

ARTICLE

Influences of Summer Water Temperatures on the Movement, Distribution, and Resource Use of Fluvial Westslope Cutthroat Trout in the South Fork Clearwater River Basin

Marika E. Dobos*

Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Moscow, Idaho 83844-1141, USA

Matthew P. Corsi

Idaho Department of Fish and Game, 3316 16th Street, Lewiston, Idaho 83501, USA

Daniel J. Schill

Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686, USA

Joseph M. DuPont

Idaho Department of Fish and Game, 3316 16th Street, Lewiston, Idaho 83501, USA

Michael C. Quist

U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Moscow, Idaho 83844-1141, USA

Abstract

Although many Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* populations in Idaho are robust and stable, population densities in some systems remain below management objectives. In many of those systems, such as in the South Fork Clearwater River (SFCR) system, environmental conditions (e.g., summer temperatures) are hypothesized to limit populations of Westslope Cutthroat Trout. Radiotelemetry and snorkeling methods were used to describe seasonal movement patterns, distribution, and habitat use of Westslope Cutthroat Trout in the SFCR during the summers of 2013 and 2014. Sixty-six radio transmitters were surgically implanted into Westslope Cutthroat Trout (170–405 mm TL) from May 30–June 25, 2013, and June 20–July 6, 2014. Sedentary and mobile summer movement patterns by Westslope Cutthroat Trout were observed in the SFCR. Westslope Cutthroat Trout were generally absent from the lower SFCR. In the upper region of the SFCR, fish generally moved from the main-stem SFCR into tributaries as water temperatures increased during the summer. Fish remained in the middle region of the SFCR where water temperatures were cooler than in the upper or lower regions of the SFCR. A spatially explicit water temperature model indicated that the upper and lower regions of the SFCR exceeded thermal tolerance levels of Westslope Cutthroat Trout throughout the summer. During snorkeling, 23 Westslope Cutthroat Trout were observed in 13 sites along the SFCR and at low density (mean \pm SD, 0.0003 ± 0.0001 fish/m²). The distribution of fish observed during snorkeling was consistent with the distribution of radio-tagged fish in the SFCR during the summer. Anthropogenic activities (i.e., grazing, mining, road construction, and timber harvest) in the SFCR basin likely altered the natural flow dynamics and temperature regime and thereby limited stream habitat in the SFCR system for Westslope Cutthroat Trout.

*Corresponding author: marika.dobos@idfg.idaho.gov

Received June 15, 2015; accepted December 21, 2015

Lotic systems are complex environments where inter- and intra-annual variation and interactions exist among a suite of physical and biological factors (Schlosser 1991; Wenger et al. 2011; Petty et al. 2012). Stream fish populations use a variety of resources (e.g., food, refuge) in lotic systems to maximize growth, reproduction, and survival at all life history stages (Schlosser 1991; Fausch et al. 2002). Suitable resources can be defined at multiple spatial scales that vary through time, and understanding how those resources vary is critical to our understanding of salmonid ecology and conservation (Fausch et al. 2002; Hillyard and Keeley 2012; Petty et al. 2012). Moreover, resources can be constrained by the physical properties of the environment and influence the long-term persistence of a population (Kruse et al. 1997; Al-Chokhachy et al. 2013).

Several abiotic (e.g., habitat, water temperature) and biotic (e.g., introduced species) factors can influence the movement and distribution of coldwater fishes (D'Angelo and Muhlfeld 2013). A critical feature influencing coldwater fishes is water temperature (Bonneau and Scarnecchia 1996; Isaak and Hubert 2004). Water temperature is related to growth and survival of fishes, often nonlinearly, through a variety of mechanisms, particularly physiological responses (Dickerson and Vinyard 1999; Isaak and Hubert 2004; Sloat et al. 2005; McMahon et al. 2007). The quality and availability of physical habitat is also important for fishes. Complex habitat that includes physical structures (i.e., wood, large boulders), deep pools, and side channels have been associated with high density and sedentary movement patterns of coldwater fishes (Fausch and Northcote 1992; Harvey et al. 1999; Rosenfeld et al. 2001). In addition to thermal and physical habitat characteristics, the movement and distribution of fishes is often influenced by displacement and replacement by other fish species, particularly nonnative species (Krueger and May 1991; Muhlfeld et al. 2009b; Corsi et al. 2013). Consequently, high water temperatures during the summer, altered habitat, and nonnative fish species can influence native salmonids (Krueger and May 1991; Shepard 2004).

Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* is a coldwater salmonid, native to and widely distributed across western North America (Shepard et al. 2005). Westslope Cutthroat Trout currently inhabit coldwater systems that vary from high-elevation, low-productivity, small streams to highly productive, large river systems (Rieman and Apperson 1989; Shepard et al. 2005; Sloat et al. 2005). The movement and distribution of Westslope Cutthroat Trout can be influenced by a variety of environmental factors, particularly water temperature (Sloat et al. 2005; DuPont et al. 2008). For example, survival of juvenile Westslope Cutthroat Trout during a laboratory experiment dramatically decreased after 30 d of constant exposure to water temperatures of 20.0°C (Bear et al. 2007). Adult Westslope Cutthroat Trout are typically found in areas where daytime water temperatures are less than 22.0°C (Bjornn and Reiser 1991; Hunt 1992; Eaton

et al. 1995). Daily fluctuations in water temperatures could allow fish to sustain higher water temperatures for short periods during the day (Dickerson and Vinyard 1999), but the upper temperature thresholds for Westslope Cutthroat Trout are frequently reached or surpassed for extended periods during the summer in some systems (Dechert and Woodruff 2003; Stevens and DuPont 2011).

Movement of fluvial Westslope Cutthroat Trout is variable among individuals and across systems (Schmetterling 2001; Zurstadt and Stephan 2004; Schoby and Keeley 2011; Stevens and DuPont 2011; Pierce et al. 2014). Cutthroat Trout can exhibit both mobile and sedentary tendencies across seasons (Brown and Mackay 1995a; Schmetterling 2001; Hilderbrand and Kershner 2004; Zurstadt and Stephan 2004; Colyer et al. 2005). Extreme movements of fishes tend to occur in response to either life history events (e.g., spawning) or changes in environmental conditions (e.g., temperature: Hilderbrand and Kershner 2000; Skalski and Gilliam 2000). The greatest movements typically occur during the spring as fish migrate for spawning (Schmetterling 2001; Zurstadt and Stephan 2004; Muhlfeld et al. 2009a). Although Westslope Cutthroat Trout regularly move long distances even in systems with a cool summer water temperature regime (<19.0°C; Zurstadt and Stephan 2004), long-distance movements during summer often reflect fish searching for coldwater refugia (e.g., Stevens and DuPont 2011). In systems where anthropogenic effects have altered the riverscape and water temperature regime, suitable resource patches can seasonally limit the distribution of coldwater species (Ebersole 2001; Poole and Berman 2001; Hillyard and Keeley 2012; Williams et al. 2015), particularly Westslope Cutthroat Trout (Stevens and DuPont 2011).

Side channels, alcoves, lateral seeps, and deep pools are often used by fishes because they help moderate extremes in water temperature (Ebersole et al. 2001, 2003; Gooseff et al. 2006). Hyporheic exchange typically occurs in unconfined depositional valleys where interactions of water with subsurface substrate can cool localized areas (Poole and Berman 2001). Stevens and DuPont (2011) found that Westslope Cutthroat Trout in the North Fork Coeur d'Alene River, Idaho, used side-channel habitat in the summer where water temperatures were 3.0–8.0°C cooler than in the main channel. High-elevation reaches, tributaries, and thermal gradients where tributaries enter a system can also provide thermal refuge for fishes during the summer (Bonneau and Scarnecchia 1996; Ebersole et al. 2001, 2003; Baird and Krueger 2003; Gooseff et al. 2006). For example, in the Adirondack River, New York, Brook Trout *Salvelinus fontinalis* and Rainbow Trout *O. mykiss* aggregated near tributary confluences where water temperatures were 0.2–3.5°C cooler than main-stem habitats lacking tributary influence (Baird and Krueger 2003). Thermal conditions in fluvial habitats during the summer are dependent on large-scale (e.g., elevation, geomorphology, gradient, precipitation) and small-scale (e.g.,

cover, depth) factors that vary among and within systems (Beechie et al. 2006; Stanford 2006). Habitat alterations can disrupt natural flow dynamics and the temperature regime of a system, thereby, influencing movement and distribution of fishes (Swanberg 1997; Poole and Berman 2001; Williams et al. 2015).

To understand the ecological significance of suitable habitat and water temperature for Westslope Cutthroat Trout in the South Fork Clearwater River (SFCR) basin during the summer, biologists must consider the temperature dynamics and physical characteristics of the riverscape and how fish respond to warm water temperatures and habitat features. In this study, movement, distribution, and habitat use of Westslope Cutthroat Trout in the SFCR basin were examined using radiotelemetry and snorkeling techniques. Understanding seasonal movement and use of habitat by Westslope Cutthroat Trout by using radiotelemetry techniques helps to identify environmental factors (e.g., water temperature, cover, channel type, substrate size) that influence the population dynamics of fish at multiple spatial scales. Snorkeling observations can supplement radiotelemetry data and provide a more comprehensive understanding of the distribution (e.g., areas lacking fish) and habitat use of Westslope Cutthroat Trout. Since summer water temperatures were hypothesized as a major factor influencing movement and distribution of Westslope Cutthroat Trout, we also modeled water temperatures throughout the SFCR basin to better understand the distribution and movement patterns in the system.

STUDY AREA

The SFCR is a third-order system in the Clearwater River basin in north-central Idaho (Strahler 1957; Figure 1). The drainage area of the SFCR is 3,052 km² and extends from its headwaters at 3,048 m above sea level (msl) to 383 msl where the SFCR joins the Middle Fork Clearwater River at Kooskia, Idaho (Dechert and Woodruff 2003). Major tributaries in the SFCR basin include the Red, American, and Crooked rivers and Newsome, Tenmile, and Johns creeks (Figure 1). Land ownership of the SFCR basin includes the U.S. Forest Service (USFS; 68%), private (29%), the U.S. Bureau of Land Management (BLM; 2%), Nez Perce Tribe (NPT; <1%), and the state of Idaho (<1%) (Cochner and Claire 2001; Dechert and Woodruff 2003).

The main tributaries of the SFCR are generally either confined in steep canyons or have unconfined valleys with broad alluvial floodplains (Siddall 1992; Dechert and Woodruff 2003; NPCC 2003). Lower regions of the Red, American, and Crooked River basins and the Newsome Creek basin flow through unconfined valleys and likely had a high degree of side channels and lateral complexities prior to land use practices (e.g., livestock grazing, placer mining, timber extraction) that began in the mid-1800s. Lower reaches of Tenmile and Johns creeks generally have moderate to high stream

gradients and are confined to steep canyons of quartzite, gneiss, schist, and granite substrate.

The main-stem SFCR originates at the confluence of the Red and American rivers and contains both confined and unconfined valley forms. The cumulative drainage area of the Red River watershed contains 41% (418 km²) of the upper SFCR basin area upstream from Tenmile Creek (river kilometer [rkm] 76.7). Although considered a tributary of the SFCR by name, the lower reaches of the Red River (downstream from rkm 27.6) contribute most of the discharge to the main-stem SFCR and is functionally a continuation of the main-stem SFCR. For this study, the SFCR was divided into three regions (i.e., upper, middle, lower) based on the physical properties of the river valley. The upper region of the main-stem SFCR (rkm 75.0–103.0) has a stream gradient of 5.9% and flows through relatively unconfined valleys that are underlain by a combination of granite, mica schist, quartz, and gneiss. The stream gradient of the middle region of the main-stem SFCR (rkm 30.0–75.0) is 11.4%, and the channel is confined to a steep, canyon-type valley of primarily granite substrate (Dechert and Woodruff 2003; NPCC 2003). The lower region of the SFCR (rkm 0.0–30.0) has a stream gradient of 4.6% and primarily flows through moderately unconfined valleys of basalt substrate.

Grazing, mining, road construction, and timber harvest have influenced the riverscape throughout much of the upper SFCR basin, especially in unconfined valleys (Siddall 1992). With the discovery of gold in 1861, mining activities altered the natural flow dynamics and degraded riparian habitats through most of the upper SFCR basin (Siddall 1992; Cochner and Claire 2001; Dechert and Woodruff 2003; Fletcher 2006). Waste ponds and tailings from large-scale mining operations remain in the upper watershed and are the focus of ongoing habitat restoration efforts (Siddall 1992). Recreational mining continues today with a number of small suction dredges currently operating along the SFCR and some major tributaries (Stewart and Sharp 2003). Commercial timber harvest, primarily clearcutting, has been a major land use that started in the 1940s. Timber harvest currently operates at a smaller scale than it has historically and is regulated by the USFS and BLM. Anthropogenic perturbations can result in altered thermal regimes of a river system that can, in turn, affect movement and distribution of fishes (Caissie 2006).

