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Abstract.–We completed a large-scale field experiment in four tributaries of the Logan River, Utah, where the largest metapopulation of imperiled Bonneville cutthroat trout (*Oncorhynchus clarkii utah*; BCT) persists. We documented the spatial and temporal distribution of BCT spawners, quantified substrate use versus substrate availability, and evaluated differences in hatch and emergence fry success between and among sites in relation to habitat characteristics. We observed considerable variability in the timing, magnitude, and duration of spawning among study areas (streams), in part as a function of a variable, multi-peaked hydrograph. Nevertheless, across study areas, > 70% of redds were constructed on the final descending limb of the hydrograph. Despite large differences in the amount of spawning substrate available, BCT utilized a narrow range of substrate and sizes (3 - 80mm) similar to that utilized by other sub-species of cutthroat trout albeit biased towards larger sizes. Water temperatures generally remained below the recommended range (6 – 17 °C) for spawning; however, the viability of this meta-population of BCT suggests the recommended temperature range for spawning is likely over-estimated for BCT and/or does not account for local thermal adaptation. Hatch and emergence survival varied from 43-77% and 39-65%, respectively, among streams, within-stream variability was substantial, and both survival rates declined significantly as a function of increased fine sediment concentrations. Egg development rates were nearly 50% longer in a high elevation tributary, where redd counts were also lowest. In high, mountain systems with short growing seasons, this incubation delay likely presents a significant growth disadvantage for age-0 trout. Our research enhances our understanding of BCT spawning ecology and early survival and provides critical information for aiding in the development of benchmarks for recovery of BCT. Effective conservation efforts for BCT should

be directed towards minimizing anthropogenic activities that result excess sedimentation in critical spawning tributaries.

In the last century, cutthroat trout (*Oncorhynchus clarkii*) have experienced large, range-wide reductions in distribution and abundance, due to the combined effects of habitat loss and fragmentation, competition and hybridization with nonnative species, disease, and overharvesting (Behnke 1992; Duncan and Lockwood 2001; Fausch 2008) and now, the additional effects of climate change (Williams et al. 2009). Today, the range of this species is extremely fragmented, with subspecies limited primarily to high elevation lakes and rivers (Behnke 2002). Consequently, of the 14 recognized subspecies of cutthroat trout, two are extinct, three are listed as threatened under the Endangered Species Act and the remaining subspecies are generally imperiled (Williams et al. 2009). Cutthroat trout prefer habitat with clear, cold water, sufficient stream flows, adequate stream side vegetation and habitat complexity and heterogeneity. Their criteria for spawning are thought to be quite specific and require a narrow range of substrate and hydrologic conditions (Hickman and Raleigh 1982; Bjorn and Reiser 1991; Behnke 1992). As a result of such stringent habitat requirements, cutthroat trout are particularly sensitive to human disturbances (e.g., livestock grazing, irrigation diversions, road construction); such sensitivity is likely most pronounced in the important spawning and highly variable early life-history stages (Duff 1988; Behnke 1992; Kershner 1995).

As spring spawners, typical in high mountain streams, the spawning and early life-history stages of cutthroat trout often correspond with the snowmelt and spring spates and are thus extremely difficult to study. While considerable information exists describing the spawning ecology and early life-history of other salmonids (e.g., salmon species; Beauchamp et al. 1994;

Isaak et al. 2007), significant gaps remain in our understanding of these life stages for Bonneville cutthroat trout (*Oncorhynchus clarkii utah*; BCT), the focus of this study (*see also* Hilderbrand 2003). As with other spring-time spawners, cutthroat trout spawning is thought to be initiated in response to seasonal changes, when environmental conditions reflect the transition from winter to spring with increasing water temperatures, increasing day length and receding flows from spring runoff (Behnke 1992). The environmental conditions that follow spring runoff (e.g., stable flows and warm water temperatures) are representative of high mountain rivers and provide ideal conditions for embryo incubation, fry emergence, and the rearing of juveniles (Behnke 1992; Kershner 1995).

While information describing the spawning ecology and early life-history of BCT is limited, a considerable body of literature provides insight into this critical stage for other species of cutthroat trout. Such studies include the description of physical characteristics of redds (e.g., Thurow and King 1994; Schmetterling 2000), the determination of age at maturity and fecundity of females (e.g., Downs et al. 1997), and the characterization of the relationship of habitat availability, habitat type, and substrate characteristics (e.g., percent fine sediment) to spawning distribution, and redd composition and redd densities (e.g., Magee et al. 1996; Joyce and Hubert 2004). However, to our knowledge, there has been a paucity of research focused on the spawning ecology of BCT, specifically, the quantification of the spawning distribution, spawning duration and timing, fecundity, egg incubation period, emergence time, and egg-to-fry survival of BCT. While restoring these imperiled cutthroat trout populations and protecting and preserving remaining healthy populations remains a top priority and concern (Budy et al. 2007; Williams et al. 2009), these data gaps challenge our ability to identify links between land management and cutthroat trout viability and thus limit the effective prioritization of conservation and recovery actions.

