Exploring the Spawning Dynamics and Identifying Limitations to the Early Life-History Survival of an Important, Endemic Fish Species

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Utah State University

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EXPLORING THE SPAWNING DYNAMICS AND IDENTIFYING LIMITATIONS TO THE EARLY-LIFE HISTORY SURVIVAL OF AN IMPORTANT, ENDEMIC FISH SPECIES

by

Sara E. Seidel

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER of SCIENCE

in

Fisheries Biology

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UTAH STATE UNIVERSITY
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2009
ABSTRACT

Exploring the Spawning Dynamics and Identifying Limitations to the Early-Life History Survival of an Important, Endemic Fish Species

by

Sara E. Seidel, Master of Science

Utah State University, 2009

Major Professors: Dr. Phaedra Budy and Dr. Brett Roper
Department: Watershed Sciences

For many native, imperiled salmonid species, the prioritization of recovery and conservation efforts hinges upon the identification of a species most limiting life stage. The early life-history stage can be a limiting life stage for fish, and given the importance of the reproductive stage to overall persistence, there is a need to better understand the spawning ecology and early life history of many salmonids. The Logan River, in northern Utah, contains one of the largest metapopulations of imperiled Bonneville cutthroat trout (BCT) throughout the Bonneville Basin. Little research has evaluated the temporal and spatial distribution of BCT spawning nor quantified their early life-history survival. In the summer of 2008, I documented the spawning ecology of BCT and quantified their early life-history survival via egg-to-fry survival field experiments in four tributaries to the Logan River. I observed considerable variability in the timing, magnitude, and duration of spawning between study streams, in part as a function of a variable, multi-
peaked hydrograph. I also conducted egg-to-fry survival experiments using incubation boxes and hatchery-fertilized, eyed cutthroat embryos and installed these boxes throughout my study streams. I found that survival was extremely variable within and among my study streams. For example, the variation I observed in survival appeared to be a function of fine sediment loads. Lastly, I observed that in the Logan River the timing of greatest intensity of both stream side and in-stream anthropogenic activities (e.g., livestock grazing, horseback riding) overlaps directly with the spawning and early life stages of BCT. Using my estimates of early survival, I revised a four-stage matrix population model for BCT in order to evaluate the hypothetical effects of anthropogenic impact on rearing areas. I determined that population growth rates are sensitive to perturbation at the egg-to-fry and fry to age-1 stages, and if even a small number of redds are destroyed through habitat degradation, a high degree of immigration of reproductively mature BCT is required to maintain the near-term persistence of this population. Future conservation efforts for BCT should be prioritized to protect areas where land-use activities are high during the sensitive spawning and early life-stage periods.
ACKNOWLEDGMENTS

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Sara E. Seidel
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INTRODUCTION

In the last century, the natural evolution of aquatic ecosystems, coupled with an increase in anthropogenic activities, has led to the fragmented distribution, and reduced density and abundance of native fishes worldwide (Griffith 1988; Liknes and Graham 1988; Behnke 1992). These population declines can be attributed to several natural and anthropogenic factors including: habitat loss and fragmentation, nonnative species introduction, hybridization with nonnative species, disease, and overharvesting (Allendorf and Leary 1988; Behnke 1992; Horan et al. 2000; Duncan and Lockwood 2001). The degree to which these factors impact native fish populations is particularly wide-ranging when considering life-stage specific responses to both natural and anthropogenic variation. For example, habitat loss and fragmentation via land-use activities such as river damming, irrigation diversions, and livestock grazing may impact the adult and juvenile life stages of a salmonid differently relative to the egg-to-fry-stage (Thurow et al. 1988; Schmetterling 2001; Allan 2004). Furthermore, fish abundance and distribution can be dynamic in response to naturally-occurring events, such as floods, fires, and drought (Kelsch 1994). As such, it is the combination of natural and anthropogenic events that pose the greatest risk to the biotic integrity and persistence of native fish populations.

Native fishes have experienced large declines in abundance and distribution throughout the western United States, where habitat loss and degradation has been pronounced in riparian ecosystems (Kauffman and Kreuger 1984). In particular, the cutthroat trout, *Oncorhynchus clarkii*, has experienced large, range-wide reductions in distribution, density, and abundance (Behnke 2002). Today, the range of this species is
extremely fragmented, with subspecies limited to high elevation lakes and rivers across the Great Basin, into portions of the Rocky Mountains, and Intermountain West, and southern portions of Canada and Alaska, in addition to coastal and interior regions of Washington, Oregon, and California (Behnke 2002). Cutthroat trout, as with many other native salmonid species, prefer high-quality habitat, complete with clear, cold-water, sufficient stream flows, adequate stream side vegetation, and habitat complexity and heterogeneity (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 perturbation (e.g., livestock grazing, irrigation diversions, road construction, river damming, timber logging). The imperiled state of many cutthroat trout subspecies has prompted their placement under state protection as species of special concern and/or federal protection as sensitive species. To date, conservation efforts towards restoring cutthroat trout populations have been prioritized towards: habitat restoration and/or improvement projects, exotic species eradication, native species translocation, and modified management of land-use activities (Harig et al. 2000; Shepard et al. 2002; Novinger and Rahel 2003).

While considerable information exists describing the spawning ecology and early life history of other salmonids (e.g., salmon species; Beland et al. 1982; Lorenz and Eiler 1989; Beauchamp et al. 1994; Geist and Dauble 1998; Isaak et al. 2007), there are significant gaps in our understanding of these life stages for Bonneville cutthroat trout (Oncorhynchus clarkii utah; BCT), the focus of this study. Despite these gaps, research has demonstrated that, similar to other cutthroat trout subspecies, BCT generally spawn during the spring and summer, with fry emerging in mid-late summer (Behnke 1992). As
with other spring spawners, cutthroat trout spawning is initiated in response to seasonal changes, where environmental conditions reflect the transition from winter to spring, with increasing water temperatures, increasing and receding flows from spring-runoff; the environmental conditions following 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). To date, studies examining the spawning ecology and quantifying early-life stage survival of BCT or cutthroat in general, include describing physical characteristics of redds (e.g., Thurow and King 1994; Schmetterling 2000), determining the age of maturity and fecundity of females (e.g., Downs et al. 1997), and defining the relationship of substrate to redd densities, as well as survival-to-emergence (STE; Young 1991; Weaver and Fraley 1993; Magee et al. 1996). To our knowledge, little research has focused on the spawning ecology of BCT throughout its range. In fact, very little research has quantified the spawning distribution, spawning duration and timing, fecundity, egg incubation period, emergence time, and egg-to-fry survival of BCT.

The continued persistence of cutthroat trout today may be due in part, to their innate ability to adapt to changing environmental and anthropogenic conditions (Lentsch et al. 1997). However, the need for biologists to better quantify the relationship between habitat characteristics and key life history stages, such as the spawning stage, is of utmost importance for the conservation of future, self-sustaining salmonid populations. Understanding the spawning ecology of an imperiled species, in light of natural and anthropogenic variation, serves as only the beginning in the prioritization of conservation efforts. To further prioritize conservation efforts for cutthroat trout species, such as BCT,
biologists need an in-depth understanding of the natural and anthropogenic mechanisms controlling and/or limiting survival at all life-stages, but particularly at the life-stages most variable and sensitive to natural and anthropogenic variation, such as the early life-stage.