In addition to Westslope Cutthroat Trout, the fish assemblage in the SFCR basin includes steelhead (anadromous Rainbow Trout) and Bull Trout *S. confluentus*, both of which are listed as “threatened” under the U.S. Endangered Species Act (South Fork Clearwater River Watershed Advisory Group 2006). A dam on the SFCR near Harpster, Idaho (rkm 21.5), impeded upstream migration of steelhead to most of the SFCR basin from its completion in 1910 until it was removed in 1963 (Woodworth 1963). Since 1962, efforts to reestablish steelhead included releasing eyed

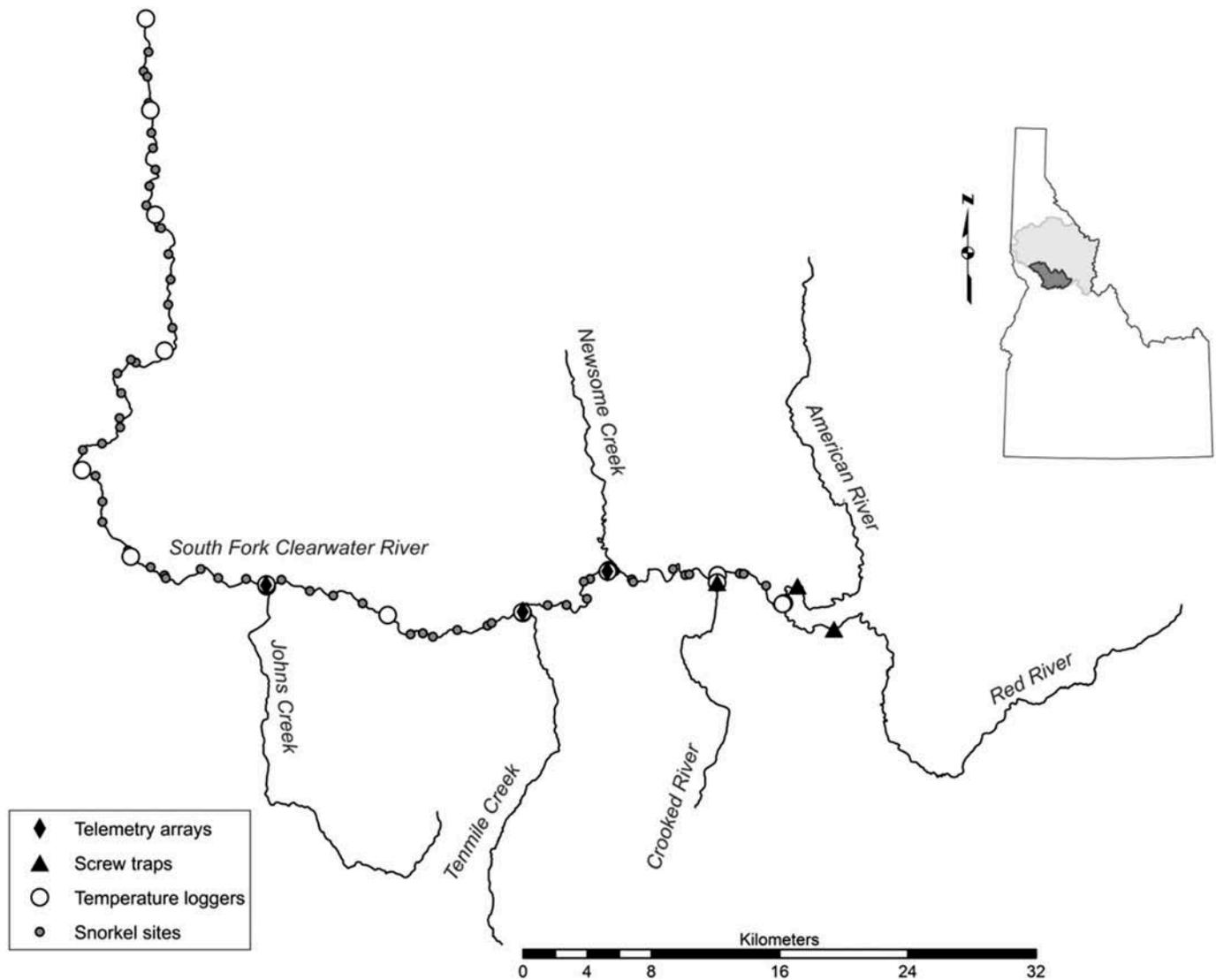


FIGURE 1. The South Fork Clearwater River, Idaho, and its major tributaries. Location of telemetry arrays (diamonds), screw traps (triangles), temperature loggers (open circles), and snorkel sites (gray circles; August 2014) are also presented.

eggs, fry, and smolts at numerous locations in the SFCR basin (Woodworth 1963; George et al. 2006). Dams in the Clearwater River basin led to the extirpation of Chinook Salmon *O. tshawytscha* in the Clearwater River watershed. In 1982, hatchery programs reintroduced Chinook Salmon (USFWS 2009). Steelhead and Chinook Salmon smolts are annually released in the SFCR basin.

Other native fishes in the SFCR basin include Pacific Lamprey *Lampetra tridentate*, Mountain Whitefish *Prosopium williamsoni*, Bridgelip Sucker *Catostomus columbianus*, Mountain Sucker *C. platyrhynchus*, Chiselmouth *Acrocheilus alutaceus*, Northern Pikeminnow *Ptychocheilus oregonensis*, Longnose Dace *Rhinichthys cataractae*, Speckled Dace *R. osculus*, Paiute Sculpin *Cottus beldingii*, Shorthead Sculpin *C. confusus*, and Torrent Sculpin *C. rhotheus* (Siddall

1992; Cochnauer and Claire 2001; Dechert and Woodruff 2003). Three nonnative species (Black Bullhead *Ameiurus melas*, Brook Trout, and Smallmouth Bass *Micropterus dolomieu*) have also been observed in the system.

METHODS

Radiotelemetry.—Radiotelemetry was used to investigate habitat use and movement of Westslope Cutthroat Trout in the SFCR basin. Fish were captured for radio-tagging using rotary screw traps and angling during the postspawning migration period (May–July in 2013, June–July in 2014). Three 1.5-m diameter rotary screw traps were operated by Idaho Department of Fish and Game from March to early November in 2013 and 2014 using standard operating

procedures described by Volkhardt et al. (2007). Rotary screw traps were located on the Red River 7.8 km upstream from its confluence with the American River, on the American River 3.1 km upstream from its confluence with the Red River, and on Crooked River 0.7 km upstream from its confluence with the main-stem SFCR (Figure 1). Angling was conducted along the SFCR on June 19 and 20 in 2013 and on June 20 through July 6 in 2014. Angling was conducted across all habitat types from the origin of the SFCR to its confluence with the Middle Fork Clearwater River.

In 2013, three sizes of individually coded radio transmitters (1.1, 2.8, and 4.3 g) manufactured by Lotek Wireless (Newmarket, Ontario) were used to tag fish. Since microscale use of a thermal refuge by an individual, radio-tagged fish was difficult to determine via measuring water temperature at a fish's location, two sizes of radio transmitters (2.2 and 4.0 g) with temperature sensors ($\pm 0.8^\circ\text{C}$) were used in 2014 to evaluate the water temperature immediately surrounding the fish at the time of detection. Prior to surgery, all tags were tested for functionality and the temperature-sensing radio transmitters were tested to ensure they accurately measured temperature. Total length (mm) and mass (g) were measured on all fish captured and tagged. Radio transmitters were surgically implanted through an incision in the peritoneal cavity along the linea alba and anterior to the pelvic girdle (Jakober et al. 1998). The antenna exited the body wall using a modified shielded-needle technique (Ross and Kleiner 1982; Hillyard and Keeley 2012). Incisions were closed with two interrupted monofilament sutures, and fish were placed in a holding container in the stream for recovery prior to release. Past studies have reported high survival and low transmitter expulsion using similar surgical procedures (Martin et al. 1995; Zale et al. 2005). Once recovered, fish were released at the location of capture. Radio transmitters were programmed (149.48 MHz in 2013, 150.34 MHz in 2014) with a continuous cycle emitting a signal every 5 or 10 s. Battery life varied from 124 to 678 d for radio transmitters without temperature sensors and from 160 to 260 d for the temperature-sensing radio transmitters. Recommendations by Zale et al. (2005) were used to ensure that radio transmitters did not exceed 3.0% (mean \pm SE, $1.55 \pm 0.08\%$) of the fish's body weight.

Radio-tagged fish were relocated using mobile techniques and fixed stations. Lotek model SRX 400 or SRX 600 receivers equipped with either a six-element or three-element directional Yagi antenna were used for mobile tracking. Fixed receivers and antennas were also placed at the confluences of Newsome, Tennile, and Johns creeks to track movement of fish entering or exiting those tributaries, which were difficult to survey due to very limited road or trail access. An attempt was made to relocate fish at least once a week during June–August 2013 and 2014. Radio-tagged fish in the SFCR were relocated at least once a month during September 2013–May 2014 or until the battery on the radio transmitter expired. Radio-tagged fish were initially tracked by vehicle and then on foot. Test trials similar

to those of Simpkins and Hubert (1998) were conducted to evaluate error in locating radio-transmitters. Location error was 0.50 m (SE, ± 0.06 m) at a distance of 5.0 m from the antenna to the radio transmitter and decreased to 0.12 m (± 0.03 m) at 2.0 m. By observing several fish visually with external antennas we further verified our accuracy in the field. Fish were considered alive when movement was observed during tracking. When a radio-tagged fish was found in the same area as its previous relocation, we attempted to disturb the fish and (or) snorkel the area to determine the fate of the fish. Locations were marked using a handheld GPS device, and the stream distance of movement between relocations of each radio-tagged fish was measured using a GIS, similar to Swanberg (1997). Seasons were defined as summer (June–August), autumn (September–November), winter (December–February), and spring (March–May). From November 2013 to April 2014, access in many portions of the SFCR basin was limited by road conditions (i.e., snow); consequently, information on winter and spring movements of fish that remained in tributaries was not available.

Habitat use by radio-tagged fish was recorded at large and small spatial scales. The channel-unit type was characterized at the location of each fish during tracking. Maximum depth of the channel unit was measured to the nearest 0.1 m. Channel-unit type was defined and categorized using a hierarchical classification system as fast-turbulent (i.e., cascade, rapid, riffle), fast-nonturbulent (i.e., run, glide), pocket water, or pool (Hawkins et al. 1993; Jakober et al. 2000). Pocket water was included as a habitat category due to the high frequency of large substrate (>500 mm in diameter) in the SFCR that created multiple localized scour pools. Microhabitat used by radio-tagged fish was defined as a 1-m^2 area centered on the location of the fish (Brown and Mackay 1995a; Muhlfield et al. 2001). Presence of cover was noted if a portion of the structure was in the 1-m^2 area. Cover was defined as large wood, undercut bank, overhanging vegetation, or large boulder (≥ 256 mm in diameter) (Petty et al. 2012). The coldest water temperatures are often at the bottom of the water column of alluvial streams with groundwater inflows, particularly at low summer flows (Nielsen et al. 1994). At each relocation of a radio-tagged fish, ambient water temperature was measured at the substrate. In 2014, the temperature transmitted by the radio transmitter was also recorded.

Stream temperature model.—We used a spatially explicit linear regression model to predict water temperatures and examine the summer temperature regime of the SFCR system (Isaak et al. 2014). Onset temperature loggers ($0\text{--}50^\circ\text{C}$ range, $\pm 0.53^\circ\text{C}$ accuracy; Onset Computer Corporation, Pocasset, Massachusetts) were deployed along the SFCR and in the lower reaches of six major tributaries (Figure 1). Temperature was recorded at 1-h intervals during the summers (July–August) of 2013 and 2014. For the temperature model, the SFCR system was delineated into stream segments typically between nodes or

junctions where segments converged (i.e., where tributaries entered: Ver Hoef and Peterson 2010). Stream segments varied in length from 67 to 1,987 m. Each segment was attributed with site-specific environmental covariates developed by Isaak et al. (2014). Elevation, percent canopy, mean channel gradient, cumulative drainage area, latitude, percentage of the catchment area classified as open water, and base flow index were used as fixed site-specific covariates attributed to the location of each temperature logger (Isaak et al. 2014). In addition to fixed-site variables, mean daily discharge and precipitation and daily maximum and minimum air temperatures were covariates in the model associated with each day during the summers 2013 and 2014 (Hague and Patterson 2014). Average daily discharge (m^3/s) of the SFCR was acquired from the U.S. Geological Survey gauging station located in Stites, Idaho. One model used daily maximum water temperatures as the dependent variable and another model used daily minimum water temperatures. Daily air temperature and precipitation data were acquired from the National Oceanic and Atmospheric Administration. Using the models, daily maximum and minimum water temperatures were predicted for all stream segments in the SFCR system for the summers of 2013 and 2014 (Al-Chokhachy et al. 2013).