In addition to being difficult to quantify and sensitive, for most salmonids, these early life stages typically exhibit high rates of natural mortality for both incubating embryos and emergent fry (e.g., Knight et al. 1999; Kershner 1995). Furthermore, a wide suite of abiotic variables (e.g., water temperature, dissolved oxygen, water velocity, gravel size, percent fine sediment) can be influential in determining early survival (Hickman and Raleigh 1982; Bjorn and Reiser 1991; Kondolf 2000) and disturbances to habitat, via land-use activities, can alter these key physical factors. Hickman and Raleigh (1982) suggest that suitable spawning criteria for cutthroat trout in general include: 1) water temperatures between 6-17°C, with optimal embryo incubation at 10°C, 2) mean water column velocities suitable for embryo incubation between 0.11-0.90 m/sec, with optimal velocities between 0.30-0.60 m/sec, and 3) a range of substrate sizes for embryo incubation between 3-80 mm and optimal between 15-60 mm. The critical value for dissolved oxygen is not known at this time for cutthroat trout embryos but is assumed to be similar to that of adult cutthroat trout; optimal dissolved oxygen levels for adult cutthroat trout is >7mg/l at ≤15°C and ≥9 mg/l at >15°C. (Hickman and Raleigh 1992). Overall, the abundance of spawning gravel is perhaps one of the most critical and limiting factors for both successful redd construction and embryo incubation (Kondolf et al. 1991). Despite these general criteria, we know extremely little about how spawning criteria differ among the different species of cutthroat trout, species that are adapted to very different environments.

Land-use activities, such as livestock grazing, can have direct and indirect detrimental impacts on spawning, as redds are extremely vulnerable to trampling by livestock and/or fine sediment accumulation via bankside disturbances from grazing livestock (Gregory and Gamett

2009). Anthropogenic activities such as road construction and irrigation diversions also have the potential to negatively affect spawning either by fine sediment increases or redd dewatering (Hickman and Duff 1978; Kershner 1995). The effects of fine sediment accumulation can be significant, as sediment caps can form over redds and smother or suffocate incubating embryos and prevent fry emergence (Tappel and Bjornn 1983; Lisle 1989). Given the challenges of quantifying early life-history survival in the wild, lab-based studies have evaluated the relationship between some of these key abiotic variables and cutthroat trout survival at the early life stage in controlled laboratory settings. Young (1991), for example, used Colorado River cutthroat trout (*O. c. pleuriticus*) eggs in a lab setting to assess the degree to which different proportions of sediment impacted early survival and concluded that egg-to-fry survival declined in respect to the percent fine sediment 13.8 mm and greater in size. Similarly, while studying the effects of water temperature reduction on survival of cutthroat trout embryos fertilized at 7°C, Hubert and Gern (1995) found survival to the hatching stage to be lower for those embryos that were at an earlier development stage when water temperatures were reduced to 3°C. While these studies have advanced our knowledge of the early life stages of cutthroat trout in general, they have not identified mechanistic linkages between habitat quality and quantity, and survival as they occur in nature.

Within the context of native trout conservation and recovery, the overall goal of our research was to gain a better understanding of, and to identify, the underlying factors controlling the spawning ecology and early life stage survival of BCT. To meet that goal, we selected four study streams that captured the natural range of habitat characteristics and BCT redd densities, and focused our research on three primary objectives: 1) documenting the spatial and temporal distribution of BCT spawning among four study streams in the Logan River drainage, 2) quantifying substrate use versus substrate availability in four study areas in the Logan River drainage, and 3) evaluating differences in hatch and emergence fry success among and within study areas as a function of variation in habitat quality and quantity.

Methods

Study Area.--Our study area is located within the Logan River drainage, in northern Utah. The headwaters of the Logan River (2,600 m elevation) originate in the Bear River Mountains of southeastern Idaho, flowing approximately 64 river km southwest into the Logan Canyon of northern Utah, eventually draining into the Little Bear River in Cache Valley (see Budy et al. 2007 for a more detailed site description; Figure 1). The upper Logan River is characterized by a fairly unconfined valley, with moderate to steep gradient channels, coarse sediment loads, and discharge ranging from 0.24 to 7.57 m^3/s. The lower reaches of the river are typified by a dissected canyon, with lower gradient channels, smaller substrate, and fluctuations in discharge from 1.41 to 29.03 m^3/s. The Logan River's hydrograph is dominated by seasonal variation in flow, with snowmelt-driven high flows in the spring (April-May) followed by relatively stable base-flow conditions throughout the remainder of the year. As is typical across the Intermountain West, anthropogenic activities that potentially affect in-stream and riparian habitat in this area are concentrated over summer and early autumn seasons (June-October) and include livestock grazing, horseback riding, dispersed camping, and off-road motorized vehicle use. The Logan River drainage is home to one of the largest remaining metapopulatons of imperiled BCT. Densities in the Logan River drainage currently far exceed those documented for any other BCT population throughout the Bonneville Basin (Budy et al. 2007), making this population ideal for ecological research and also a conservation priority.

Based on a pilot study of all tributaries and a subset of mainstem areas in 2007, we *a priori* chose four study streams within the Logan River drainage to conduct our research (Table 1; Figure 1). Spawn Creek (1800 m in elevation) is a small, spring-fed, 1st-order tributary to Temple Fork, with perennial flows largely controlled by groundwater input, and mean summertime water temperatures of 9°C. Temple Fork (1745 m in elevation), also a perennial creek and a tributary to the mainstem of the Logan River, originates from Temple Springs with stream flow largely driven by spring runoff, with mean summertime temperatures of 10°C. Beaver Creek (2000 m in elevation) and Franklin Basin (2052 m in elevation) each originate from headwater springs in southern Idaho, with perennial stream flows dominated by spring-runoff, and mean summer water temperatures of 10°C and 8°C, respectively. Franklin Basin and Beaver Creek join to form the mainstem of the Logan River. We chose these sites because they represented a wide range of redd densities and habitat characteristics. In addition, Spawn Creek, anecdotally known as a primary area for BCT spawning (Fleener 1951; Bernard and Israelsen 1982), was the site of a recent restoration project, where a fenced exclosure was constructed to prevent cattle access to the entirety of the stream, except for the first 200 meters (Hansen and Budy 2011). In contrast, Temple Fork is susceptible to livestock grazing and the associated impacts of riparian grazing during the spring and summer months.

