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ARTICLE

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Abstract

Little is known about the variability in the spatial and temporal distribution of spawning potamodromous trout despite decades of research directed at salmonid spawning ecology and the increased awareness that conserving life history diversity should be a focus of management. We monitored a population of fluvial–resident Bonneville Cutthroat Trout *Oncorhynchus clarkii utah* in a tributary to the Logan River, Utah, from 2006 to 2012 to gain insight into the distribution and timing of spawning and what factors may influence these spawning activities. We monitored Bonneville Cutthroat Trout using redd surveys with multiple observers and georeferenced redd locations. We documented an extended spawning period that lasted from late April to mid-July. The onset, median, and end of spawning was best predicted by the mean maximum water temperature during the first 13 weeks of the year ($F = 130.4$, df = 5, $R^2 = 0.96$, $P < 0.0001$) with spawning beginning and ending earlier in years that had warmer water temperatures prior to spawning. The distribution of redds was clumped each year and the relative density of redds was greater in a reach dominated by dams constructed by beavers *Castor canadensis*. Both dam failure and construction appeared to be responsible for creating new spawning habitat that was quickly occupied, demonstrating rapid temporal response to local habitat changes. Bonneville Cutthroat Trout appeared to establish and defend a redd for up to 2 d, and spawning most often occurred between similar-sized individuals. Spawning surveys for potamodromous trout are an underutilized tool that could be used to better understand the distribution and timing of spawning as well as determine the size and trends of the reproducing portion of populations of management concern. Without efforts to document the diversity of this important aspect of potamodromous trout life history, prioritization of conservation will be problematic.

Understanding and conserving the breadth of species diversity is at the heart of fisheries management (Allendorf and Waples 1996). In Pacific salmon *Oncorhynchus* spp., a primary focus of management is the maintenance of populations within the same species (i.e., stocks) that use different spawning locations or spawn at different times in the same area, thus maintaining reproductive isolation, which promotes microevolution and population stability (Quinn 2005; Schindler et al.

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2010). Potamodromous trout populations of western North America also exhibit a variety of spawning movement patterns including adfluvial (i.e., lake rearing and stream spawning; Cope 1956; Downs et al. 2006; Holecek and Walters 2007; Barnett and Paige 2013), fluvial (i.e., larger spawning and rearing movements within streams; Colyer et al. 2005; Al-Chokhachy and Budy 2008; Pierce et al. 2009), and tributary residency (Young 1995), and multiple movement patterns are often demonstrated within a single watershed (Al-Chokhachy and Budy 2008). The diversity of potamodromous trout spawning movements is thought to be part of a complex set of life history characteristics that have evolved in response to frequent changes in the spatial and temporal availability of suitable habitat (Gresswell et al. 1994; Northcote 1997; Dunham et al. 2003).

To effectively manage the life history diversity of potamodromous trout will require a comprehensive understanding of the abundance of the reproducing portion of a population, as well as the spatial and temporal distribution of spawning (e.g., Isaak and Thurow 2006; Falke et al. 2010). Of additional importance is the need to quantify how landscape characteristics and fluvial processes can influence the variability of the spatial and temporal patterns of spawning, which often requires in-depth monitoring approaches that integrate continuous views of the river over a variety of spatial scales (Torgersen et al. 2001; Gresswell et al. 2006). Although information related to the timing of spawning migrations of salmonid species have been described (Gresswell et al. 1994; Brenkman et al. 2001; Muhlfeld et al. 2009), there remains a paucity of data for potamodromous trout describing the annual variation in distribution and timing of spawning or specific spawning activities such as the number of fish on a redd, the length of time spent of a redd, and the interaction between different "stocks" such as resident and fluvial or adfluvial spawners (Northcote and Lobon-Cervia 2008). The limited knowledge of spawning activity for potamodromous trout is not surprising given the challenges of monitoring spawning activity in tributaries that have low densities of spawners and are small and difficult to access (Budy et al. 2012).

Redd surveys are a common method for assessing spawning activity in salmonids because they are relatively inexpensive and nondisruptive (Dunham et al. 2001; Holecek and Walters 2007). Monitoring salmonid redds can provide some of the life history data required to determine the conservation status of the fish. These data can include estimates of the abundance of spawning adults (Rieman and Myers 1997), the spatial and temporal dynamics of adult populations (Zimmerman and Reeves 2000; Isaak and Thurow 2006), distribution and quality of spawning habitat (Magee et al. 1996), and information regarding within and across population diversity (Rieman and McIntyre 1996). However, the current knowledge related to the spatial, temporal, and behavioral patterns of salmonid spawning is largely skewed as many studies have focused on coastal populations of obligate anadromous species that return to relatively well-defined spawning areas and spawn over relatively short time periods (Quinn 2005). Even when studies have focused on potamodromous trout they have tended to be on adfluvial populations (Irvine 1978) or select populations with high recreational value that exhibit more predictable fluvial or adfluvial spawning movements (e.g., Kaeding and Boltz 2001).

Here, we used 7 years of redd survey data to investigate the spatial and temporal spawning patterns and activity on redds for Bonneville Cutthroat Trout *O. clarkii utah*. This study took place within a recently fenced stream section with a number of beaver dams. The goal of this study was to merge the use of redd count methods with observational data to better understand the spawning ecology of Bonneville Cutthroat Trout. The specific objectives of this study were to determine (1) the annual variation in the duration and temporal distribution of spawning, (2) the influence of discharge and water temperature on the duration and temporal distribution spawning, (3) the annual variation in the spatial distribution of redds, (4) the influence local disturbances (i.e., beaver dam construction and failure) on the spatial distribution of redds, and (4) the number and size of fish on redds and the length of time redds are occupied.

STUDY AREA

Our study took place in Spawn Creek, a third-order tributary to Temple Fork Creek, which flows into the Logan River in northern Utah (Figure 1). Spawn Creek is a small stream (catchment area = 13.6 km^2) with a mean bankfull width of 2.6 m (Hansen and Budy 2011). Spawn Creek receives substantial groundwater inputs resulting in a mean annual water temperature of 6.3°C and a mean annual discharge of 0.13 m^3/s. During the Bonneville Cutthroat Trout spawning season daily mean temperatures range from a low of 4°C in May to a high of 16°C in July and stream discharge ranges from 0.16 to 1.04 m^3/s. Water clarity is high during the spawning period except for short time periods following intense rainstorm events or failure of upstream beaver dams (Hansen and Budy 2011).

