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ARTICLE

Temperature-Related Changes in Habitat Quality and Use by Bonneville Cutthroat Trout in Regulated and Unregulated River Segments

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Abstract

The availability of suitable habitat is often viewed as one of most important limiting factors for animal populations. In this study, we examined the composition and spatial distribution of stream habitat based on summer water temperature using airborne thermal imagery, floating temperature surveys, and fixed temperature data loggers in a regulated and unregulated segment of the Bear River in Idaho and Wyoming. We also used temperature-sensitive radio telemetry tags to measure water temperature in habitats used by Bonneville cutthroat trout *Oncorhynchus clarkii utah*. We found that when available water temperatures increased in the Bear River, cutthroat trout in the regulated segment continuously selected cooler habitats that followed a similar rate of increase as available water temperatures. In the unregulated segment, cutthroat trout did not select significantly cooler available water temperatures when measured over the entire study period. However, cutthroat trout in the unregulated segment did select cooler water temperatures during the peak period of high water temperatures in July. In the regulated river segment, patches of habitat with hospitable water temperatures were small, infrequent, and widely distributed. Whereas, in the unregulated river segment, habitat patches with hospitable water temperatures were larger, more frequent, and in closer proximity to one another. Our data indicate that during the peak of summer temperatures the availability of habitat below the thermal maxima of cutthroat trout becomes very limited, but they are able to locate and use these small patches of habitat during the warmest part of the summer.

Ecologists have traditionally studied resource availability and selection by identifying the proportion of habitat types an animal uses relative to its availability. Resource selection occurs when an animal uses or avoids a resource in greater or lesser proportion to its availability (Manly et al. 2002; Rosenfeld 2003). More recently, resource availability studies have also focused on the spatial distribution of resources by examining the level of connectivity between suitable habitat patches (Isaak et al. 2007). Resource connectivity across a landscape is critical for dispersing individuals to recolonize suitable habitats after local extinctions from disturbance events (Pascual-Hortal and Saura 2006; Baguette and Dyck 2007). The connectivity of resource patches within an animal's landscape is directly related to the quantity and size of these patches. As suitable resource patches become larger and more abundant, the probability of connectivity between patches will increase, enabling animals to disperse over larger areas and increasing the source population's viability and persistence over time.

In mobile animal populations, individuals must first choose a landscape to live in and subsequently decide about the use of resource patches, search modes, and responses to movement barriers that they encounter within the landscape (Orians and Wittenberger 1991; Manly et al. 2002). Individuals perceive and react to resources within their landscape at different spatial scales and hierarchical levels (Poole 2002; Girvetz and Greco 2007). When an animal chooses a landscape (i.e., home range), this decision is based upon available resources needed to survive, but it may only use portions of the landscape for a particular

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resource (e.g., food, shelter). Hence, ecologists are often challenged with determining which resources primarily influence the distribution and abundance of their study species (Edwards and Cunjak 2007). For ectothermic animals, metabolic rate, energy consumption, and growth are strongly dependent on temperature conditions that can fluctuate seasonally and daily (Sinokrot and Stefan 1993; Buckley et al. 2008; Mather et al. 2008). Ectotherms often select habitat to thermoregulate a preferred internal body temperature that attempts to optimize metabolic processing, but can be constrained by the limited availability of temperature to maximize growth (Grant and Dunham 1988). Both terrestrial and aquatic ectotherms use a broad range of environmental temperatures to thermoregulate toward a preferred internal body temperature by selecting habitat that cools or heats body temperature as needed. Hence, connection between habitats that cool and heat internal body temperatures during contrasting seasonal or even daily periods can be essential for thermoregulation in ectothermic animals (Burrow et al. 2001).

In lotic ecosystems, the natural range of stream temperatures and flow patterns typically influence the community of aquatic organisms that inhabit streams worldwide, ranging from coldwater- or coolwater-adapted stream communities to tropical stream ecosystems (Anderson et al. 2006). Habitat alterations that modify natural stream temperature cycles may be a direct cause of native species extinctions or may facilitate replacement by nonnative species with a broader temperature tolerance (Poole and Berman 2001; Lessard and Hayes 2003). Given that many of the largest river systems in North America, Europe, and Asia are impounded to some degree (Nilsson et al. 2005), a prominent source of habitat alteration that greatly influences the thermal characteristics of stream ecosystems is damming of rivers (Poole and Berman 2001; Lessard and Hayes 2003). Dams can directly influence downstream temperature regimes by releasing cool hypolimnetic water or warm epilimnetic water (Poole and Berman 2001; Lessard and Hayes 2003). Dams that release water warmer than normal river temperatures and higher stream discharges during warm summer months can create habitats that may overwhelm the natural pattern of temperature regimes and change the composition of organisms found in an ecosystem. While the majority of the dams in the United States are small, surface-release dams, few studies have considered the effects of warmwater releases on the availability of habitat for downstream coldwater species (Lessard and Hayes 2003).

Salmonid fishes are coldwater species that require water temperatures in the range of 12–15°C for optimal growth (Coutant 1977). Salmonids typically show signs of stress when maximum water temperature exceeds 22°C for less than 1 d (Dickerson and Vinyard 1999; Dunham et al. 2003; Johnstone and Rahel 2003) and may attempt to thermoregulate by finding coolwater refuges within larger areas that exceed stressful temperature levels (Ebersole et al. 2001; Schrank et al. 2003; Boxall et al. 2007). Temperature alterations in rivers due to dams that release epilimnetic water have had unintended effects on the quantity, quality, and spatial arrangement of habitats used by coldwater species (Angilletta et al. 2008). Identifying the range and spatial distribution of available habitat can provide an understanding of its limitation during periods of high summer water temperature. With predicted average increases in global temperatures in the range of 1–6°C over the next 50–100 years (Solomon et al. 2007), understanding how temperature may limit habitat availability will be increasingly important in predicting species responses to climate change.

Bonneville cutthroat trout *Oncorhynchus clarkii utah* is a salmonid fish native to streams, rivers, and lakes in the Bonneville basin of the western United States (Trotter 2008). Historically, fluvial populations of Bonneville cutthroat trout spawned in headwater tributary streams and juvenile fish migrated to main-stem habitat in major river systems to achieve adult size. More recently, dams and irrigation diversions have greatly modified stream discharge patterns in many rivers, and in these areas, may have eliminated all suitable habitat for salmonids during periods of peak summer temperatures. As a result of these impacts, a critical barrier to completing the life cycle of fluvial cutthroat trout may now exist in the last remaining main-stem habitats for this species.

In this study, we examined the spatial and temporal distribution of stream habitat in relation to water temperature. We compared the availability of stream habitat in river segments above and below a major impoundment as a means of assessing how flow alteration can influence the frequency, size, and distribution of suitable habitat for cutthroat trout. Our study followed seasonal changes in temperature during summer to determine whether peak summer temperatures exceeded maximum lethal temperatures for Bonneville cutthroat trout. In conjunction, we monitored habitat selection by Bonneville cutthroat trout to determine the range of temperature occupied when the availability of suitable habitat may have been limited by maximum summer water temperature in regulated and unregulated reaches. By measuring habitat use and availability, we determined whether summer temperature extremes acted to limit the availability of suitable habitat in regulated and unregulated river reaches and whether any differences had corresponding influences on the behavior and habitat selection by Bonneville cutthroat trout.