Redd Counts.--We refer to the sample areas within which we surveyed for redds, within each study stream, as "study areas." We initiated biweekly redd counts during the last week of April (2008) in each of our four study areas to document the spatial and temporal distribution of BCT spawning, and continued until spawning activity ceased in July (2008). These study areas constituted the majority of spawning activity as observed during the pilot study of 2007; redd counts were conducted throughout approximately 2.5 km of each stream, depending on stream topography. In each study area, we identified the presence and location of new redds and classified a redd as an area of cleaned gravel with a characteristic pocket and pillow shape (Hassemer 1993) and recorded the location of each redd using a hand-held Global Position

System unit. We also marked the vegetation near each redd with flagging tape to visually identify redds and prevent double-counting in subsequent surveys. In addition, all efforts were made to visually identify fish presence, whether directly on a redd or nearby.

Discharge and Water Temperature.--We used a combination of stage-height recorders and discharge measurements to project an hourly discharge value throughout spawning in each of our four study areas. In addition, we installed temperature data loggers in each of our four study areas; each logger was set to record temperature every hour.

Spawning Substrate Use and Availability.--To describe the physical characteristics of spawning substrate used by BCT in our four study areas, we measured the gravel composition along the width of each redd via 100-count Wolman pebble surveys (Wolman 1954). Given the conservation status of BCT and our desire to not disturb any redds, the gravel immediately adjacent to each redd was assumed to be of a similar composition to the gravel that was encountered by the spawning female prior to redd construction (Thurow and King 1994). To avoid bias, we measured a randomly selected subset of redds during different times (every one to two weeks as based on new redd activity) throughout the spawning season in each of our four study areas. All attempts were made to measure the gravel composition of an arbitrary but logistically feasible minimum of 30% of the total redds per study area.

We conducted 55 Wolman pebble surveys in each of our four study areas to characterize substrate availability (Wolman 1954). We delineated each study area (~2.5 km) into eleven 200-m reaches. Within each 200 m reach, we then defined twenty 10-m segments, parallel to stream flow. We then randomly selected five of the twenty transects in each reach to conduct a 100-count pebble survey. We assessed the distribution of available substrate in each study area within the range recommended for cutthroat trout spawning (i.e., 3-80mm; Hickman and Raleigh 1982), and calculated the proportion of substrate used versus the proportion available for each substrate size category.

Egg-to-Fry Survival Experiment

In order to assess differences in fry hatch and emergence success of BCT, we placed hatchery (local fluvial Bear Lake strain) brood-stock, eyed eggs (i.e., day 20 of development at time of installation) into slotted egg incubation boxes and buried the boxes in locations throughout the Logan River drainage on 1 July 2008. Mean daily water temperatures at the time of installation as recorded by the temperature loggers at the egg-box level were 11.4 °C in Spawn Creek, 9.1 °C in Temple Fork, 7.2 °C in Franklin Basin and 10.4 °C in Beaver Creek. Our primary goal was to install egg boxes in sites where spawning had been observed during the 2008 redd counts. Sites in which egg boxes were installed are referred to hereafter as “study sites.” To determine appropriate sites for egg box installation, we randomly selected a subset of redds in each of our four study areas, and selected nearby sites for our egg boxes, after assessing flow and substrate characteristics via a Wolman pebble survey.

In total, we installed 96 egg boxes throughout our four study areas, with 24 egg boxes installed in each study area; these 24 eggs boxes were separated into 4 study sites, with 6 egg boxes installed per study site. We used an egg box design based on Harris (1973) and modified according to Wood and Budy (2009). Each egg box (tubular in shape) was 10 cm long by 10 cm wide, and constructed of rigid, tubular polypropylene, with an approximate slot size of 1 mm by 5 mm to allow adequate delivery of water and oxygen, while still preventing the escape of sac fry and emergent fry. We equipped each egg box with lightweight, flexible polyethylene caps perforated with small holes (1.5 mm). Each egg box was filled with spawning sized gravel and 100 eyed, hatchery-fertilized BCT eggs (Utah Division of Wildlife Resources, Mantua Fish

Hatchery). The top 3-4 cm of each box was left empty to allow room for emerging fry. While we did not record the mean size or shape of the gravel used in the egg boxes, every effort was made to use similar sized gravel in each egg box. Each study site consisted of a T-post driven into the stream bed, with six egg boxes attached to the base of the T-post by wire, buried approximately 10-15 cm into the gravel to approximate the natural conditions of a spawning cutthroat trout (Smith 1941). In addition, each study site was equipped with a temperature data logger, buried at the depth of the egg boxes and set to record temperature every hour.

In order to assess survival to both the hatch and emergence stages and compensate for the differing water temperatures among the streams, we first used periodic temperature readings and a relationship between development times and mean temperatures from Merriman (1935) to predict hatch and emergence timing for each of our study sites. At the times predicted for the completion of each stage, we removed half of our egg boxes (n=3) at hatch and the remaining at emergence. If live eggs or live sac-fry were present when we checked the egg boxes at the actual installation site, we reinstalled those egg boxes to allow for further hatching or emergence development. After the majority of eggs had emerged, we transported all egg boxes back to the laboratory, where all fry and any remaining eggs were counted. Survival was calculated as the number of fry alive divided by the number of eggs at initiation.

Based on past research of the deleterious impacts of fine sediment accumulation on incubating embryos and developing fry, we evaluated for potential relative differences in fine sediment accumulation within the egg boxes for both the hatch and emergence stages. We collected the accumulated substrate from each egg box, and oven dried (110 °C for approximately 12 hours) and weighed fine sediment, as defined as less than 4 mm in diameter.