Bonneville Cutthroat Trout are native to Spawn Creek and the Logan River watershed, which has been identified as one of the largest remaining strongholds of this subspecies (Lentsch et al. 2000; Budy et al. 2007). The majority of Bonneville Cutthroat Trout spawning in the upper Logan River likely takes place in Temple Fork and Spawn Creek (Budy et al. 2007, 2012). Both resident and fluvial life history forms of Bonneville Cutthroat Trout spawn in Spawn Creek (Bernard and Israelsen 1982; Budy et al. 2007). The mean length of Bonneville Cutthroat Trout based on 5 years of electrofishing surveys throughout the watershed was 236 mm (SD = 44, n = 1,531: Budy et al. 2007). Other salmonid species in the study area include Brown Trout *Salmo trutta* and Brook Trout *Salvelinus fontinalis*. Brown Trout are primarily found in the lower 1,500 m of Spawn Creek, while Brook Trout are primarily associated with beaver ponds in the upper 500 m of the study area.

We evaluated spawning Cutthroat Trout in the lower 2,500 m of Spawn Creek, from the confluence with Temple Fork Creek

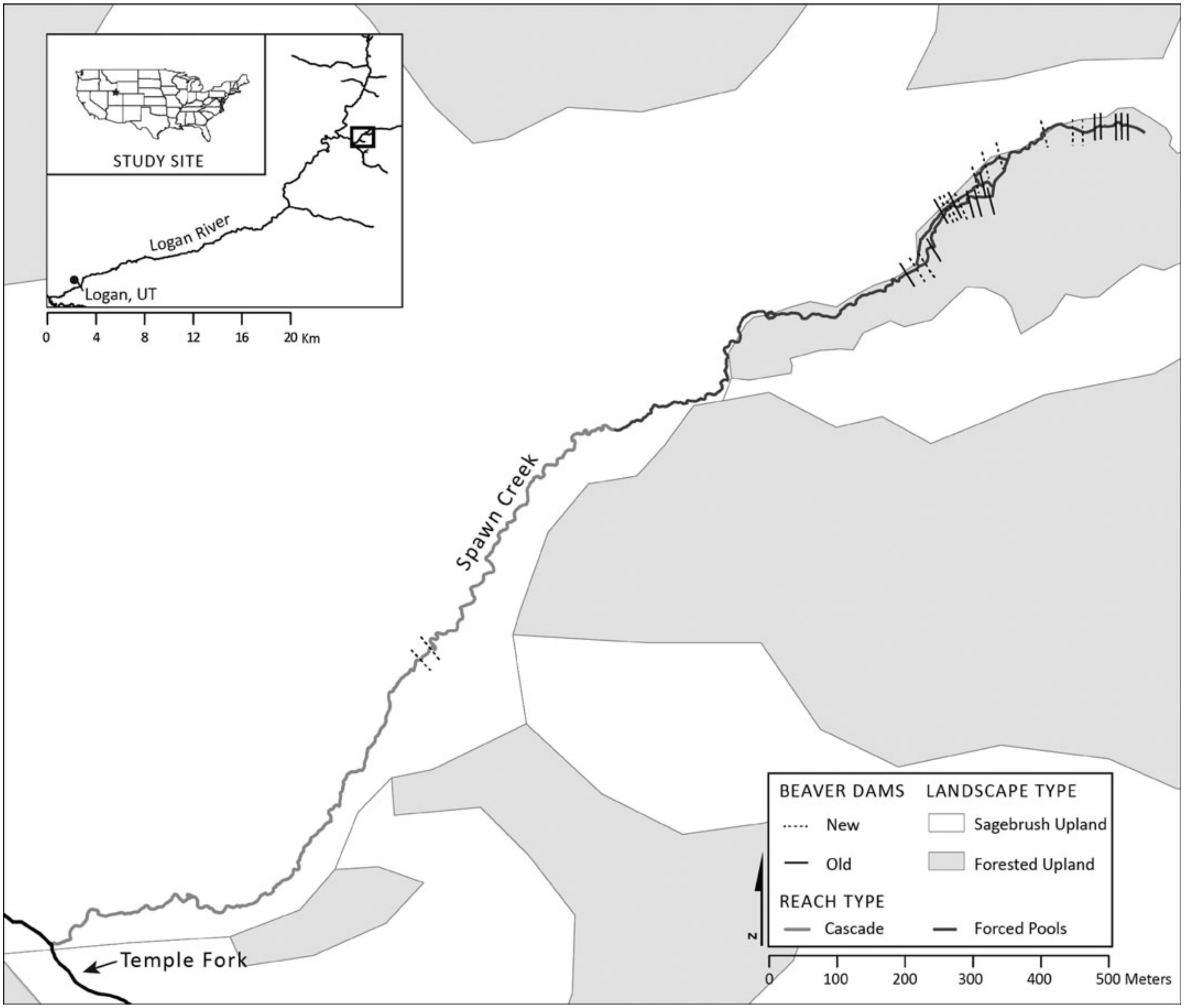

FIGURE 1. Location of the Logan River watershed within Utah and the Spawn Creek study site within this watershed. The Spawn Creek study site is composed of a lower forced-pool reach and an upper cascade reach. Beaver dams built before 2006 (Old) and from 2006 to 2012 (New) are depicted by perpendicular lines on the stream.

upstream to a series of beaver dams (Figure 1). All but the lower 200 m of this section of stream was fenced in 2006 to exclude cattle grazing (Hansen and Budy 2011). We divided the study area into two distinct reaches on the basis of vegetation type, valley confinement, and stream characteristics (Figure 1) (Brierley and Fryirs 2005). Reach 1 consists of the lower 1,300 m of the study area and is within a sagebrush *Artemesia tridentate* upland landscape type. The majority of reach 1 is forced pool–riffle with mostly gravel and cobble substrate (Lokteff et al. 2013). Reach 2 extends from 1,300 to 2,500 m above the mouth of Spawn Creek and is within a forested (trembling aspen *Populus tremuloides* and conifers Pinaceae) upland landscape type. The majority of reach 2 is cascading with more cobble and boulder substrate and less sinuosity than reach 1. Both reaches have limited direct cover over the stream, and therefore, spawning fish can be observed throughout most of the spawning season.