While the degree of research quantifying the survival, growth, and habitat requirements of adult and juvenile cutthroat trout has been comprehensive (e.g., Fraley and Shepard. 2005; Sloat et al. 2001; Budy et al. 2007), our breadth of knowledge of the early life-stage of these species is limited. This life stage represents an additional gap in our knowledge, as the early life-history stage of fishes can often be the most vulnerable life stage, typically exhibiting high rates of natural mortality for both incubating embryos and emergent fry (Knight et al. 1999). The early life-stage is often the most sensitive and vulnerable to natural and human-induced perturbation. In addition to natural and anthropogenic impacts (e.g., drought, flood, livestock grazing, road construction), the early life-stages can be challenging to study, as a wide suite of abiotic variables (e.g., water temperature, dissolved oxygen, water velocity, gravel size, fine sediment) can be influential in determining survival (Hickman and Raleigh 1982; Bjorn and Reiser 1991; Kondolf 2000). Understanding the relationships among abiotic variables such as water temperature, dissolved oxygen, water velocity and substrate size to early life-stage survival is critical to the management of salmonid species, as these variables have the potential to affect survival through mechanistic links to embryo incubation and fry emergence (Beland et al. 1982). Furthermore, disturbances to habitat, via land-use activities, can alter these key abiotic variables and in the process, decrease survival at the early life stage. Biologists make every effort to prevent these potential impacts through
increased conservation efforts and the modification of land-use activities, but often the data required to make such conservation decisions is lacking.

Bonneville cutthroat trout, the species of focus in this study, are endemic to the Bonneville Basin, and are currently restricted to 35% of their native range, as the result of both natural and anthropogenic events (e.g., habitat loss, nonnative species introduction, overharvesting; Duff 1988; Behnke 1992; Hepworth 1997). Despite their status as a protected and endemic species, our ecological knowledge of BCT spawning and early life-stage survival is limited. The Logan River in northern Utah is home to one of the largest remaining metapopulations of imperiled BCT. Bonneville cutthroat trout densities in the Logan River are currently the greatest of any other documented BCT populations throughout the Bonneville Basin (Budy et al. 2007), making this population both ideal for ecological research and a conservation priority.

Given the importance of the reproductive stage to overall persistence, there is a need to quantify and better understand the spawning ecology (both spatial and temporal components) and early life-history stages of BCT. With our research, we strived to gain a better understanding of and to identify the underlying factors controlling the spawning ecology and early life-stages of BCT within the Logan River drainage. To do this, we selected 4 study streams that captured a range of habitat characteristics and BCT redd densities and focused our research to three primary objectives: 1) documenting the spatial and temporal distribution of BCT spawning in four study streams in the Logan River drainage, 2) evaluating differences in egg emergence success between sites, as related to variation in habitat and land-use activities, and 3) modeling the impacts of BCT redd
destruction via hypothetical habitat degradation, on the long-term population trend of BCT in a selected study stream, Temple Fork, as a case study.
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 rkm southwest into the Logan Canyon of northern Utah, eventually draining into the Little Bear River in Cache Valley (see Budy et al. 2007 for more site information; Figure 1). The upper Logan River is characterized by a fairly unconfined, flat valley, with high velocity flows (1.1 m$^3$/s) capable of transporting coarse sediment loads. The lower reaches of the river are characterized by a steep, dissected canyon, with relatively low velocity (0.63 m$^3$/s) and smaller substrate (personal observation). High, spring snowmelt (April-May) and relatively stable base flow conditions (August-October) characterize the river’s hydrograph, creating a hydrograph strongly dominated by seasonal variation in flow. Average summertime (May-August) temperatures range from 10°C in the headwaters to 13.5°C in the lower reaches of the river. Major tributaries in the Logan River drainage, relative to this study, include Temple Fork (1745 m in elevation) Spawn Creek (1st-order tributary to Temple Fork; 1800 m in elevation), Franklin Basin (2052 m in elevation) and Beaver Creek (2000 m in elevation) (Table 1). Franklin Basin and Beaver Creek come together to form the mainstem of the Logan River. The Logan River is home to three native fish species, including the mottled sculpin (Cottus bairdii), the mountain whitefish (Prosopium williamsoni) and the endemic Bonneville cutthroat trout; the lower reaches of the Logan River are dominated by introduced brown trout (Salmo trutta). In addition, anthropogenic activities in this area, including livestock grazing, horseback riding,
dispersed camping, and off-road motorized vehicle use, are concentrated over relatively short summer and fall seasons.

We a priori chose four study streams within the Logan River drainage to conduct our study (Table 1). These study streams included paired mid-elevation tributaries, Temple Fork and Spawn Creek, and paired high-elevation tributaries, Franklin Basin and Beaver Creek.
Beaver Creek. Spawn Creek is a small, spring-fed tributary, with perennial flows largely controlled by groundwater input, and average summertime temperatures of 9°C. Spawn Creek 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 2007; Hansen and Budy; in review). Tributary, Temple Fork, also a perennial creek, originates from Temple Springs with streams flow largely driven by spring-runoff, with average summertime temperatures of 10°C. Beaver Creek and Franklin Basin each originate from headwater springs in southern Idaho, with perennial stream flows dominated by spring-runoff, and average summertime temperatures of 10°C and 8°C, respectively.

Study Species

The native range of BCT once spanned throughout the Lake Bonneville Basin, encompassing regions of Wyoming, Nevada, Utah, and Idaho (Duff 1988; Hepworth et al. 1997). Bonneville cutthroat trout are listed as a sensitive species by the USFS and BLM and a species of special concern in the state of Utah, and are managed within geomorphic management units throughout the Bonneville Basin. Furthermore, BCT are currently managed under an interagency conservation agreement among Utah, Idaho, Nevada, and Wyoming (Lentsch et al. 1997), in which a primary objective is to determine baseline conditions for the reproductive and early life-history stage of BCT.

Within the Logan River drainage, Spawn Creek is anecdotally known as one primary area for BCT spawning (Fleener 1951; Bernard and Israelsen 1982; personal communication Brett Roper). While biologists recognize the importance of Spawn Creek
as a primary spawning and nursery area for BCT, these fish do occupy more than 25 km of the Logan River and its tributaries, and supplemental spawning areas must exist in order to support the large metapopulation of BCT within the Logan River drainage.