METHODS

Study Area

We conducted our study in two main-stem sections of the Bear River in southeastern Idaho and western Wyoming. In each section of the river, we quantified the spatial and temporal distribution of available habitat as categorized by water temperature and compared habitat use by Bonneville cutthroat trout using radiotelemetry tags with temperature-sensing capabilities. The Bear River watershed lies within the states of Utah, Idaho, and Wyoming, and covers approximately 18,648 km^2 (Figure 1). The Bear River is surrounded by mountains and is the largest

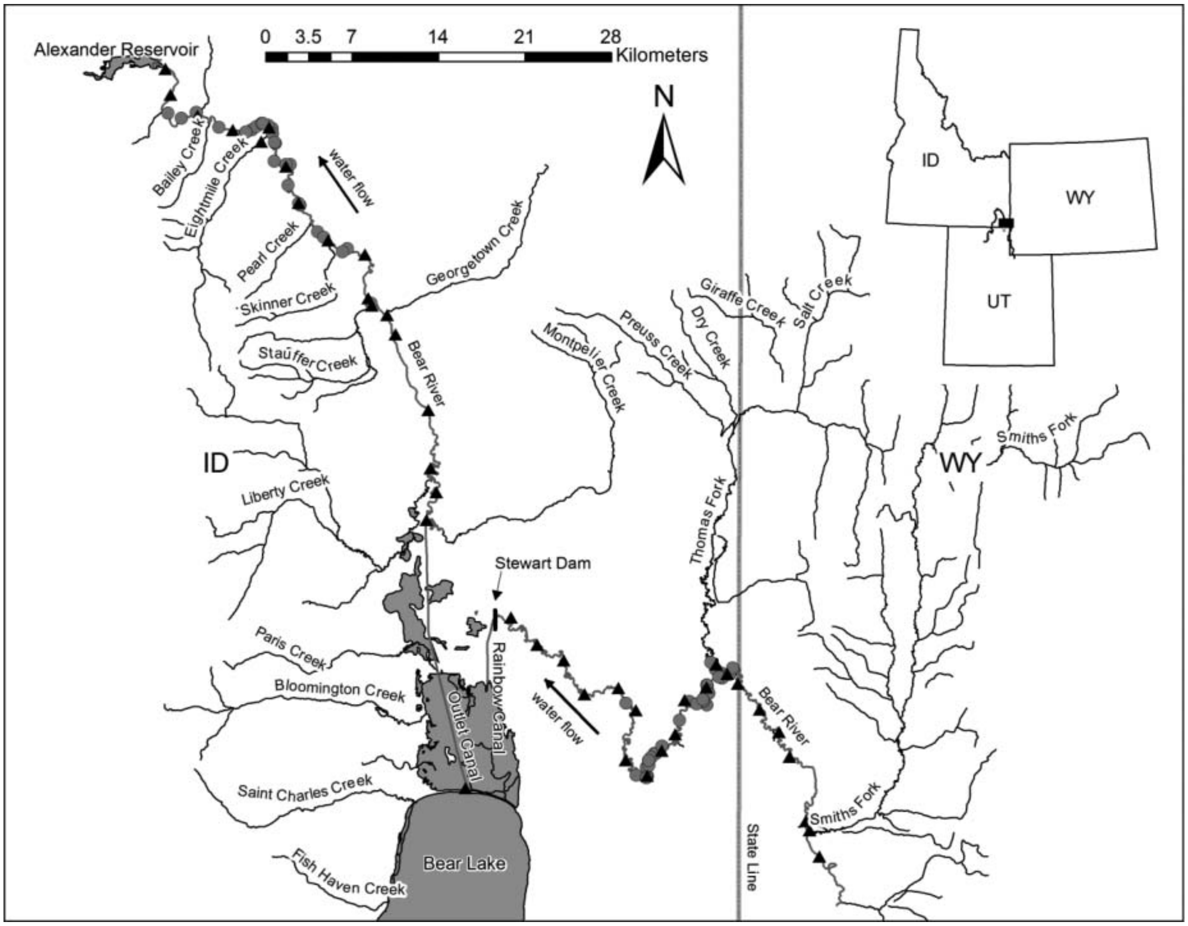

FIGURE 1. The Bear River watershed illustrating the location of the two study areas. The regulated segment begins at Alexander Reservoir and continues upstream to the lower end of the outlet canal of Bear Lake. The unregulated segment begins at the Stewart Dam diversion and continues upstream to the confluence with the Smiths Fork. The locations of 34 temperature loggers are marked by solid triangles, and the tagging location of 84 cutthroat trout are indicated by circle markers. Inset map indicates the location of the study segments (solid square) within the Bear River watershed of Idaho, Wyoming, and Utah.

river in North America that does not empty into an ocean. The main channel of the Bear River has a length of over 885 km from the headwaters in the Uinta Mountains of Utah to its mouth at Great Salt Lake, also in Utah. Although the river makes almost a 1,000-km journey to its final destination, the headwaters and mouth are only 120 km apart (Denton 2007). Climate within the Bear River watershed is semiarid continental, with cold winters and hot dry summers when temperatures often reach as high as 37°C. Private land (50%) allocation is predominant in the watershed, and 47% is under public land management and 3% is classified for a variety of other purposes. The Bear River has a history of human-induced alterations through land management such as dams, irrigation diversions, agricultural production of lands, livestock grazing, and logging. Human-related use of water from the Bear River is allocated primarily for hydroelectric power, irrigation, livestock, and domestic consumption.

Near the town of Dingle, Idaho, Stewart Dam separates the Bear River into two river segments with contrasting flow regimes that potentially influence thermal patterns in each river segment (Figure 1). Stewart Dam is located in the center of the study area and changes the Bear River from being a primarily unregulated river to an artificially regulated system by diverting the entire river into nearby Bear Lake (Figure 1). The water is stored for irrigation purposes until early summer and is pumped back into the Bear River via the Lifton pumping station and outlet canal (see Hillyard 2009 for comparative flow data). These two river segments provide a setting to compare habitat availability and use by Bonneville cutthroat trout and to identify the potential differences in thermal habitat characteristics between a regulated and unregulated river segment within the Bear River.

The regulated segment in this study begins at Alexander reservoir (North American Datum 83 [NAD83]; 12T 442940 E, 4721552 N; 1,746 m above sea level [asl]), near Soda Springs, Idaho, and continues upriver to the outlet of Bear Lake (NAD83; 12T 474047 E, 4662418 N; 1,806 m asl), and has a total length of 93 km (Figure 1). The unregulated segment has a total length of 81 km and begins at Stewart Dam (NAD83; 12T 476175 E, 4677502 N; 1,811 m asl) and continues upriver to 2.5 km above

TABLE 1. Spatial and temporal sampling resolution for the three methods used to quantify temperture-related habitat availability for Bonneville cutthroat trout in the Bear River, Idaho and Wyoming.

	Sampling resolution	
Method	Spatial	Temporal
Floating temperature surveys	1 m	Weekly
Temperature loggers	5 km	0.5 h
Thermal imagery	0.9 m^2	1 d

the Smiths Fork (NAD83; 12T 503849 E, 4654038 N; 1,880 m asl), near Cokeville, Wyoming (Figure 1).

Habitat Availability

We used three different methods to identify and quantify the spatial and temporal variation in available habitat, as characterized by water temperature. Each method has its own inherent limitation in measuring various spatial and temporal scales at which patterns can be detected in water temperature (Table 1). We used stationary temperature data loggers to provide continuous temporal monitoring of water temperature over the study period, but with limited spatial representation. In contrast, we used airborne thermal infrared remote sensing (TIR), to provide fine-scale spatial representation of temperature patterns, but with no temporal changes. Finally, we developed an innovative method, hereafter referred to as "floating temperature surveys" (FTS), to integrate both temporal and spatial measures of habitat availability.

Temperature loggers.—We systematically placed 34 Onset StowAway Tidbit (Onset, Bourne, Massachusetts) temperature loggers in the Bear River approximately 5 km apart from each other (Figure 1). Five additional temperature loggers were placed in tributaries thought to be used by Bonneville cutthroat trout. Each temperature logger was secured in a 15 × 5-cm polyvinyl chloride (PVC) pipe and then attached to a length of rebar that was hammered into the river bottom. Temperature loggers were placed approximately 6 cm from the bottom of the river and recorded temperature (±0.2°C) at 30-min intervals. This method had high temporal resolution, but the spatial resolution was limited to the 34 locations in the river.

Thermal imagery.—Airborne TIR imagery was collected by Watershed Sciences, Inc. (Corvallis, Oregon) during July 24–26, 2006, between 1200 and 1600 hours. This period corresponded to the warmest part of the summer and optimal time to capture the maximum thermal contrast between main-stem river water temperatures, subsurface upwelling, and adjacent terrestrial features. Thermal images were collected with a Space Instruments FireMapper 2.0 sensor mounted on the underside of a Bell Jet Ranger helicopter. A high-resolution, true color, digital camera (Nikon D2X with 24-mm lens) was comounted with the TIR sensor. Both cameras were positioned to look vertically down from the aircraft and take simultaneous images as the helicopter flew downstream. The TIR sensor was set to acquire images at a rate of approximately one image every 2 s. The flight altitude ranged from 300 to 400 m above ground and was based upon stream size and sinuosity. With these parameters, the imagery spatial resolution (i.e., pixel size) was 0.9 m^2. This method provided data that could be used for fine-scale spatial analysis of the size and arrangement of thermal resources within each segment but was temporally limited to a "snapshot" because sampling was only done during 1 d of the summer in each river segment. Our analyses of TIR data assumed that TIR measurements represented the temperature of a completely mixed water column at a particular location in the river based on measurements from the surface. We compared the nearest stationary temperature data logger to the corresponding TIR measurement taken during the closest time of day to estimate the difference between the two methods.