Lokteff et al. (2013) collected information on the presence and status of beaver dams throughout the study area and identified 26 beaver dams, 24 of which were in reach 2 (Figure 1). Here, we classified the dams into old (existed prior to the study initiation in 2006) and new (built between 2006 and 2012) to consider how beaver dams can potentially influence the spatial distribution of redds.

METHODS

Redd surveys.—We modified the typical redd survey protocol for salmon and trout (e.g., Gallagher et al. 2007) because redds of potamodromous trout can be hard to detect due to their inherently small size and the prevalence of other natural disturbances to the substrate (Magee et al. 1996). Therefore, we defined a redd as a location occupied by two or more Cutthroat Trout engaged in spawning behavior. We defined spawning behavior as fish holding side by side, digging, spawning (eggs and/or milt being released), or aggressive behavior (chasing other fish from the area). We conducted redd surveys in Spawn Creek beginning in mid-April and ending in mid-July. The number of observers and frequency of observations varied over the course of the study, but in general, we completed a minimum of one survey per week (Table 1). The number of days surveyed per year ranged from 16 in 2006 to 47 in 2009, and the number of observers ranged from one in 2006 to six in 2008. Twelve observers participated in the study. Experienced observers (>5 years experience, $n = 3$) trained inexperienced observers by conducting three redd surveys in or near the study area with the experienced observer showing inexperienced observers how to identify redds. Surveys were conducted between 0930 and 1600 hours and generally took between 1.5 and 3.0 h to complete depending upon the number of spawning fish encountered.

Although we did not mark the locations of redd observations with flags or stakes to avoid biasing subsequent surveys (Gallagher et al. 2007), we georeferenced each redd observation to aid in identifying unique redds and assess the spatial and temporal distribution of redds (sensu Klett et al. 2013; see below). We recorded the location of each redd from the streambank nearest to the redd using a hand-held GPS unit. We waited to record the GPS location until the positional error was <7.5 m (as measured by the GPS unit). We used 7.5 m as the cutoff for a positional error based on our field experience, as well as the tradeoff between getting a more accurate GPS location and the length of time it took for the positional error to improve as a surveyor collected GPS data at a location. With this level of error we typically obtained the location of a redd within 2–3 min, and using this method our mean recorded position error was 3.8 m (SD = 1.4, $n = 669$; this mean positional error is based on redds recorded from 2008 to 2012 because the exact error was not recorded from 2006 to 2007, only that it was <7.5 m). We imported GPS redd locations into a GIS database and determined the distance to the nearest point on the stream layer. Redd locations that plotted >25 m from the stream (five redds or 0.54% observed) were excluded from the analysis. The nearest stream coordinate was used to replot the remaining redd observations on the stream layer. We then recorded the distance of each redd observation from the mouth of Spawn Creek.

We developed a rule set to characterize which georeferenced redd observations were spatially and temporally unique (i.e., a unique redd). Any redd observations that were within 15 m of each other (i.e., twice the error rate of the GPS) and recorded in <4 d were assumed to be a single redd; we acknowledge that integrating the spatial error of the GPS likely provided conservative estimates of unique spawning sites. We chose ≤4 d based on our experience and the limited evidence reported in the literature (Smith 1941; Schmetterling 2000). Thus, redd observations that were either >15 m apart or observed >4 d apart (or both) were considered unique redds. When a redd was observed multiple times we used the mean date of observation as the date of redd presence and the mean distance from the mouth as the location of the redd (Zimmerman and Reeves 2000). To estimate the relative spawning intensity across years and between reaches we calculated annual redd density index as

$$\frac{n}{l} \times \frac{1}{s} \times 100$$

where n is the number of redds, l is the length of the reach, and s is the number of redd surveys (Baxter et al. 1999; Gortazar et al. 2007). We incorporated the number of surveys to allow for comparisons between years of different survey effort.

Discharge and temperature monitoring.—We monitored stream discharge and water temperature in Spawn Creek and the Logan River annually to assess the influence of these attributes on the timing and duration of spawning. Earlier research in Spawn Creek suggested discharge was an important factor influencing migration and spawning activity (Bernard and Israelsen 1982; Budy et al. 2012), and discharge and water temperature have been found to influence spawning activity in other potamodromous trout populations (Liknes and Graham 1988; Behnke 1992). We measured stage height with a water level gauge located at the mouth of Spawn Creek and developed a stage–discharge relationship through intermittent measurements of discharge at the water level gauge using a flow meter. An exponential regression model was fit to the data to predict the discharge ($y = 0.0007 \times e^{0.1153x}$, $R^2 = 0.92$, $p < 0.0003$). We used two temperature probes placed in the lower 400 m of Spawn Creek to collect mean, maximum, and minimum daily water temperatures. All discharge and temperature data for the Logan River was obtained from the Utah State Water Research Lab (http://uwrl.usu.edu/).

Temporal distribution of spawning.—We examined the temporal distribution of redds between years by plotting the cumulative proportion of redds by week of the year. We used a Kolmogorov–Smirnov two-sample test to test whether the temporal distribution of redds was different between years and adjusted P-values of pairwise comparisons between years to account for multiple tests using the step-down Bonferroni method (Holm 1979). We estimated the duration and temporal distribution of spawning by plotting the mean number of redds recorded each week of the spawning period from mid-April (week 13) to mid-July (week 30). We calculated the day when 5, 50, and 95% of the redd observations were made each year as a measure of onset, median, and end, respectively, of the spawning period (Warren et al. 2012).