**Bonneville Cutthroat Trout Spawning**

To quantify the spatial distribution of BCT spawning in the Logan River drainage, we conducted pilot BCT spawning surveys during the summer of 2007 (May–July). We surveyed all running tributaries, in addition to several reaches along the mainstem of the Logan River, from Right Hand Fork (1698 m in elevation) to Franklin Basin (2052 m in elevation), encompassing more than 25 km, using topographic maps and GPS points from the US Forest Service (USFS) and the Utah Division of Wildlife Resource (UDWR) surveys citing potential spawning areas. Based on results from this pilot study, we then selected the paired sites of Temple Fork, Spawn Creek, Beaver Creek, and Franklin Basin for intensive study of BCT spawning ecology and early life-stage survival in 2008, because these sites represented a range of redd densities and habitat characteristics; these four sites will be referred to as our “study streams” throughout the paper. The areas in which we surveyed for redds within each study stream will be referred to as “study areas.”

**Redd Counts**

To determine the onset of spawning in each of our four study areas, we initiated biweekly redd counts during the last week of April 2008. In previous years, redd counts at Spawn Creek revealed the onset of spawning near the end of April/beginning of May. We selected a study area within each study stream to consistently survey for redds twice
a week (Table 1). These study areas constituted the majority of spawning as observed during 2007. With the respective onset of spawning in each study area, we continued our biweekly redd counts and identified the presence and location of new redds. We classified a redd as an area of cleaned gravel, with a characteristic pocket and pillow shape (Hassemer 1993) and marked the location of each redd using a hand-held Global Position System (GPS) unit. To visually identify redds, we also marked vegetation near each redd with flagging tape. In addition, all efforts were made to record fish presence, whether directly on a redd or nearby.

**Stage-Height Recorder Installation**

Based on previous monitoring, the onset of BCT spawning appears to be strongly linked to spring run-off within the Logan River (Fleener 1951; Bernard and Israelsen 1982). Therefore, one of our primary goals was to evaluate the relationship of site-specific discharge to the onset and duration of spawning activity in each of our four study areas. We developed a discharge and stage-height (water height) relationship for each of our four study areas, as to accurately predict daily discharge during the course of the spawning season. To ensure continuous monitoring of water height in our four study areas, we installed 1.5 m stage-height recorders (TruTrack) during the fall of 2007. We programmed each stage-height recorder to take a measurement of water height every hour.

**Discharge**

We measured discharge following the protocol of Harrelson et al. (1994), measuring discharge at the same cross-section of each stream during every survey. For
our smaller stream systems of Temple Fork, Spawn Creek, and Beaver Creek, we measured water velocity (m/s) and water depth (m) at 20 equidistant cross-sections along a transect, for a reading time of 40 seconds. In Franklin Basin, we measured water velocity and water depth at 30 equidistant points, for a reading time of 40 seconds, in order to most accurately determine discharge, given the stream’s large size. We measured discharge six times between October 2007 and August 2008 in each of our four study areas.

To predict site-specific discharge over the course of the spawning season in each site, we created site-specific scatter plots with stream discharge plotted against water height (as determined from the stage-height recorder during the time frame in which discharge was measured). We predicted daily discharge prior to spawning and throughout the entire spawning season in our four study areas based on an exponential trend line fit to each scatter plot and the corresponding exponential equation.

Temperature

To evaluate potential impacts of stream temperature on the timing, duration, magnitude and onset of spawning, we installed temperature loggers (Hobo pendant temperature loggers 64k) in each of our four study areas in July of 2007. We downloaded temperature recorders prior to spawning in late-April and at the conclusion of the summer in late-August.
Bonneville Cutthroat Trout Redd Characteristics

We conducted microhabitat surveys to quantify the physical characteristics of BCT redds in Spawn Creek and Temple Fork, measuring characteristics of redds of approximately 30% of the total redds per study area. To avoid bias, we measured a randomly selected subset of redds during different times throughout the spawning season in Spawn Creek and Temple Fork. We measured water velocity and water depths, using a Marsh-McBirney flow meter and top-setting wading rod, at a range of locations both within and beside each redd (Thurow and King 1994; Schmetterling 2000). Specifically, we measured water velocity at 0.60 times the depth of the water column (i.e., average water column velocity), along with water depth in the following locations: inside the redd pocket, directly upstream of the redd pocket, directly beside the redd pocket, near the beginning of the pillow, and at the crest of the pillow. In addition, we characterized redd dimensions by measuring the width and length of the redd pocket, and the pillow length of each redd. We also characterized the gravel composition directly beside each redd, by conducting 100-count pebble counts for each redd. The gravel directly beside 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). In total, we measured the physical characteristics of 61 redds in Temple Fork and 38 redds in Spawn Creek.
Table 1. Characteristics of our four study streams. Average baseflow (m³/s) calculated as the average daily flows (m³/s) during baseflow conditions, August-October.

<table>
<thead>
<tr>
<th>Study stream</th>
<th>Average baseflow (m³/s)</th>
<th>Average width (m)</th>
<th>Length of survey reach (m)</th>
<th>Elevation (m)</th>
<th>Spawning previously documented, Y/N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spawn Creek</td>
<td>0.11</td>
<td>1.85</td>
<td>2200</td>
<td>1800</td>
<td>Y</td>
</tr>
<tr>
<td>Temple Fork</td>
<td>*</td>
<td>3.71</td>
<td>2500</td>
<td>1745</td>
<td>Y</td>
</tr>
<tr>
<td>Beaver Creek</td>
<td>0.04</td>
<td>4.41</td>
<td>3000</td>
<td>2000</td>
<td>Y</td>
</tr>
<tr>
<td>Franklin Basin</td>
<td>0.31</td>
<td>8.41</td>
<td>3000</td>
<td>2052</td>
<td>Y</td>
</tr>
</tbody>
</table>

*=No reliable estimate available, but based on geomorphology, baseflow expected to be between Spawn Creek and Beaver Creek. Refer to hydrographs in Figure 5 for more information.

Egg-to-Fry Survival Experiment

We placed hatchery-reared, eyed cutthroat trout eggs into slotted egg incubation boxes, buried beneath the gravel, in 16 locations throughout the Logan River (Figure 2). We used an egg box design based on Harris (1973) but modified to quantify early life-stage survival for brown trout in the Logan River (Wood and Budy, in press). Each egg box was constructed using rigid, tubular polypropylene, with an approximate slot size of 1 mm x 5 mm, as to allow for the 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, secured with small plastic zip ties and perforated with small holes (1.5 mm in diameter).

We selected study sites in relation to current spawning activity in each site; our primary goal was to install egg boxes in sites where spawning had been observed during the 2008 redd counts. We will refer to sites in which egg boxes were installed 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. Installing egg boxes directly over or next to current redds would have been detrimental to incubating embryos of a protected species; therefore, we instead selected nearby sites, similar in flow and substrate characteristics. We measured water velocity and water depth along a transect at each potential study site, and assessed substrate composition by conducting 100-count pebble counts, as to ensure that physical characteristics were within the recommended range for cutthroat trout spawning and embryo incubation (Hickman and Raleigh 1982).