Relative differences in within egg box sedimentation were expressed as the proportion of fines standardized by the maximum weight of fines observed across all boxes.

Statistical Analysis

For our third objective, evaluating differences in hatch and emergence fry success among and within sites as a function of variation in habitat quality and quantity, we first used a single factor ANOVA test of hatch and emergence survival rates both among and within study areas. Across site tests compared the mean hatch or emergence survival (dependent variable) across each of four study areas. Within site tests compared the hatch or emergence survival (dependent variable) of each set of three egg boxes within each study area (n= 16). Second, as survival values range 0-1 (binomial link function), we used logistic regression to assess the relationship between mean hatch and emergence survival (dependent variables) as a function of fine sediment (independent variable) measured in each of the 16 study sites, across our four study areas (SAS Institute 2005). We standardized the proportion of fine sediment by the maximum weight of fines for both hatch (208 g) and emergence (291 g). Lastly, in order to assess whether sedimentation was more influential at earlier (hatch) or later (emergence) development stages, we compared the statistical significance between fine sediment accumulations at the hatch versus the emergence stage at all study sites, also using a single factor ANOVA.

We assessed statistical significance OF all tests using an *a priori* α-level of 0.05.

Results

Redd Counts.--We observed substantial variability in the timing, magnitude, and duration of BCT spawning among our four study areas during the 2008 spawning season. Notably, the onset of spawning in our two mid-elevation tributaries occurred a month earlier (mid-May) than in our high-elevation tributaries (mid-June; Figure 2). We identified the onset of spawning in our mid-elevation tributaries during May 2008 and first counted redds on 13 May at Spawn Creek and 15 May at Temple Fork (Figure 2). In Spawn Creek, spawning peaked on 19 May; we observed two peaks in spawning in Temple Fork, with the first peak occurring on 9 June and the second peak occurring on 23 June. In these stream areas, spawning continued through to the first week of July 2008, commencing on 7 July, with 128 and 213 redds counted in Spawn Creek and Temple Fork, respectively. In the high-elevation streams, the first redds were identified on 10 June and 16 June, respectively, at Franklin Basin and Beaver Creek (Figure 2), and spawning peaked in early July and was completed 15 July and 23 July for Beaver Creek, and Franklin Basin, respectively.

In total, from May to July 2008, we counted 388 BCT redds throughout tributaries: Temple Fork (85.2 redds/km), Spawn Creek (58.2 redds/km), Beaver Creek (7.6 redds/km), and Franklin Basin (8.0 redds/km). Redds identified in Beaver Creek and Franklin Basin contributed 12% to the total number of redds counted, whereas Temple Fork and Spawn Creek contributed 55% and 33%, respectively.

Discharge and Water Temperature

The winter of 2007/2008 was characterized by an above average snowfall in Logan River drainage, followed by three distinct peaks in the hydrograph during spring and summer months (USGS 2010). Similarly, we observed three distinct, well-spaced peaks in discharge in three of our four study streams (Figure 2). Characteristics of spawning (e.g., timing, magnitude, duration, frequency) appeared to be largely controlled by the respective hydrology of each stream.

In Temple Fork, spawning activity began with a mean daily discharge of 0.5 m^3/s on 15 May. Discharge at this time was extremely low, with flows receding from the stream's first large peak in discharge (Figure 2). As discharge increased to a second peak on 20 May, spawning ceased, but resumed again on a very small scale, following the second peak. Spawning increased rapidly after the third and final peak in discharge on 2 June, with 86% of the redds constructed after the third peak (Figure 2).

In contrast to Temple Fork, stream flows at Spawn Creek were considerably lower at the onset of spawning, with a mean daily discharge of 0.1 m^3/s. Spawn Creek is primarily spring-fed and no pronounced spring-time peaks in discharge were observed (Figure 2). However, we observed the onset of spawning during the lowest spring-time flow. Discharge gradually increased in Spawn Creek during the course of spawning, reaching a peak of 0.2 m^3/s on July 3.

Similar to the hydrology at Temple Fork, both high-elevation tributaries experienced three peaks in discharge. The magnitude of these peaks, though, was much larger than at Temple Fork. Beaver Creek experienced its first peak event on 20 May (Figure 2). Spawning at Beaver Creek started approximately 12 days after the second peak in discharge at a discharge of 0.9 m^3/s. Spawning activity was relatively low, but stable, as discharge increased to a third and final peak on 18 June. As discharge receded, spawning peaked, with 83% of the total redds created after the third peak.

Franklin Basin also experienced its first peak in discharge on 20 May, but with a considerably higher discharge (Figure 2), as compared to Beaver Creek. Spawning started on the descending limb of the hydrograph's second peak, at a discharge of 10.2 m^3/s, with one redd identified (Figure 2). As discharge increased to a third peak, spawning started to increase slightly, and six redds were observed before the peak. We counted zero redds during a redd count on 19 June, four days before the third and final peak. Seventy one percent of the total redds counted were identified after the last peak.

Daily mean temperatures during the spawning season were variable and fluctuated largely in response to flow (Figure 3). The daily range in water temperatures during the spawning season (May- July) ranged from 4.1-14.0 °C in Temple Fork, 3.7-16.7 °C in Spawn Creek, 3.1-10.9 °C in Franklin Basin, and 3.9-13.0 °C in Beaver Creek. In the colder, high elevation streams Beaver Creek and Franklin Basin, spawning activity appeared to increase after mean daily stream temperatures remained above 7 °C.