TABLE 1. Summary statistics for redds and environmental conditions for Bonneville Cutthroat Trout in Spawn Creek, Utah, 2006–2012. Q = discharge (m^3/s), RDI 1 = redd density index in reach 1 (see Methods for calculation), RDI 2 = redd density index in reach 2. Number of survey days = number of days redd surveys were conducted, Number of surveys = number of individual surveys (includes multiple surveys on same day), Average number of surveys/week = mean number of redd surveys conducted per week for weeks 13–30 each year (this mean only includes 1 survey/d from week 24 in 2008 and 2009 when we conducted 4–5 surveys/d as part of an intensive survey effort), Number of observers = number of observers used each year, Average days between surveys = mean number of days between each survey, Number of redds observed = total number of redds observations by all observers summed for all surveys in that year, Number of unique redds = an estimate of how many redd observations were of the same redd (see Methods), % unique redds observed once = an estimate of percent unique redds that were only detected once during the survey period, Average daily maximum Q (weeks 1–13) = the mean maximum discharge (m^3/s) during weeks 1–13, Average daily maximum Q (Apr–Jul) = the mean maximum discharge (m^3/s) during the spawning period (April–July), Average daily maximum temperature (weeks 1–13) = mean maximum water temperature (C°) during weeks 1–13, Average maximum temperature (Apr–Jul) = mean maximum water temperature (C°) during the spawning period (April–July), Onset date = day of the year 5% of redd observations made, Median date = day of the year 50% of redd observations made, End date = day of the year 95% of redd observations made.

Year	Number of survey days	Number of surveys	Average number of surveys/week	Number of observers	Average days between surveys	Number of redds observed	Number of unique redds	% unique redds observed once	Average daily maximum Q (weeks 1–13)	Average daily maximum Q (Apr–Jul)	Average daily maximum temperature (weeks 1–13)	Average daily maximum temperature (Apr–Jul)	Onset date	Median date	End date	RDI 1	RDI 2
2006	16	16	0.9	1	6.1	81	78	96.2		0.39	6.2	10.5	124	143	172	17.8	23.5
2007	24	24	1.3	2	4.0	136	117	88.0	0.14	0.14	6.2	12.4	119	138	161	15.1	29.9
2008	25	50	1.7	5	2.6	203	131	81.7	0.08	0.14	4.7	10.9	133	154	174	12.9	19.1
2009	47	66	2.8	6	2.0	242	131	63.4	0.09	0.14	5.1	10.8	134	155	177	11.3	18.0
2010	39	40	2.2	3	2.0	108	98	91.8	0.09	0.10	6.0	11.4	124	152	168	9.0	13.0
2011	23	23	1.3	3	4.1	78	63	79.4	0.11	0.29	4.7	9.3	136	157	171	19.4	8.5
2012	23	23	1.3	5	3.1	73	69	92.8	0.07	0.12	6.5	13.7	121	139	155	8.0	18.2
Total	197	242	1.6	12	3.4	921	687	84.7	0.10	0.19	6.5	11.3	127	148	168	13.4	18.6

Influence of discharge and temperature on temporal distribution of spawning.—To assess the influence of abiotic factors on the onset, median, and end of spawning we built a set of linear models using day of calendar year of the onset, median, and end of spawning as the dependent variables and different measures of discharge and temperature from Spawn Creek and the Logan River as the independent variables. We evaluated models using discharge and temperature factors for Spawn Creek and the Logan River separately (i.e., temperature variables for Spawn Creek and the Logan River were not used in the same model) to determine whether proximate or more distant cues influenced timing of spawning. Variables we included in the models were mean flow and temperature metrics in periods well prior to spawning (using calendar year, weeks 1–13), just prior to spawning (week 13), during peak spawning (weeks 17–27), and the day of the year was noted when the peak discharge was the greatest. We hypothesized that the onset of spawning would be earlier and end earlier in years with lower maximum discharge and higher water temperatures. We tested for both additive and interaction effects. We modeled the separate dependent variables as factors and thus included each dependent variable in a single model. An additive model would indicate the onset, median, and end of spawning were similarly affected by the independent variables. Evidence of an interaction effect would suggest that onset, median, and end of spawning were influenced by different variables. We used Akaike's information criterion corrected for small sample size (AIC_c) to assess our candidate models (Burnham and Anderson 1998) and considered models within two ΔAIC_c as the most plausible and models > 10 ΔAIC_c not supportable by the data.

Spatial distribution of redds.—We plotted the cumulative frequency of redds by stream distance to determine whether the spatial distribution of redds differed across years (Isaak and Thurow 2006). We tested for differences in the spatial distribution of unique redds between years with a two-sample Kolmogorov–Smirnov test (described above; Dunham et al. 2001). We tested whether there was a spatial pattern (uniform, random, or clumped) within the study area each year by summing up the number of redds in 500-m segments of stream. We hypothesized that redds would have a clumped distribution based on differences in the two reach types in the study area. We used the ratio of the variance in redd counts per 500-m segment of stream to the mean number of redds per segment (i.e., index of dispersion) as an indication of distribution pattern. Ratios for uniform distributions will be <1, random distributions will be ~ 1, and clumped distributions will be >1. A chi-square test was used to test the significance of the ratio. We binned redd observations in 500-m segments so that each segment would have a minimum predicted number of redds of six or more to conform to chi-square assumptions (Zar 1984). For all analyses, we set our critical value as $P < 0.1$ to balance the probability of committing type I and II errors.

Influence of beaver dams on spatial distribution of redds.—We suspected that beaver dams in Spawn Creek (Bernard and Israelsen 1982; Lokteff et al. 2013) could influence the distribution of redds as changes in flows related to the construction and failure of dams are thought to create spawning habitat and habitat heterogeneity that benefit fish populations (Collen and Gibson 2001; Pollock et al. 2004). To assess the influence of beaver dam construction and failure on the spatial distribution of redds we compared the redd density index with the location of dams (new and old) and the failure of dams.