Figure 2. Study design for egg-to-fry experiments, with (A) schematic representation of study sites within one study stream, with the dashed line separating the number of boxes removed at the hatch stage and at the emergence stage, respectively and (B) schematic layout of study sites within each study stream, separated by mid-elevation tributaries and high-elevation tributaries.
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 in each study site (Figure 2). Each egg box was filled with spawning sized gravel, as recommended for cutthroat spawning (Hickman and Raleigh 1982) and incubated with 100 eyed, hatchery-fertilized cutthroat eggs (Utah State Division of Wildlife Resources Manuta Fish Hatchery), leaving the top 3 or 4 cm of each box empty, as to allow room for emerging fry. A 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, as to approximate the natural conditions of a spawning cutthroat trout (Figure 2; Smith 1941). In addition, each study site was equipped with a temperature logger (Hobo pendant temperature logger 64k), buried at the approximate depth of the egg boxes and set to record a temperature reading every hour.

Using periodic temperature readings and values derived in the literature (Merriman 1935), we predicted hatch and emergence timing throughout our study sites. In order to assess survival to both the hatch and emergence stages, we pulled half of our egg boxes ($n=3$) at hatch and the remaining at emergence (Figure 2). We transported all egg boxes back to our lab at Utah State University, where all fry and any remaining eggs were counted and preserved. Furthermore, to assess relative differences in fine sediment accumulation within our egg boxes, for both the hatch and emergence stages, we collected the accumulated substrate from each egg box, and dried ($110^\circ$C, for approximately 12 hours) and weighed all substrate <4mm.
Stage-Based Population Trend Model

The early life stage is an important and critical stage to the persistence of many salmonid populations, but data are often lacking, making it difficult to model near-term population growth. During our egg-to-fry study, we observed egg box destruction via cattle. Based on these direct impacts of anthropogenic activities, we modeled the degree to which perturbation (i.e., decreased survival at egg-to-fry stage) via hypothetical habitat degradation (e.g., recreational use, livestock grazing) impacted the near-term population growth rate ($\lambda$) at a tributary site, Temple Fork, as an example. We used our empirical estimates of emergence survival from our egg-to-fry experiments, combined with our redd count data, to evaluate the sensitivity of lambda to perturbation at the egg-to-fry stage. To do this, we revised a four-stage matrix population model (Hilderbrand 2003; McHugh 2006) and examined the potential impact of decreased survival at the egg-to-fry stage on $\lambda$, given empirical estimates of survival rates for stage-0, stage-1, stage-2, and stage-3+ BCT, as well as the observed near-term population growth rate ($\lambda$) at this tributary in the Logan River (Figure 3; Budy et al. 2007). Each of our four stages was developed based on age data for Logan River BCT, with stage-0, stage-1, stage-2, and stage-3+ representing age-0, age-1, age-2, and ages 3 and older, respectively. Length at stage-3+ was defined as >225mm and considered reproductively mature (Budy et al. 2009). For these fish, we used the following length-fecundity relationship derived from BCT sampled in the Logan River to estimate stage-3+ fecundity: $(4.96 \times 10^{-6}) \times TL^{3.26} \times \frac{1}{2} \times S_{ef}$, where TL represents total length measured in mm, $\frac{1}{2}$ denotes the fraction of eggs that are females (i.e., the sex ratio; Fleener 1951), and $S_{ef}$ denotes the survival rate from egg to fry. Given the baseline value of $S_{ef}$ (0.65), the net fecundity for stage-3+ was 75,
which represents the annual reproductive contribution to the fry stage (i.e., number of eggs surviving to fry) per adult female (Fig. 3).

After constructing our matrix model, we assessed the impact of increasing levels of redd destruction on egg-to-fry survival via multiple redd-destruction scenarios. We did not have data on the lengths of fish that created the redds surveyed in Temple Fork. Therefore, in order to calculate an average number of eggs-per-redd, we substituted the average length of stage-3+ BCT sampled during fish surveys in Temple Fork in 2008 (i.e., ~274mm) into our length-fecundity relationship (shown above) to obtain an average of 439 eggs-per-redd (Budy et al. 2009). The baseline conditions (i.e., before redd destruction) reflected the ratio of the number of eggs surviving to emergence (60780), based on our estimate of emergence survival (65%) and the total number of eggs for 100% survival (93507). We then projected a stable stage distribution and calculated the corresponding number of individuals in each stage class (stage-1, stage-2, stage-3+) relative to those in stage-0 (Figure 3). For this simple example, we assumed that habitat suitable for spawning was unsaturated (i.e., density independence), a constant environment, and that redd destruction affected only egg-to-fry survival.

We then manipulated the numerator of the ratio described above to reflect increasing degrees of redd loss. For example, to emulate destruction of 10 redds we subtracted 4390 eggs from our baseline total of 60780 eggs to get a new ratio reflecting 60% egg-to-fry survival (i.e., 56390/93507). Using a generalized reduced gradient method of optimization, we then solved for the level of immigration (consisting of new stage-3+ BCT) required to compensate for the redd loss and stabilize the near-term population growth rate at Temple Fork to \( \lambda = 1 \), calculated over a 5-yr projection interval.
We recognize and note that while a time period of five years is appropriate and realistic for management purposes, it is shorter than the time-period required to reach a stable age distribution. However, our goal was simply to capture the magnitude of population decline that could be possible due to the effects of hypothetical habitat degradation and the number of immigrants that would be required to stabilize that decline over a realistic time horizon for management, assuming that redd destruction affected only egg-to-fry survival and no other aspects of population structure.

**Statistical Analysis**

To test for statistically significant differences in redd characteristics among Spawn Creek and Temple Fork, we ran single factor ANOVA tests for all water velocity, water depth, redd dimension, and substrate measurements, using an α-level of 0.10. To test for statistically significant differences in redd characteristics within redds in Spawn Creek and Temple Fork, we ran 2-way t-tests for unequal variance for all water velocity, and water depth measurements, using an α-level of 0.10.

We compared across site variability in survival, based on mean study site-specific hatch and emergence survival rates using single factor ANOVA tests. In addition, we also compared within site variability in survival rates, based on mean study site-specific hatch and emergence survival, using single factor ANOVA tests. We assessed the statistical significance for all ANOVA tests using an α-level of 0.10. Furthermore, we used logistic regression analysis to evaluate the relationship between mean percent survival (hatch and emergence) and abiotic variables such as fine sediment and water temperature, using an α-level of 0.10. Lastly, we compare the statistical significance
between fine sediment accumulations at the hatch versus the emergence stage, using a single factor ANOVA test, at an \( \alpha \)-level of 0.10.

Figure 3. The baseline stage-structured life cycle model for BCT in the Temple Fork tributary of the Logan River, UT. Survival, as well as fecundity values for stage-3+ BCT, are depicted by arrows connecting stages (top). The life cycle model is also shown in matrix format (bottom). \( N_t \) represents the number of individuals in each stage at a given time step (initial condition values are shown), \( N_{t+1} \) represents the number of individuals at the next time step. The immigration vector \( I_t \) was augmented at stage-3+ using simulation, represented by an X, to determine the number of new, reproductively mature stage-3+ BCT immigrants that are required to compensate for increasing levels of redd destruction (i.e., lower emergence survival).
RESULTS

Redd Counts

General Observations

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 4). In total, from May-July 2008, we counted 388 BCT redds throughout tributaries, Temple Fork, Spawn Creek, Beaver Creek and Franklin Basin. 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 (Table 2).