Snorkel surveys.—Because radiotelemetry data only provided information on the subset of the population that was radio-tagged, snorkeling was used to provide additional insight on the influence of environmental factors on Westslope Cutthroat Trout in the SFCR system. Enumeration of fishes from snorkeling has been widely used to quantify abundance and density of salmonids (Schill and Griffith 1984; Zubik and Fraley 1988; Thurow et al. 2006). Snorkeling also provided information on the large-scale distribution and resource use of Westslope Cutthroat Trout in the SFCR and their possible associations with other fishes.

The main-stem SFCR was divided into 1-km segments from its origin at the junction of the Red and American rivers to its confluence with the Middle Fork Clearwater River. The sampling frame consisted of 103 potential sample segments; 52 of these segments were systematically selected (Figure 1). Within the selected segments, a single channel unit (e.g., pool, riffle, run) was randomly sampled. Sites that could not be safely snorkeled due to high current velocity were removed and replaced with a new randomly selected site. Eleven additional sites were randomly selected for a total of 63 sites that were sampled. At each site, the channel unit was categorized as a pool, riffle, run, or pocket water using the same definitions used for the radiotelemetry portion of the study.

Snorkeling was conducted from August 5 to 18, 2014, between 1000 and 1730 hours when light conditions were optimal using standard snorkeling methods described by Thurow (1994). Snorkelers attended a training workshop prior to the snorkeling event to help ensure fish species were correctly identified and lengths were accurately estimated. Maximum visibility was measured at each site as the

maximum distance a snorkeler could identify the markings of an imitation fish underwater on the day of the snorkeling event (Schill and Griffith 1984). Snorkelers were spaced laterally across the SFCR either upstream or downstream from the start of the site (Zubik and Fraley 1988). We attempted to observe all fish present in each site by maximizing the number of snorkelers. The number of snorkelers varied from two to nine depending on mean stream width, current velocity, and maximum visibility. Snorkelers identified and enumerated all fishes observed. Snorkelers communicated counts during surveys to reduce double-counting and undercounting fish (Zubik and Fraley 1988). The lengths of all Rainbow Trout and Westslope Cutthroat Trout were estimated and grouped as either medium (150–300 mm) or large (>300 mm). Westslope Cutthroat Trout and Rainbow Trout less than 150 mm were excluded from the analysis due to uncertainty in species identification (Campton and Utter 1985; Baumsteiger et al. 2005).

Habitat characteristics were quantified for each site. Site length was measured along the thalweg, and three transects were established perpendicular to the direction of the flow at 25, 50, and 75% of the site length (Sindt et al. 2012). Mean wetted width (m) was calculated from the three transect measurements (Meyer and High 2011). Depths were taken at 25, 50, and 75% of the wetted channel widths along each transect. Substrate composition was visually estimated as a percentage of different substrate categories along a 2-m strip centered on each transect. Substrate was categorized using a modified Wentworth scale (Cummins 1962) as silt or sand (<2 mm in diameter), gravel (2–64 mm), small cobble (65–128 mm), large cobble (129–256 mm), boulder (>256 mm), or bedrock (Brown and Mackay 1995a; Muhlfeld et al. 2001). Cover was categorized using the same criteria used for the radiotelemetry portion of the study (i.e., overhanging vegetation, undercut bank, large wood). The area of each piece of cover was estimated as the mean of three width measurements multiplied by the length of the structure (Sindt et al. 2012). Temperature loggers were deployed at each site immediately after snorkeling to record temperature at 1-h intervals for 24 h. Using the nearest temperature logger that was continuously recording throughout the summer for the temperature models, the diel maximum and minimum stream temperatures at each site were adjusted to a single, randomly chosen date within the snorkeling period to index water temperature. The area of a site was calculated as the thalweg length times the mean of the three width measurements. Counts of fish were divided by the area of the channel unit to estimate fish density at each site.

Data analysis.—Relocations of radio-tagged fish were imported into ArcMap GIS version 10.1 (Environmental Systems Research Institute, Redlands, California). The first detection was excluded from the analysis to avoid any influence of surgery on movement. Daily movement rate between relocations was estimated as the stream distance traversed divided by the days at large. Mean movement by month was summarized from June 2013 through August 2014.

Downstream movement was denoted as a negative value. Home range was defined as the stream distance between the most upstream and most downstream detections of individual radio-tagged fish in the summer (Vokoun and Rabeni 2005; Schoby and Keeley 2011). Linear regression was used to evaluate home range size as a function of body length of radio-tagged fish. Only fish that survived and were tracked throughout the summer were included in the linear regression analysis.

A kernel density estimator was used to examine proportional use of the main-stem SFCR by radio-tagged Westslope Cutthroat Trout (Vokoun 2003). The density estimate is based on a histogram of detections of radio-tagged fish along the main-stem SFCR and lower Red River. Areas that were used more frequently by fish were represented by peaks in the utilization distribution. The univariate kernel density estimator was defined as

$$\hat{f}(x) = \frac{1}{nh} \sum_{i=1}^n K\left(\frac{x - X_i}{h}\right),$$

where h was the bandwidth and $K(x)$ was the Gaussian kernel function (Vokoun 2003; Vokoun and Rabeni 2005). A Sheather–Jones plug-in method was used to select the appropriate bandwidth (Jones et al. 1996). A kernel density function was estimated for detections in the main-stem SFCR in the months of June, July, and August of 2013 and 2014. The lower 27.6 km of the Red River downstream from the South Fork Red River (a large tributary of Red River) was also included because it functions as the primary extension of the main-stem SFCR. The upper Red River (i.e., >27.6 km from the confluence with the American River) is comparable in size (e.g., drainage area = 129.4 km²) to the American (237.2 km²) and Crooked (184.7 km²) rivers and was considered a tributary.

Logistic regression models were developed to predict the probability of occurrence for Westslope Cutthroat Trout in the SFCR using snorkeling data (Porter et al. 2000; Fransen et al. 2006). The occurrence of zeros can result from an ecological effect (true zeros) or error in observing individuals despite their presence (false zeros: Martin et al. 2005). Although we would have preferred to sample sites repeatedly to get an estimate of fish detection probability, logistics prevented us from conducting replicate samples. We assumed that the number of false zeros in the snorkel data was minimized by trained snorkelers actively seeking fish in each site and correctly identifying species and the fact that multiple snorkelers were used so that the entire site was observed with some overlap among snorkelers.

Prior to generating a priori models, a suite of candidate biological and physical variables known to influence Westslope Cutthroat Trout were evaluated using Pearson's product-moment pairwise correlation coefficients. Ecologically relevant variables

that were not highly correlated (Pearson's $r \leq |0.70|$) were retained for a priori candidate models (Porter et al. 2000; Sindt et al. 2012). If variables were highly correlated, one was excluded to prevent multicollinearity. However, if ecologically relevant variables were correlated but likely had different influential effects on Westslope Cutthroat Trout, both variables were used. The saturated model was the most parameterized of the candidate models and included maximum and minimum water temperatures, region (i.e., lower, middle, or upper region), mean depth, estimated proportion of site that had large substrate, area of cover provided by wood, and Rainbow Trout density as explanatory variables. Overdispersion of the saturated model was evaluated using the estimated \hat{c} (Burnham and Anderson 2002); overdispersion was not a concern ($\hat{c} = 0.81$). An information-theoretic approach using Akaike's information criterion corrected for small samples (AIC_c) was used to rank 23 candidate models (Akaike 1973; Burnham and Anderson 2002). Top models were those with an AIC_c value that was within 2.0 of the best model (i.e., $\Delta AIC_c \leq 2$). Top models were evaluated using Akaike weights (w_i) and McFadden's ρ^2 (McFadden 1974; Burnham and Anderson 2002). The summary statistic ρ^2 is analogous to r^2 in a linear model, but because the dependent variable is binary, the correlations between predictor and dependent variables are lower (Porter et al. 2000). Values between 0.20 and 0.40 were considered to have satisfactory model fit (Steinberg and Colla 1991). All statistical analyses were performed in R (R Development Core Team 2013).

RESULTS

Radiotelemetry

Sixty-eight Westslope Cutthroat Trout were captured and implanted with radio transmitters from May 30–July 9, 2013, (35 fish) and June 20–July 6, 2014, (33 fish). Twenty-one of the radio-tagged fish in 2013 were captured with screw traps; the others were captured by angling. Several adult Westslope Cutthroat Trout exhibited postspawning characteristics (i.e., dark coloration, loose skin on abdomen, eggs not present during surgery). Total length of radio-tagged fish varied from 170 to 405 mm (mean \pm SD, 280.8 \pm 55.5 mm) and mass varied from 40 to 548 g (227.0 \pm 134.3 g). Forty-five fish (20 in 2013 and 25 in 2014) were known to have survived and were tracked through the summers of 2013 and 2014. Eighteen fish (11 in 2013 and 7 in 2014) died or shed their tag during the summer. Two radio transmitters were found inside mink *Neovision vision* dens and two were found in or near campgrounds. One transmitter was found in regurgitated material from an unknown predator on land. The number of relocations for each radio-tagged fish varied from 1 to 34 (11.1 \pm 6.7) during the summer. The number of days between relocations using mobile tracking techniques during the summer varied from 1 to 52 d (5.4 \pm 5.3 d). Five fish were relocated in the SFCR every month during the winter, three of which had batteries that expired during the spring of 2014. Due to winter

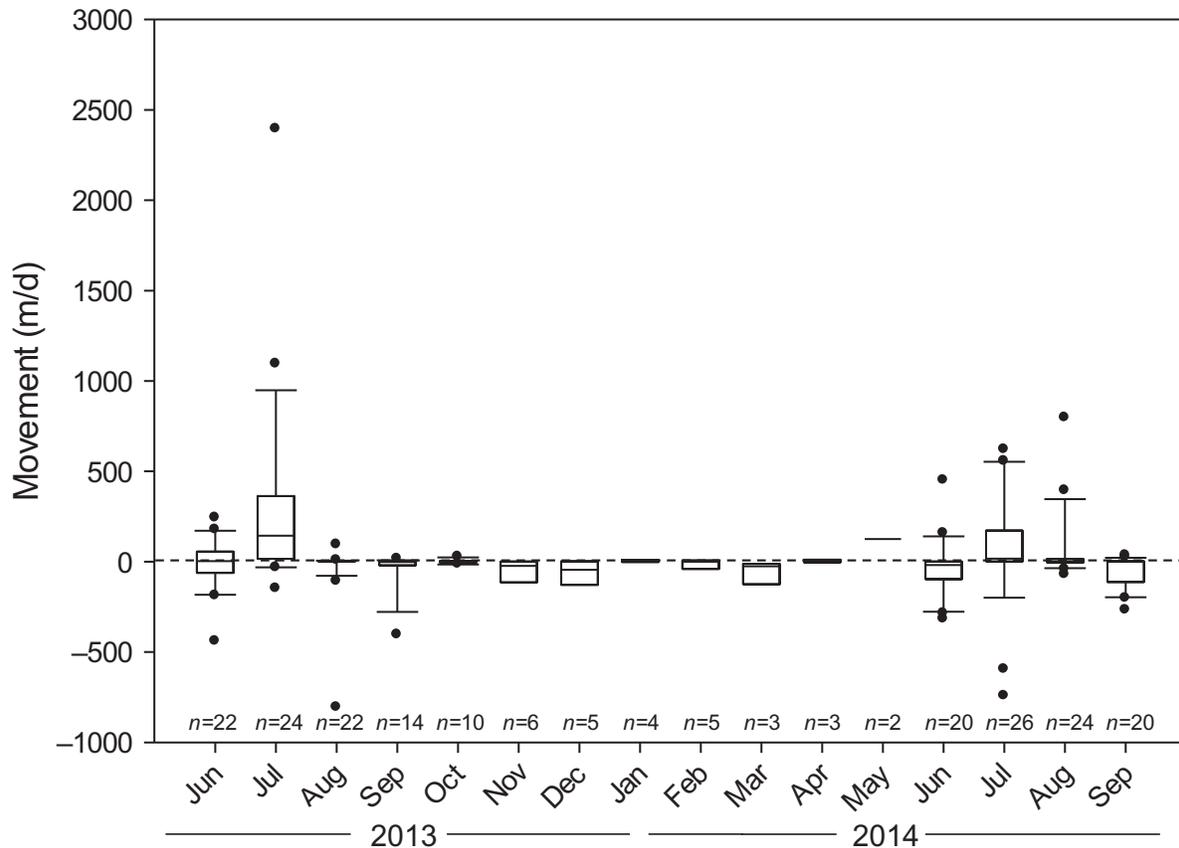


FIGURE 2. Movement rates of radio-tagged Westslope Cutthroat Trout by month in the South Fork Clearwater River basin in 2013 and 2014. Positive values indicate upstream movement and negative values indicate downstream movement. Box plots are shown with medians, first and third quartiles, and outliers (black points).

conditions, fish that remained in tributaries throughout the winter were not relocated.