Substrate Use and Availability

Bonneville cutthroat trout used a relatively narrow range of substrate throughout our four study areas, but primarily within the range of 3-80 mm (Figure 4). We did observe a few exceptions to this pattern in Temple Fork and Spawn Creek, where fish used a small proportion of larger particles (≥ 90 mm; Figure 4). We quantified the percentage of substrate considered suitable for cutthroat trout spawning (i.e., 3-80mm; Hickman and Raleigh 1982) as approximately 55% in Temple Fork, 81% in Spawn Creek, 26% in Franklin Basin, and 60% in Beaver Creek.

Egg-to-Fry Survival Experiments

Egg-to-hatch survival (i.e., hatch survival rate) varied substantially both among and within our four study areas (Figure 5; Table 2). Egg boxes in Temple Fork and Beaver Creek supported high rates of hatch survival, with mean hatch survival rates of 77% and 74%, respectively. In contrast, mean hatch survival rates were lower in Spawn Creek and Franklin Basin, with 43% and 60% of eggs hatching, respectively (Table 2). Hatch survival rates were variable across our four study areas (*P*=0.12; Table 3). We also observed a large degree of spatial variability in hatch survival across sites within some, but not all, study areas (e.g., Franklin Basin (*P*=0.06*;* Table 3*)* and Spawn Creek (*P*=0.03*;* Table 3).

Similar to the pattern of hatch survival rates, emergence survival rates also varied among and within our four study areas (Figure 5). Emergence survival rates were relatively high in Temple Fork and Beaver Creek, with mean emergence survival rates of 65% and 57%, respectively (Table 2). Franklin Basin and Spawn Creek supported lower rates of emergence survival, with mean emergence survival rates of 41% and 39%, respectively. Despite this variability, mean study area emergence survival rates were not significantly different among the four areas (Table 3). Emergence survival rates were variable within individual study sites for both Franklin Basin (*P*=0.03*;* Table 3) and Spawn Creek (*P*=0.11*;* Table 3) study areas, ranging from 1-61% and 6-60%, respectively (Table 2).

We observed a relatively wide range of fine sediment accumulation within egg boxes throughout our 16 study sites, with many boxes having little accumulated sediment and a few being nearly full (Table 2). Across study areas fine sediment accumulation within egg boxes was lowest in study sites in Temple Fork and Beaver Creek and higher levels in some study sites throughout Spawn Creek and Franklin Basin. We observed a significant, negative relationship between survival, for both hatch and emergence, and fine sediment (Table 3; Figure 7).

Mean daily water temperatures during the course of the experiment were similar and close to the optimal temperature for cutthroat trout embryo incubation in all study areas except Franklin Basin. Mean daily water temperatures during the course of the experiment were 9.0 °C and 10.7 °C in mid-elevation tributaries, Temple Fork and Spawn Creek, respectively and 10.2 °C and 7.2 °C in high-elevation tributaries, Beaver Creek and Franklin Basin, respectively

(Figure 7). Mean daily stream discharge in general during the course of the egg-to-fry experiment was 0.3 m^3/s in Temple Fork, 3.7 m^3/s in Franklin Basin, 0.1 m^3/s in Spawn Creek, and 0.38 m^3/s in Beaver Creek.

Embryo developmental rates in study sites within the high-elevation tributary, Franklin Basin, were considerably later in comparison to our other study sites. Embryo development progressed rapidly in study sites at Spawn Creek and Beaver Creek, with hatching completed on 12 July, only 12 days after installation. Stream conditions in Temple Fork also supported rapid development, with hatching completed at 14 days after installation. In contrast, fry in Franklin Basin finished hatching 22 days after installation. Fry completed emergence on 28 July in Temple Fork, Spawn Creek, and Beaver Creek, only 28 days after installation, and a full 11 days before emergence completed in Franklin Basin (7 August).

Discussion

Although we observed BCT spawning during a similar time frame (e.g, May-August) as other subspecies of cutthroat trout, we also observed large variability in the onset, magnitude and duration of spawning in response to, in part, a unique, multi-peaked hydrograph. Cutthroat trout strategize to maximize fitness and survival of young in challenging mountain environments by spawning on the descending limb of the hydrograph, such that subsequent flow and water temperatures will be at near optimal conditions for embryo incubation and the rearing of young after hatch (Hickman and Raleigh 1982; Bjorn and Reiser 1991; Behnke 1992). For example, Thurow and King (1994) observed Yellowstone cutthroat trout (YCT; *O. c. bouvieri*) spawning on the descending limb of the hydrograph in Pine Creek, Idaho, and likewise, Schmetterling

(2000) noted that the spawning period of Westslope cutthroat trout (WSCT; *O. c. lewisi*) in four tributaries in western Montana occurred after a single peak flow event in May.

Despite the importance of strong annual cues, flexibility in spawn timing in response to a dynamic hydrograph is an evolutionarily robust life-history strategy that has been observed for other species of cutthroat trout. Accordingly we observed pronounced differences in the timing, magnitude, and duration of spawning between just our mid-elevation and high-elevation tributaries. Humboldt cutthroat trout (*O. clarkia*), for example, a closely related species to the Lahontan cutthroat trout (*O. c. henshawi)* in Nevada (Nelson et al. 1987) similarly demonstrated two discrete spawning periods following two discrete peak flow events in April and May, respectively. As such, we believe the variation we observed in the timing of BCT spawning among our four study areas may be explained, in part, by characteristics of the hydrograph. The spring and summer of 2008 represented a somewhat unique year for the Logan River, both spatially and temporally, with three peak flow events occurring from May-July (USGS 2010). More typically, the Logan River has either one, large snowmelt driven pulse or two smaller pulses, with the majority of spawning likely occurring on the descending limb of the final peak in the hydrograph. In this study, while we did observe spawning initiating in response to the first two peak flow events of the spring and summer, the majority of spawning was delayed until after the third peak flow event, when spawning conditions (e.g., water temperature, discharge) appeared closer to optimal conditions. Interestingly, in Spawn Creek, one of our small, first order study tributaries, the spring-runoff spate is insignificant in magnitude and the hydrograph demonstrates little variability due to perennial spring inputs. In this study area, BCT may be cueing into flows either at Temple Fork and/or the mainstem of the Logan River as they stage and migrate through to Spawn Creek (Figure 1) and/ or stream water temperature (e.g., Homel and Budy 2008; Seidel 2009).