Mid-Elevation Tributary Sites

We identified the onset of spawning in our mid-elevation tributaries during May 2008. We counted 13 redds on May 13 at Spawn Creek, and 13 redds on May 15 at Temple Fork (Figure 3; Table 2). Spawning continued through to the first week of July 2008, with 128 and 213 redds counted in Spawn Creek and Temple Fork, respectively. In Spawn Creek, spawning peaked on May 19, with 15 redds counted (Figure 4). We observed two peaks in spawning in Temple Fork, with the first peak occurring on June 9 and the second peak occurring on June 23; 31 redds each, were identified during the respective spawning peaks (Figure 4).
Figure 4. Number of BCT redds counted during the 2008 spawning season in tributaries, Beaver Creek, Franklin Basin, Spawn Creek, and Temple Fork, from top to bottom. Note changes in the y-axis scale.
Table 2. Timing, magnitude, and duration of BCT spawning, and mean daily water temperatures (°C) for the 2008 BCT spawning season, of our four study streams in the Logan River.

<table>
<thead>
<tr>
<th>Study stream</th>
<th>Onset of spawning</th>
<th>End of spawning</th>
<th>% of total redd count</th>
<th>Duration of spawning</th>
<th>Mean temperature (season average)</th>
<th>Temperature range °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temple Fork</td>
<td>5/15</td>
<td>7/7</td>
<td>55% (213 of 388)</td>
<td>54 days</td>
<td>4.98-9.17 (7.32)</td>
<td>4.1-14.04</td>
</tr>
<tr>
<td>Fork Creek</td>
<td>5/13</td>
<td>7/3</td>
<td>33% (128 of 388)</td>
<td>53 days</td>
<td>5.66-10.71 (9)</td>
<td>3.68-16.68</td>
</tr>
<tr>
<td>Franklin Basin</td>
<td>6/10</td>
<td>7/23</td>
<td>6% (24 of 388)</td>
<td>44 days</td>
<td>3.88-7.96 (7.27)</td>
<td>3.05-10.94</td>
</tr>
<tr>
<td>Beaver Creek</td>
<td>6/16</td>
<td>7/15</td>
<td>6% (23 of 388)</td>
<td>30 days</td>
<td>4.43-10.61 (9.24)</td>
<td>3.89-12.98</td>
</tr>
</tbody>
</table>

Table 3. Peak flow events and associated discharge characteristics of our four study streams in the Logan River during the 2008 BCT spawning season.

<table>
<thead>
<tr>
<th>Study stream</th>
<th>Date of 1st Peak (discharge-m³/s)</th>
<th>Date of 2nd Peak (discharge-m³/s)</th>
<th>Date of 3rd Peak (discharge-m³/s)</th>
<th>Average Discharge Range (m³/s)</th>
<th>Discharge Range (m³/s)</th>
<th>% of redds after final peak</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temple Fork</td>
<td>5/8 (0.85)</td>
<td>5/20 (1.28)</td>
<td>6/2 (0.84)</td>
<td>0.46-1.28 (0.60)</td>
<td>0.34-1.39</td>
<td>86%</td>
</tr>
<tr>
<td>Fork Creek</td>
<td>4/29 (0.1297)</td>
<td>5/9 (0.118)</td>
<td>n/a</td>
<td>0.09-0.15 (0.12)</td>
<td>0.08-0.38</td>
<td>100%</td>
</tr>
<tr>
<td>Franklin Basin</td>
<td>5/20 (17.1)</td>
<td>6/2 (15.91)</td>
<td>6/24 (13.71)</td>
<td>1.69-13.71 (7.37)</td>
<td>1.65-14.97</td>
<td>71%</td>
</tr>
<tr>
<td>Beaver Creek</td>
<td>5/20 (1.96)</td>
<td>6/4 (4.59)</td>
<td>6/18 (1.97)</td>
<td>0.34-1.97 (0.88)</td>
<td>0.33-2.44</td>
<td>83%</td>
</tr>
</tbody>
</table>

**High-Elevation Tributaries**

The timing of spawning was quite different between our mid-elevation tributaries and high-elevation tributaries. The first redds were identified on June 10 and June 16, respectively, at Franklin Basin and Beaver Creek (Figure 4; Table 2). We counted 23 redds throughout the duration of spawning (June 10-July 15) in Beaver Creek (Table 2); spawning peaked on July 1, with 7 redds counted (Figure 4). Similar to Beaver Creek, redd densities were extremely low in Franklin Basin, with a total of 24 redds counted from June 10-July 23 (Table 2).
Discharge

The winter of 2007/2008 was characterized by a heavier-than-normal snowfall in the Logan Canyon, subsequently resulting in not one, but three distinct pulses or peaks in the hydrograph during the following spring and summer months (http://waterdata.usgs.gov/nwis/rt). More typically, the Logan River has one, large snowmelt driven pulse, with the majority of spawning occurring on the descending limb of the hydrograph. In three of our study streams, we observed three distinct, well-spaced peaks in discharge (Figure 5). Subsequently, characteristics of spawning (e.g., timing, magnitude, duration, frequency) appeared to be largely controlled by the respective hydrology of each stream.

Mid-Elevation Tributary Sites

In Temple Fork, spawning activity was initiated in response to an average daily discharge of 0.52 m³/s on May 15; discharge at this time was extremely low, with flows receding from the creek’s first large peak in discharge (May 8 at 0.85 m³/s). As discharge increased to a second peak (May 20 at 1.28 m³/s), 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 (June 2 at 0.84 m³/s), with 86% of the redds constructed after the third peak (Table 3; Figure 5). Discharge fluctuated considerably during the spawning season, ranging from 0.34 m³/s to 1.39 m³/s. Average daily discharge throughout the duration of spawning was 0.60 m³/s (range, 0.46-1.28 m³/s; Table 3).

In contrast to Temple Fork, stream flows at Spawn Creek were considerably lower at the onset of spawning, with an average daily discharge of 0.09 m³/s. Spawn
Creek experienced only two spring-time peaks in discharge (Figure 5); the first peak occurred on April 29, with a discharge of 0.12 m$^3$/s, and discharge peaked again on May 9, at 0.12 m$^3$/s. We observed the onset of spawning on the descending limb of the hydrographs second peak; discharge gradually increased in Spawn Creek during the course of spawning, reaching a peak of 0.15 m$^3$/s on July 3. Compared to Temple Fork, discharge was far more constrained in Spawn Creek during the spawning season, ranging from a low of 0.08 m$^3$/s to a high of only 0.38 m$^3$/s. Average daily discharge during the spawning season ranged from 0.09 m$^3$/s to 0.15 m$^3$/s, with an average daily discharge of 0.12 m$^3$/s (Table 3).