Floating temperature surveys.—For this technique we used a drift boat or canoe, temperature sensors, and a Trimble XT GPS unit (Trimble Navigation Limited, Sunnyvale, California). This sampling method operated by mounting a metal bar (6 m long by 25 mm in diameter) perpendicular to the hull of the boat. Two Onset Hobo U10-001 temperature data loggers (Onset Computer Corporation, Pocasset, Massachusetts) with four data capture ports were used to attach water temperature sensor cables. We attached eight water temperature sensor cables across the length of the bar, and spaced them 1 m apart. Temperature sensors were suspended in the first 5–10 cm from the surface of the water column. The temperature data loggers recorded temperature and time every 5 s while the boat drifted through a river segment. To record the spatial location of temperature readings, we used a Trimble GeoXT GPS unit and differentially corrected the locations to obtain submeter accuracy. Both data sets were downloaded to a computer and merged to form a georeferenced thermal data set using the MERGE procedure in SAS 9.1.3 (SAS Institute, Inc., Cary, North Carolina). We conducted floating temperature surveys in each segment at least once a week from July to August 2006. Because the Bear River was wider than the sampling area of the equipment, we alternated the sampling effort between sides of the river every 15 min. This procedure helped to incorporate lateral spatial heterogeneity of thermal patches in the river.

Habitat Use by Cutthroat Trout

In order to identify water temperature in habitats used by Bonneville cutthroat trout, we implanted fish with radiotelemetry tags that were designed to record and transmit water temperature measurements from the source of their signal transmission. We sampled and tagged cutthroat trout during two time periods: 4 October–22 November 2005 and 11 April–14 July 2006. Bonneville cutthroat trout were collected from the Bear River using a Coffelt model VVP-15 drift-boat-mounted electrofishing unit. We attempted to tag at least one cutthroat trout in every three river kilometers in order to ensure a broad geographic representation in the sample of individuals. We surgically implanted radio transmitters from Advanced Telemetry Systems (models F1820 and F1830; ATS, Isanti, Minnesota) into the body cavity of the fish. Each radio transmitter was equipped with a temperature (±0.1°C) and mortality sensor and was uniquely encoded with a specific frequency (148.000–149.999 MHz). We used two sizes of transmitters to tag a wide size range of cutthroat trout because excessive transmitter mass may affect fish performance. Cutthroat trout were tagged with transmitters that weighed less than 3% of their total body mass by using 12-g transmitters for fish that weighed at least 400 g and 9-g transmitters for fish weighing at least 250 g.

Surgery on an individual fish to be tagged was initiated by anesthetizing it in a water bath with tricaine methanesulfonate (MS-222) in a dosage of approximately 60 mg/L in water. After a fish was lethargic, it was measured for total length (TL; ±1 mm) and wet mass (±1 g), and then placed on a surgery tray where a 3.5-cm ventral incision was made along the abdomen and immediately anterior to the pelvic girdle. A 15-cm long, grooved, directional tool was then inserted into the incision and slid posterior to the pelvic girdle. The tool aided in guiding a 15-cm catheter needle to puncture the body wall posterior to the pelvic girdle. The antenna of the transmitter was then inserted through the needle shaft until it exited the opposite end. By pulling on the antenna, the transmitter was pulled into the body cavity of the fish. The incision was closed with three surgical staples. Upon completion of the surgery cutthroat trout were immediately put back into the river in a holding area and monitored until swimming ability was reestablished. The surgery process typically took an average of 2 min to complete.

During the course of the study, we recorded habitat use by locating radio-tagged cutthroat trout on a weekly basis using vehicle, fixed-wing aircraft, or boat. We used a truck-mounted, five-element Yagi antenna in areas accessible by roads or a boat-mounted, three-element Yagi antenna in areas accessible by boat. If any particular cutthroat trout was not located for an extended period of time (e.g., two or more weeks), aerial tracking was used to survey a larger spatial extent. If an individual was located by air, we would return to determine a more precise estimate of location on the ground. At each tracking location, fish location was georeferenced with a handheld global positioning device and the water temperature used by cutthroat trout was recorded from the radio transmitter signal information.

We also monitored the movements of radio-tagged cutthroat trout with the use of fixed telemetry stations. These stations were used to identify movement of tagged cutthroat trout in and out of the two large tributaries in the unregulated segment (Figure 1). Telemetry stations consisted of an ATS model R4500 receiver connected to two five-element Yagi antennas mounted at each site: one pointing upstream and one pointing downstream. This configuration allowed us to determine the direction that cutthroat trout were moving. The stations were powered by two 12-V, deep-cycle batteries that were exchanged with recharged batteries every 2 weeks.

Statistical Analyses

In order to describe habitat use versus availability we calculated and compared average weekly mean (AWmean) water temperatures collected from temperature-sensitive telemetry tags, temperature loggers, and floating temperature surveys. To determine AWmean habitat use, we averaged water temperatures used by cutthroat trout for each day tracked in each segment of the river. We then averaged the daily means to obtain an AWmean of temperatures used by cutthroat trout in each study segment. For habitat available, we calculated AWmean temperatures for both temperature loggers and floating temperature surveys. Using the temperature logger data, we first obtained a daily mean for each logger, consisting of the hours in the day in which we tracked tagged cutthroat trout (i.e., 0900–2100 hours). We then calculated a weekly average for each logger. Finally, we calculated the AWmean for each segment by averaging the average weekly values for each logger within a segment. The floating temperature surveys were conducted once a week in each segment. Therefore, we calculated average temperature for each of the eight sensors and then again averaged those values to obtain an AWmean water temperature for each segment.

To determine whether cutthroat trout were using habitats with cooler water temperatures, as available water temperature increased, we used linear regression and a one-tailed *t*-test to determine whether the observed regression slope was significantly different than the expected slope. If cutthroat trout were randomly using water temperatures in available habitat we would expect a 1:1 ratio relationship between available water temperatures and water temperatures used during the study period. Therefore, we used linear regression to evaluate the relationship between AWmean used water temperatures (telemetry tags) and AWmean available water temperatures for both temperature loggers and floating temperature surveys. We then used a *t*-test to determine if the observed slope was significantly ($P < 0.05$) different than the expected slope of 1. We used a binomial test of significance to determine whether the elevation of the observed regression line differed from the expected elevation of the directly proportional line.

The airborne TIR data had a very high spatial resolution but low temporal resolution; therefore, we used this method to identify the proportion of available habitat related to water temperature within 0.5°C temperature categories and to calculate thermal habitat patch characteristics. To calculate the proportion of habitat related to water temperature, we summed the number of pixel values within each 0.5°C category and then divided by the total number of pixel values within the segment. We also calculated the average (±95% confidence interval [CI]) temperature for the TIR imagery for each study segment by summing all pixel values then dividing by the number of pixels.