Fish used large portions of the SFCR basin throughout the year, and movement of radio-tagged fish was variable among seasons. Monthly movement patterns of radio-tagged fish indicated that movement was highly variable in July (Figure 2). Mean summer movement was 0.07 km/d (SE, ± 0.03 km/d) and mean movement in July was 0.29 km/d (± 0.06 km/d). Downstream movement (signified by a negative value) was observed as water temperatures decreased. Mean movement was -0.04 km/d (± 0.01 km/d) for autumn and -0.02 km/d (± 0.01 km/d) for winter. Five fish located in tributaries during the summer moved downstream into either the main-stem SFCR or lower Red River in August–September in 2013 and 2014. One fish was observed moving downstream into the main-stem SFCR from the Red River in January 2013. Eight fish in the main-stem SFCR were tracked through January and found to overwinter between rkm 49.0 and rkm 51.7, typically in deep pools and runs. The direction of movement in February and March 2014 was also primarily downstream. Upstream movement occurred during the spawning period in April and May. Mean spring

movement was 0.01 km/d (± 0.04 km/d). Out of five radio-tagged fish tracked through the spring, two were detected in the lower 4.8 km of Mill Creek on June 3. Another fish was assumed to have moved into Mill Creek given its detection history, and two fish remained in the main-stem SFCR throughout the spring.

Kernel density estimates indicated that fish were patchily distributed throughout the main-stem SFCR upstream of rkm 30.0 and in tributaries during the summer (Figure 3). The mean summer home range of Westslope Cutthroat Trout was 9.0 km (SD, 8.9 km). Fish length was weakly correlated with home range size ($r = -0.11$, $P = 0.03$). Two distinct movement patterns of Westslope Cutthroat Trout in the SFCR basin were observed. Twenty-six fish (11 in 2013 and 15 in 2014) remained in the main-stem SFCR or in the lower Red River over the entire summer (hereafter termed “main-stem” fish). In contrast, nine radio-tagged fish in 2013 and nine in 2014 moved into tributaries by July (hereafter termed “tributary” fish). The upper region of the SFCR and lower region of Red River was used by 10 fish in August compared with 20 fish that used the middle region (Figure 3). Mean TLs were 306.9 mm (SD, ± 59.3 mm) for main-stem fish and

253.5 mm (± 40.1 mm) for tributary fish. The mean summer home range was 3.9 km (± 5.0 km) for main-stem fish and 16.5 km (± 8.1 km) for tributary fish. Two tributary fish in 2013 and one in 2014 moved back into the main-stem SFCR in August. In July and August, main-stem fish were concentrated between rkm 45.0 and rkm 75.0 where water temperatures were generally the coldest (Figure 3).

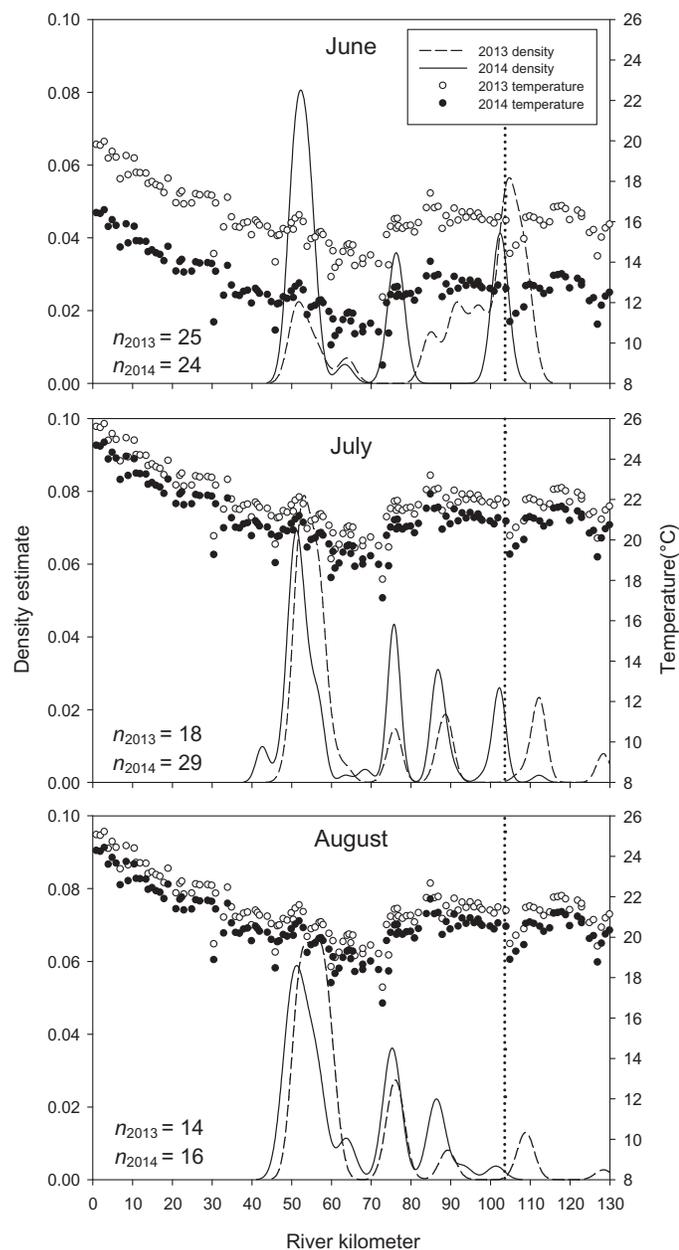


FIGURE 3. Monthly kernel density estimates for summer detections of radio-tagged Westslope Cutthroat Trout in the main-stem South Fork Clearwater River and lower Red River (starting at rkm 103 [dotted vertical reference line]) in 2013 (dashed line) and 2014 (solid line). The number of fish detected by year and month and predicted monthly mean maximum water temperatures for 2013 (open circles) and 2014 (closed circles) are included.

During the summer, radio-tagged fish were located in areas where water temperatures were between 10.0°C and 25.0°C (mean \pm SE, 17.5 \pm 0.13°C; Figure 4). In 2014, both the ambient water temperature and temperature measured by the temperature-sensing radio transmitters in 23 fish were recorded at 185 relocations. The relationship between ambient water temperature and radio transmitter temperature in 2014 showed that 68% of the temperatures recorded by the radio transmitter were at least 0.1°C colder than the ambient water temperature measured at the location of the fish. Ninety percent of the temperatures recorded by the radio transmitter were within 1.0°C and 70% were within 0.5°C of the ambient water temperature on the substrate. At two relocations when ambient water temperature was relatively cool (14.0–15.0°C), the radio transmitter temperature was nearly 2.5°C warmer than the ambient temperature.

Radio-tagged fish occupied a variety of different channel-unit types during the summer (Table 1). In June, fish generally occupied riffle and pool habitats. In July and August, most fish

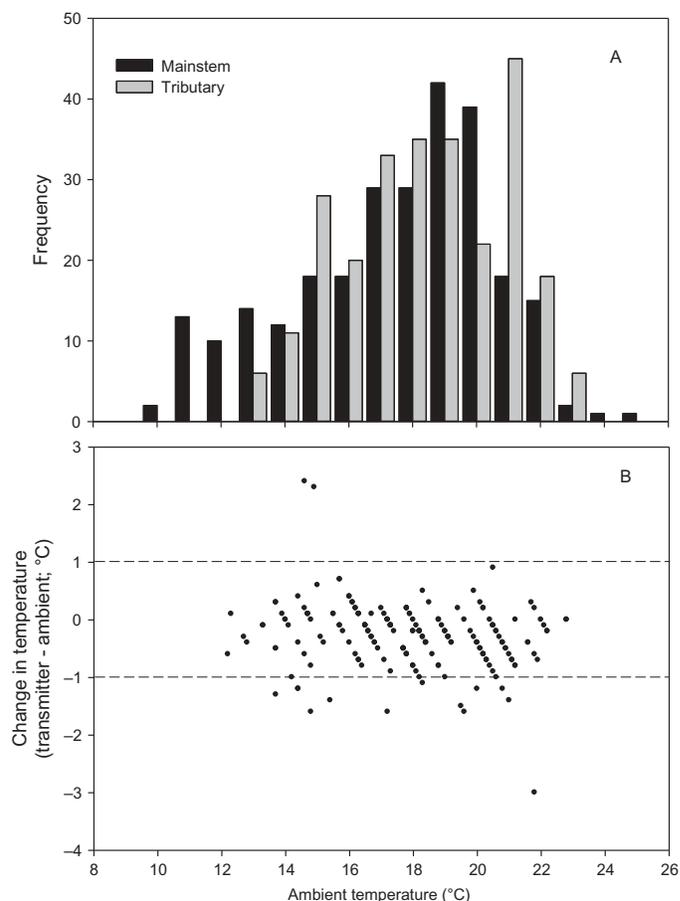


FIGURE 4. (A) Ambient temperature for all fish detected in the South Fork Clearwater River, Idaho, (black bars) and in tributaries (gray bars) from June to August in 2013 and 2014, and (B) the difference between ambient and transmitter temperature as a function of ambient water temperature.

TABLE 1. Total number of detections and proportional use of channel-unit type, depth, and cover type by radio-tagged Westslope Cutthroat Trout in the South Fork Clearwater River basin, Idaho, by season in 2013 and 2014. Seasons were defined as summer (June–August), autumn (September–November), winter (December–February), and spring (March–May). Data for detections in the main stem and in the tributaries were grouped separately. NA = data were not available due to ice cover or high flow events.

Habitat characteristics	2013		2013–2014		2013–2014		2014		2014	
	Summer		Autumn		Winter		Spring		Summer	
	Total or mean	SE	Total or mean	SE	Total or mean	SE	Total or mean	SE	Total or mean	SE
	Main-stem detections									
Number of detections	296		63		13		27		217	
Channel unit type										
Rapid	0.068	0.029	0.011	0.011	0.000	0.000	0.000	0.000	0.099	0.055
Riffle	0.306	0.045	0.139	0.070	0.000	0.000	0.000	0.000	0.176	0.059
Pocket	0.068	0.025	0.110	0.017	0.167	0.000	0.162	0.085	0.150	0.029
Run	0.208	0.049	0.260	0.059	0.417	0.068	0.200	0.200	0.436	0.130
Glide	0.017	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pool	0.333	0.012	0.480	0.119	0.417	0.068	0.638	0.234	0.139	0.033
Depth (m)										
0.0–0.5	0.126	0.032	NA	NA	NA	NA	NA	NA	0.021	0.021
0.6–1.0	0.318	0.079	NA	NA	NA	NA	NA	NA	0.526	0.040
1.1–1.5	0.159	0.046	NA	NA	NA	NA	NA	NA	0.352	0.071
1.6–2.0	0.039	0.031	NA	NA	NA	NA	NA	NA	0.024	0.013
2.1–2.5	0.033	0.033	NA	NA	NA	NA	NA	NA	0.029	0.029
2.6–3.0	0.033	0.033	NA	NA	NA	NA	NA	NA	0.006	0.006
>3.0	0.292	0.054	NA	NA	NA	NA	NA	NA	0.042	0.033
Cover type										
Large boulder	0.261	0.010	0.058	0.058	NA	NA	NA	NA	0.257	0.055
Large wood	0.033	0.022	0.000	0.000	NA	NA	NA	NA	0.002	0.002
Undercut bank	0.013	0.007	0.000	0.000	NA	NA	NA	NA	0.005	0.005
Overhanging vegetation	0.000	0.000	0.000	0.000	NA	NA	NA	NA	0.000	0.000
Combination	0.011	0.002	0.000	0.000	NA	NA	NA	NA	0.019	0.012
None	0.682	0.020	0.942	0.058	NA	NA	NA	NA	0.717	0.068
	Tributary detections									
Number of detections	88		14						56	
Channel unit type										
Rapid	0.050	0.040	0.000	0.000	NA	NA	NA	NA	0.058	0.043
Riffle	0.501	0.090	0.091	0.074	NA	NA	NA	NA	0.197	0.058
Pocket	0.037	0.023	0.000	0.000	NA	NA	NA	NA	0.071	0.056
Run	0.059	0.034	0.000	0.000	NA	NA	NA	NA	0.214	0.132
Glide	0.015	0.009	0.000	0.000	NA	NA	NA	NA	0.015	0.015
Pool	0.192	0.107	0.573	0.022	NA	NA	NA	NA	0.302	0.074
Depth (m)										
0.0–0.5	0.512	0.145	NA	NA	NA	NA	NA	NA	0.373	0.141
0.6–1.0	0.252	0.080	NA	NA	NA	NA	NA	NA	0.527	0.059
1.1–1.5	0.064	0.036	NA	NA	NA	NA	NA	NA	0.000	0.000
1.6–2.0	0.128	0.072	NA	NA	NA	NA	NA	NA	0.100	0.082
2.1–2.5	0.044	0.044	NA	NA	NA	NA	NA	NA	0.000	0.000
2.6–3.0	0.000	0.000	NA	NA	NA	NA	NA	NA	0.000	0.000
>3.0	0.000	0.000	NA	NA	NA	NA	NA	NA	0.000	0.000

TABLE 1. Continued.