High-Elevation Tributary Sites

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 May 20, at 1.96 m$^3$/s (Table 3; Figure 5). Spawning at Beaver Creek started approximately 12 days after the 2nd peak in discharge (June 4 at 4.59 m$^3$/s), at a discharge of 0.94 m$^3$/s (Table 3). Spawning activity was relatively low, but stable, as discharge increased to a 3rd and final peak on June 18 (1.96 m$^3$/s; Table 3). As discharge receded, spawning peaked, with 83% of the total redds created after the 3rd peak (Table 3). Discharge fluctuated on a relatively large scale in Beaver Creek, ranging from 0.33 m$^3$/s to 2.44 m$^3$/s throughout the duration of the spawning season, with an average daily discharge of 0.88 m$^3$/s (range, 0.34-1.97 m$^3$/s; Table 3).
Figure 5. Number of BCT redds counted (bars) and average daily discharge (line; m³/s) during the 2008 BCT spawning season in tributaries, Beaver Creek, Franklin Basin, Spawn Creek, and Temple Fork, from top to bottom. Note changes in left and right y-axis scales.
Franklin Basin also experienced its first peak in discharge on May 20, but with a considerably higher discharge of 17.1 m$^3$/s (Table 3; Figure 5), as compared to Beaver Creek. Spawning started on the descending limb of the hydrographs 2$^{nd}$ peak (June 2 at 15.91 m$^3$/s), at a discharge of 10.22 m$^3$/s, with one redd identified (Figure 5). As discharge increased to a 3$^{rd}$ peak, spawning started to increase slightly, with six redds before the peak. We counted zero redds during a redd count on June 19, four days before the 3$^{rd}$ and final peak (June 24 at 13.71 m$^3$/s). Seventy one percent of the total redds counted were identified after the last peak (Table 3). Flows in Franklin Basin represented the highest of our four sites during the spawning season, with discharge ranging from 1.64 m$^3$/s to 14.97 m$^3$/s. Average daily discharge ranged from 1.69 m$^3$/s to 13.71 m$^3$/s during the spawning season, with an average of 7.37 m$^3$/s (Table 3).

Temperature

Daily mean temperatures during the spawning season were variable and fluctuated largely in response to peak flow events, producing a rather unpredictable temperature regime. Mean daily temperatures ranged from 7.32°C and 9.04°C in mid-elevation tributaries, Temple Fork and Spawn Creek, respectively, to 7.27°C and 9.24°C in high-elevation tributaries, Franklin Basin and Beaver Creek, respectively (Table 2).

Bonneville Cutthroat Trout Redd Characteristics

We measured the physical characteristics of 38 BCT redds in Spawn Creek (30% of total redds counted) and 61 redds in Temple Fork (29% of total redds counted). We observed significant differences in water velocities and water depths among redds in Temple Fork and Spawn Creek, as measured at five points in or around the redd (Figure
Furthermore, in both Temple Fork and Spawn Creek, substrate composition, as measured beside redds, ranged from <4mm to 90mm in diameter, with all D values (e.g., D16, D50, D84) significantly different between redds at Temple Fork and Spawn Creek (Table 4).

In addition to among-site differences in redd characteristics, we also observed significant within-site differences in water velocity and water depth among redds in Temple Fork. Specifically, water velocity significantly decreased from above redds into the redd pocket, with an average velocity above the redd of 0.59 m/s (SD, 0.17; range, 0.27-1.03; Figure 6), and an average pocket velocity of 0.52 m/s (SD, 0.15; range, 0.07-0.83; Figure 6). Furthermore, water velocity increased significantly from the redd pocket, to the pillow crest (0.66 m/s; SD, 0.18; range, 0.00-0.99; Table 4). Water depth increased significantly from above the redd into the redd pocket, with an average water depth above redds of 14.98 cm (SD, 5.51; range, 3.81-30; Figure 6) and in the redd pocket, as 18.54 cm (SD, 6.03; range, 5.08-30; Figure 6). In addition, water depth decreased significantly from the redd pocket to the pillow crest, with an average water depth of 14.71 cm (SD, 5.55; range, 5.08-30; Figure 6) at the pillow crest.

In contrast to Temple Fork, average water velocities in redds at Spawn Creek did not follow a significant pattern (Table 4). Water depths, though, followed a similar pattern as observed in Temple Fork; in particular, water depth increased significantly from above redds into the redd pocket, with an average water depth of 11.24 cm (SD, 3.50; range, 6-18; Figure 6) above the redd pocket. Water depth from the pocket to pillow crest followed a decreasing pattern, with an average water depth of 14.13 cm (SD, 4.12; range, 8-26; Figure 6) in the pocket, to an average water depth of 9.55 cm (SD, 2.88;
range, 4-18; Figure 6) at the start of the pillow, ending with an average water depth of 8.82 cm (SD, 2.74; range, 4-18; Figure 6) at the pillow crest.

_Egg-to-Fry Survival Experiments_

We observed large variability in sac fry survival, both among and within our four study areas (Figure 7). Egg boxes in Temple Fork and Beaver Creek supported high rates of hatch survival, with mean hatch survival rates of 77% and 74%, respectively (Table 7). In contrast, mean hatch survival rates were lower in Spawn Creek and Franklin Basin, with 43% and 60% of fry hatching, respectively (Table 5). While hatch survival rates were variable across our four study areas, this variability was not statistically significant (Table 6). In respect to within-site variability in survival rates, we observed large spatial variability in sac fry survival at Franklin Basin, and to a lesser degree, in Spawn Creek (Figure 7). Hatch survival rates of individual study sites in Franklin Basin were variable and significantly different, ranging from 21%-83% (Table 5).

Similarly, variability in mean hatch survival rates among individual study sites in Spawn Creek were significantly different, ranging from 22%-79% (Table 5). In contrast, hatch survival rates were relatively homogenous and not significantly different across individual study sites at Beaver Creek and Temple Fork, with mean hatch survival rates ranging from 65%-84% in Temple Fork, and 67%-81% in Beaver Creek (Table 5). Similar to the pattern we observed in hatch survival rates, emergence survival rates also showed considerable variation among and within our four study areas (Figure 7).
Figure 6. Comparative box-and-whisker plots of average water velocity (m/s), and water depth (cm) in redd pocket, beside redd pocket, above redd pocket, at start of pillow and pillow crest, and redd dimension (cm) characteristics of 61 BCT redds in Temple Fork and 38 BCT redds in Spawn Creek. The lower and upper whiskers correspond to the 5th and 95th percentiles, respectively. The solid and dashed lines represent the median and mean, respectively, with outliers identified by dark circles.
Table 4. Results of single-factor ANOVAs and 2-way t-tests, testing differences between average water velocities (m/s), water depth (cm), redd dimensions (cm), and substrate (mm) among and within study streams, Temple Fork and Spawn Creek.