Spawning activity at redds.—From 2009 to 2012 we quantified spawning activity at each redd location to document the number of fish per redd, the size-class of fish on or near a redd (i.e., within the same habitat unit), and the time spent on a redd. Once the location of a redd was recorded with GPS (see above), we visually estimated the size of fish occupying the redd using length classes as defined by Budy et al. (2007) that correspond to distinct age-classes: <150 mm (age 1), 150–225 mm (age 2), and >225 mm (age 3 +). Observers were trained with cutouts of fish of known length prior to beginning surveys or they had multiple years experience capturing and tagging similar-sized fish in Spawn Creek and Temple Fork. Fish were classified as either being associated with the redd (i.e., defending, digging, directly spawning in redd) or as being in the immediate area of the redd but not a direct contributor to the redd construction or spawning activity. We assumed some of these fish in the immediate area could be "sneakers" (Gross 1991). We recorded how much time individuals spent building and defending a redd to confirm our assumptions that redd observations more than 4 d apart were likely unique. To test this assumption we determined the proportion of redds detected more than once during our surveys with the assumption that if fish are not observed at a location where they were previously observed, the fish were no longer spawning.

RESULTS

Redd Surveys, Water Discharge, and Temperature

Between 2006 and 2012, we conducted 242 individual surveys on 197 d and recorded 921 redd observations (Table 1). We made observations at 687 unique redds based on our distance and time criteria. Most years we found that increases in discharge in the Logan River and Spawn Creek coincided with increased numbers of fish of the largest (>225 mm) size-class being observed in the study stream, which was assumed to represent the beginning of the spawning migration (weeks 13–14; Figure 2).

Across all years mean discharge in the Logan River declined prior to the end of the spawning period in Spawn Creek (Table 1; Figure 2). However, discharge in Spawn Creek was variable and showed no consistent pattern across years (Figure 3). In Spawn Creek water temperatures increased over the spawning period across all years, but each year the trend was disrupted by sharp decreases for short time periods (Figure 3). The mean daily water temperature per week at the onset of spawning was 7.9°C (mean daily minimum = 5.0°C, mean daily maximum = 11.9°C), and

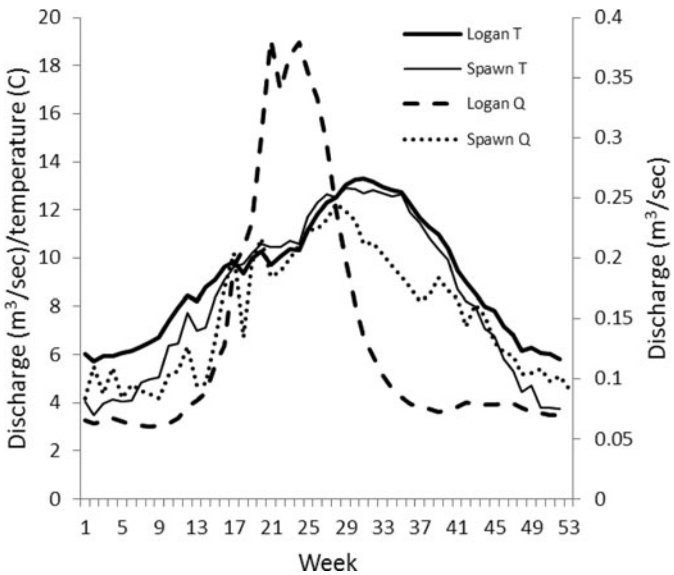

FIGURE 2. Mean weekly discharge (Q; m^3/s) and temperature (T; C°) in the Logan River and Spawn Creek, 2006–2012. Logan River discharge and temperature and Spawn Creek temperature are depicted on the left *y*-axis. Spawn Creek discharge is depicted on the right *y*-axis.

the mean number of redd observations per week was highest when temperatures reached 12–14°C (Figure 3). There was no relationship between the mean daily maximum water temperature during weeks 1–13 and year ($P = 0.9$, $R^2 = 0.003$).

Temporal Distribution of Spawning

The onset of spawning began as early as April 23 (week 17) and spawning continued through July 9 (week 28; Figure 3). The spawning period lasted between 38 and 71 d across all years, and the temporal distribution of spawning varied significantly between years (e.g., adjusted $P \leq 0.035$). Spawning occurred earlier and ended earlier in 2006, 2007, 2010, and 2012 when mean daily temperatures for weeks 1–13 were warmer than those in 2008, 2009, and 2011 (Figure 3). The median date for spawning across all years was the last week in May (week 22), but it ranged over 3 weeks from mid-May (week 20) to the first week in June (week 23; Table 1; Figure 3).

The most supported model describing the onset, median, and end of spawning included mean daily maximum water temperature in Spawn Creek during weeks 1–13 ($F = 130.4$, df = 5, $P \leq 0.0001$, $R^2 = 0.96$; Figure 4; Table 2). There was little support for the next best model, which included the mean daily maximum discharge in the Logan River (model weight = 0.022).

Spatial Distribution and Density of Redds

The mean distance between redds was 24.7 m (SD = 39.5; range, 0–246 m) across years. Each year most spawning occurred in single pairs with few large congregations, although there were one or two locations each year where multiple redds (3–5) were built within 5–10 m either over the same time (i.e., 1–2 weeks) or throughout the spawning period. In all years the index of dispersion ratio was >1 indicating a clumped distribution of redds (index range: 2.2–3.8, $\chi^2 > 20.5$, $P < 0.015$; Figure 5). The spatial distribution of redds differed significantly between 2011 and all other years ($P < 0.03$). There was an overall decreasing trend in the redd density index from 2006 to 2012 ($P = 0.02$, $R^2 = 0.69$), and reach 1 had a lower density of redds in all years compared with reach 2 except in 2011 (Table 1).

Prior to the study there were 11 existing beaver dams and during the study beavers built 15 more dams (Figure 1). Most of the new dams were built in the fall of 2010 or throughout 2011 (12 of 15 new dams) with only one new dam built in 2007 and two built in 2009 (both of which were on side channels). Two dams built in the fall of 2010 were the only ones present in reach 1 during the study (Figure 1). The new dams in reach 1 appeared to influence the spawning distribution in 2011 as we observed spawning on the newly deposited gravel where the stream entered these new ponds and downstream of the dams where outflow from the dams had created new channels (Figures 1, 6). In contrast, few redds were counted in these locations in previous years. By the 2012 spawning season, both of these dams were completely filled by sediment, and the dams had partially breached. A similar though less dramatic change in distribution occurred when a large beaver dam in the upper 500 m of the study area failed on May 8, 2008. Prior to this failure most of the flow in this area went through a series of beaver ponds and was distributed among multiple small channels. Following the dam failure, most of the stream flow was in a single stream channel with newly exposed gravel-sized substrate. An increase in the proportion of redds in the upper 500 m segment was evident in 2008 and 2009 (Figures 5, 6).

