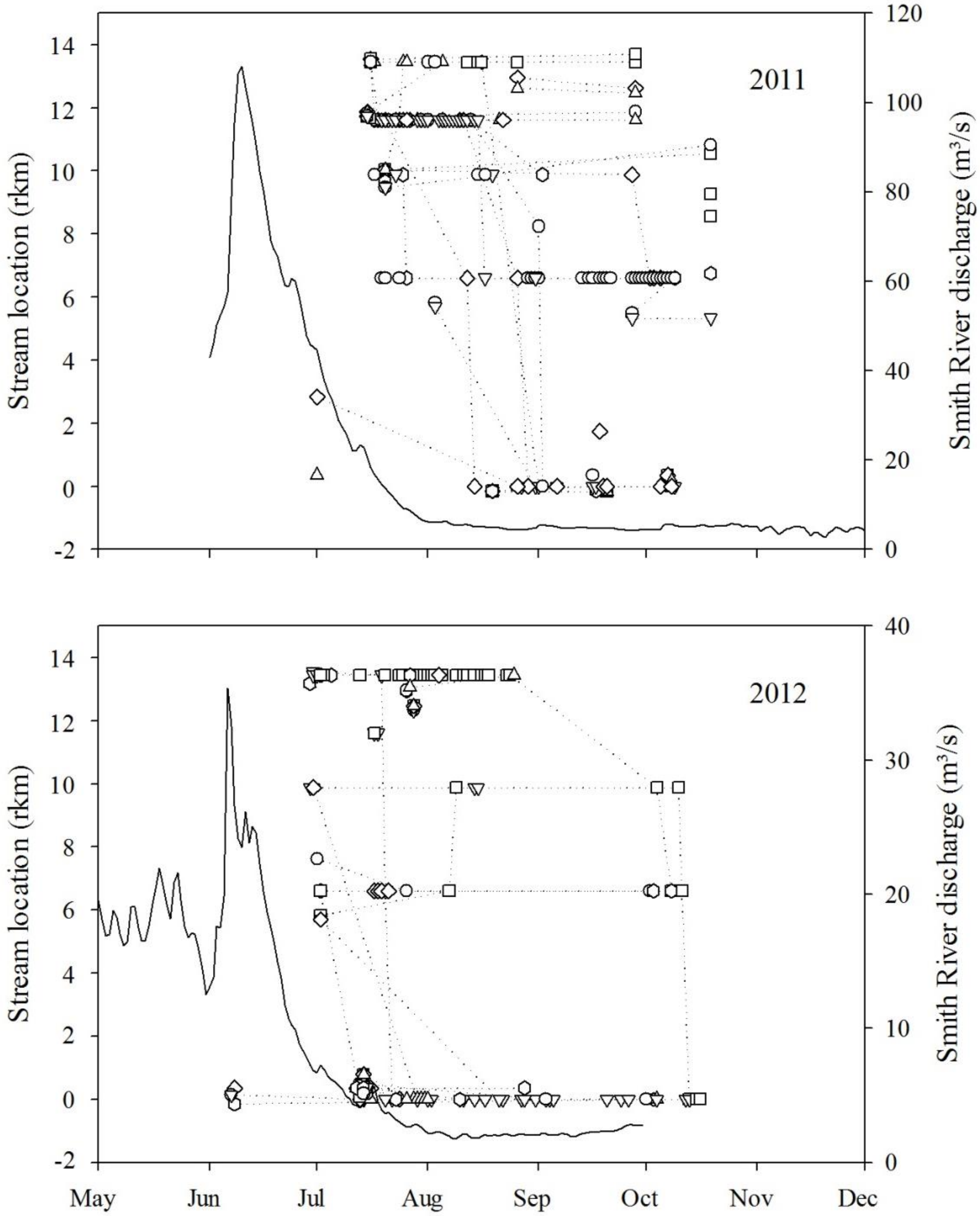

Figure 38. Observed movements of tagged rainbow × cutthroat hybrid trout in 2011 and 2012. Symbols represent individual fish and lines represent movements (or lack thereof) of those individuals. Symbols without connecting lines indicate fish that were tagged and never relocated. Stream location is the distance from the confluence with the Smith River. Values below 0 rkm represent fish either above or below the confluence in the Smith River. Solid lines represent daily Smith River discharges.

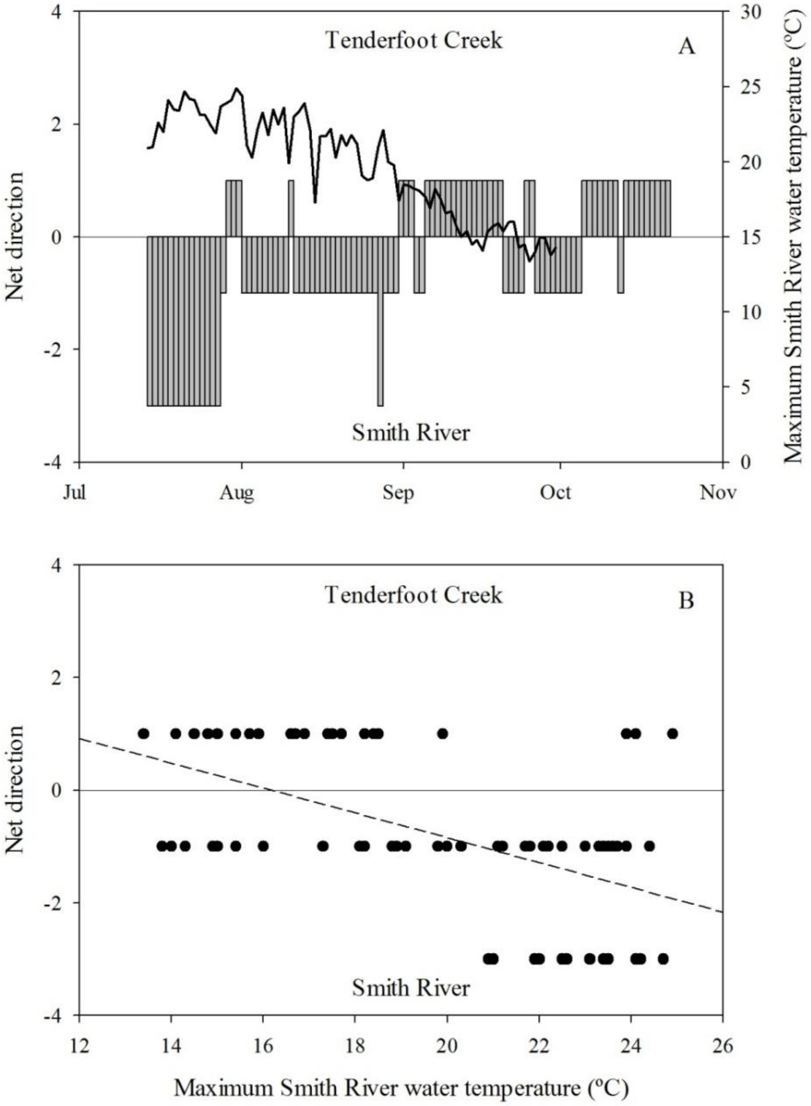

Figure 39. (A) Net direction of the three rainbow × cutthroat hybrid trout detected on the confluence station when water temperature was high in 2012. Bars represent the net location of the three rainbow × cutthroat hybrid trout inferred from detections on the upstream and downstream antennas of the confluence station. Negative values indicate occupation in the Smith River, whereas positive values indicate upstream occupation in Tenderfoot Creek. The solid line represents daily maximum Smith River water temperatures. (B) Net direction of the three rainbow × cutthroat hybrid trout detected on the confluence station when water temperature was high in 2012 and maximum Smith River water temperature. Dots represent the net direction of the three individuals inferred from detections on the upstream and downstream antennas of the confluence station. Negative values indicate occupation in the Smith River, whereas positive values indicate upstream occupation in Tenderfoot Creek.