In order to describe the patch characteristics (i.e., number of patches, mean patch size, and mean patch distance) for three thermal habitat types, we had to extract from the thermal imagery data pixel values that represented Bear River water

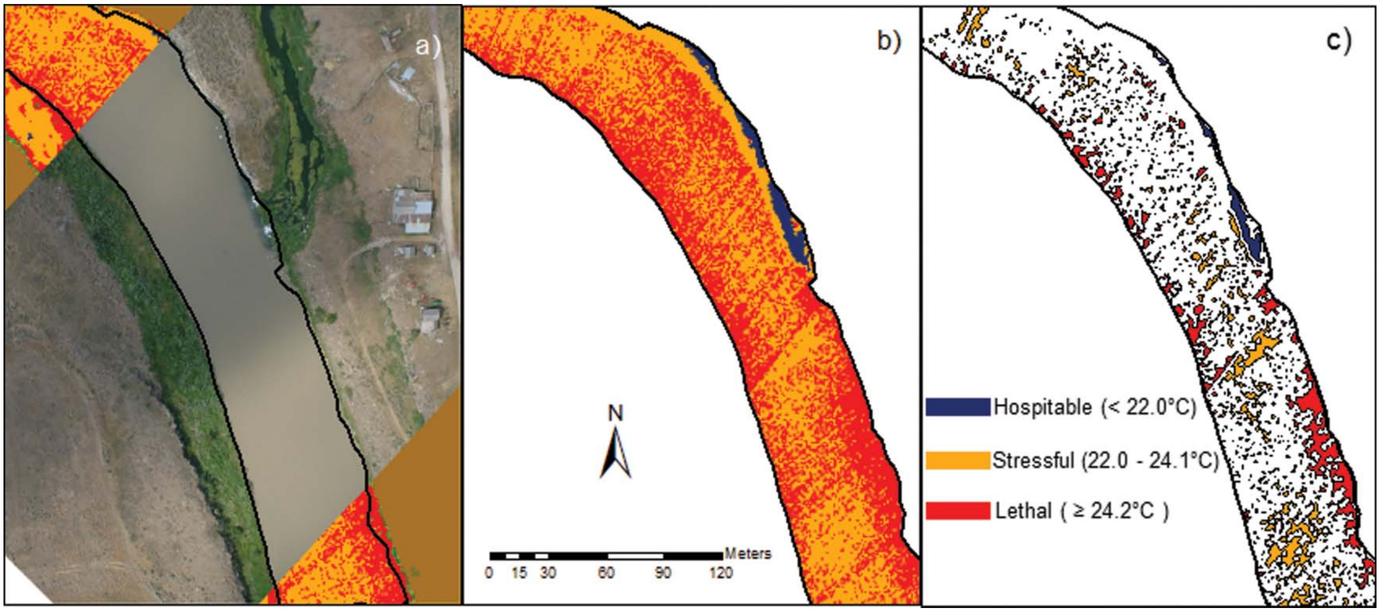

FIGURE 2. Images of the steps used to create polygons of three thermal habitat types (<22°C, hospitable; 22.0–24.1°C, stressful; ≥24.2°C, lethal) using ArcGIS 9.2 (ESRI, Redlands, California). (**a**) Georeferenced digital aerial photograph and thermal infrared remote sensing image, with a color scheme that contrasted the water from terrestrial environments, were used to create a polygon of the river edge. (**b**) Water temperatures specific to the Bear River were extracted using the polygons created in panel a. (**c**) Polygons of the three thermal habitat types created from extracted Bear River temperatures in panel b.

temperatures and exclude pixels representing terrestrial areas also captured with the imagery. Using the TIR imagery, we created a raster image consisting of pixel values representing only river temperatures by digitizing a polygon of the river edge. The boundary of the wetted stream channel was defined by combining digital aerial photographs with TIR images that were taken in sequence with each other and georeferenced using ArcGIS 9.2 (ESRI, Redlands, California; Figure 2a). A color scheme that best defined the contrast between the water and terrestrial edge was then applied using the symbology tool. This new raster image was used to calculate the proportion of water temperatures within 0.5°C temperature categories and overall mean temperature (Figure 2b).

We also used the digitized thermal image to calculate the patch characteristics for three thermal habitat types, which included water temperatures <22°C (hospitable), 22.0–24.1°C (stressful), and ≥24.2°C (lethal). We established these habitat types from past thermal physiology studies of cutthroat trout (Heggenes et al. 1991; De Staso and Rahel 1994; Meeuwig et al. 2004) and specifically for Bonneville cutthroat trout using the incipient lethal temperature (i.e., temperature lethal to 50% of a test population; LT50) of 24.2°C developed by Johnstone and Rahel (2003). Patch characteristics were calculated using ArcGIS 9.2 and the Patch Analyst 4 extension (R. Rempel, Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, Thunder Bay, Ontario) by reclassifying the original pixel values into categorized thermal habitats. We used the Patch Grid tool from the Patch Analyst 4 extension to create polygons (i.e., patches) for each thermal habitat type. In order to ensure the analysis only included habitat patches that were large enough to be identified and occupied by cutthroat trout of the size we studied, we removed habitat patches that were 5 m^2 or less as a minimum estimate of the space requirements for salmonids in streams of this size we studied (Grant and Kramer 1990). We then used the remaining habitat patches to calculate the patch characteristics for each thermal habitat type within each segment (Figure 2c).

RESULTS

Radio-Tagging

A total of 84 Bonneville cutthroat trout (32 from the regulated segment, 52 from unregulated segment) were implanted with temperature-sensitive radio transmitters between 4 October 2005 and 14 July 2006. Radio-tagged cutthroat from the regulated segment averaged 366 ± 64 mm (mean ± SD) TL (range, 294–474 mm) and 563 ± 309 g mass (range, 240–1,140 g). In the unregulated segment, radio-tagged cutthroat averaged 394 ± 39 mm TL (range, 335–545 mm) and 672 ± 256 g mass (range, 380–1,800 g). We tracked individual radio-tagged cutthroat trout for 0–328 d (mean = 172 d), depending on the fate of the fish or transmitter battery life. A total of 1,186 tracking locations were recorded for the 84 radio-tagged cutthroat trout, with an average of 14 locations per fish (range, 0–410).

Habitat Availability

Temperature loggers.—Based on the stationary temperature loggers, we observed that daytime (0900–2100 hours) water