Spawning Activity at Redds

The mean number of individual Cutthroat Trout observed on redds ranged from two to five (mean = 2.2, SD = 0.46), and up to 10 other individuals (mean = 0.74, SD = 1.3) were observed adjacent to redds. Cutthroat Trout >150 mm made up 97% of all fish on redds, and 80% of all fish near redds. Fish of the same size-class appeared to pair together more often, as 67% of all redds had only a single pair of either 150–225-mm trout (40%) or a single pair of >225-mm trout (27%) present. The remainder of the redds were occupied by either mixed size-classes of fish and/or more than a single pair. No redds were occupied by only fish <150 mm.

Despite the mean time between redd surveys being 3.4 d across all years, most redds (85%) were only observed once (i.e., fish were only observed spawning at a location during one survey; mean observations of a redd = 1.4, minimum = 1, maximum = 11, SD = 1.02, $n = 687$). This pattern, which suggests fish occupy redds for very short durations, was further supported in 2009 and 2010 when the mean time between surveys was 2 d and a mean of 78% of redds were observed only once.

FIGURE 3. Mean number of Cutthroat Trout redds per week (grey bars), mean daily maximum water temperature (solid line; C°), and mean daily maximum discharge (dashed line; m^3/s) per week in Spawn Creek from 2006 to 2012. Gaps in discharge data are due to failures of data loggers.

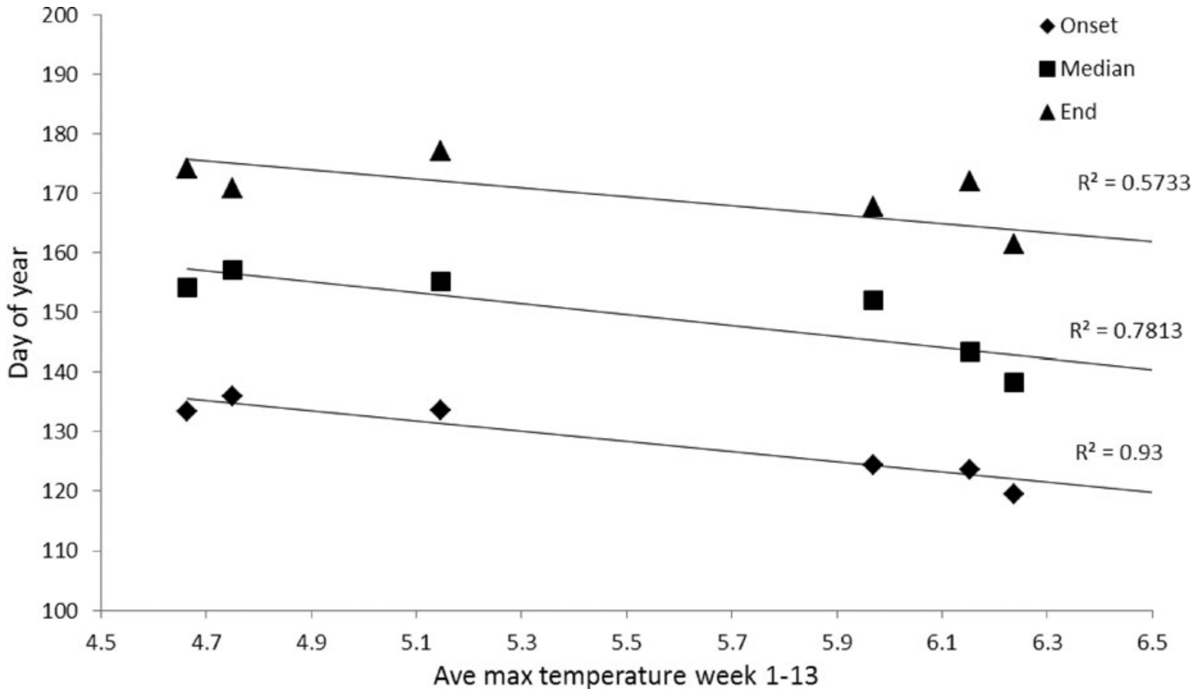

FIGURE 4. Cumulative proportion of Cutthroat Trout redds observed by week in Spawn Creek relative to stream distance from the mouth, 2006–2012.

DISCUSSION

Our study provides insight into the complexity of potamodromous trout spawning ecology, and provides a platform for further research. Furthermore, we consider our results to be a case study in identifying the diversity of life history patterns of Cutthroat Trout in headwater streams; understanding the diversity of such patterns can be used in directing local management actions (e.g., timing and intensity of livestock grazing; Peterson et al. 2010) as well as devising population and species conservation frameworks (Haak et al. 2010). This study is one of the first to investigate the spawning activity of stream-dwelling Bonneville Cutthroat Trout over several spawning seasons. We found Bonneville Cutthroat Trout spawning occurred over several months and generally involved two similarly sized fish that often spent less than 2 d spawning and guarding a redd. Our use of redd surveys for Bonneville Cutthroat Trout allowed us to assess the spatial and temporal variability in spawning activity and patterns, and thus provided insight into the diversity and factors associated with this important life history component.

Temporal Distribution of Spawning

We observed a protracted spawning period lasting 6–11 weeks, during which time relatively small numbers of redds were observed in any one survey (typically <10% of the total estimated number of redds each year per survey). The duration of spawning observed for Bonneville Cutthroat Trout is consistent with observations from other subspecies of potamodromous Cutthroat Trout (Gresswell et al. 1997; Muhlfeld et al. 2009). This wide temporal distribution of spawning activity may be an especially important adaptation of potamodromous trout in

TABLE 2. Top three models predicting the onset, median, and end of spawning. The top model (described in the first row) is an additive model with temperature in Spawn Creek during the first 13 weeks of the year (weeks 1–13). LR = Logan River, SC = Spawn Creek, ΔAIC_c = the difference between each model's AIC_c score and the top model's AIC_c score, Model weight = conditional probability for each model. Group defines onset, median, and end times of spawning.