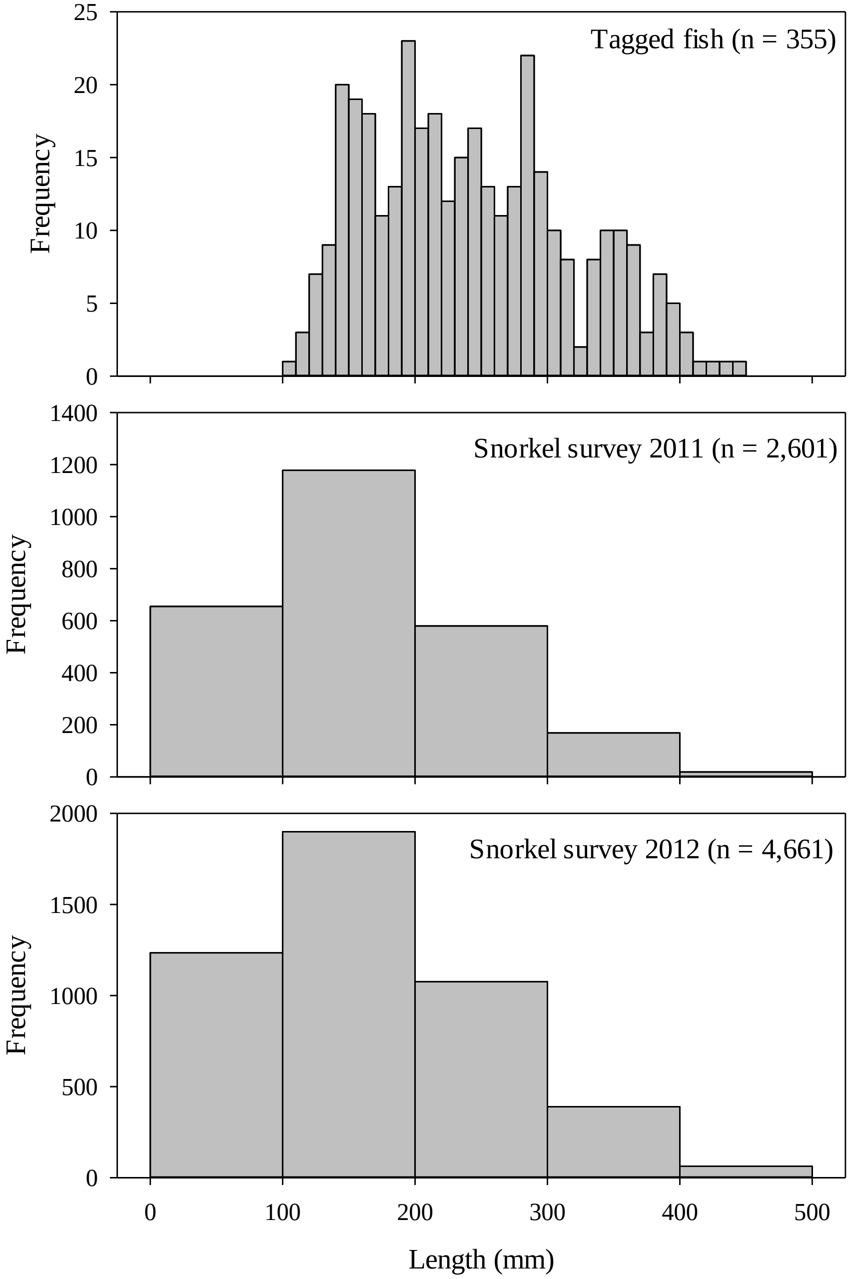

Figure 40. Length-frequency distributions of rainbow × cutthroat hybrid trout tagged in Tenderfoot Creek from August of 2010 to July of 2012 and observed during snorkel surveys in Tenderfoot Creek in August of 2011 and 2012. Fish measuring less than 100 mm were too small to tag and not measured and therefore not included in the distribution of tagged fish.