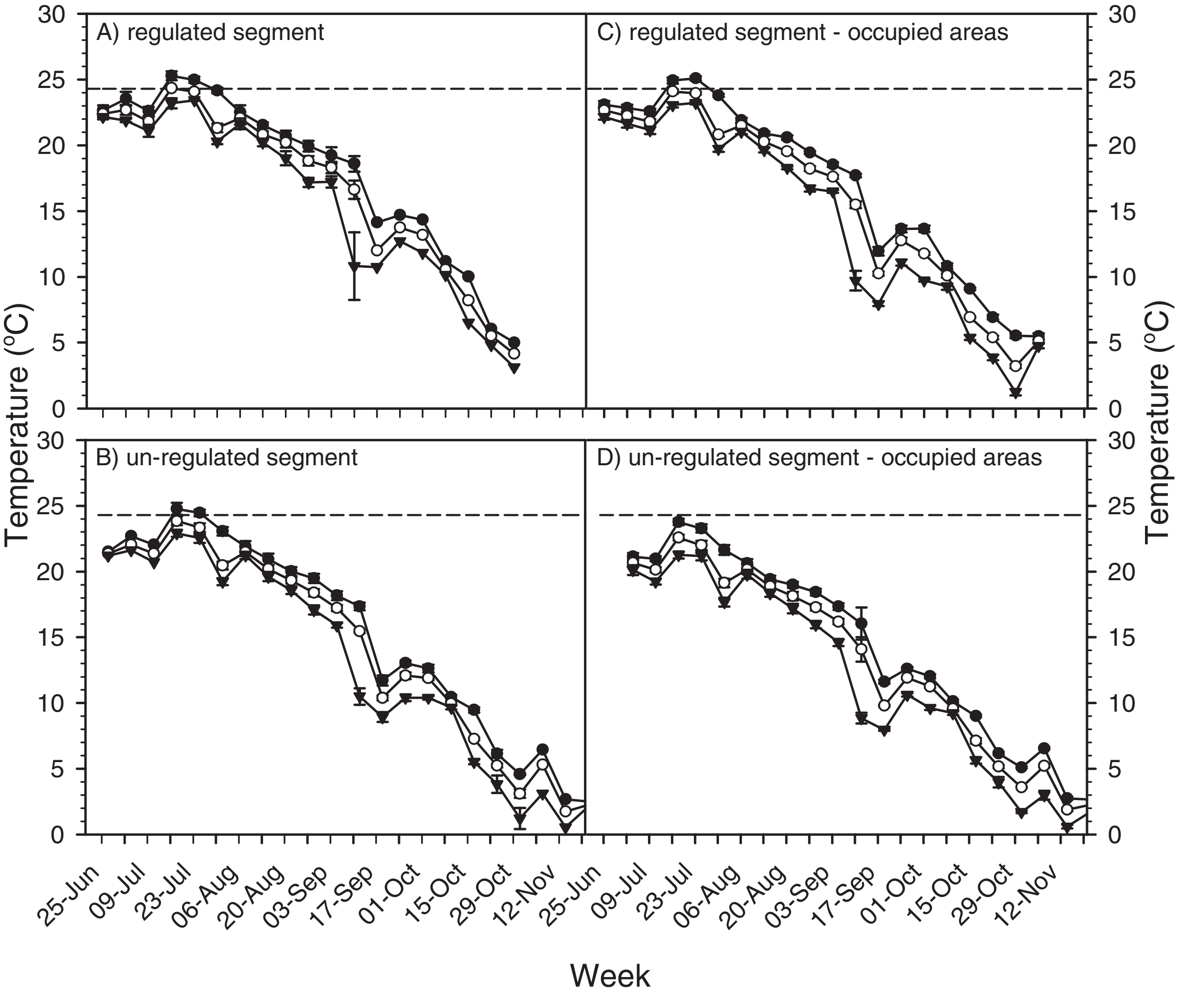

FIGURE 3. Average weekly maximum (AWmax, solid circles), average weekly mean (AWmean, open circles), and average weekly minimum (AWmin, solid triangles) water temperatures (°C) (± 95% CI) in (**A**) a regulated segment of the Bear River or (**B**) an unregulated segment of the Bear River. Panels (**C**) and (**D**) represent a subset of areas in (A) and (B) that exclude areas where Bonneville cutthroat trout were never observed to occupy. The horizontal dashed line at 24.2°C represents the inflection probability where 50% of the population will die (incipient lethal) based on the criterion by Johnstone and Rahel (2003).

temperatures increased from the end of June, peaked near the last week of July, then declined through November of 2006 (Figure 3a, b). The highest average weekly maximum (AWmax) in the regulated segment was 25.3 ± 0.3°C and 24.8 ± 0.5°C in the unregulated segment, both of which exceeded the lethal temperature of 24.2°C for Bonneville cutthroat trout (Figure 3a, b). In addition, AWmean temperatures approached the upper lethal temperature in the regulated segment but was lower in the unregulated segment (Figure 3a, b). Average weekly minimum (AWmin) temperatures mirrored mean temperatures but were 1–2°C lower. In both study segments there were areas that were never observed to be occupied by radio-tagged cutthroat trout (Figure 1). When we excluded those areas in calculating temperature regimes of available habitat, temperatures were lower in occupied areas compared with areas that included unoccupied areas (Figure 3c, d). However, the regulated segment continued to include AWmax temperatures that were 1.0–1.5°C above incipient lethal temperature levels during the warmest part of the summer (Figure 3c). In contrast, thermal regimes in the unregulated segment fell below lethal thresholds for Bonneville cutthroat trout for both AWmax and AWmean temperatures (Figure 3d).

Thermal imagery.—Thermal imagery data provided a fine-scale spatial representation of water temperatures in the Bear River during the warmest period of the summer. There were differences in the proportion of temperature-characterized habitat between the two study segments. The regulated segment had mean, median, and mode temperatures of 24, 25, and 25°C, respectively, and a distribution weighted towards warmer temperatures. The unregulated segment had a larger proportion of cooler temperatures and mean, median, and mode temperatures calculated at 21, 22.5, and 22.5°C, respectively.

When we classified the proportion of habitat that fell into three temperature categories: hospitable (<22.0°C), stressful

(22.0–24.1°C), and lethal ($\geq$24.2°C), there were distinct differences in the abundance and spatial distribution of the three thermal habitat types in the two study segments. The regulated segment was limited to only 0.02% of the total available habitat with hospitable water temperatures. Habitat patches with lethal water temperatures were most abundant, comprising 78% of the total habitat, and almost 21.9% of the remaining habitat patches contained water temperatures categorized as stressful. In the unregulated segment, 15% of the total available habitat was composed of patches with hospitable water temperatures, 84% was considered stressful, and only 1% of habitat patches consisted of lethal water temperatures.

In addition to differences in the frequency of thermal habitat categories between the two study segments, there were also differences in the spatial arrangement of habitat patches, including number of patches, mean patch size, and mean patch distance (Figure 4a, b). In the regulated segment, only three patches of habitat contained hospitable water temperatures. Hospitable patches had an average size of 77 m^2 and were widely distributed, with an average distance of 9,514 m between patches. In this segment, habitat patches with stressful water temperatures were more abundant than hospitable patches with a total of 757 patches and on average were 342 m^2 in area and 3,058 m apart. Habitat patches with lethal temperatures were the most abundant, totaling 1,097, largest in size at 1,324 m^2, and closer together, measuring 600 m apart (Figure 4a). In contrast, the unregulated segment had 462 habitat patches categorized as hospitable with an average size of 738 m^2 and average distance between patches of 279 m. Habitat patches with stressful water temperatures were most abundant and largest in size, totaling 535 patches with an average area of 2,685 m^2 and average distance apart of 120 m. Habitat patches composed of lethal water temperatures consisted of 77 patches with an average area of 9 m^2 and an average distance apart of 89 m (Figure 4b). In comparison with the nearest available data logger anchored above the stream bottom and taken at the same time of day, TIR measurements were, on average, 0.65°C, or 1.89%, higher than data logger measurements.

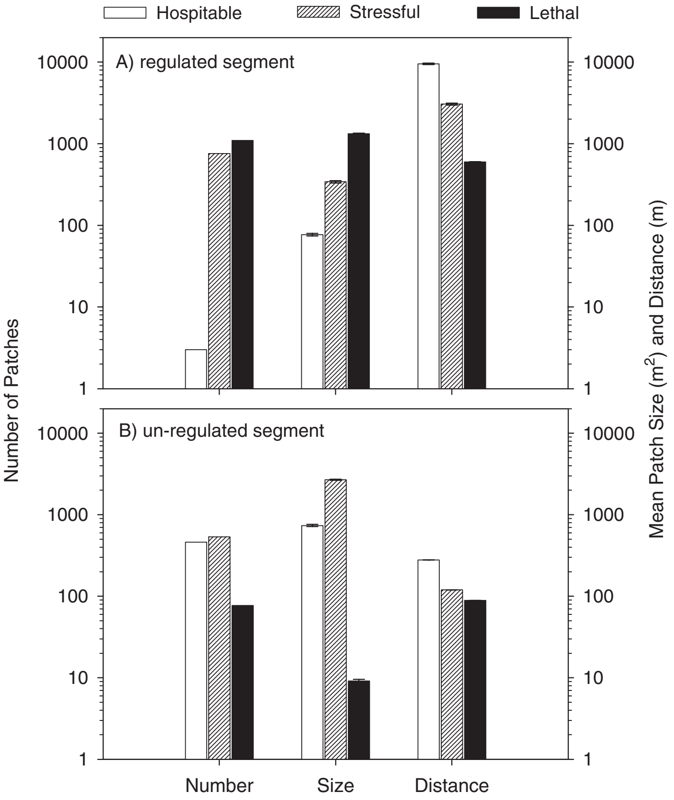

FIGURE 4. Mean (± 1 SE) habitat characteristics based on thermal imagery data used to calculate the number of patches, mean patch size, and mean distance between patches for the three thermal habitat types in (**A**) regulated and (**B**) unregulated segments of the Bear River.

Floating temperature surveys.—We conducted 14 floating temperature surveys (seven in the regulated segment and seven in the unregulated segment) during 13 July–6 October 2006 to combine estimates of both spatial and temporal variation in Bear River water temperature (Figure 5). Thermal profiles of AWmax temperatures for both segments revealed similar patterns to the temperature logger profiles. However, this method captured more spatial variability of available water temperatures. During the study period, AWmax temperatures increased from the first week in July and peaked between the third and fourth week of July (Figure 5). In both segments, AWmax water temperatures exceeded the lethal temperature for cutthroat trout; although, these high temperatures occurred on separate consecutive weeks. In the regulated segment, AWmax temperatures peaked at 25.5°C during the last week of July (Figure 5a). In the unregulated segment, AWmax temperatures peaked on the third week in July at 24.6°C (Figure 5b).