Water temperature is also known to play an important role in cutthroat trout spawning (Behnke 2002), and notably, the temperature ranges we observed in our four study streams were considerably lower than spawning temperatures observed for other subspecies of cutthroat trout. In each of our four study streams, water temperatures were often below the recommended range for cutthroat trout spawning (e.g., 6 -17 °C; Hickman and Raleigh 1982) throughout the spawning season. Furthermore, in the coldest, high elevation streams, BCT appeared to delay spawning until stream temperatures remained above 7 °C. Thurow and King (1994) observed YCT spawning in a mean water temperature range of 10 - 14 °C, a minimum water temperature range of 4 - 9 °C, and a maximum water temperature range of 16 - 20 °C. In addition, the onset of spawning was not observed until mean daily temperatures were above 10 °C and minimum daily temperatures above 4 °C; however, they did not measure or report associated discharge. In this study, the unique multi-peaked hydrograph contributed to non-linear patterns of warming and cooling across the spring season, in contrast to a consistent pattern of warming along a descending limb of the hydrograph, and temperatures were colder than reported elsewhere during spawning. Given the extremely large size and viability of this meta-population of BCT (Budy et al. 2007), we suggest the recommended temperature range for spawning in the published Habitat Suitability Index for cutthroat trout in general (Hickman and Raleigh 1982) is likely over-estimated and/or does not account for local thermal adaptation (e.g., Keleher and Rahel 1996; Jensen et al. 2003).

While discharge and temperature may provide important cues for spawning, suitable substrate must be available for successful spawning, incubation and emergence (Kondolf and

Wolman 1993; Kondolf 2000). Tributary streams, such as those studied herein, often represent ideal spawning conditions including a high availability of suitable sized substrate (Bjornn and Reiser 1991; Knapp and Vredenburg 1996; Magee et al. 1996). While we documented BCT spawning over a large spatial scale, from mid-to-high elevation tributaries, the size range of substrate used was relatively narrow but still corresponded with the size range available. For example, Franklin Basin is dominated by a steep gradient and cobble-boulder sized substrate with limited suitable spawning gravel available. The spawning habitat that is available is sub-optimal, restricted to marginal areas along the bank and silty in composition; these areas along the bank are also highly susceptible to cattle intrusion during the spring and summer months (Seidel 2009; Hansen and Budy 2011). Our observed low redd counts appeared to coincide with the low abundance of available spawning substrate in Franklin Basin (and perhaps also colder stream temperatures; see above). These results confirm that even in systems where fish densities are high overall and habitat is near pristine, the local abundance of spring-spawning salmonids may be limited at the reproductive stage, if spawning substrate availability is low and/or stream conditions are unsuitable for the successful spawning and rearing of young (Magee et al. 1996; Knapp et al. 1998).

Despite differences in the amount of available spawning substrate among our four study areas, BCT appeared to primarily utilize substrate within the range recommended for cutthroat trout spawning in all four study areas (e.g., 3 - 80mm, Hickman and Raleigh 1982). BCT used substrate similar to that of WSCT (e.g., 0.07 - 50.8 mm, Magee et al. 1994; 6 – 110 mm, Schmetterling 2000) but of sizes greater than the range observed for Snake River spotted cutthroat trout (*O. c. [proposed] behnkei*; 2 – 20 mm; Joyce and Hubert 2004). The variability observed in spawning substrate use among subspecies of cutthroat trout may simply be a function of fish size (i.e., larger fish utilize large substrate) and/or available substrate.

While we made every effort to accurately identify the onset of spawning and the presence of redds, our study did have important and obvious limitations and constraints. Observer error can limit the accuracy and precision of redd counts, when counts are used as a technique to monitor adult fish populations (Dunham et al. 2001; Al-Chokhachy et. al 2005; Muhlfeld et al. 2006). The purpose of our redd counts, though, was not to monitor and/or estimate adult BCT populations, but rather, to provide critical information in furthering our understanding of the temporal and spatial distribution of BCT throughout the Logan River drainage. Nevertheless, observers may have underestimated the number of redds and/or the date of the onset of spawning, especially in our high-elevation study streams, where flow conditions were high and turbid into late June. However, we might expect that in years when the magnitude, frequency, and duration of peak flows events is smaller, flow and water conditions (i.e., turbidity levels) could potentially be suitable for spawning earlier in the spring and summer than what we observed in 2008. As such, our identification of the onset of BCT spawning in our four study areas may have been accurate, and the low density of redds observed in Franklin Basin and Beaver Creek may simply be a function of a shorter available spawning season, due to hydrologic stream conditions (e.g., Hickman and Raleigh 1982; Thurow and King 1994).