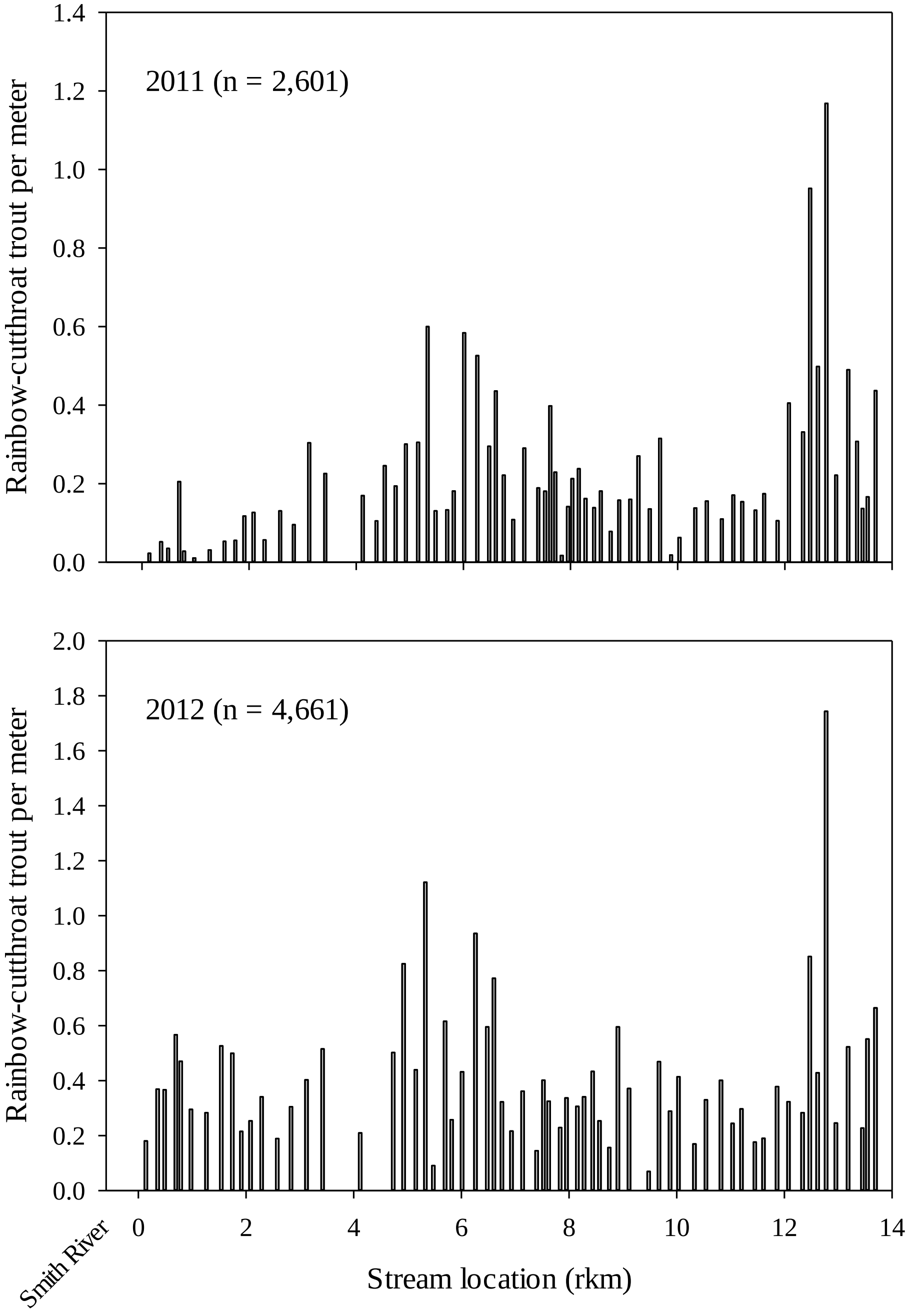

Figure 41. Distributions of rainbow × cutthroat hybrid trout determined by snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012. Bars represent the numbers of rainbow-cutthroat trout observed per linear meter of stream.

Figure 42. An out-migrant rainbow × cutthroat hybrid trout captured in the downstream confluence weir in July of 2011. Note the vibrant colors and low body mass indicative of post-spawning condition.

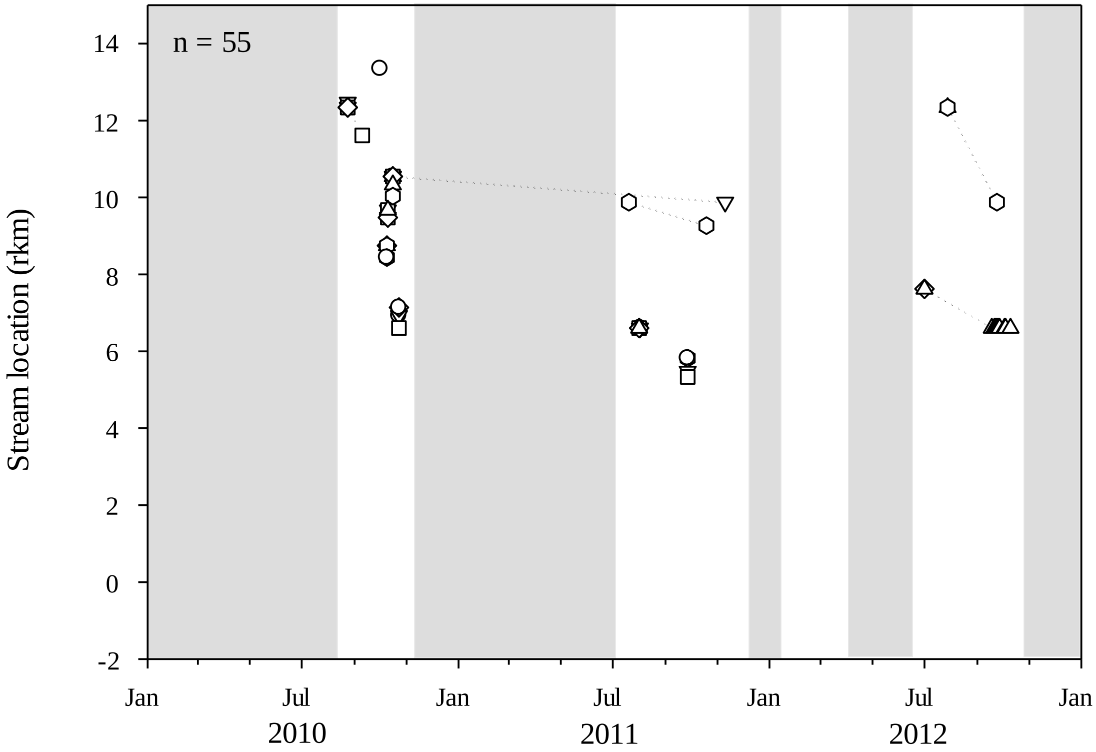

Figure 43. Observed movements of all tagged Brook Trout from 2010 to 2012. Thirty eight fish were tagged in 2010, 12 in 2011, and 5 in 2012. Symbols represent individual fish and lines represent movements (or lack thereof) of those individuals. Symbols without connecting lines indicate fish that were tagged and never relocated. Translucent gray areas indicate when fixed stations were not operating. Stream location is the distance from the confluence with the Smith River.

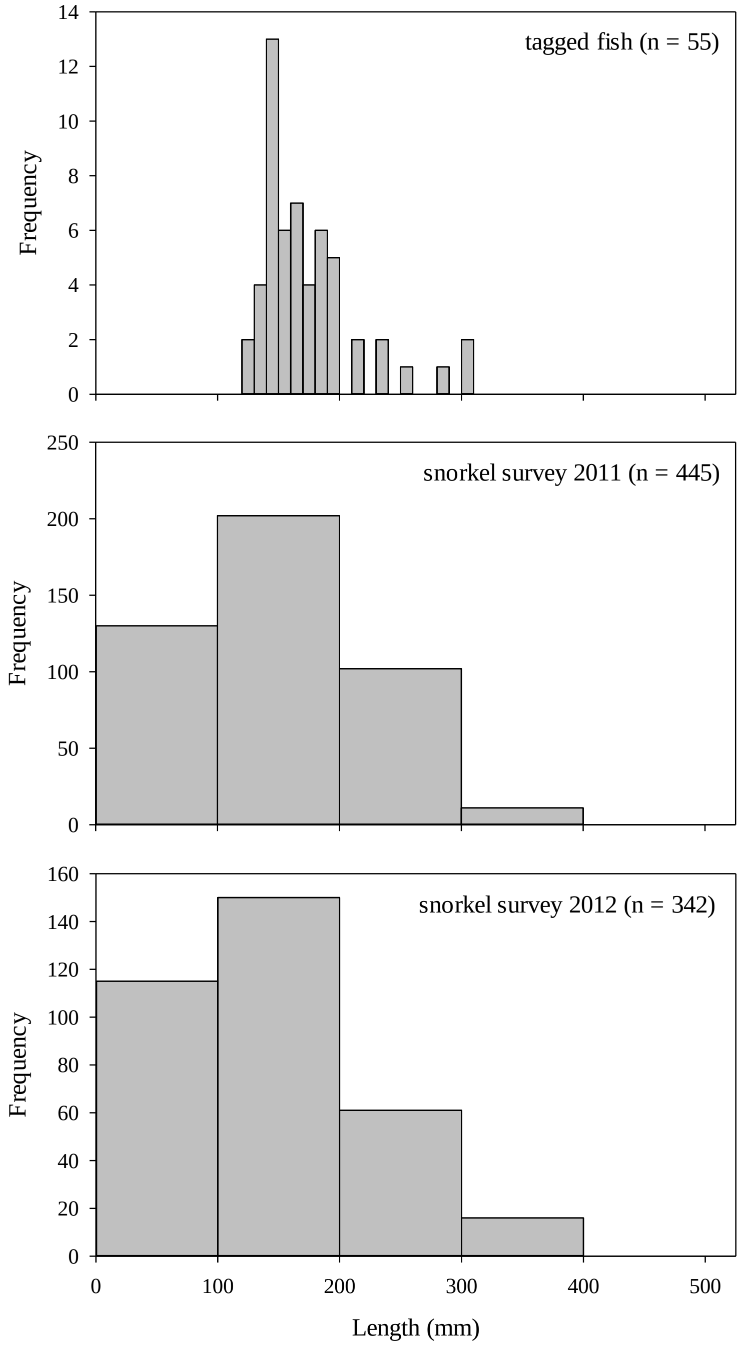

Figure 44. Length-frequency distributions of Brook Trout tagged in Tenderfoot Creek from August of 2010 to July of 2012 and observed during snorkel surveys in Tenderfoot Creek in August of 2011 and 2012. Fish measuring less than 100 mm were too small to tag and not measured and therefore not included in the distribution of tagged fish.