<table>
<thead>
<tr>
<th>Among study streams</th>
<th>Statistical test</th>
<th>Characteristic</th>
<th>Measurement</th>
<th>DF</th>
<th>F-statistic</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Single-factor ANOVA</td>
<td>Adjacent to pocket</td>
<td>Water velocity (m/s)</td>
<td>1, 91</td>
<td>25.97</td>
<td>&lt;0.0001</td>
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<td>Single-factor ANOVA</td>
<td>Above pocket</td>
<td>Water velocity (m/s)</td>
<td>1, 94</td>
<td>27.64</td>
<td>&lt;0.0001</td>
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<tr>
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<td>Pocket</td>
<td>Water velocity (m/s)</td>
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<td>17.59</td>
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<td>Start of pillow</td>
<td>Water velocity (m/s)</td>
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<td>Pillow crest</td>
<td>Water velocity (m/s)</td>
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<td>28.20</td>
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<tr>
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<td>1, 96</td>
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<td>1, 97</td>
<td>15.73</td>
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<td>Water depth (cm)</td>
<td>1, 97</td>
<td>27.64</td>
<td>&lt;0.0001</td>
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<tr>
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<td>Single-factor ANOVA</td>
<td>Pillow crest</td>
<td>Water depth (cm)</td>
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<td>37.13</td>
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<td>Pocket width (cm)</td>
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<td>Substrate</td>
<td>D84</td>
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<td>6.84</td>
<td>0.0104</td>
</tr>
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</table>

Within study stream:

Temple Fork:

<table>
<thead>
<tr>
<th></th>
<th>2-way t-test</th>
<th>Above pocket into pocket</th>
<th>Water velocity (m/s)</th>
<th>1, 114</th>
<th>-2.74</th>
<th>0.0071</th>
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<tr>
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<td>Water velocity (m/s)</td>
<td>1, 117</td>
<td>-2.54</td>
<td>0.0125</td>
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<tr>
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<td>Pocket to pillow crest</td>
<td>Water velocity (m/s)</td>
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<td>-5.14</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Start of pillow to pillow crest</td>
<td>Water velocity (m/s)</td>
<td>1, 115</td>
<td>-2.69</td>
<td>0.0083</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Adjacent to and above pocket</td>
<td>Water depth (cm)</td>
<td>1, 119</td>
<td>0.89</td>
<td>0.3783</td>
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<tr>
<td></td>
<td>2-way t-test</td>
<td>Above pocket into pocket</td>
<td>Water depth (cm)</td>
<td>1, 119</td>
<td>3.41</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td>2-way t-test</td>
<td>Pocket to start of pillow</td>
<td>Water depth (cm)</td>
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<td>3.85</td>
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<td></td>
<td>2-way t-test</td>
<td>Pocket to pillow crest</td>
<td>Water depth (cm)</td>
<td>1, 119</td>
<td>3.66</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Start of pillow to pillow crest</td>
<td>Water depth (cm)</td>
<td>1, 120</td>
<td>-0.15</td>
<td>0.8773</td>
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</tbody>
</table>

Within study stream:

Spawn Creek:

<table>
<thead>
<tr>
<th></th>
<th>2-way t-test</th>
<th>Above pocket into pocket</th>
<th>Water velocity (m/s)</th>
<th>1, 72</th>
<th>0.68</th>
<th>0.4988</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Pocket to start of pillow</td>
<td>Water velocity (m/s)</td>
<td>1, 73</td>
<td>-1.14</td>
<td>0.2565</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Pocket to pillow crest</td>
<td>Water velocity (m/s)</td>
<td>1, 65</td>
<td>-1.56</td>
<td>0.1225</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Start of pillow to pillow crest</td>
<td>Water velocity (m/s)</td>
<td>1, 69</td>
<td>-0.59</td>
<td>0.5952</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Adjacent to and above pocket</td>
<td>Water depth (cm)</td>
<td>1, 73</td>
<td>-0.65</td>
<td>0.5162</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Above pocket into pocket</td>
<td>Water depth (cm)</td>
<td>1, 74</td>
<td>3.47</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Pocket to start of pillow</td>
<td>Water depth (cm)</td>
<td>1, 66</td>
<td>5.61</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Pocket to pillow crest</td>
<td>Water depth (cm)</td>
<td>1, 64</td>
<td>6.62</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>2-way t-test</td>
<td>Start of pillow to pillow crest</td>
<td>Water depth (cm)</td>
<td>1, 74</td>
<td>1.14</td>
<td>0.2570</td>
</tr>
</tbody>
</table>
Mean emergence survival rates were relatively high in Temple Fork and Beaver Creek, with mean emergence survival rates of 65% and 57%, respectively (Table 5). Franklin Basin and Spawn Creek supported lower rates of emergence survival, with mean emergence survival rates of 41% and 39%, respectively (Table 5). Despite this variability, mean emergence survival rates were not significantly different among our four study areas (Table 6). Mean emergence survival rates were variable and significant among individual study sites in both Franklin Basin and Spawn Creek (Table 6), ranging from 1%-61% and 6%-60%, respectively (Table 5). We observed higher mean emergence survival rates among study sites in Temple Fork and Beaver Creek, ranging from 42%-84% and 44%-65%, respectively (Table 5).

We observed a wide-range of fine sediment accumulation within egg boxes throughout our 16 study sites. Fine sediment accumulation within egg boxes was relatively low in study sites in Temple Fork and Beaver Creek (Table 5). In contrast, we observed high levels of fine sediment in some study sites throughout Spawn Creek and Franklin Basin (Table 5). We observed a significant, negative relationship between survival, for both hatch and emergence, and fine sediment (Table 6; Figure 8).

On average, we observed a higher survival rate to the sac fry stage than to the emergent fry stage throughout our study sites; survival from hatch to emergence declined from 6-30% throughout the majority of our study sites. As a necessary artifact of our experimental design (see methods), we needed to conduct two experiments; as a result of our experimental design, mean emergence survival was higher than mean hatch survival in two of our 16 study sites.
Figure 7. Percent hatch and emergence survival for study sites (1, 2, 3, and 4) 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.
Table 5. Egg-to-fry survival rates (hatch and emergence), hatch and emergence times, and measurements of key abiotic variables for tributary sites. Daily mean temperature (°C) was calculated over the course of each study sites’ respective hatch and emergence periods.