Model description	df	AIC_c	ΔAIC_c	Model weight
SC temperature, weeks 1–13	5	128.6		0.957
LR discharge, weeks 1–13	5	136.1	7.5	0.022
SC temperature, weeks 1–13 × group	7	136.8	8.2	0.016

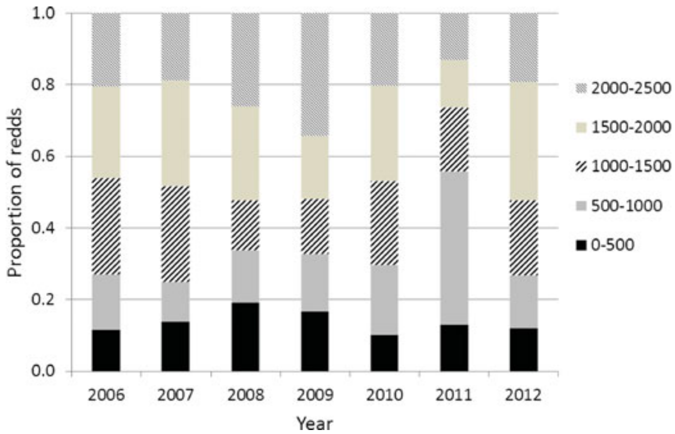

FIGURE 5. Relationship between the mean maximum daily water temperature (C°) during weeks 1–13 (prior to spawning) and the day of the year of onset (5%), median (50%), and end (95%) of Cutthroat Trout spawning in Spawn Creek, 2006–2012. [Color figure available online.]

small headwater streams; predation risk would be limited because the density of spawning fish, both daily and seasonally, would be reduced (sensu Quinn et al. 2003), and the complete loss of a brood year due to stochastic events such as flooding, landslides, and fires would be avoided (Hilderbrand and Kershner 2000; Budy et al. 2012).

The timing of redd construction changed among years with most of the variation occurring at the beginning of the spawning period rather than at the end. After week 27 (July 5), we never

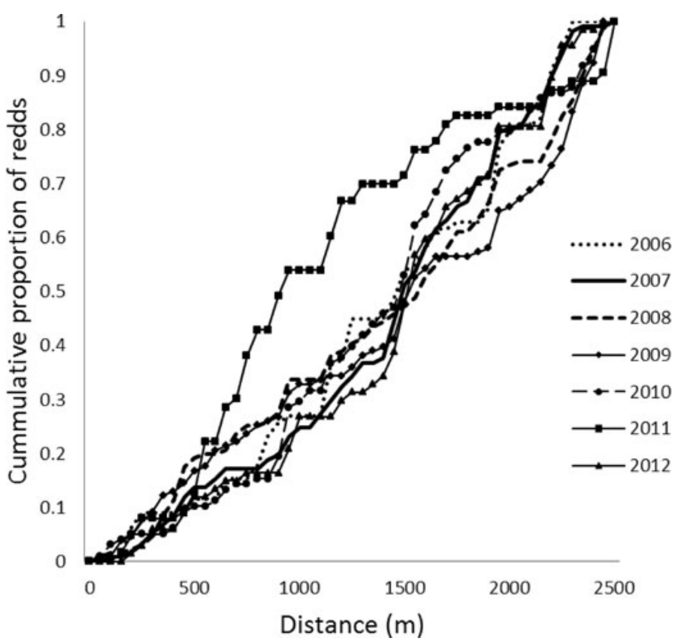

FIGURE 6. Proportion of all Cutthroat Trout redds observed by year and by 500-m segment of stream starting at the mouth (0–500) and moving upstream. Stream segments were lumped together for display but the spatial distribution of redds was assessed for spatial pattern (uniform, random, and clumped) using 250-m segments.

observed more than a single redd during a survey. However, we observed considerable differences in the intensity of redd construction from April 15 to May 15. Accordingly, we observed that the mean water temperature during weeks 1–13 was the best predictor of the onset, median, and end of spawning, whereas there was no correlation between spawn timing and discharge. In contrast, other studies have observed that Cutthroat Trout begin spawning on the descending limb of the hydrograph (Bjornn and Reiser 1991; Thurow and King 1994; Gresswell et al. 1997; Schmetterling 2000; DeRito et al. 2010; Budy et al. 2012). However, these studies either did not have or use temperature data well before spawning (i.e., January–March) or their studies were of short duration (1–2 years). Bonneville Cutthroat Trout in Spawn Creek began spawning on both the rising and falling limb of the hydrograph. This may be due in part to the spring-dominated, stable, and relatively low discharge in Spawn Creek, which likely differs from many headwater systems where hydrographs are much more variable in time (Poff and Ward 1989; Budy et al. 2012).

The onset of spawning within and between species of potamodromous trout has been correlated with stream temperature (Thurow and King 1994; Knapp and Vredenburg 1996); however, the specific temperature where spawning begins can vary considerably across populations (Bjornn and Reiser 1991). This variation suggests potamodromous trout may exhibit greater flexibility in the onset of spawning. The ability to spawn earlier in the spring permits a longer growing period for newly hatched young. In contrast, eggs laid late in the summer may not permit sufficient time for juvenile fish to grow to a size where they are likely to survive through the winter. This explains why spawning ended about the same time each year even though conditions in the spring were variable. Budy et al. (2012) found that spawning in other Logan River tributaries at higher elevations began a month later than at Spawn Creek, even though these tributaries were less than 20 km apart.

Spatial Distribution and Density

Redds were not evenly distributed throughout the stream, and the location of redds within the stream differed among years. Spatial clustering of salmonid redds within a year has been reported by others (Bozek and Rahel 1991; Magee et al. 1996; Isaak and Thurow 2006) at various scales (i.e., within and between drainages) and is attributed to the inherent patchy nature of suitable spawning habitat. Thus, in small tributary streams the location and extent of suitable spawning habitat is likely not only patchily distributed, but also changes between years because of a variety of variable disturbances operating at different temporal scales (Magee et al. 1996; Dunham et al. 2003).