Habitat Use by Cutthroat Trout

During the warmest period of the summer (i.e., 1 July–15 August 2006), Bonneville cutthroat trout used habitats with temperatures that were cooler or similar to most available habitat depending upon the study segment they were in (Figure 5). Each of the three methods used to measure temperatures in available habitats identified similar trends in the thermal profile of the Bear River during the summer; although, slight variations in AWmean values for each method were identified each week during the warmest portion of the summer (Figure 5a, b). In the regulated segment, cutthroat trout used habitats with average temperatures cooler than average temperatures in available habitats during the last 2 weeks of July and first week of August of 2006 (Figure 5a). In the unregulated segment, cutthroat trout used habitats with average temperatures around 21.5–22.0°C during the first 4 weeks of the study period (Figure 5b). The third week in July was the warmest week in the unregulated segment and during this time period cutthroat trout used average temperatures in habitats that showed the largest difference between average temperatures measured in available habitats (Figure 5b).

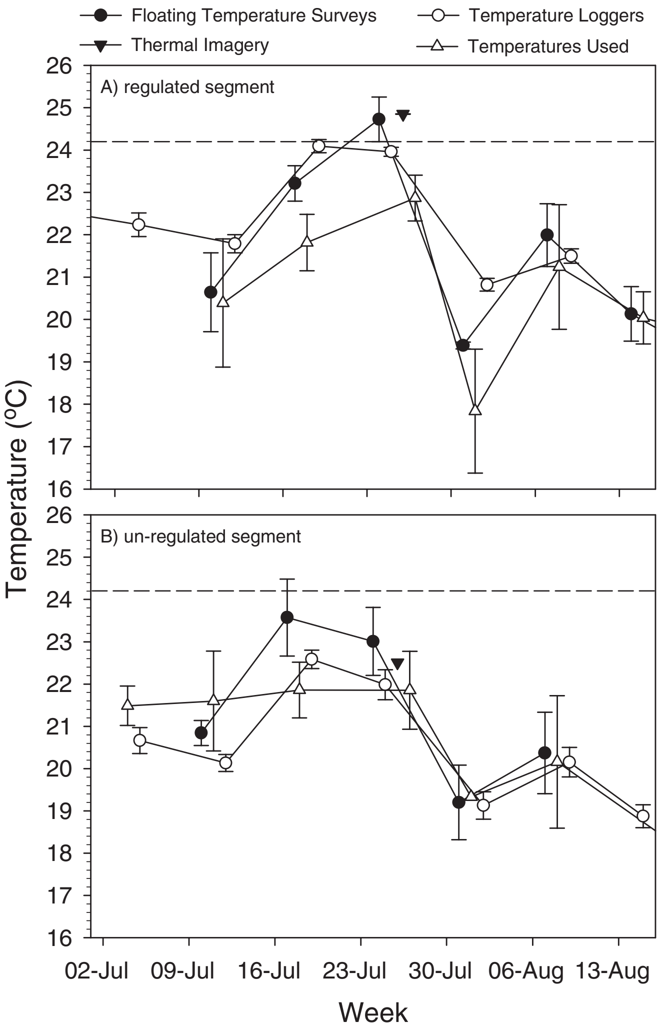

FIGURE 5. Weekly variation in mean available water temperatures (°C) (± 95% CI) measured with floating temperature surveys (solid circles), temperature loggers (open circles), and 1 week of thermal imagery (solid triangle) along with water temperatures used (°C) (± 95% CI) by Bonneville cutthroat trout (open triangles) in the (**A**) regulated and (**B**) unregulated segments of the Bear River, Idaho and Wyoming, during the study period of 2006. The horizontal dashed line at 24.2°C represents the inflection probability where 50% of the population will die (Johnstone and Rahel 2003).

During the warmest period of the summer, temperature loggers periodically measured average daily river temperatures that were near or exceeded the LT50 for Bonneville cutthroat trout, but few cutthroat trout using these high river temperatures were identified. In the regulated segment, only one cutthroat trout was recorded in habitat with a water temperature higher than the incipient lethal temperature of 24.2°C, despite the observation that average daily river temperatures exceeded lethal temperatures for a 2-week continuous period. In the unregulated segment, average daily river temperatures exceeded the lethal temperature for cutthroat trout for a shorter period of time, and during this time two fish using habitats categorized as having lethal temperature were identified. Overall, 98% of the relocations from cutthroat trout during this time period were in habitats cooler than the average daily river temperature.

Linear regression analysis of the relationship between AWmean river temperatures versus temperatures used by cutthroat trout revealed an increase in water temperature selected as available water temperature increased in the Bear River. In the regulated segment, the observed rate of increase was similar to the expected directly proportional increase, whether we compared available water temperature based on temperature loggers ($t_{1,5} = 0.45$, $n = 6$, $P < 0.25$; Figure 6a) or by means of floating temperature surveys ($t_{1,5} = 0.45$, $n = 6$, $P < 0.25$; Figure 6b); however, in both comparisons the elevation of the line was significantly lower than the expected 1:1 relationship (binomial test: $P < 0.05$; Figure 6a, b). In the unregulated segment, the relationship between available water temperature and that used by cutthroat trout deviated more strongly than the expected 1:1 relationship (Figure 6c, d), but was only different from a slope of 1 based on the floating temperature survey data ($t_{1,5} = 2.65$, $n = 5$, $P < 0.05$; Figure 6d) and not the temperature data loggers ($t_{1,5} = 1.36$, $n = 6$, $P < 0.10$; Figure 6c). Cutthroat trout in the unregulated segment only appeared to be selective when available water temperature was above 22–23°C.

To compare the frequency of temperatures used by cutthroat trout with their corresponding frequency of occurrence in the Bear River, we compiled the distribution of temperatures using the thermal imagery data and the distribution of temperatures used by Bonneville cutthroat trout during the warmest period of the summer (i.e., 1 July–15 August) and recorded from radiotelemetry data. In the regulated segment, thermal imagery data recorded a range of temperatures from 18.0°C to 28.1°C. Only 0.02% of the available habitat had temperatures less than the stressful limit of 22°C and 0.12% below the lethal limit of 24.2°C (Figure 7a). In contrast, cutthroat trout used habitats that had temperatures ranging between 11.8°C and 24.3°C (Figure 7a). Sixty-three percent of the habitat used by cutthroat trout had temperatures below 22°C and 98% had temperatures below 24.2°C (Figure 7a). In the unregulated segment, thermal imagery data ranged between 17.5°C and 28.5°C (Figure 7b). Twelve percent of the available habitat had a temperature below 22°C and 99% was below 24.2°C (Figure 7b). Temperature in habitat used by Bonneville cutthroat trout in the unregulated segment ranged between 18.5°C and 24.8°C (Figure 7b). We observed that 59% of the habitat used by cutthroat trout had a temperature below the stressful limit of 22°C and 97% was below the incipient lethal temperature of 24.2°C (Figure 7b).

The distribution of Bonneville cutthroat trout during peak summer temperatures was correlated with tributary confluences in the regulated segment; whereas in the unregulated segment, cutthroat trout distribution was more dispersed. In the regulated segment, cutthroat trout were primarily located near the confluences of Bailey Creek and Eightmile Creek (Figure 8a). In the unregulated segment, cutthroat trout were more evenly distributed throughout the upper portion of the study segment where most of the coolwater patches existed