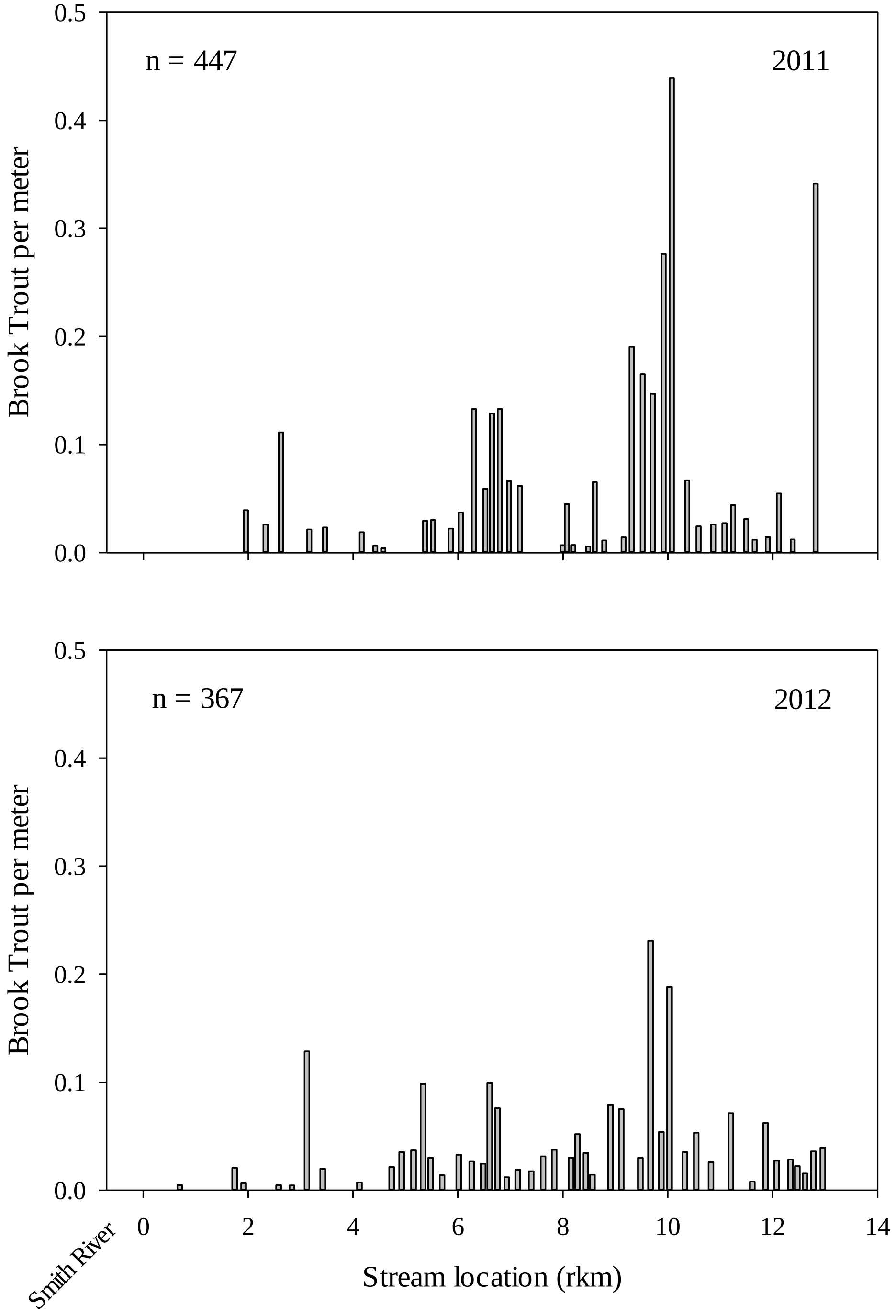

Figure 45. Distributions of Brook Trout determined by snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012. Bars present the numbers of Brook Trout observed per linear meter of stream.