Habitat characteristics	2013		2013–2014		2013–2014		2014		2014	
	Summer		Autumn		Winter		Spring		Summer	
	Total or mean	SE	Total or mean	SE	Total or mean	SE	Total or mean	SE	Total or mean	SE
Cover type										
Large boulder	0.063	0.049	1.000	0.000	NA	NA	NA	NA	0.165	0.062
Large wood	0.034	0.018	0.000	0.000	NA	NA	NA	NA	0.214	0.118
Undercut bank	0.044	0.026	0.000	0.000	NA	NA	NA	NA	0.068	0.039
Overhanging vegetation	0.000	0.000	0.000	0.000	NA	NA	NA	NA	0.015	0.015
Combination	0.034	0.018	0.000	0.000	NA	NA	NA	NA	0.286	0.118
None	0.826	0.088	0.000	0.000	NA	NA	NA	NA	0.252	0.011

were found in pocket water, runs, and pools both in the SFCR and its tributaries. Fish in the main stem were relocated in areas with large boulders at 27% of the detections during both summers. In 2013, two fish were relocated at areas that had a combination of large boulders and large wood. One main-stem fish in 2013 used only large wood as a form of cover. In tributaries, 33% percent of summer detections in 2013 and 65% in 2014 were at or near instream cover. Of the fish associated with cover in tributaries, 47% in 2013 and 20% in 2014 were exclusively associated with large boulders. Twenty-five percent of the fish in 2013 and 37% in 2014 were exclusively associated with large wood. Fish detected in tributaries were also found near undercut banks, overhanging vegetation, and various combinations of cover.

Temperature Model

Water temperatures increased from late June through early July in 2013 and 2014. Data from the temperature loggers indicated that daily summer maximum temperatures in the SFCR were 10.8–28.4°C in 2013 and 8.6–27.6°C in 2014. Peak stream temperatures occurred on July 2 in 2013 and July 30 in 2014. The mean daily summer maximum temperature in the main-stem SFCR was 20.5°C (SE, $\pm 0.6^\circ\text{C}$) in 2013 and 18.9°C ($\pm 0.5^\circ\text{C}$) in 2014. Temperature trends in the tributaries were similar to those in the main-stem SFCR; however, tributaries were generally cooler than most reaches in the SFCR (Figure 5). Mean daily maximum summer temperatures were high in the lower reaches of Red River ($19.8 \pm 0.3^\circ\text{C}$ in 2013, $18.3 \pm 0.4^\circ\text{C}$ in 2014), American River ($20.3 \pm 3.6^\circ\text{C}$ in 2013, $18.8 \pm 0.5^\circ\text{C}$ in 2014), Crooked River ($19.0 \pm 0.3^\circ\text{C}$ in 2013, $16.7 \pm 0.4^\circ\text{C}$ in 2014), and Newsome Creek ($19.3 \pm 0.4^\circ\text{C}$ in 2013, $20.3 \pm 0.3^\circ\text{C}$ in 2014). Mean daily maximum summer temperatures were much cooler in Johns ($16.6 \pm 0.4^\circ\text{C}$ in 2013, $14.9 \pm 0.4^\circ\text{C}$ in 2014) and Tenmile creeks ($15.8 \pm 0.3^\circ\text{C}$ in 2013, $16.7 \pm 0.2^\circ\text{C}$ in 2014).

The spatial temperature model performed well and explained 91.5% of the variability in observed daily maximum water temperatures and 92.0% in observed daily minimum temperatures. Mean maximum predicted temperature for the summers of 2013 and 2014 exhibited a nonlinear temperature profile for the SFCR (Figure 6). The model indicated that 61% of the main-stem SFCR in 2013 and 74% in 2014 were predicted to have mean summer maximum water temperatures less than 22.0°C. On the warmest day, the availability of thermally suitable habitat in the main-stem SFCR decreased to 15% in 2013 and 2014.

Snorkel Surveys

We surveyed 5.7 km (5.5%) of the main-stem SFCR in August 2014. In the upper region, 1.4 km (4.9%) of the SFCR was surveyed, 2.5 km (5.6%) was surveyed in the middle region, and 1.8 km (5.9%) was surveyed in the lower region (Table 2). Westslope Cutthroat Trout were only observed upstream from rkm 33.7 during snorkel surveys (Figure 7). Twenty-three Westslope Cutthroat Trout were observed in 12 of the 63 sample sites in the SFCR resulting in low estimated densities (mean \pm SD, 0.0003 ± 0.0008 fish/m²) at these sites. The highest density of Westslope Cutthroat Trout (0.005 fish/m²) was observed at rkm 68.7. Thirteen of the observed Westslope Cutthroat Trout were greater than 300 mm. Other species observed in the SFCR were Rainbow Trout, Chinook Salmon, Mountain Whitefish, suckers *Catostomus* spp., dace *Rhinichthys* spp, sculpins *Cottus* spp., and Northern Pikeminnow. Smallmouth Bass were observed in sites downstream from rkm 20.0 and five Bull Trout were observed at sites near the confluence of Tenmile Creek (rkm 76.6).

The two top logistic models relating biotic and abiotic variables to the presence of Westslope Cutthroat Trout in the SFCR were identified (Table 3). The cumulative AIC weight for the top two models was 0.44; McFadden's ρ^2 values were

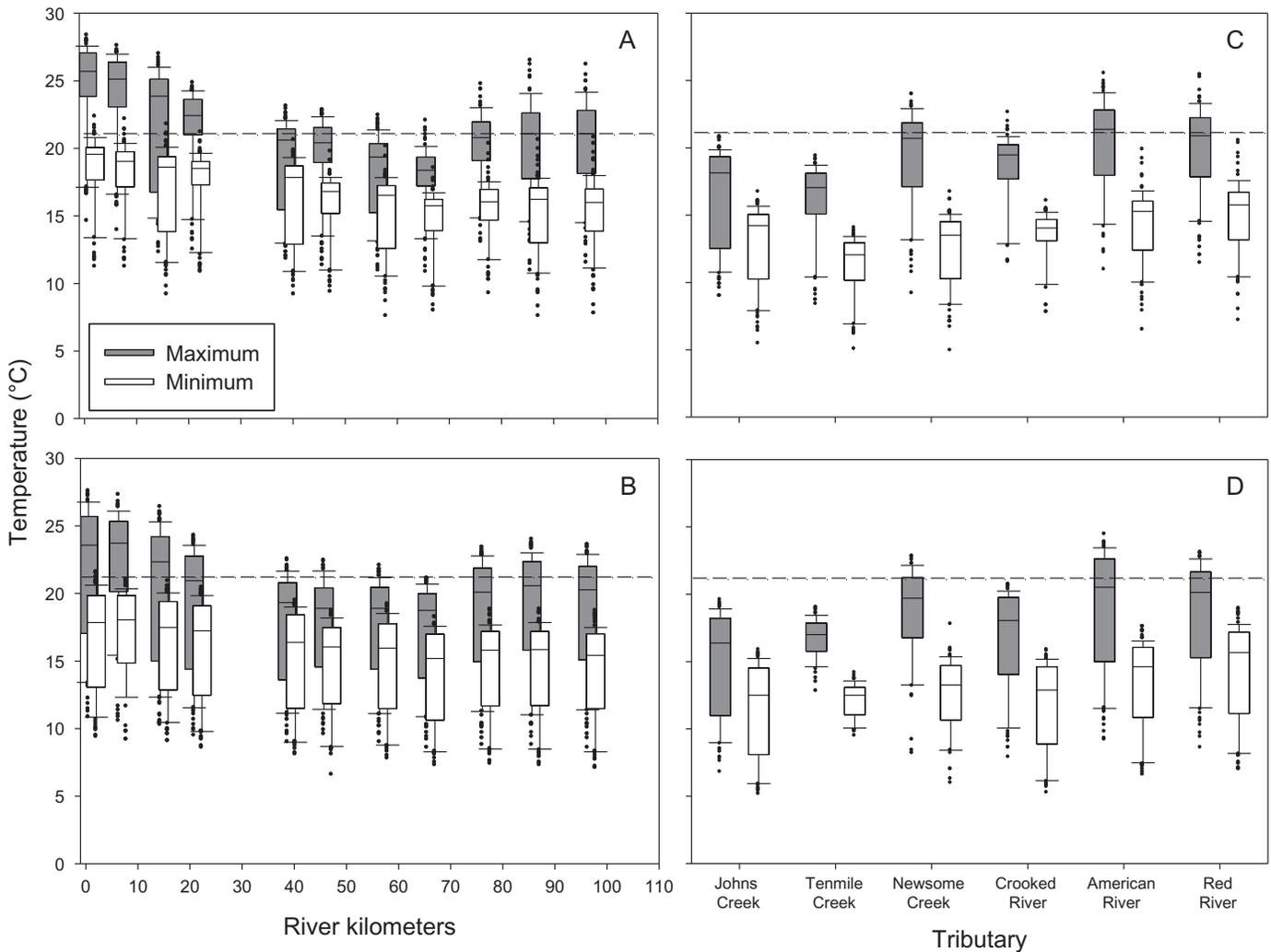


FIGURE 5. Variation of daily maximum temperatures in the South Fork Clearwater River, Idaho, (June–August) in (A) 2013 and (B) 2014 and for six major tributaries in (C) 2013 and (D) 2014. Box plots are shown with medians, first and third quartiles, and outliers (black points). The upper thermal limit (22.0°C) of adult Westslope Cutthroat Trout is represented by the dashed horizontal reference line.

0.15 and 0.19. Maximum water temperature occurred in both of the top models, and large substrate occurred in one of the models. Westslope Cutthroat Trout were negatively related to maximum water temperature and were not observed in sites where the maximum temperature exceeded 21.7°C during the snorkeling event. Westslope Cutthroat Trout presence was positively related to large substrate.

DISCUSSION

The timing of downstream autumn and winter movements and use of wintering habitat of radio-tagged fish in the SFCR basin were similar to those reported by other radiotelemetry studies investigating movement of fluvial Westslope Cutthroat Trout (Brown and Mackay 1995a; Jakober et al. 1998; Schmetterling 2001; Schoby and Keeley 2011).

Movement patterns in the SFCR indicated that radio-tagged fish typically moved downstream in late August through September from areas where they resided during the summer. Deep-pool habitat is thought to be important to winter survival of Westslope Cutthroat Trout (Brown and Mackay 1995a; Jakober et al. 1998). Use of deep overwintering habitat is likely attributed to stable winter conditions and a lower probability of subsurface ice formation (Lindstrom and Hubert 2004). Overwintering in the main-stem SFCR primarily occurred between rkm 49.0 and rkm 55.0 in deep pools and runs. As many as four radio-tagged fish aggregated in the same channel unit in the main-stem SFCR during winter. Use of deep pools by Westslope Cutthroat Trout for overwintering habitat was also reported in the Ram River basin, Alberta (Brown and Mackay 1995a), and in the upper Salmon River, Idaho (Schoby and Keeley 2011). Similarly, Westslope

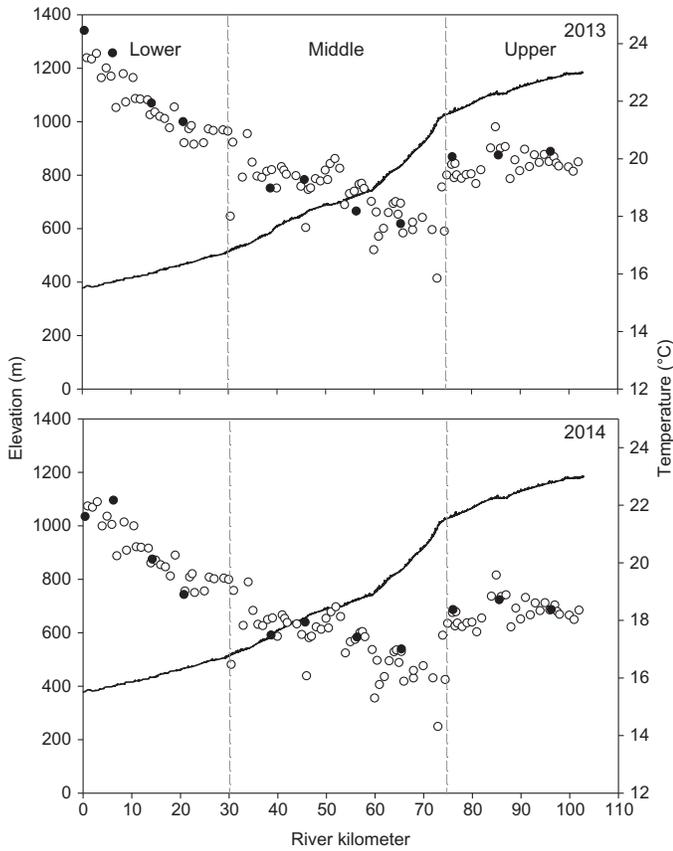


FIGURE 6. Elevation (above sea level; solid line) and mean summer (June–August) maximum temperature profiles consisting of measured (solid circles) and predicted (open circles) temperatures in 2013 and 2014 in the South Fork Clearwater River, Idaho. Locations of breaks for lower, upper, and middle regions are shown.