In addition to the constraints on our ability to identify the onset of spawning, it is important to understand the somewhat unavoidable limitations of estimating hatch and emergence survival even with a large-scale field experiment and substantial degree of effort. Our estimates of survival are likely an overestimation of survival under natural conditions. Incubating embryos, sac fry and emergent fry were protected, by a large degree, from both abiotic and biotic factors, such as scouring flows, predation (e.g., by sculpin, *Cottus bairdii*), and to a certain degree, anthropogenic impacts (e.g., trampling from recreationists and/or grazing livestock; Kershner 1995; DeVries 1997; Gregory and Gamett 2009). In contrast, some boxes may have experienced artificially high sediment accumulation based simply on small microhabitat differences in location within the artificial redd (see further discussion below). Despite these potential limitations, our estimates of BCT hatch and emergence survival provided an excellent description of the relative variability in early survival among a wide range of habitat conditions and provides novel information on a life stage for which there was little previously known.

In our experiments, we observed variability in hatch and emergence survival rates both among but also within our four study areas, especially throughout study sites in tributaries, Spawn Creek and Franklin Basin. Such variability is likely driven by important microhabitat site differences in intragravel conditions such as the proportion of fine sediment and other substrate characteristics (Bjorn and Reiser 1991). The negative relationship between salmonid early life-stage survival and fine sediment we observed herein has been firmly and mechanistically documented in the literature (e.g., Chapman 1988; Julien and Bergeron 2006). Further, using Colorado River cutthroat trout (*O. c. pleuriticus*) eggs in a lab setting, Young (1991) assessed the degree to which different proportions of sediment impacted early survival, concluding that egg-to-fry survival was highest with geometric mean particle sizes 13.8 mm and greater. Kondolf (2000) similarly highlights the importance of water flow through redds for the delivery of dissolved oxygen and the removal of metabolic waste. Fine sediment accumulation within the incubation gravel can greatly impede these critical and necessary processes and may explain the differences we observed in hatch survival in emergence survival in Franklin Basin. In contrast, in Spawn Creek, we actually observed a low mean hatch survival and a low mean amount of fine sediment in one of our four study sites, highlighting the role of other environmental conditions, perhaps outside of the egg boxes. Further, it is also important to note that the level of fine sediment we observed in our egg boxes may be a function of natural conditions, anthropogenic conditions, our egg box design, or some combination of the three. Regardless of the ultimate determinate of the proportion fines, the negative relationship we observed between fine sediment and hatch and emergence survival rates has important and obvious implications for land-use management and BCT conservation (e.g., McHugh et al. 2004). In systems or areas that are naturally near the upper limits for fine sediments, even a small degree of increase in sedimentation can have large effects on early survival. Based on these results, if protection of BCT is a management priority, efforts should be made to prevent excessive sedimentation in critical spawning streams.

In addition to fine sediment, water temperature also serves as a key physical factor that has a strong, mechanistic influence on salmonid early life-stage survival and embryo development. In our study, embryo development was delayed in the cold, high-elevation tributary, Franklin Basin, and fry emerged approximately 10 days later in Franklin Basin than in Temple Fork, Spawn Creek, and Beaver Creek. The relationship between delayed cutthroat trout embryo development and cooler and/or decreasing water temperatures has been documented extensively in the lab (e.g., Merriman 1935; Stonecypher et al. 1994; Hubert and Gern 1995), with Hickman and Raleigh (1982) recommending optimal water temperatures for cutthroat trout embryo incubation at 10 °C. Mean daily water temperatures in all study sites except Franklin Basin were close to the optimal temperature for embryo incubation, while in contrast, mean daily temperatures observed in study sites in Franklin Basin were on average at least 2 °C cooler over the course of the experiment (e.g., ~7 °C). Fry that emerge earlier in the summer may have a greater potential to reach the critical body size need to successfully survive winter, as opposed to fry that emerge later in the season and lack the body size and mass needed to endure the harsh winter conditions common in the Logan River drainage (Cerven 1973; Smith and Griffith 1994). Based on the results of our spawning surveys, as well as our egg-to-fry survival experiments, high-elevation tributary, Franklin Basin appears to be naturally less suited for both spawning and embryo incubation, relative to the conditions observed in the other three tributaries. These results have important implications for local restoration activities (Budy et al. 2007) and demonstrate a template for prioritizing conservation actions more broadly.

The conservation and recovery of imperiled, native fish species poses several significant recovery challenges. Specifically, identifying the life stage(s) most limiting for a given fish species and then prioritizing conservation efforts accordingly can be a complicated and challenging endeavor (e.g., Budy and Schaller 2007; Williams et al. 2009). Our study is one of few to quantify both the spawning ecology and early life-history survival of cutthroat trout via a large-scale, replicated field study. The variability we observed in the timing of BCT spawning, and redd densities appeared to be strongly linked to variation in in-stream habitat conditions (e.g., discharge, substrate), and as such, has important implications for the conservation and restoration of spawning habitat for BCT range wide. In addition, the results of our BCT egg-to-fry survival experiments highlighted the deleterious effects of fine sediment to hatch and emergence survival. By conducing this studying in a system where the quality and connectivity of habitat still supports a very large metapopulation of BCT, our research enhances our understanding of cutthroat trout spawning ecology and early survival and provides critical information for aiding in the development of benchmarks for the recovery and persistence of BCT in this as well as other systems.

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Table 1. Mean baseflow, mean width, length of survey reach and elevation of our four study streams of our four study streams. Mean baseflow calculated as the mean daily flows during baseflow conditions, August to October.

Study stream	Mean baseflow (m^3/s)	Mean width (m)	Length of survey reach (m)	Elevation (m)
Spawn Creek	0.11	1.85	2200	1800
Temple Fork	0.37	3.71	2500	1745
Beaver Creek	0.04	4.41	3000	2000
Franklin Basin	0.31	8.41	3000	2052

Table 2. Egg-to-fry survival rates (hatch and emergence), hatch and emergence times, and measurements of key abiotic variables for tributary sites. Daily mean temperature was calculated over the course of each study sites' respective hatch and emergence periods. Egg boxes were installed in all study sites on 1 July, 2008.