In addition to the inherent patchy nature of spawning habitat it appeared that the relative density and distribution of redds was affected by beaver dams either being constructed or failing. Other researchers have demonstrated that beaver dams and frequent pond failures can create novel habitat for salmonids

(Pollock et al. 2007). In our study we found considerable redistribution of spawning following the failure of dams in the upper section of the study area in 2008 and 2009 and the creation of two large beaver dams in the lower reach of Spawn Creek in late 2010. The construction of two new dams in the lower reach in 2011 also appears to have increased the density of redds in the lower reach. However, field observations suggest spawning fish were only temporarily impeded from passing around the new dams, and further study suggests beaver dams do not regularly restrict Cutthroat Trout movement upstream or downstream in Spawn and Temple creeks (Lokteff et al. 2013). Other dams built during the study appeared to have less influence on the density and distribution of redds, possibly because they were built in the upper part of the study area where there were already a large number of dams. Also, they were smaller (lower crest height) and/or they were built on side channels and had less influence on flow.

Historically, beavers were likely to be more common in the Logan River watershed just as they were in much of North America (Naiman et al. 1988; White and Rahel 2008). In general, beaver dams in mountainous high gradient streams (e.g., the Logan River) reduce local gradient and capture sediment directly (Butler and Malanson 1995), and when they fail can produce stream reaches with lower gradients and more sediment than the surrounding stream reaches. Wood associated with beaver dams also adds hydraulic roughness to channels, which increases the capture and sorting of sediments and the availability of spawning locations (Buffington et al. 2004). Beaver activity can also create a wide variety of other habitats necessary for different life stages of trout (e.g., habitat complementation: White and Rahel 2008). Beavers are now again active in all the major spawning tributaries of the Logan River including Spawn Creek, and our study shows how responsive Cutthroat Trout spawning can be to newly created spawning areas resulting from beaver dam construction or failure. Observations during the fall and winter also suggest adult Cutthroat Trout overwinter in the beaver ponds, which could further promote more spawning in the upper reach (Jakober et al. 1998; Randall 2012).

The decreasing trend noted in our redd density index may be an indication that Bonneville Cutthroat Trout populations declined over the period of our study. Budy et al. (2007) monitored the population of Bonneville Cutthroat Trout throughout the Logan River watershed to determine the trend in overall population abundance and determined the population growth rate may have declined from 2001 to 2005. Further study has indicated this trend is still negative (P. Budy, unpublished data). Our findings support the conclusions of Budy et al. (2007), which are alarming since the Logan River Cutthroat Trout population is one of the largest and most intact Bonneville Cutthroat Trout populations with high densities of fish and relatively intact habitat. Spawning surveys could be a useful part of population assessment especially in more isolated Cutthroat Trout populations where population estimates may be costly due to low fish densities.

Spawning Activity on Redds

Bonneville Cutthroat Trout spawned with similarly sized fish, a pattern that could reflect a separation between fluvial and resident spawning fish (Bernard and Israelsen 1982; Budy et al. 2007). Bonneville Cutthroat Trout that demonstrate fluvial migratory patterns are known to enter tributary streams in the spring to spawn and are typically larger than resident Bonneville Cutthroat Trout (Bernard and Israelsen 1982; Meyer et al. 2003). Small fish ($<$150 mm) observed during our surveys likely represent mostly sexually immature fish (Downs et al. 1997) and or "sneaker" activity (Gross 1991). It is unknown what proportion of the spawning fish comprised resident forms, but we assume there was a mixture of all size-classes; however, this is an area that requires further study. We acknowledge that our surveys likely underrepresented spawning activity of small fish ($<$150 mm), which are more difficult to detect with visual surveys than are the larger size-classes. Although potamodromous trout can mature at sizes as small as 100 mm, the few studies that have specifically examined size at maturity of Cutthroat Trout have found the majority of sexually mature fish are $>$150 mm (Fleener 1952; Downs et al. 1997).

Our results indicated that Bonneville Cutthroat Trout spend very little time building and defending their nests. Schmetterling (2000) also observed that Westslope Cutthroat Trout *O. clarkii lewisi* spent a maximum of 2 d on a redd. This pattern of spawning activity likely reflects the low fecundity of potamodromous trout compared with semelparous anadromous salmonids (Quinn 2005). With lower fecundity, a shorter time spent on redds likely reduces predation risks for iteroparous, potamodromous trout (e.g., Stapp and Hayward 2002), thus enhancing lifetime reproductive success (Seamons and Quinn 2010). However, repeat spawning frequency is poorly understood in most potamodromous trout populations.

CONCLUSION

Maintaining diversity within a species is a central tenet of conservation (Lawton 1995; Rieman and Dunham 2000; Hilborn et al. 2003). For many potamodromous trout populations, knowledge of the diversity of life history patterns, including spawning ecology (e.g., Northcote and Lobon-Cervia 2008), is remarkably limited but not surprising given the challenges of sampling and monitoring potamodromous trout populations in headwater streams. However, identifying the within- and across-population diversity is critical for setting conservation targets to enhance species persistence (Haak et al. 2010; Schindler et al. 2010).

The results of our study illustrate a case study of the variability of one facet of life history for the population considered herein, and illustrate the need to identify how such diversity varies among other populations of potamodromous trout. Understanding such diversity may become increasingly important in identifying and prioritizing restoration and conservation strategies to enhance species persistence (Haak and Williams 2012; Segurado et al. 2013). Accurately characterizing life history patterns (e.g., spawning distribution and timing) can additionally help identify management strategies (e.g., angling regulations, cattle grazing) to minimize the detrimental effects on target populations (Gregory and Gamett 2009; Peterson et al. 2010). We understand that conducting redd surveys will be a challenge for spring-spawning potamodromous trout, but spring surveys are successfully carried out under a variety of conditions for other salmonids precisely because these data are so necessary to describe spawning diversity and improve management of the species.

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