Cutthroat Trout used ponds made by beavers *Castor canadensis* in tributaries to the Bitterroot River, Montana (Jakober et al. 1998).

In the spring, fluvial Westslope Cutthroat Trout typically exhibit their longest seasonal movements as they move into tributaries to spawn (Brown and Mackay 1995b; Schmetterling 2001; Schoby and Keeley 2011; Pierce et al. 2014). Westslope Cutthroat Trout sometimes travel more than 30 km upstream to spawn (Schmetterling 2001; Schoby and Keeley 2011) and distances over 50.0 km have been recorded (Bjornn and Mallet 1964; Pierce et al. 2014). Unfortunately, we were unable to determine the upstream extent of movement in tributaries due to access limitations. Although the number of radio-tagged fish in our study was low, upstream movement was observed from April to July in 2013. Two radio-tagged fish were observed and one was assumed to have moved into Mill Creek, a tributary to the main-stem SFCR (rkm 53.6), in May and June 2013. In addition, several fish captured in screw traps in late spring near the confluences of the Red, American, and Crooked rivers had physical characteristics that indicated postspawning conditions. The timing of the suspected spawning movements (May–June) coincided with what has been reported for Westslope Cutthroat Trout in the Flathead (Muhlfeld et al. 2009a) and Blackfoot rivers, Montana (Schmetterling 2001; Pierce et al. 2014), Ram River basin (Brown and Mackay 1995b), and upper Salmon River (Schoby and Keeley 2011). Although patterns observed during the winter and spring are interesting and contribute to our knowledge on the ecology of Westslope Cutthroat Trout, the most important patterns observed in this study were during the summer.

After spawning, Westslope Cutthroat Trout generally migrate downstream (Schmetterling 2001; Zurstadt and Stephan 2004; Schoby and Keeley 2011), but movement

TABLE 2. Channel-unit type, number of units, total stream length snorkeled, and proportion of each channel-unit type that was snorkeled in the upper, middle, and lower regions of the main-stem South Fork Clearwater River. Mean depths, SEs, and counts of Westslope Cutthroat Trout (Cutthroat Trout) and Rainbow Trout greater than 150 mm TL. NA = data were not available due to sample size.

Channel type	Number of units	Length (m)	Proportion	Mean depth (m)	SE	Cutthroat Trout	Rainbow Trout
Upper region							
Pocket water	1	68.0	0.05	0.48	NA	0	18
Pool	2	276.5	0.20	0.83	0.31	0	2
Riffle	3	163.5	0.12	0.27	0.05	5	12
Run	11	874.0	0.63	0.42	0.04	4	13
Middle region							
Pocket water	5	362.5	0.14	0.69	0.13	5	94
Pool	7	743.5	0.29	1.12	0.12	2	78
Riffle	4	232.0	0.09	0.38	0.10	2	21
Run	11	1,203.5	0.47	0.82	0.05	5	104
Lower region							
Pocket water	0	0.0	0.00	NA	NA	NA	NA
Pool	4	395.0	0.22	0.61	0.14	0	5
Riffle	5	284.5	0.16	0.51	0.21	0	6
Run	9	1,102.0	0.62	0.58	0.11	0	4

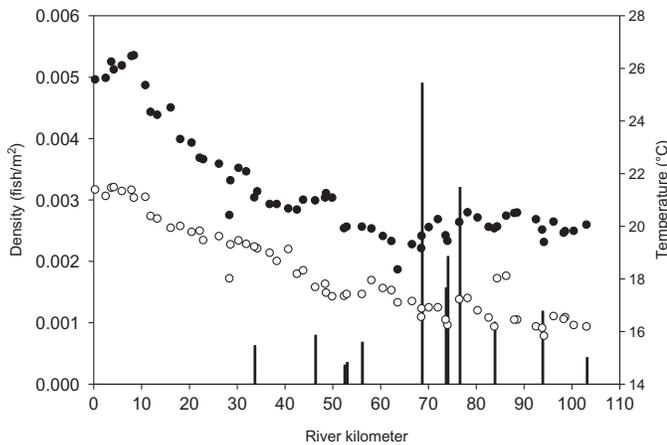


FIGURE 7. Densities of Westslope Cutthroat Trout (vertical bars) observed at snorkel sites along the main-stem South Fork Clearwater River, Idaho, in August 2014. Maximum (solid circles) and minimum (open circles) water temperatures at the sites are included.

during the summer varies depending on the system (Schmetterling 2001; Zurstadt and Stephan 2004). Radio-tagged fish in the SFCR basin generally moved downstream in early June supporting findings of other studies. Summer water temperatures in the main-stem SFCR and some of its major tributaries (i.e., Red and American rivers and Newsome Creek) exceeded thermal levels that commonly induce stress in Westslope Cutthroat Trout ($>22.0^{\circ}\text{C}$; Bjornn and Reiser 1991; Stevens and DuPont 2011). All of the radio-tagged fish that were detected in the upper region of the SFCR, except two, moved into tributaries as water temperatures were increasing. Warm water temperatures and decreased use by radio-tagged fish indicated that the upper region of the SFCR provided the least suitable conditions for Westslope Cutthroat Trout. At a smaller spatial scale, 68% of the radio-tagged fish in 2014 were located in water temperatures colder than the “ambient” temperature. As such, water temperature was an important factor influencing Westslope Cutthroat Trout

movement and habitat use at both large and small spatial scales in the SFCR basin.

The riverscape of the SFCR system includes all flow pathways in the drainage and is imposed by the geomorphology of the system (Frissell et al. 1986; Stanford 2006). The riverscape can be delineated into multiple hierarchical levels to define the scale of resource use by fishes. In this study, these concepts provide context for why different spatial scales of habitat evaluations are linked to the resource use of fishes. Large-scale variables such as drainage area, elevation, channel gradient, substrate type, and valley form can be indicators of suitable habitat (e.g., groundwater influence, large in-stream boulders) for fishes at a large spatial scale. Channel habitat features (e.g., substrate size, groundwater influences) provide small-scale resources for fishes that would be difficult or impossible to detect at a large scale.

Regions can be broadly categorized as confined or unconfined depending on the constraints of the valley (Moore and Gregory 1989; Beechie et al. 2006). Streams confined by steep, rigid canyons are typically straight with little lateral complexity (Moore and Gregory 1989; Montgomery and Buffington 1997). Erosive by nature, stream channels in confined canyons typically have a higher frequency of high-gradient channel types (e.g., step-pools, cascades) and are not typically cooled by hyporheic processes via groundwater influence (Stanford 2006). Instead, water temperatures of such systems are often influenced by tributary contributions and from shade (Stanford 2006; Tonina and Buffington 2009). Consequently, we would expect Westslope Cutthroat Trout to migrate to cold thermal refugia (e.g., high-elevation reaches of the main-stem river or into tributaries) in the SFCR basin where summer temperatures are limiting. The Lochsa, North Fork Clearwater, and St. Joe rivers and Kelly Creek in northern Idaho provide comparable examples of generally confined systems with steep, rigid geomorphic features that have similar temperature regimes as the SFCR. In those systems, Westslope Cutthroat Trout move to high-

TABLE 3. Model selection results from multiple logistic regression models relating biotic and abiotic variables to the presence of Westslope Cutthroat Trout from snorkel surveys in the South Fork Clearwater River (SFCR), Idaho, in August of 2014. Variables included maximum temperature ($^{\circ}\text{C}$), large substrate (%), the lower, middle, and upper regions of the SFCR (Region_i), mean depth (m), area of wood (m^2), and Rainbow Trout density (RBT; fish/m^2). The parameter estimates, number of parameters (K), Akaike’s information criterion corrected for small sample size (AIC_c), measure of each model relative to the best model (ΔAIC_c), model weight (w_i), and McFadden’s $\hat{\rho}^2$ are included. Only the top models (i.e., models with $\Delta\text{AIC}_c < 2.0$) and saturated model are presented.

Models	K	AIC_c	ΔAIC_c	w_i	$\hat{\rho}^2$
Top models					
$10.41 - 0.73(\text{Temp}_{\text{max}}) + 4.17(\text{Substrate}_{\text{large}})$	3	55.73	0.00	0.24	0.19
$15.24 - 0.81(\text{Temp}_{\text{max}})$	2	56.13	0.39	0.20	0.15
Saturated model					
$-4.27 + 0.46(\text{Temp}_{\text{max}}) - 1.53(\text{Temp}_{\text{min}}) + 16.42(\text{Region}_M) + 14.39(\text{Region}_U) + 0.42(\text{Depth}_{\text{mean}}) + 6.01(\text{Substrate}_{\text{large}}) - 0.09(\text{Wood}) - 42.95(\text{RBT})$	10	60.99	8.72	0.00	0.29

elevation reaches of the main-stem river during the summer (Hunt 1992).

Unconfined valleys often have depositional properties and are characterized by low channel gradient, high sinuosity, abundant side channels, and extensive floodplains (Moore and Gregory 1989; Beechie et al. 2006; Stanford 2006). Heterogeneous water temperatures at small spatial scales are common in unconfined valleys and can provide thermal refuge for fishes during the summer (Ebersole et al. 2001; Tonina and Buffington 2009). Channel complexity in unconfined valleys may also provide a variety of habitat (e.g., deep pools, cover) for multiple life history stages of Cutthroat Trout (Harvey et al. 1999). Systems such as the Blackfoot, Coeur d'Alene (Idaho), and upper Salmon rivers, are generally unconfined and have large floodplains with substantial lateral complexity (Gregory and Walling 1973). After postspawning migrations, Westslope Cutthroat Trout typically remain sedentary throughout the summer in these systems (Schmetterling 2001; DuPont and Stevens 2011; Schoby and Keeley 2011).

The SFCR basin has a combination of both confined reaches in steep canyons and unconfined reaches with larger floodplains. As such, mobile and sedentary summer movement patterns would be expected in the SFCR basin given the different geomorphic characteristics. The middle region of the main-stem SFCR (rkm 30.0–75.0) consists of steep canyons of rigid granite substrate and has moderate to high stream gradients. Based on previous studies (i.e., Hunt 1992; Zurstadt and Stephan 2004), we might expect that fish would move into high-elevation reaches of the system, especially with unconfined valley habitat available in the upper region. However, radio-tagged fish in the middle region of the SFCR had small summer home ranges and were largely sedentary throughout the summer. Similarly, 61% of the Westslope Cutthroat Trout observed during snorkeling were in the middle region of the SFCR. Colder water temperatures in the middle region of the SFCR likely provided thermally suitable habitat for Westslope Cutthroat Trout during the summer. Cold water temperatures during the summer in main-stem rivers can largely be attributed to cold water inflows from pristine watersheds. Specifically, the Gospel–Hump Wilderness Area is 83,386 ha in area and located between the Salmon and South Fork Clearwater rivers; contributions from tributaries (e.g., Johns [293.0 km²] and Tenmile [138.9 km²] creeks) in the Gospel–Hump Wilderness Area help to reduce water temperatures for fish in the middle region of the main-stem SFCR during the summer. Warm water temperatures during the summer in the lower and upper regions of the SFCR might also constrain fish to the middle region.

In contrast to the confined reaches of the SFCR, the lower region of the main-stem SFCR (i.e., downstream of rkm 30.0) has low channel gradient and large floodplains in unconfined valleys. Likewise, the upper region of the main-stem SFCR and the lower regions of the Red, American, and Crooked rivers have low to moderate channel gradient and flow through

unconfined valleys with large floodplains. Based on previous research of Westslope Cutthroat Trout behavior in such systems (e.g., Schmetterling 2001; Schoby and Keeley 2011; Stevens and DuPont 2011), we expected Westslope Cutthroat Trout to remain relatively sedentary during the summer after postspawning movement in these areas. Instead, as water temperatures increased, radio-tagged fish in the upper SFCR basin typically moved long distances upstream in tributaries. Few Westslope Cutthroat Trout used the upper region of the main-stem SFCR or the lower portions of the Red, American, and Crooked rivers or Newsome Creek in August. Similarly, movement of radio-tagged fish and observations from snorkeling found no evidence that Westslope Cutthroat Trout inhabited the lower region of the SFCR during the summer. It is likely that the low elevation of the lower region influences summer water temperatures. The ubiquity of Smallmouth Bass in the lower region during snorkeling supports this concept. Also, despite the geomorphology of the lower and upper regions of the SFCR basin, current and historical land use practices (i.e., livestock grazing, mining, timber harvest, log drives) have altered the system in those areas (Poole and Berman 2001; Dechert and Woodruff 2003; Caissie 2006; Fletcher 2006). Features that are important for Westslope Cutthroat Trout during the summer such as thermal refuge, deep pools, and structure (e.g., large boulders, wood) are lacking in the upper region of the SFCR.