Site	Number of days to hatch ending	Mean hatch survival (%)	Mean water temperature (°C)	Mean fine sediment (g)	Number of days to emergence ending	Mean emergence survival (%)	Mean water temperature (°C)	Mean fine sediment (g)
Mid-Elevation Tributaries								
Temple Fork 1	14	65	8.99	26	28	42	9.45	34
Temple Fork 2	14	80	8.99	19	28	63	9.44	32
Temple Fork 3	14	84	8.51	22	28	84	8.99	36
Temple Fork 4	14	80	8.48	43	28	72	8.97	30
Spawn Creek 1	12	23	10.73	125	28	6	10.80	238
Spawn Creek 2	12	22	10.68	15	28	31	10.79	88
Spawn Creek 3	12	79	10.60	63	28	60	10.74	32
Spawn Creek 4	12	49	10.60	40	28	60	10.73	69
Mean		*60*	*9.70*	*44*		*52*	*9.99*	*70*
High-Elevation Tributaries								
Beaver Creek 1	12	67	10.18	26	28	61	11.21	49
Beaver Creek 2	12	74	9.95	22	28	44	10.36	58
Beaver Creek 3	12	75	9.91	29	28	65	10.28	91
Beaver Creek 4	12	81	9.86	16	28	58	10.23	49
Franklin Basin 1	22	21	6.98	141	38	1	7.50	291
Franklin Basin 2	22	62	7.04	56	38	48	7.65	124
Franklin Basin 3	22	75	6.65	85	38	61	7.09	117
Franklin Basin 4	22	83	6.39	25	38	55	6.67	55
Mean		*67*	*8.37*	*50*		*47*	*8.87*	*104*

Table 3. Results of statistical tests for BCT hatch and emergence survival. Across site tests compared the mean hatch or emergence survival at each of the four study areas. Within site tests compared the hatch or emergence survival (dependent variables) of each set of three egg boxes within each study area. See Methods for additional detail.

	Measurement	Statistical test	DF	F-statistic	P-value
Hatch stage survival					
	Across study sites	Single factor ANOVA	3, 12	2.44	0.12
	Temple Fork	Single factor ANOVA	3, 8	1.08	0.41
	Spawn Creek	Single factor ANOVA	3, 8	4.92	0.03
	Beaver Creek	Single factor ANOVA	3, 8	1.79	0.23
	Franklin Basin	Single factor ANOVA	3, 8	3.78	0.06
	Mean hatch fine sediment vs. mean hatch survival (all study sites combined)	Logistic regression	1	n/a	<0.001
Emergence stage survival					
	Across study sites	Single factor ANOVA	3, 12	1.38	0.30
	Temple Fork	Single factor ANOVA	3, 8	2.58	0.13
	Spawn Creek	Single factor ANOVA	3, 8	2.80	0.12
	Beaver Creek	Single factor ANOVA	3, 8	0.27	0.84
	Franklin Basin	Single factor ANOVA	3, 8	5.24	0.03
	Mean emergence fine sediment vs. mean emergence survival (all study sites combined)	Logistic regression	1	n/a	<0.001
Hatch vs. Emergence					
	Fine sediment	Single factor ANOVA	1, 29		0.20

Figure 1. Map of the Logan River drainage, in northern Utah. Study streams are highlighted and include mid-elevation tributaries, Temple Fork and Spawn Creek and high-elevation tributaries, Franklin Basin and Beaver Creek. The river flows from north to southwest.

Figure 2. Number of BCT redds counted (bars) and average daily discharge (line; m^3/s) during the 2008 BCT spawning season in Beaver Creek, Franklin Basin, Spawn Creek, and Temple Fork, from top to bottom.

Figure 3. Number of BCT redds counted (bars) and average daily temperature (line; °C) during the 2008 BCT spawning season in Beaver Creek, Franklin Basin, Spawn Creek, and Temple Fork, from top to bottom. Note changes in right and left y-axis scales.

Figure 4. Proportion of substrate used versus substrate available in Beaver Creek, Franklin Basin, Spawn Creek, and Temple Fork, from top to bottom. Substrate size was measured using a Wolman pebble count; sizes represent minimum size bins.

Figure 5. Percent hatch and emergence survival for study sites (from low to high elevation) in study streams Beaver Creek, Franklin Basin, Spawn Creek, and Temple Fork, from top to bottom. Dark bars represent percent hatch survival and gray bars represent percent emergence survival. The dashed line represents the mean survival, as averaged over hatch and emergence, per study stream. Please note that we did conduct two separate experiments to assess hatch and emergence survival separately, and therefore, while emergence survival appears to be higher than

hatch survival in two study sites in Spawn Creek, survival was estimated from two separate experiments for hatch and emergence. Error bars are 1 standard error.

Figure 6. Relationship between level of fine sediment, calculated as proportion of fines, standardized by the maximum weight of fines, and (A) percent hatch survival (logit(hatch probability) = -0.0110 * fine sediment + 1.220; Wald chi-square for slope = 86.1594, $P<0.001$) and (B) percent emergence survival (logit [emergence] = -0.0128 * fine sediment + 1.0647; Wald chi-square for slope = 151. 5350, $P<0.001$).

Figure 7. Mean daily temperatures in Spawn Creek, Beaver Creek, Temple Fork, and Franklin Basin during the course of the egg-to-fry experiment (1 July – 8 August). Minimum and maximum temperature thresholds refer to the temperature range recommended for cutthroat trout spawning. The optimal temperature line refers to the optimal temperature recommended for cutthroat trout embryo incubation (Hickman and Raleigh 1982).