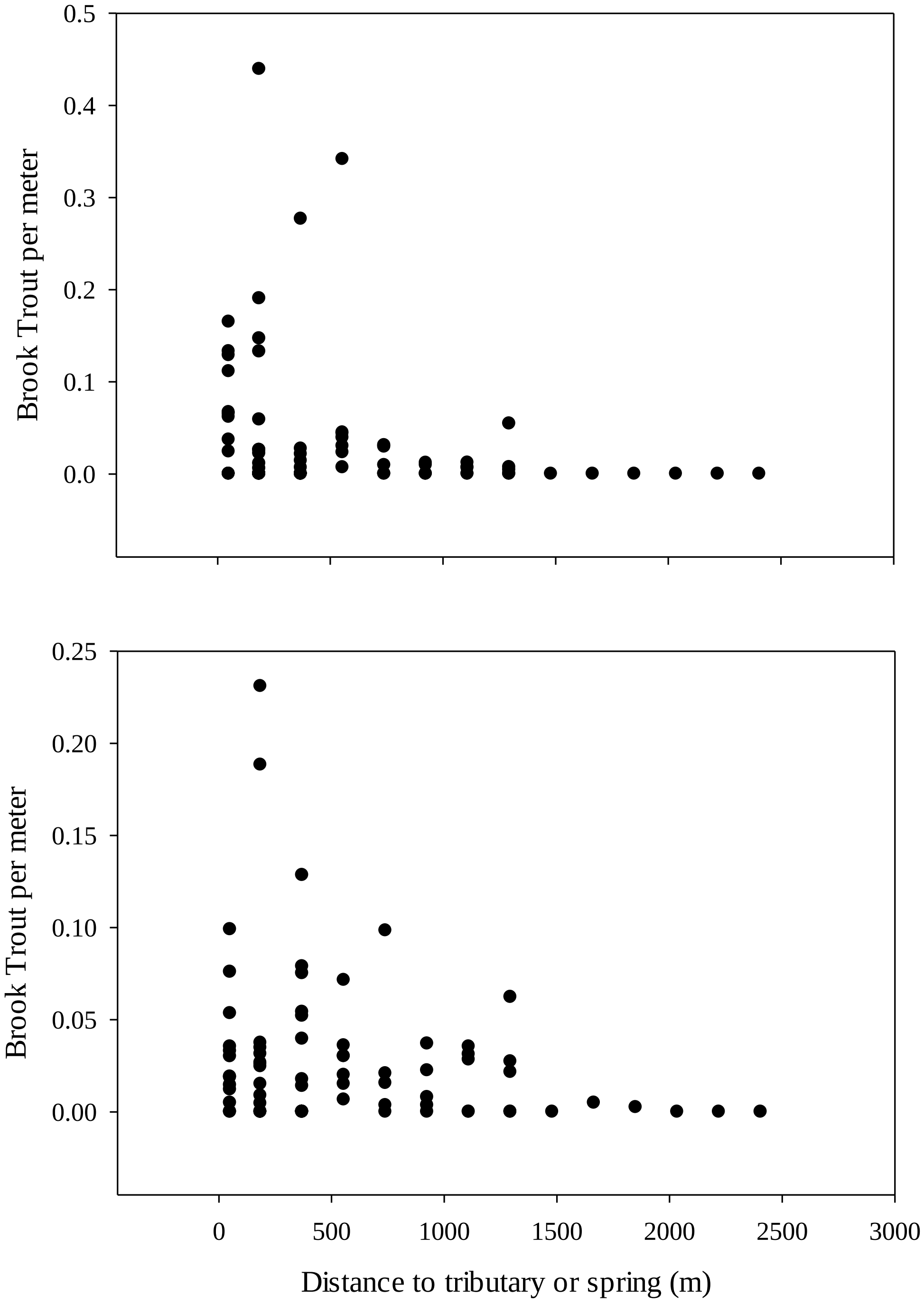

Figure 46. Densities of Brook Trout and distance to the nearest tributary or spring estimated during snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012.

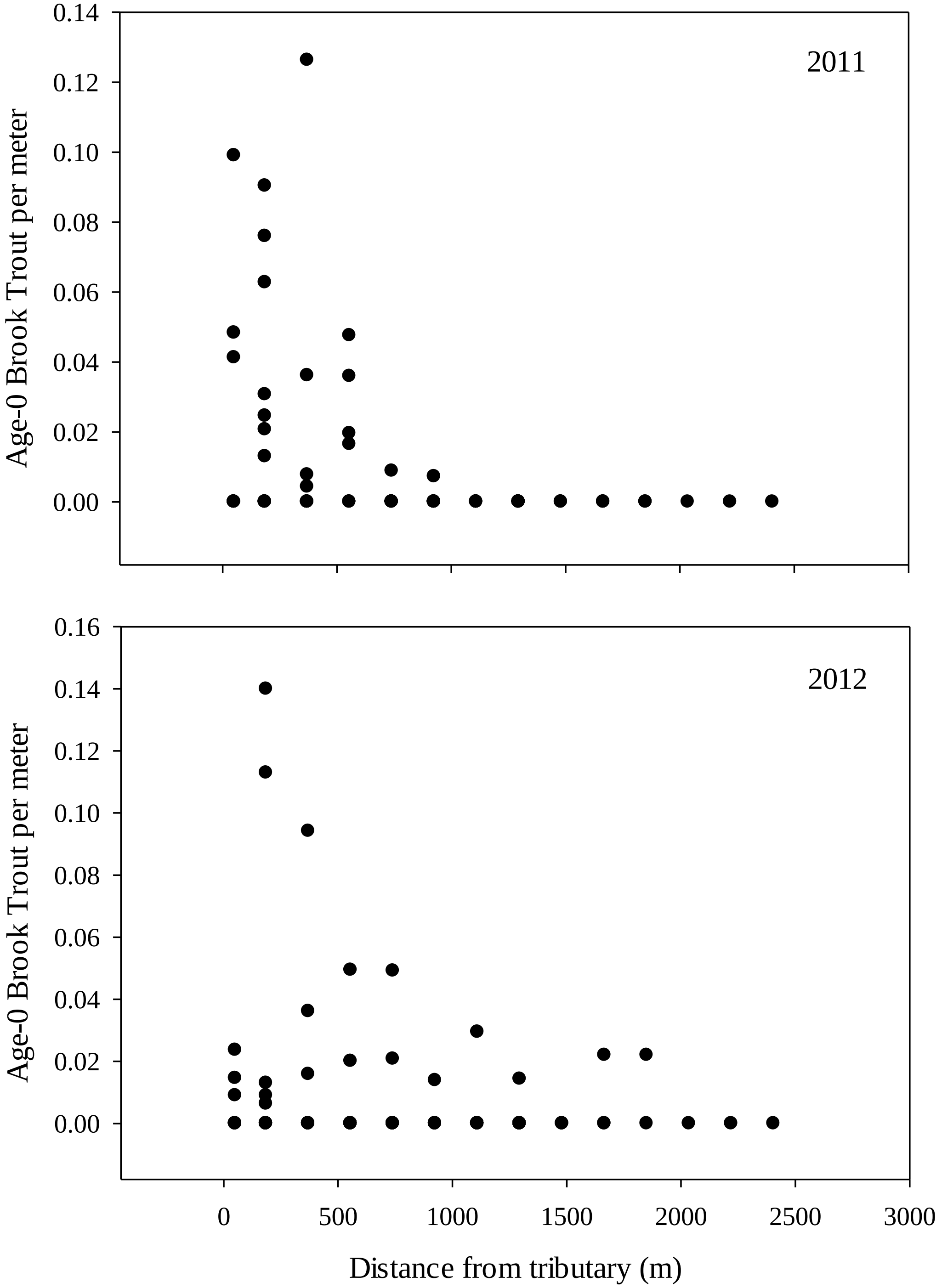

Figure 47. Densities of Brook Trout under 100 mm and distance to the nearest tributary estimated during snorkel surveys in Tenderfoot Creek in late August of 2011 and 2012.

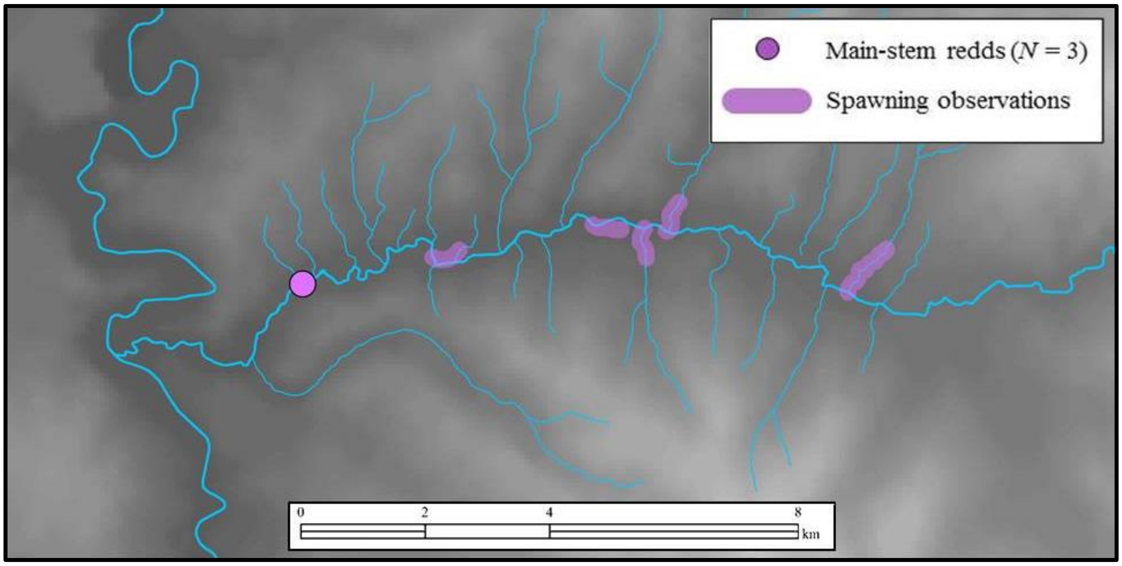

Figure 48. Spawning locations of Brook Trout in Tenderfoot Creek observed from 2010 to 2012.