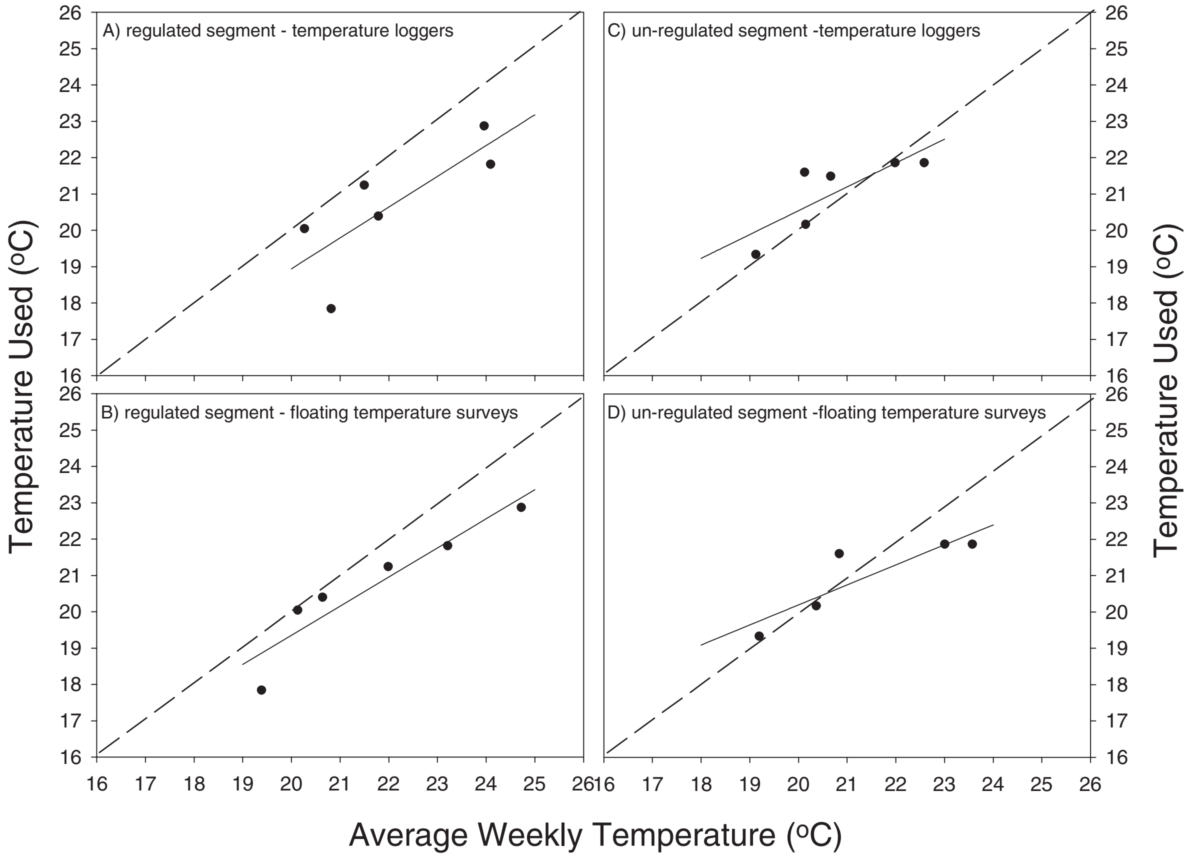

FIGURE 6. The relationship between available water temperature in the Bear River versus water temperature selected by Bonneville cutthroat trout for a regulated segment of the Bear River where water temperature was recorded with (**A**) temperature loggers or (**B**) by means of floating temperature surveys, and for an unregulated segment of the Bear River where water temperature was recorded (**C**) with temperature loggers or (**D**) by means of floating temperature surveys. In all panels the dashed line represents the 1:1 line.

(Figure 8b). Movement rates of fish in the two study segments also differed dramatically during the warmest period of the summer. Cutthroat trout in the regulated segment moved an average of 701 ± 815 m; whereas, in the unregulated segment they moved an average of 7,964 ± 5,886 m.

DISCUSSION

During peak summer temperatures, the availability of habitat categorized with hospitable water temperatures was limited for Bonneville cutthroat trout in the Bear River. From the first week of July until the middle of August, water temperatures often exceeded the upper lethal limits for cutthroat trout during the warmest part of the day in almost all habitats measured by three different methods. Patches of cooler water were present in both regulated and unregulated study segments of the Bear River, but the quantity, size, and spatial distribution of these refuges differed between the two segments. In the regulated segment of the Bear River, coolwater patches were confined to tributary mouths in just three locations. In the unregulated segment, coolwater patches were distributed more evenly throughout the study segment, including a large patch of cool water that resulted from the input of the Smiths Fork tributary. Our data suggest that high discharge rates of warm water in the regulated segment are diluting the formation of coolwater refugia as seen in other studies (Webb and Walling 1997; Lessard and Hayes 2003; Ahearn et al. 2005). Radiotelemetry of Bonneville cutthroat trout in both study segments revealed that fish selected habitat that was cooler than average water temperatures during the hottest part of the summer, but were less selective and more mobile when temperatures were cooler.

During the study period, ambient water temperatures in both the unregulated and regulated study segments of the Bear River exceeded both stressful (22.0°C) and incipient lethal (24.2°C) temperatures for Bonneville cutthroat trout. Thermal tolerance studies on various coldwater species have shown that high water temperatures (>22.0°C) negatively influence growth and survival, but the probability of mortality is dependent upon the exposure time to high temperature (Dickerson and Vinyard 1999; Johnstone and Rahel 2003; Meeuwig et al. 2004). For instance, Johnstone and Rahel (2003) identified that the probability of mortality increased significantly for Bonneville cutthroat

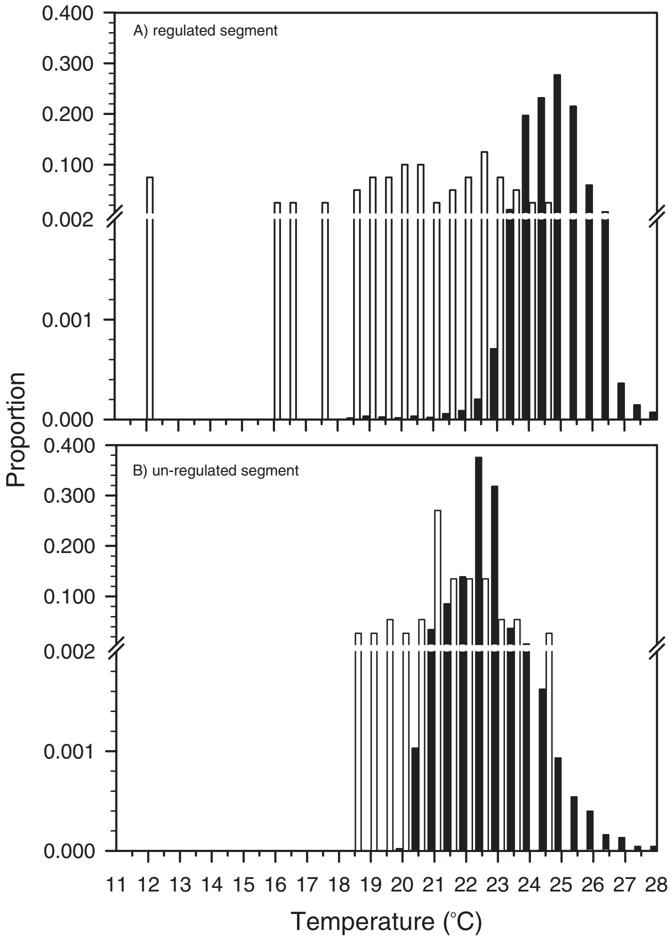

FIGURE 7. Proportion of pixel values (0.9 m^2) grouped into 0.5°C temperature categories from thermal imagery (solid bars) collected within the (**A**) regulated and (**B**) unregulated segments within the Bear River, Idaho and Wyoming, during 24–27 July 2006, and the proportion of temperatures in habitats used by Bonneville cutthroat trout (open bars) in the Bear River during the warmest period of the summer (1 July–15 August 2006) and recorded from radiotelemetry data.

trout when exposed to constant water temperatures of 25.5°C for more than 11 h. In our study, temperature loggers placed throughout the regulated segment recorded water temperatures that approached or exceeded 25.5°C for up to 10 h on five consecutive days. In the unregulated segment, water temperatures were recorded near 25.5°C for only 5 h during two consecutive days. Despite exposure to high water temperatures, survival can be mediated for coldwater species if there is a wide diel temperature range (i.e., ± 10°C) because cooler periods allow fish to repair physiological damages that may occur during injurious levels of high water temperature (Breck 1988; Schrank et al. 2003). In the Bear River, minimum daily water temperatures in the two study segments appeared to offer limited relief when maximum water temperatures were highest. When maximum water temperatures in the regulated segment reached 27°C, daily minimum water temperatures declined to 22°C, remaining within stressful limits for salmonid fishes. In the unregulated segment, maximum daily water temperatures reached 26°C and a minimum of 19°C, providing a less stressful range for the fish during nighttime periods. However, given the high maximum water temperatures and limited range of diel temperatures in both segments, coolwater sources probably play a critical role in sustaining Bonneville cutthroat trout in the Bear River.