Although water temperatures were associated with the movement and distribution of Westslope Cutthroat Trout in the SFCR basin, the availability of other local resources (e.g., shade, cover, food) may also be important for Westslope Cutthroat Trout at small scales (Hilderbrand and Kershner 2000). Physical structures (i.e., boulders, large wood, overhanging vegetation, undercut banks) can facilitate the formation of deep pools, which in turn, provide shade that lowers water temperature and cover from predators (Griffith and Smith 1993; Rosenfeld et al. 2000; Poole and Berman 2001). Depth was important for Westslope Cutthroat Trout in the Coeur d'Alene River (Stevens and DuPont 2011) and in Trestle Creek (Bonneau et al. 1995) in northern Idaho during the summer. Fish in tributaries of the SFCR were more frequently found near cover than fish that remained in the main-stem SFCR. Snorkeling and radiotelemetry indicated that Westslope Cutthroat Trout in the main-stem SFCR were found in various channel-unit types and at various depths. Little woody structure was observed in the main-stem SFCR during snorkeling; only five (8.0%) sites had woody cover. Radio-tagged fish and those fish observed during snorkeling were often in association with large boulders. Of the habitat that was examined by snorkeling, mean depth was greatest in the middle region. Only two pools were sampled in the upper region compared with seven in the middle region suggesting a general lack of deep-water habitat in the upper region. Available channel-unit habitat was not quantified for this

study; therefore, the use of small-scale habitat by fish should be interpreted with caution.

Management Implications

Overexploitation, habitat degradation, and introduction of nonnative trout have been attributed to the decline of Westslope Cutthroat Trout across their distribution (Rankel 1971; Liknes and Graham 1988; Krueger and May 1991; Shepard et al. 1997). Although we did not evaluate angler harvest in the SFCR basin, Westslope Cutthroat Trout are highly susceptible to exploitation (MacPhee 1966; Ball 1971; Johnson and Bjornn 1975), and we found two transmitters in or near campgrounds in tributaries to the SFCR as evidence of angler harvest. The main-stem SFCR is managed as a catch-and-release fishery for Westslope Cutthroat Trout and adipose-fin-intact Rainbow Trout. However, harvest of Westslope Cutthroat Trout is allowed in tributaries to the SFCR. Future work should consider evaluating harvest of Westslope Cutthroat Trout in the SFCR basin. However, given the movement patterns and distribution of Westslope Cutthroat Trout during the summer, water temperature and habitat quality were likely the primary limiting factors influencing fluvial fish in the main-stem SFCR.

Thermally suitable habitat for Westslope Cutthroat Trout was primarily in the middle region of the SFCR. Large-scale mining and logging operations that began in the mid-1800s have altered the riverscape of the SFCR basin. Disturbance to the floodplain from dredging in unconfined reaches can increase the erosion of stream banks, decrease channel roughness and complexity, and cause pools to fill with sediment (Thomas 1985; Harvey and Lisle 1998). Logging and road construction can also result in channelized streams, increased stream bank erosion, and sedimentation (Eaglin and Hubert 1993). These factors can have direct effects on the water temperature regime of a system by disrupting hyporheic processes. In the upper SFCR basin where habitat was greatly altered by anthropogenic activities, water temperatures during the summer frequently exceeded the thermal limits of Westslope Cutthroat Trout.

Our observations suggest that the behavior (e.g., movement to tributaries, small-scale selection of thermal refuge) of Westslope Cutthroat Trout reflects the thermal constraints of the system and availability of suitable habitat during the summer. Therefore, management and conservation efforts should focus on areas in the upper SFCR basin (e.g., Red, American, and Crooked rivers and Newsome Creek) that have experienced habitat degradation from mining, logging, and grazing practices (Siddall 1992; Dechert and Woodruff 2003). Currently, several agencies are rehabilitating streams and riparian habitats in the unconfined valley portions of the SFCR (Fletcher 2006). Additional restoration that improves the condition of riparian habitat and reduces water temperatures, especially in the upper SFCR basin, could enhance

habitat quality and ultimately help secure fluvial Westslope Cutthroat Trout populations.

ACKNOWLEDGMENTS

We thank K. Griffin, T. Venable, and Idaho Department of Fish and Game personnel for their assistance with data collection. We also thank E. Buzbas, J. Rachlow, B. Shepard, and four anonymous reviewers for providing comments on an earlier version of this manuscript. Funding for this project was provided by the Idaho Department of Fish and Game through Federal Aid in Sport Fish Restoration. The Idaho Cooperative Fish and Wildlife Research Unit is jointly sponsored by the University of Idaho, U.S. Geological Survey, Idaho Department of Fish and Game, and Wildlife Management Institute. This project was conducted under the University of Idaho's Institutional Animal Care and Use Committee Protocol 2012-142. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest.
- Al-Chokhachy, R., S. J. Wenger, D. J. Isaak, and J. L. Kershner. 2013. Characterizing the thermal suitability of instream habitat for salmonids: a cautionary example from the Rocky Mountains. *Transactions of the American Fisheries Society* 142:793–801.
- Baird, O. E., and C. C. Krueger. 2003. Behavioral thermoregulation of Brook Trout and Rainbow Trout: comparison of summer habitat use in an Adirondack River, New York. *Transactions of the American Fisheries Society* 132:1194–1206.
- Ball, K. W. 1971. Initial effects of catch-and-release regulations on Cutthroat Trout in an Idaho stream. Master's thesis. University of Idaho, Moscow.
- Baumsteiger, J., D. Hankin, and E. J. Loudenslager. 2005. Genetic analyses of juvenile steelhead, Coastal Cutthroat Trout, and their hybrids differ substantially from field observations. *Transactions of the American Fisheries Society* 134:829–840.
- Bear, E. A., T. E. McMahon, and A. V. Zale. 2007. Comparative thermal requirements of Westslope Cutthroat Trout and Rainbow Trout: implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society* 136:1113–1124.
- Beechie, T. J., M. Liermann, M. M. Pollock, S. Baker, and J. Davies. 2006. Channel pattern and river-floodplain dynamics in forested river systems. *Geomorphology* 78:124–141.
- Bjornn, T. C., and J. Mallet. 1964. Movements of planted and wild trout in an Idaho river system. *Transactions of the American Fisheries Society* 93:70–76.
- Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–139 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society, Special Publication 19, Bethesda, Maryland.
- Bonneau, J. L., and D. L. Scarnecchia. 1996. Distribution of juvenile Bull Trout in a thermal gradient of a plunge pool in Granite Creek, Idaho. *Transactions of the American Fisheries Society* 125:628–630.
- Bonneau, J. L., R. F. Thurow, and D. L. Scarnecchia. 1995. Capture, marking, and enumeration of juvenile Bull Trout and Cutthroat Trout in small, low-

- conductivity streams. *North American Journal of Fisheries Management* 15:563–568.
- Brown, R. S., and W. C. Mackay. 1995a. Fall and winter movements of and habitat use by Cutthroat Trout in the Ram River, Alberta. *Transactions of the American Fisheries Society* 124:873–885.
- Brown, R. S., and W. C. Mackay. 1995b. Spawning ecology of Cutthroat Trout (*Oncorhynchus clarki*) in the Ram River, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 52:983–992.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edition. Springer-Verlag, New York.
- Caissie, D. 2006. The thermal regime of rivers: a review. *Freshwater Biology* 51:1389–1406.
- Campton, D. E., and F. M. Utter. 1985. Natural hybridization between steelhead trout (*Salmo gairdneri*) and Coastal Cutthroat Trout (*Salmo clarki clarki*) in two Puget Sound streams. *Canadian Journal of Fisheries and Aquatic Sciences* 42:110–119.
- Cochnauer, T., and C. Claire. 2001. Evaluate status of Pacific Lamprey in the Clearwater River Drainage, Idaho. Annual Report to the Bonneville Power Administration, Project 2000-028-00, Portland, Oregon.
- Colyer, W. T., J. L. Kershner, and R. H. Hilderbrand. 2005. Movements of fluvial Bonneville Cutthroat Trout in the Thomas Fork of the Bear River, Idaho–Wyoming. *North American Journal of Fisheries Management* 25:954–963.
- Corsi, M. P., L. A. Eby, and C. A. Barfoot. 2013. Hybridization with Rainbow Trout alters life history traits of native Westslope Cutthroat Trout. *Canadian Journal of Fisheries and Aquatic Sciences* 70:895–904.
- Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturalist* 67:477–504.
- D'Angelo, V. S., and C. C. Muhlfeld. 2013. Factors influencing the distribution of native Bull Trout and Westslope Cutthroat Trout in streams of western Glacier National Park, Montana. *Northwest Science* 87:1–11.
- Dechert, T., and L. Woodruff. 2003. South Fork Clearwater River subbasin assessment and total maximum daily loads. Idaho Department of Environmental Quality and U.S. Environmental Protection Agency, DEQ-646, TM79, Technical Report, Boise.
- Dickerson, B. R., and G. L. Vinyard. 1999. Effects of high chronic temperatures and diel temperature cycles on the survival and growth of Lahontan Cutthroat Trout. *Transactions of the American Fisheries Society* 128:516–521.
- DuPont, J., E. Lider, M. Davis, and N. Horner. 2008. Movement, mortality, and habitat use of Coeur D'Alene River Cutthroat Trout. Idaho Department of Fish and Game, Project 07-57, Annual Report, Boise.
- Eaglin, G. S., and W. A. Hubert. 1993. Effects of logging and roads on substrate and trout in streams of the Medicine Bow National Forest, Wyoming. *North American Journal of Fisheries Management* 13:844–846.
- Eaton, J. G., J. H. McCormick, B. E. Goodno, D. G. O'Brien, H. G. Stefany, M. Hondzo, and R. M. Scheller. 1995. A field information-based system for estimating fish temperature tolerances. *Fisheries* 20(4):10–18.
- Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2001. Relationship between stream temperature, thermal refugia and Rainbow Trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. *Ecology of Freshwater Fish* 10:1–10.
- Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2003. Cold water patches in warm streams: physiochemical characteristics and the influence of shading. *Journal of the American Water Resources Association* 39:355–368.
- Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences* 49:682–693.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52:483–498.
- Fletcher, C. 2006. Biological opinion and concurrence for the Newsome Creek watershed rehabilitation project. U.S. Fish and Wildlife Services, Project 2007-F-0061, Boise, Idaho.
- Fransen, B. R., S. D. Duke, L. G. McWethy, J. K. Walter, and R. E. Bilby. 2006. A logistic regression model for predicting the upstream extent of fish occurrence based on geographical information systems data. *North American Journal of Fisheries Management* 26:960–975.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 12:199–214.
- George, B., J. McGehee, D. Munson, T. Klucken, and W. Boore. 2006. Clearwater Fish Hatchery. Idaho Department of Fish and Game, Project 06-19, Annual Report, Boise.
- Gooseff, M. N., J. K. Anderson, S. M. Wondzell, J. LaNier, and R. Haggerty. 2006. A modeling study of hyporheic exchange pattern and the sequence, size, and spacing of stream bedforms in mountain stream networks, Oregon, USA. *Hydrological Processes* 20:2443–2457.
- Gregory, K. J., and D. E. Walling. 1973. *Drainage basin form and processes*. Edward Arnold, London.
- Griffith, J. S., and R. W. Smith. 1993. Use of winter concealment cover by juvenile Cutthroat and Brown trout in the south fork of the Snake River, Idaho. *North American Journal of Fisheries Management* 13:823–830.
- Hague, M. J., and D. A. Patterson. 2014. Evaluation of statistical river temperature forecast models for fisheries management. *North American Journal of Fisheries Management* 34:132–146.
- Harvey, B. C., and T. E. Lisle. 1998. Effects of suction dredging on streams: a review and an evaluation strategy. *Fisheries* 23(8):8–17.
- Harvey, B. C., R. J. Nakamoto, and J. L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident Coastal Cutthroat Trout (*Oncorhynchus clarki*) during the fall and winter. *Canadian Journal of Fisheries and Aquatic Sciences* 56:2161–2166.
- Hawkins, C. P., J. L. Kershner, P. A. Bisson, M. D. Bryant, L. M. Decker, S. V. Gregory, D. A. McCullough, C. K. Overton, G. H. Reeves, R. J. Steedman, and M. K. Young. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18(6):3–12.
- Hilderbrand, R. H., and J. L. Kershner. 2000. Conserving inland Cutthroat Trout in small streams: how much is enough? *North American Journal of Fisheries Management* 20:513–520.
- Hilderbrand, R. H., and J. L. Kershner. 2004. Are there differences in growth and condition between mobile and resident Cutthroat Trout? *Transactions of the American Fisheries Society* 133:1042–1046.
- Hillyard, R. W., and E. R. Keeley. 2012. Temperature-related changes in habitat quality and use by Bonneville Cutthroat Trout in regulated and unregulated river segments. *Transactions of the American Fisheries Society* 141:1649–1663.
- Hunt, J. P. 1992. Catchability and vulnerability of Westslope Cutthroat Trout to angling and movements in relation to seasonal changes in water temperature in northern Idaho. Master's thesis. University of Idaho, Moscow.
- Isaak, D. J., and W. A. Hubert. 2004. Nonlinear response of trout abundance to summer stream temperatures across a thermally diverse montane landscape. *Transactions of the American Fisheries Society* 133:1254–1259.
- Isaak, D. J., E. Peterson, J. V. Hoef, S. Wenger, J. Falke, C. Torgersen, C. Sowder, A. Steel, M. J. Fortin, C. Jordan, A. Reusch, N. Som, and P. Monestiez. 2014. Applications of spatial statistical network models to stream data. *WIREs (Wiley Interdisciplinary Reviews): Water* 1:277–294.
- Jakober, M. J., T. E. McMahon, and R. F. Thurow. 2000. Diel habitat partitioning by Bull Charr and Cutthroat Trout during the fall and winter in Rocky Mountain streams. *Environmental Biology of Fishes* 59:79–89.
- Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by Bull Trout and Cutthroat Trout in Montana headwater streams. *Transactions of the American Fisheries Society* 127:223–235.