DISCUSSION

Tenderfoot Creek as a Thermal Refuge

Contrary to expectations, Tenderfoot Creek was not used as a thermal refuge by salmonids when water temperatures in the Smith River were high. High water temperatures can adversely affect growth, development, and reproductive capacity by suppressing appetite and reducing ability to compete for resources (Elliott 1991; DeStaso and Rahel 1994). Fish therefore select a specific range of temperatures, unique to species, to reduce stress and optimize growth, feeding, development, and reproduction when presented with a thermal gradient (Jobling 1981; Golovanov 2013). Such gradients can be vertical in orientation (Sutterlin and Stevens 1992), or horizontal (Bonneau and Scarnecchia 1996) as in the confluence of Tenderfoot Creek with the Smith River. During periods of high ambient water temperature, trout move to areas of cooler temperature (Stevens and DuPont 2011; Hillyard and Keeley 2012) and may seek thermal refuge in coldwater tributaries in systems where main-stem river temperatures are high (Kaeding 1996; Baird and Krueger 2003). Steelhead and Chinook Salmon in the Columbia River frequently used coldwater tributaries during spawning migrations, often remaining in such areas for days at a time when main-stem river conditions were too warm (Goniea et al. 2006; Keefer et al. 2009). However, none of my tagged fish exhibited this refuge-seeking behavior when water temperatures in the Smith River were stressful. Perhaps conditions in the Smith River were not stressful enough to warrant upstream movement into Tenderfoot Creek, Tenderfoot Creek was not cool enough to be used as a thermal refuge, fish were finding thermal refuge within the Smith River itself, or social interactions among fish, such as territoriality, mediated thermoregulatory behavior.

Thermal conditions in the Smith River were not extreme enough to affect the survival of salmonids, but their growth, feeding, development, and reproductive capacity may have been adversely affected. Long-term upper incipient lethal temperatures of all taxa were surpassed at least twice in the Smith River in 2012. Frequency of exposure to these temperatures was not enough to be lethal; even when temperatures surpassed long-term UILTs and upper growth limits on consecutive days, they were maintained for only a few hours before decreasing to less stressful levels. Bonneville Cutthroat Trout persisted under diel cycling conditions of 16-26 ºC, which temporarily exceeded their 7-d UILT of 24.2 ºC, but experienced reduced appetite and lethargy (Johnstone and Rahel 2003). When mean daily temperatures in the Columbia River exceeded 20 °C, use of coldwater tributaries by steelhead increased exponentially, but such conditions often persisted for weeks at a time (Keefer et al. 2009). In contrast, mean daily temperatures in the Smith River never exceeded 20 °C for more than 3 days.

The temperature gradient at the confluence of Tenderfoot Creek and the Smith River may have been too gradual for fish to detect. Trout in the geothermally-heated lower Firehole River, where maximum temperature reached 29.6 °C, used a 9 ºC cooler tributary to thermoregulate in late summer (Kaeding 1996). Brook and Rainbow Trout in Moose River, New York, used tributaries that averaged about 6 ºC cooler than the main-stem river, where maximum temperature reached 26.4 °C (Baird and Krueger 2003). Rainbow Trout in northeastern Oregon streams used thermal refugia that averaged 3-8 ºC less than ambient stream temperature (Ebersole et al. 2001). In contrast, Tenderfoot

Creek was never more than 3.65 °C cooler than the Smith River at the confluence, where the maximum temperature recorded was 24.9 °C. Much cooler temperatures existed in the upper reaches of Tenderfoot Creek but fish were not observed moving out of the Smith River to use these areas. Fish can select among slightly different temperatures, but only when in close proximity; the cues necessary to elicit thermoregulatory behavior apparently were not prominent enough to cause large-scale movement of tagged fish.

Fish in the Smith River were probably finding thermal refuge elsewhere. Rather than leave the main stem, Brook Trout in the Shavers Fork watershed in West Virginia used cool microhabitats such as coldwater upwellings and tributary confluences to thermoregulate (Petty et al. 2012). Similarly, fish may be using cool microhabitats in the Smith River. Topography in the upper Smith River basin, including Tenderfoot Creek, is characterized by deep canyons. Canyon walls provide shade that keep water cool (Ebersole et al. 2003a) in addition to creating deep bluff pools. The deep bluff pools in the Smith River may provide sufficient thermal refuge for trout. Even in late summer, pools in the Smith River can exceed 3 m in depth and can be cooler close to the bottom; I have observed fish there. Rainbow Trout in southern California aggregated in cooler water at the bottom of pools when surface water temperatures surpassed 27 °C (Matthews and Berg 1997). Brown Trout occupied the deepest parts of pools in Wilfin Beck, U.K., because water temperatures were coolest there, despite higher dissolved oxygen concentrations in the warmer layers of water above (Elliott 2000). Ground water influence and hyporheic flow also provide areas of thermal refuge to salmonids (Baird and Krueger 2003; Ebersole et al. 2003b; Olsen and Young 2008). The Smith River contains such areas, especially close to the confluence of Tenderfoot Creek. I observed numerous fish in the outflow of Tenderfoot Creek, suggesting that the tributary contributes cool direct and subsurface flow within the Smith River. Radio-tagged steelhead and Chinook Salmon used the plumes of tributaries within the main-stem Columbia River where water temperatures were lower (Goneia et al. 2006; Keefer et al. 2009). Fish are probably finding enough thermal refuge in the Smith River to avoid needing to physically move upstream into Tenderfoot Creek. Moreover, by remaining in the main stem, fish have access to forage in the warmer, more productive water, thereby expending little energy but still avoiding prolonged exposure to stressful temperatures (Petty et al. 2012).

Absence of movement of Brown Trout into Tenderfoot Creek may have been mediated by territoriality. Deep pools within Tenderfoot Creek were usually occupied by only one or two large individuals greater than 400 mm, and although other species were present, no other Brown Trout were present. These large, presumably dominant individuals may have defended preferred habitat from conspecifics. The largest trout excluded others from the coldest areas in northeastern Oregon streams (Ebersole et al. 2001), and large, adult Bluegill prevented smaller juveniles from occupying areas of optimum temperature in a laboratory setting (Beitinger and Magnuson 1975). A higher proportion (79.5%) of Tenderfoot Creek residents exceeded 400 mm in length than did Smith River residents (67%), suggesting that large, socially dominant fish claimed territories in the thermally superior habitat of Tenderfoot Creek and may have inhibited smaller individuals from immigrating when thermal conditions were stressful in the Smith River.