Past studies have found that various fish species will identify and occupy habitats with more optimal water temperatures when prevailing water temperatures are stressful (van den Avyle and Evans 1990; Torgersen et al. 1999; Dunham et al. 2003), but few studies have identified the spatial distribution of thermal refuges in lotic systems (for example, see Ebersole et al. 2001, 2003). In this study, we identified the spatial distribution and characteristics of coolwater patches that may be important for survival of Bonneville cutthroat trout in the Bear River during peak summer temperatures. The spatial distribution and characteristics of coolwater refuges showed dramatic differences between the two study segments. In the regulated segment, there were only three patches with hospitable water temperatures for cutthroat trout to occupy during peak highs. In addition, these patches were small, with an average size of 77 m^2 and average distance between patches of 9,514 m, and the location of these patches was associated with tributary confluences. Due to localized disturbances near the mouths of tributaries (e.g., dewatering, pollution), the potential for localized patch extinctions is elevated because fish are limited in their ability to find distant coolwater patches without extended exposure to lethal water temperatures (Russell et al. 2003; Isaak et al. 2007). In contrast, the unregulated segment contained 462 patches of habitat with hospitable water temperature and had an average patch size of 738 m^2 and average distance between patches of 279 m. The Smiths Fork was the main upstream tributary of the Bear River that contributed a large supply of cool water, while springs and subsurface flows probably offered smaller sources of cooler water, as found in other studies (Cardenas et al. 2008; Olsen and Young 2009). In the regulated segment, there were a number of springs and coldwater tributaries identified with the thermal imagery. However, high summer water temperatures and high discharge rates from Bear Lake appear to buffer these sources as potential coolwater refuges once they reach the Bear River.

Epilimnetic water releases from dams can influence the longitudinal thermal profile of downstream river segments, and high summer discharge rates can decrease the potential formation of coolwater habitat (Webb and Walling 1997; Lessard and Hayes 2003; Ahearn et al. 2005). Typically, water temperatures in natural river systems increase downstream; however, in regulated rivers, water temperatures may be warmest directly below discharge structures when water releases are from epilimnetic sources. These warm water temperatures decrease farther downstream, as cooler secondary sources enter the primary stream flow. For instance, Lessard and Hayes (2003) studied the influence of surface release dams on water temperatures within 10 rivers. They identified that water temperatures increased

FIGURE 8. Distribution of tracking locations of Bonneville cutthroat trout in the (**A**) regulated and (**B**) unregulated segments of the Bear River, Idaho and Wyoming, during 1 July–15 August 2006.

directly below nine different dams (from +0.4°C to +5.5°C) when compared with water temperatures 2 to 3 km downstream and in comparison to sites upstream. In contrast, other studies have shown water temperatures in regulated river segments below dams are significantly cooler (Ward and Stanford 1979; Marshall et al. 2006). These results typically occur when water is released from cooler hypolimnetic zones within the impoundment, especially during stratification. In Bear Lake, warm surface water is pumped into an outlet canal at the Lifton pumping station and then delivered back to the Bear River channel during the summer irrigation season. As a consequence, the longitudinal thermal regimes of the unregulated and regulated segments were similar to those observed by Lessard and Hayes (2003). In the unregulated segment, downstream water temperatures were, on average, 2.2°C higher than upstream water temperatures. Water temperatures directly below the outlet were, on average, 1.0°C higher than water temperatures entering Bear Lake. Finally, in the regulated segment, water temperatures at the outlet of Bear Lake were, on average, 0.9°C higher than downstream water temperatures.

In addition to warmwater releases that altered the longitudinal thermal regime of the Bear River, high discharge rates potentially reduce the formation of coolwater refugia in the regulated segment. During the warmest part of the summer, discharge rates in the regulated segment fluctuated between 14.2 and 25.5 m^3/s (500 and 900 ft^3/s), and in the unregulated segment discharges were between 4.25 and 12.7 m^3/s (150 and 450 ft^3/s) (Hillyard 2009). In the regulated segment, higher discharge rates are influenced by the release of water from the surface of Bear Lake at the head of the segment to meet irrigation demands downstream. During summer, warm epilimnetic water forms due to solar radiation and relatively warm water is released downstream. The combination of high water temperatures and epilimnetic discharges essentially prevents the formation of coolwater habitat from groundwater and tributary sources, as other studies have found (Lessard and Hayes 2003; Caissie 2006; Webb et al. 2008). Coolwater sources contribute a greater proportion of cool water in relationship to warmer primary stream flow when discharges are lower (Constantz 1998; Caissie 2006; Webb et al. 2008). For instance, Webb and Walling (1997) studied water temperatures on a regulated river downstream from Wimbleball Lake in Somerset, UK, and identified cool water originating from springs had a greater influence on river temperatures when the amount of warm water released from the reservoir was decreased. Discharge rates in the unregulated segment remained lower than the regulated segment throughout the summer. As a result, cool water from the Smiths Fork, which enters the Bear River at the top of the study segment, altered main-stem Bear River water temperatures from lethal levels above the confluence to hospitable levels, for approximately 5 km downstream. Lower discharge rates also allowed spring and subsurface inputs to supply additional patches of cool water. Variable discharge rates between the two study segments appeared to influence the spatial distribution and abundance of thermal refuges, which in turn may be influencing the distribution patterns of cutthroat trout between the two study segments.

The spatial and temporal distribution of habitats characterized by water temperature appeared to influence the movement and distribution of Bonneville cutthroat trout during peak summer temperatures. In the regulated segment when summer water temperatures were highest, tracking locations of radio-tagged cutthroat trout were clumped near the confluence of Bailey and Eightmile creeks, whereas in the unregulated segment, tagged cutthroat trout were more evenly distributed. Cutthroat trout distributions were similar to the spatial arrangement of coolwater refuges in each study segment, suggesting thermal refuges during high water temperatures are important. Thermal refuges are a significant component to the survival and distribution of coldwater species living in environments that can experience extreme temperature even for short periods (Ebersole et al. 2001; Dunham et al. 2003; Boxall et al. 2007). The attributes of thermal refuges that are most likely to determine the distribution of coldwater species are size, frequency, and connectivity between patches. For example, Ebersole et al. (2001) identified that the abundance of Chinook salmon *O. tshawytscha* and steelhead *O. mykiss*, in the Grande Ronde River, Oregon, was positively correlated to the size and frequency of coolwater input. We found similar results in both study segments; the distribution of cutthroat trout was associated with cooler reaches within each segment, and in particular, cutthroat trout in the regulated segment were limited to small patches of thermal refuges within two locations. The movement of cutthroat trout during high water temperatures was positively associated with connectivity between patches. Therefore, in the regulated segment, due to the size, frequency, and connectivity between thermal refuges, cutthroat trout are more limited to shorter movement during high temperature periods. The restricted movement opportunities for cutthroat trout in the regulated segment may increase the potential for competition for other resources (i.e., food) as well vulnerability to angling pressure and predators that in turn may result in added stress and mortality.

Conclusions and Management Implications

The Bear River watershed has suffered from significant habitat alteration, but native populations of Bonneville cutthroat trout still persist and may continue to do so, given appropriate actions to protect and improve habitat quality (Binns and Remmick 1994; Schrank et al. 2003; Denton 2007). Our findings suggest that water temperature is influencing the distribution of cutthroat trout in main-stem Bear River habitats primarily during periods of peak summer temperatures. Predicted increases in the frequency and severity of high temperature events due to global climate change (Keleher and Rahel 1996; Rahel et al. 1996; Ficke et al. 2007) and the potential for increased consumption of surface water sources (Vörösmarty et al. 2000; Ficke et al. 2007) makes it likely that regulated rivers and native coldwater species in these systems will suffer additional negative impacts. Climate change analyses predict a loss of low-elevation habitats for coldwater species, essentially limiting their distribution to higher elevations (Rahel et al. 1996). Unfortunately, dams from these regulated systems may inhibit important long-range movement of fish from downstream habitat into upstream segments (Schoby and Keeley 2011). Similarly, the future demand for water consumption resulting from climate change and human population growth will probably increase the pressure for development of additional impoundments. Future dam construction and operations should consider the effects they may have on the movement potential and thermal refuges for native fishes and limit negative impacts that can result from dams as seen in the regulated segment of this study. Future management plans for Bonneville cutthroat trout in the Bear River should focus on increasing the spatial heterogeneity of thermal refuges and decrease ambient main-stem Bear River water temperatures. One management objective may be the restoration and reconnection of coldwater tributaries that are currently diverted without regard for impacts to native fish populations.

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