- Johnson, T. H., and T. C. Bjornn. 1975. Evaluation of angling regulations in management of Cutthroat Trout. Idaho Department of Fish and Game, Project F-59-R-6, Job Performance Report, Boise.
- Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. *Journal of the American Statistical Association* 91:401–407.
- Krueger, C. C., and B. May. 1991. Ecological and genetic effects of salmonid introductions in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 48:66–77.
- Kruse, C. G., W. A. Hubert, and F. J. Rahel. 1997. Geomorphic influences on the distribution of Yellowstone Cutthroat Trout in the Absaroka Mountains, Wyoming. *Transactions of the American Fisheries Society* 126:418–427.
- Liknes, G. A., and P. J. Graham. 1988. Westslope Cutthroat Trout in Montana: life history, status, and management. Pages 53–60 in R. E. Gresswell, editor. *Status and management of Cutthroat Trout*. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Lindstrom, J. W., and W. A. Hubert. 2004. Ice processes affect habitat use and movements of adult Cutthroat Trout and Brook Trout in a Wyoming foothills stream. *North American Journal of Fisheries Management* 24:1341–1352.
- MacPhee, C. 1966. Influence of differential angling mortality and stream gradient on fish abundance in a trout-sculpin biotope. *Transactions of the American Fisheries Society* 95:381–387.
- Martin, S. W., J. A. Long, and T. N. Pearsons. 1995. Comparison of survival, gonad development, and growth between Rainbow Trout with and without surgically implanted dummy radio transmitters. *North American Journal of Fisheries Management* 15:494–498.
- Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero-tolerance ecology: improving ecological inference by modeling the source of zero observations. *Ecology Letters* 8:1235–1246.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. Pages 105–142 in P. Zarembka, editor. *Frontiers in econometrics*. Academic Press, New York.
- McMahon, T. E., A. V. Zale, F. T. Barrows, J. H. Selong, and R. J. Danehy. 2007. Temperature and competition between Bull Trout and Brook Trout: a test of the elevation refuge hypothesis. *Transactions of the American Fisheries Society* 136:1313–1326.
- Meyer, K. A., and B. High. 2011. Accuracy of removal electrofishing estimates of trout abundance in Rocky Mountain streams. *North American Journal of Fisheries Management* 31:923–933.
- Montgomery, D. R., and J. M. Buffington. 1997. Channel-reach morphology in mountain drainage basins. *Geological Society of America Bulletin* 109:596–611.
- Moore, K. M. S., and S. V. Gregory. 1989. Geomorphic and riparian influences on the distribution and abundance of salmonids in a Cascade mountain stream. U.S. Forest Service General Technical Report PSW-110.
- Muhlfeld, C. C., D. H. Bennett, and B. Marotz. 2001. Fall and winter habitat use and movement by Columbia River Redband Trout in a small stream in Montana. *North American Journal of Fisheries Management* 21:170–177.
- Muhlfeld, C. C., T. E. McMahon, D. Belcer, and J. L. Kershner. 2009a. Spatial and temporal spawning dynamics of native Westslope Cutthroat Trout, *Oncorhynchus clarki lewisi*, introduced Rainbow Trout, *Oncorhynchus mykiss*, and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1153–1168.
- Muhlfeld, C. C., T. E. McMahon, M. C. Boyer, and R. E. Gresswell. 2009b. Local habitat, watershed, and biotic factors influencing the spread of hybridization between native Westslope Cutthroat and introduced Rainbow Trout. *Transactions of the American Fisheries Society* 138:1036–1051.
- Nielsen, J. L., T. E. Lisle, and V. Ozaki. 1994. Thermally stratified pools and their use by steelhead in Northern California. *Transactions of the American Fisheries Society* 123:613–626.
- NPCC (Northwest Power and Conservation Council). 2003. Clearwater sub-basin plan. A Mountain Snake province subbasin plan. NPCC, Portland, Oregon.
- Petty, J. T., J. L. Hansbarger, B. M. Huntsman, and P. M. Mazik. 2012. Brook Trout movement in response to thermal refugia within a complex Appalachian riverscape. *Transactions of the American Fisheries Society* 141:1060–1073.
- Pierce, R., C. Podner, T. Wendt, R. Shields, and K. Carim. 2014. Westslope Cutthroat Trout movements through restored habitat and coanda diversions in the Nevada Spring Creek complex, Blackfoot basin, Montana. *Transactions of the American Fisheries Society* 143:230–239.
- Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. *Environmental Management* 27:787–802.
- Porter, M. S., J. Rosenfeld, and E. A. Parkinson. 2000. Predictive models of fish species distribution in the Blackwater drainage, British Columbia. *North American Journal of Fisheries Management* 20:349–359.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna.
- Rankel, G. 1971. Life history of St. Joe River Cutthroat Trout. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-60-R-2, Annual Completion Report, Boise.
- Rieman, B. E., and K. A. Apperson. 1989. Status and analysis of salmonid fisheries: Westslope Cutthroat Trout synopsis and analysis of fishery information. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-73-R-11, Final Report, Boise.
- Rosenfeld, J., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile Cutthroat Trout (*Oncorhynchus clarki*) and Coho Salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:766–774.
- Ross, M. J., and C. F. Kleiner. 1982. Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. *Progressive Fish-Culturist* 44:41–43.
- Schill, D. J., and J. S. Griffith. 1984. Use of underwater observations to estimate Cutthroat Trout abundance in the Yellowstone River. *North American Journal of Fisheries Management* 4:479–487.
- Schlösser, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704–712.
- Schmetterling, D. A. 2001. Seasonal movements of fluvial Westslope Cutthroat Trout in the Blackfoot River drainage, Montana. *North American Journal of Fisheries Management* 21:507–520.
- Schoby, G. P., and E. R. Keeley. 2011. Home range and foraging ecology of Bull Trout and Westslope Cutthroat Trout in the upper Salmon River basin, Idaho. *Transactions of the American Fisheries Society* 140:636–645.
- Shepard, B. B. 2004. Factors that may be influencing nonnative Brook Trout invasion and their displacement of native Westslope Cutthroat Trout in three adjacent southwestern Montana streams. *North American Journal of Fisheries Management* 24:1088–1100.
- Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of Westslope Cutthroat Trout within the western United States. *North American Journal of Fisheries Management* 25:1426–1440.
- Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for Westslope Cutthroat Trout in the upper Missouri River basin, Montana. *North American Journal of Fisheries Management* 17:1158–1172.
- Siddall, P. 1992. South Fork Clearwater River habitat enhancement Nez Perce National Forest. Report to the Bonneville Power Administration, Project 84-5, Portland, Oregon.
- Simpkins, D. G., and W. A. Hubert. 1998. A technique for estimating the accuracy of fish locations identified by radiotelemetry. *Journal of Freshwater Ecology* 13:263–268.
- Sindt, A. R., M. C. Quist, and C. L. Pierce. 2012. Habitat associations of fish species of greatest conservation need at multiple spatial scales in wadeable

- Iowa streams. *North American Journal of Fisheries Management* 32:1046–1061.
- Skalski, G. T., and J. F. Gilliam. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology* 81:1685–1700.
- Sloat, M. R., B. B. Shepard, and R. G. White. 2005. Influence of stream temperature on the spatial distribution of Westslope Cutthroat Trout growth potential within the Madison River basin, Montana. *North American Journal of Fisheries Management* 25:225–237.
- South Fork Clearwater River Watershed Advisory Group. 2006. South Fork Clearwater River TMDL implementation plan. Idaho Department of Environmental Quality, Boise.
- Stanford, J. A. 2006. Landscapes and riverscapes. Pages 3–21 in F. R. Hauer and G. A. Lamberti, editors. *Methods in stream ecology*, 2nd edition. Academic Press, Burlington, Massachusetts.
- Steinberg, D., and P. Colla. 1991. LOGIT: a supplementary module for SYSTAT. SYSTAT, Evanston, Illinois.
- Stevens, B. S., and J. M. DuPont. 2011. Summer use of side-channel thermal refugia by salmonids in the North Fork Coeur d'Alene River, Idaho. *North American Journal of Fisheries Management* 31:683–692.
- Stewart, D., and D. Sharp. 2003. A recreational suction dredge mining water quality study on South Fork Clearwater River, Idaho County, Idaho. Idaho Department of Environmental Quality, Water Quality Summary Report 34, Boise.
- Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. *Transactions American Geophysical Union* 38:913–920.
- Swanberg, T. R. 1997. Movements of and habitat use of fluvial Bull Trout in the Blackfoot River, Montana. *Transactions of the American Fisheries Society* 126:735–746.
- Thomas, V. G. 1985. Experimentally determined impacts of a small, suction gold dredge on a Montana stream. *North American Journal of Fisheries Management* 5:480–488.
- Thurow, R. F. 1994. Underwater methods for study of salmonids in the Intermountain West. U.S. Forest Service General Technical Report INT-GTR-307.
- Thurow, R. F., J. T. Petersen, and J. W. Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating Bull Trout abundance in first to third order streams. *North American Journal of Fisheries Management* 26:217–232.
- Tonina, D., and J. M. Buffington. 2009. Hyporheic exchange in mountain rivers I: mechanics and environmental effects. *Geography Compass* 3:1063–1086.
- USFWS (U.S. Fish and Wildlife Service). 2009. Dworshak, Kooskia, and Hagerman National Fish Hatcheries: assessment and recommendations, appendix B: briefing document; summary of background information. USFWS, Pacific Region, Hatchery Review Team, Portland, Oregon.
- Ver Hoef, J. M., and E. E. Peterson. 2010. A moving average approach for spatial statistical models of stream networks. *Journal of American Statistical Association* 105:6–18.
- Vokoun, J. C. 2003. Kernel density estimates of linear home ranges for stream fishes: advantages and data requirements. *North American Journal of Fisheries Management* 23:1020–1029.
- Vokoun, J. C., and C. F. Rabeni. 2005. Home range and space use patterns of Flathead Catfish during the summer-fall period in two Missouri streams. *Transactions of the American Fisheries Society* 134:509–517.
- Volkhardt, G. C., S. L. Johnson, B. A. Miller, T. E. Nickelson, and D. E. Seiler. 2007. Rotary screw traps and inclined plane screen traps. Pages 235–266 in D. H. Johnson, B. M. Shrier, J. S. O'Neal, J. A. Knutzen, X. Augerot, T. A. O'Neil, and T. N. Pearson, editors. *Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations*. American Fisheries Society, Bethesda, Maryland.
- Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the USA* 108:14175–14180.
- Williams, J. E., H. M. Neville, A. L. Haak, W. T. Colyer, S. J. Wenger, and S. Bradshaw. 2015. Climate change adaptation and restoration of western trout streams: opportunities and strategies. *Fisheries* 40:304–317.
- Woodworth, J. R. 1963. Reintroduction of steelhead trout into the South Fork Clearwater River and the Lemhi River, 1962. Idaho Department of Fish and Game, Project 221.2-IDA-1.5, Annual Report, Boise.
- Zale, A. V., C. Brooke, and W. C. Fraser. 2005. Effects of surgically implanted transmitter weights on growth and swimming stamina of small adult Westslope Cutthroat Trout. *Transactions of the American Fisheries Society* 134:653–660.
- Zubik, R. J., and J. J. Fraley. 1988. Comparison of snorkel and mark-recapture estimates for trout populations in large streams. *North American Journal of Fisheries Management* 8:58–62.
- Zurstadt, C. F., and K. Stephan. 2004. Seasonal migration of Westslope Cutthroat Trout in the Middle Fork Salmon River drainage, Idaho. *Northwest Science* 78:278–285.