Spawning and Life Histories of Fishes in Tenderfoot Creek

All salmonids in the Smith River basin used Tenderfoot Creek for spawning, some more extensively than others. Indeed, the greatest driver of movement in my study system was reproduction. Movement plays a large role in the completion of salmonid life histories (Northcote 1997; Torgersen et al. 1999). I observed large upstream migrations into Tenderfoot Creek during known spawning periods, physiological signs of spawning, and the presence of age-0 individuals, which together provide conclusive evidence that Brook Trout, Brown Trout, Mountain Whitefish, and rainbow × cutthroat hybrid trout used Tenderfoot Creek as a spawning ground and their offspring used it as a nursery ground. The remote, undeveloped, and anthropogenically undisturbed watershed of Tenderfoot Creek is unaffected by high levels of sedimentation that could affect the survival of eggs, embryos, and juveniles (Chapman 1988; Kauffman and Hughes 2006). Groundwater discharge has not been reduced, such that areas of upwelling that provide oxygenated water to eggs in redds are abundant, and thermal regimes remain unaffected (except perhaps by climate change). Tenderfoot Creek therefore provides excellent spawning and nursery habitat and is used accordingly. Maintenance of connectivity in the Smith River system is therefore critical to the continued use of this tributary by spawning salmonids.

Compared to other systems, the number of Brown Trout redds observed in Tenderfoot Creek was low. For example, in 50 rkm of the Logan River, Utah, and its tributaries, about 6 times as many Brown Trout redds per rkm were observed (Wood and Budy 2009), and in the Credit River, Ontario, Brown Trout redd density was about 1.5

times that of Tenderfoot Creek (Zimmer and Power 2010). Brown Trout spawning effort in Tenderfoot Creek was probably slightly higher than I observed. In telemetry studies of salmonids, an individual’s spawning area is often defined as the farthest upstream location occupied during a spawning migration (Henderson et al. 2000; Pierce et al. 2009). Two tagged individuals therefore probably spawned above 6.6 rkm, where redd counts were not performed in 2011 and 2012. Even so, these were only two of eleven tagged fish that displayed spawning-related movement, suggesting that only limited spawning occurred above rkm 6.6. Brown Trout also spawn in other tributaries of the Smith River, as well as the main stem itself (Grisak et al. 2012). Tenderfoot Creek was used for spawning by Brown Trout, but not extensively.

Not surprisingly, the estimated total number of Brown Trout juveniles in Tenderfoot Creek was also low. More than twice as many juveniles were captured migrating out of Duck Creek, a tributary of Hebgen Lake, Montana, of similar size and drainage area as Tenderfoot Creek (Watschke 2006). However, the relatively low number of Brown Trout juveniles captured during electrofishing surveys and counted during snorkel surveys was probably an artifact of sampling bias or of emigration to the Smith River. Juvenile Brown Trout may have occupied habitats that were not sampled, as juvenile surveys were restricted to shallow habitats. Large age-0 and age-1 juvenile Brown Trout may occupy deep water that is not suitable for backpack electrofishing (Hayes and Baird 1994). Juvenile Brown Trout that may have been present but not observed during snorkel surveys may have been hiding in the substrate (Heggenes and Saltveit 1990; Hayes and Baird 1994). Compared to single-pass electrofishing, underwater observation was less efficient and more variable for determining abundance of age-0 and older trout in the Kakanui River, New Zealand, because of substrate hiding behavior (Hayes and Baird 1994). Alternatively, juvenile Brown Trout may have emigrated to the Smith River shortly after emergence to find more favorable habitat and protection from large, piscivorous conspecifics in Tenderfoot Creek.

Tenderfoot Creek provided quality habitat and was a permanent residence for large, dominant Brown Trout. Smaller, colder tributaries tend to be less productive and offer less space for individual trout; larger fish therefore tend to occupy larger water in lower reaches or the main-stem river where food is more abundant and temperatures are more optimal for growth (Meyer et al. 2003; Parra et al. 2009). However, the opposite was true in Tenderfoot Creek, strongly suggesting high habitat quality. The lack of Brown Trout 100-200 mm long in Tenderfoot Creek, skewed size structure, low abundance, and much higher density of Brown Trout in the Smith River suggest that most Brown Trout leave and mature in the Smith River, returning to spawn or to establish territories in the optimal habitat of Tenderfoot Creek after they have reached a large, competitively dominant size. Large resident Brown Trout may have left Tenderfoot Creek to overwinter in the Smith River after PIT antenna stations stopped operating, as Brown Trout often return to localized summer habitats (Harcup et al. 1984; Clapp et al. 1990) after overwintering elsewhere (Zimmer et al. 2010). However, such downstream migrations to overwintering habitat typically occur in November following spawning (Clapp et al. 1990; Meyers et al. 1992), which would have been prior to station shutdown at Tenderfoot Creek. No Brown Trout were detected moving past any station later than October 26 in any year. Accordingly, I think that after reaching an effectively dominant size, resident Brown Trout establish permanent residence in the optimal habitat of Tenderfoot Creek.

Tenderfoot Creek was an important spawning ground for Mountain Whitefish. Whereas 7.5% of PIT-tagged Mountain Whitefish in the Methow River, Washington, where Mountain Whitefish were the most abundant species, moved into one of three tributaries to spawn over 4 years (Benjamin et al. 2014), I observed a larger proportion (19.5%) moving into Tenderfoot Creek (a single tributary) in a single year (2012). Tenderfoot Creek also offers exceptional summer habitat for Mountain Whitefish. Summer abundances were much lower in Big Creek, a tributary of the Middle Fork of the Salmon River, Idaho, of similar size and habitat quality to Tenderfoot Creek (Lance and Baxter 2011).

Mountain Whitefish may have used Tenderfoot Creek as a foraging ground. I observed two distinct movement patterns (spring visitors and summer residents) that both entered Tenderfoot Creek in the spring. Upstream spring migrations of Mountain Whitefish into tributaries were also observed in the Grande Ronde River system in Idaho (Baxter 2002) and in the Sheep River, Alberta (Davies and Thompson 1976), and thought to be related to foraging activity. As drift feeders, Mountain Whitefish rely on sight to feed. When visibility in the main-stem Grande Ronde River deteriorated because of spring run-off, Mountain Whitefish entered the clearer waters of the Wenaha River, a major tributary of the Grande Ronde River, possibly to feed more effectively (Baxter 2002). Similarly, Tenderfoot Creek stays relatively clear compared to the Smith River, both throughout the year and during spring runoff. Mountain Whitefish were probably entering Tenderfoot Creek in spring to forage in more favorable feeding conditions.

Spring spawning of rainbow × cutthroat hybrid trout may provide additional forage opportunities, although no eggs were found in the stomach contents of Sheep River Mountain Whitefish despite the presence of spawning Rainbow Trout (Davies and Thompson 1976).

The majority of Mountain Whitefish made a large upstream migration in the spring, a large spawning migration in autumn, and a migration to over-wintering habitat after spawning in late autumn. In general, these findings are consistent with those of Davies and Thompson (1976) and Baxter (2002). My findings also support the capacity for Mountain Whitefish to display multiple, distinct movement patterns within a single population, underscoring the complexity of movement that Mountain Whitefish exhibit as a species. Such diversity in movement patterns also suggests that Mountain Whitefish may use more than one tributary in a lifetime (Baxter 2002).

Tenderfoot Creek was an important spawning and nursery ground for Smith River rainbow × cutthroat hybrid trout. My estimate of rainbow × cutthroat hybrid trout juvenile abundance there was nearly four times that in Duck Creek (Watschke 2006). However, the inability to estimate variability associated with my estimate necessitates caution in any comparisons. Regardless, the combination of captured juveniles and outmigrants and observed upstream movement in spring suggests heavy use of Tenderfoot Creek as a spawning ground and nursery area by rainbow × cutthroat hybrid trout and is consistent with radio-telemetry studies conducted in the Missouri River drainage by Montana Fish, Wildlife, and Parks (Grisak et al. 2012). The higher abundance of fish greater than 200 mm in the Smith River and large number of smaller individuals in Tenderfoot Creek suggest that many rainbow × cutthroat hybrid trout may leave Tenderfoot Creek to mature in the Smith River after reaching an appropriate size. Moreover, Tenderfoot Creek may also serve as a spawning ground and nursery area for Rainbow Trout from the Missouri River. A female Rainbow Trout tagged in the Missouri River migrated up the Smith River and into Tenderfoot Creek to spawn in the spring of 2010 (Grisak et al. 2012).

My findings suggest that multiple movement patterns may exist for rainbow × cutthroat hybrid trout, but the specifics of these movement patterns remain unclear. Similar to Mountain Whitefish, many individuals remained in Tenderfoot Creek throughout the summer, and although only a few individuals were observed moving downstream in autumn, relocations across years suggested that many overwintered in the Smith River whereas others remained in Tenderfoot Creek. Sedentary and mobile factions of populations of Rainbow and Cutthroat Trout are common (Trotter 1989; Hilderbrand and Kershner 2000; Johnson et al. 2010), as are downstream migration following spawning in summer and migration to overwintering habitat (Brown and Mackay 1995; Jakober et al. 1998). Notably, the majority of the downstream migration in the summer of 2011 occurred almost a month later than in 2012. Smith River discharges were much higher in 2011 than in 2012, especially during peak run-off in spring. Additionally, temperatures in Tenderfoot Creek and the Smith River were lower in 2011 than in 2012. Higher discharges and lower water temperatures probably delayed rainbow × cutthroat hybrid trout spawning and the subsequent post-spawn downstream migration. Spawning of hatchery Rainbow Trout was delayed by keeping water temperatures cold (Morrison and Smith 1986). Rainbow Trout in Hebgen Lake, Montana, migrated into Duck Creek earlier in a year when water temperatures were 1 °C higher (Watschke 2006).

Brook Trout are probably sedentary within Tenderfoot Creek and its tributaries. I never detected any tagged Brook Trout on the fixed PIT antenna station at the confluence at any time during the study, and the low proportion of relocated individuals suggests that their movements are rare and restricted. Densities of juvenile Brook Trout in Tenderfoot Creek were low compared to those in smaller systems (Lamothe 2002; Petty et al. 2005). However, I probably underestimated the use of Tenderfoot Creek by Brook Trout as a spawning ground and nursery area. Most Brook Trout spawning activity occurred in tributaries and side channels that I did not survey. Brook Trout are typically associated with tributaries and springs in river systems (Baird and Krueger 2003; Petty et al. 2012). Indeed, densities of Brook Trout less than 100 mm in Tenderfoot Creek were associated with tributaries and springs, suggesting that they had emigrated from nearby natal habitats therein. Barrel Coulee, for example, is a major tributary of Tenderfoot Creek that forms a large 0.8 ha pond before entering the main-stem Tenderfoot Creek. Exploratory snorkeling there revealed numerous Brook Trout. Thorough sampling of side channels, springs, and tributaries would probably provide a more accurate estimate of Brook Trout spawning effort and juvenile abundance than I achieved.

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

Tenderfoot Creek plays multiple roles in the life histories and movements of Smith River salmonids; successful management will require consideration of each of these roles. Tenderfoot Creek was used by all salmonids present as a spawning and nursery ground, and for some taxa, such use was extensive. Indeed, the predominant driver of movement was reproduction. Tenderfoot Creek may therefore be an important source of recruitment, especially for Mountain Whitefish and rainbow × cutthroat hybrid trout. Human alteration that increases sedimentation and affects groundwater discharge, especially logging practices and road construction, would diminish the quality of Tenderfoot Creek as a spawning area and rearing ground and should therefore be limited.

Additionally, movements may have been driven by trophic and overwintering requirements. Quality of habitats in river systems varies temporally and spatially (Gowan and Fausch 2002). For example, Tenderfoot Creek may have provided excellent foraging habitat for Mountain Whitefish in spring, but provided suboptimal foraging opportunities in summer, and proven altogether inhospitable in winter. Salmonids move to adapt to these changing conditions and exploit optimal conditions for growth and survival (Gowan and Fausch 2002; Young et al. 2010; Petty et al. 2012). Such movement necessitates connectivity between Tenderfoot Creek and the Smith River throughout the year, not only during spawning seasons.

I found multiple movement patterns within populations that may require management strategies specific to each. In the case of large Brown Trout, Tenderfoot Creek provides a permanent residence. The relatively few, dominant, and territorial

Brown Trout within Tenderfoot Creek may indicate a refuge-related residence pattern that has developed gradually. More likely, Tenderfoot Creek may offer preferred, high-quality habitat for mature Brown Trout. Regardless, the Smith River Brown Trout fishery is popular and a source of revenue for the outdoor recreational industry, the town of White Sulphur Springs, and Montana Fish, Wildlife and Parks. Ensuring access to tributary fisheries may therefore be important. However, management strategies of such populations must consider their low abundances and susceptibility to overharvest; catch-and-release regulations for tributaries may therefore be appropriate.

Although I observed no direct refuge-seeking behavior during periods of thermal stress, Tenderfoot Creek may still act as a thermal refuge in unexpected ways. Salmonids use confluence areas and tributary plumes to thermoregulate (Goneia 2006; Keefer et al. 2009), and the large number of fish observed below the confluence suggests that the role of Tenderfoot Creek as a thermal refuge may take place in the Smith River itself. Furthermore, this role may expand and become more explicit if warming trends continue. If so, human activities that reduce groundwater discharge (e.g., construction of impervious surfaces such as parking lots) and increase stream temperature (e.g., development of riparian corridors) should be avoided. A more comprehensive study of the temperature dynamics and movements of salmonids at the confluence of Tenderfoot Creek and the Smith River would build upon the findings of my project and could provide insight into the roles that other tributaries in the system play as thermal refuges.

Preserving connectivity throughout the Smith River watershed is essential. Other tributaries may play similar roles to that of Tenderfoot Creek. Moreover, salmonids in the Smith River system may also use multiple tributaries throughout their life histories.

Riverine fisheries are not spatially restricted and therefore require management on a watershed-scale to ensure access to needed habitats. Removal of existing barriers to movement, prevention of future barriers, and limitation of human development in the watershed will help maintain the fishery resources of the Smith River basin. However, to fully understand the Smith River fishery and apply appropriate management measures, further research on the role of all of its tributaries and movements of its fishes is necessary. An expanded but simplified version of my study to encompass all of the system’s major tributaries would enhance our understanding of fish movements and interchange in the Smith River system.

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