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Installation Date</th>
<th>Date of Hatch</th>
<th>Average Hatch Survival (%)</th>
<th>Average Temperature °C</th>
<th>Average Fine Sediment (g)</th>
<th>Date of Emergence</th>
<th>Average Emergence Survival (%)</th>
<th>Daily Mean Temperature °C</th>
<th>Average Fine Sediment (g)</th>
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<tr>
<td><strong>Mid-Elevation Tributaries</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Temple Fork Site 1</td>
<td>7/1/08</td>
<td>7/14/08</td>
<td>65</td>
<td>8.99</td>
<td>26</td>
<td>7/28/08</td>
<td>42</td>
<td>9.45</td>
<td>34</td>
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<td>7/14/08</td>
<td>80</td>
<td>8.99</td>
<td>19</td>
<td>7/28/08</td>
<td>63</td>
<td>9.44</td>
<td>32</td>
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<tr>
<td>Temple Fork Site 3</td>
<td>7/1/08</td>
<td>7/14/08</td>
<td>84</td>
<td>8.51</td>
<td>22</td>
<td>7/28/08</td>
<td>84</td>
<td>8.99</td>
<td>36</td>
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<td>7/14/08</td>
<td>80</td>
<td>8.48</td>
<td>43</td>
<td>7/28/08</td>
<td>72</td>
<td>8.97</td>
<td>10</td>
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<td>7/12/08</td>
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<td>10.73</td>
<td>125</td>
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<td>10.80</td>
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<tr>
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<td>7/12/08</td>
<td>22</td>
<td>10.68</td>
<td>15</td>
<td>7/28/08</td>
<td>31</td>
<td>10.79</td>
<td>88</td>
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<tr>
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<td>7/1/08</td>
<td>7/12/08</td>
<td>79</td>
<td>10.60</td>
<td>63</td>
<td>7/28/08</td>
<td>60</td>
<td>10.74</td>
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<td>7/28/08</td>
<td>60</td>
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<td>52</td>
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<td><strong>High-Elevation Tributaries</strong></td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>Beaver Creek Site 1</td>
<td>7/1/08</td>
<td>7/13/08</td>
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<td>10.18</td>
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<td>7/28/08</td>
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<td>9.95</td>
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<td>7/28/08</td>
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<td>7/28/08</td>
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<td>91</td>
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<td>7/28/08</td>
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<td>10.23</td>
<td>49</td>
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<td>Franklin Basin Site 1</td>
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<td>7/23/08</td>
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<td>6.98</td>
<td>141</td>
<td>8/9/08</td>
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<td>7.50</td>
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<td>7/23/08</td>
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<td>7.04</td>
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<td>8/9/08</td>
<td>48</td>
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<tr>
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<td>9/8/08</td>
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<td>7.69</td>
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<td>6.67</td>
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<td><strong>Average</strong></td>
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<td>8.37</td>
<td>30</td>
<td>47</td>
<td>8.87</td>
<td>104</td>
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Table 6. Results of statistical tests for BCT hatch and emergence survival. Across site tests compared the average hatch or emergence survival at each of the 16 study sites, across our four study areas. Site-specific tests compared the hatch or emergence survival of each set of three egg boxes across our four study areas. In addition, we used logistic regression to assess the relationship between average hatch and emergence survival to the average level of fine sediment measured in each of the 16 study sites, across our four study areas. Lastly, we compared the average fine sediment collected at the hatch stage to the average fine sediment collected at the emergence stage for all study sites.

<table>
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<tr>
<th>Measurement</th>
<th>Statistical test</th>
<th>DF</th>
<th>F-statistic</th>
<th>P-value</th>
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<td>Across sites (average survival at all 16 study sites)</td>
<td>Single factor ANOVA</td>
<td>3, 12</td>
<td>2.44</td>
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<td>3, 8</td>
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<td>Single factor ANOVA</td>
<td>3, 8</td>
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<td>1.79</td>
<td>0.2262</td>
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<td>3, 8</td>
<td>3.78</td>
<td>0.0588</td>
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<td>Average hatch fine sediment vs. average hatch survival (all study sites combined)</td>
<td>Logistic regression</td>
<td>1, n/a</td>
<td>n/a</td>
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<td><strong>Emergence stage survival</strong></td>
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<td></td>
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<td>Single factor ANOVA</td>
<td>3, 12</td>
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<td>Single factor ANOVA</td>
<td>3, 8</td>
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<td>Average emergence fine sediment vs. average emergence survival (all study sites combined)</td>
<td>Logistic regression</td>
<td>1, n/a</td>
<td>n/a</td>
<td>&lt;0.001</td>
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<td><strong>Hatch vs. Emergence</strong></td>
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<td>Fine sediment</td>
<td>Single factor ANOVA</td>
<td>1, 29</td>
<td>0.1973</td>
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</table>
Figure 8. Relationship between level of fine sediment, calculated as a relative index of fines per study site 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).
Mean daily water temperatures (°C) during the course of the experiment were 9.01°C and 10.68°C in mid-elevation tributaries, Temple Fork and Spawn Creek, respectively (Figure 9; Table 7) and 10.17°C and 7.20°C in cooler high-elevation tributaries, Beaver Creek and Franklin Basin, respectively (Table 7). Mean daily water temperatures (°C) during the course of the experiment were close to the optimal temperature for cutthroat trout embryo incubation (10°C; Hickman and Raleigh 1982), with the exception of Franklin Basin, whereas mean daily water temperatures (°C) were far below the optimal range. We observed a significant negative relationship between temperature (°C) and hatch survival rates (logit(hatch probability) = -0.1325 * temperature + 1.7674; Wald chi-square for slope = 13.7482, P=0.002), and a nonsignificant relationship between temperature (°C) and emergence survival rates (logit(emergence probability) = 0.080 * temperature – 0.480; Wald chi-square for slope = 0.0528, P=0.8183).

Embryo developmental rates in study sites within high-elevation tributary, Franklin Basin were considerably delayed in comparison to our other study sites. Embryo development progressed rapidly in study sites at Spawn Creek and Beaver Creek, with fry hatching on July 12, only 11 days after installation (note embryos were 20 days into development at installation). Stream conditions in Temple Fork also supported rapid growth, with fry hatching on July 14, 13 days after installation. Fry in Franklin Basin hatched on July 22, approximately 20 days after installation. Fry emerged on July 27 in Temple Fork, Spawn Creek, and Beaver Creek, only 57 days after installation, and a whole 10 days before fry emerged in Franklin Basin (August 8).
Stage-Based Population Trend Model

Based on the results of our population model, population growth rates appear to be highly sensitive to perturbation at the early life stages (e.g., egg-to-fry, fry-to-year 1); population growth rates decreased predictably in response to increasing degrees of redd destruction (i.e., lower levels of egg-to-fry survival; Figure 10). In addition, in years...
when anthropogenic activities contribute to a lower egg-to-fry survival, a substantial rate of immigration of new, reproductively mature BCT is required to stabilize the long-term population trend in Temple Fork (Figure 10). For example, with the destruction of 10 redds, 17 immigrants are required to stabilize the average long-term population growth rate ($\lambda$) to 1 after 5 years; as the level of redd destruction increases to 130 redds destroyed, the immigration rate required to further stabilize the average long-term population growth rate increases to 1147 adults (Figure 10).

Figure 10. Number of redds hypothetically destroyed and corresponding population growth rates ($\lambda$), with number of immigrants referring to the number of new reproductively mature BCT required to immigrate into Temple Fork, per time step, in order to stabilize the average near-term population growth rate ($\lambda$).
DISCUSSION

The successful management and conservation of imperiled, native fish species requires a wide breath of knowledge concerning specific life-history strategies, in light of natural and anthropogenic variation (Wilcove et al. 1998; Fausch et al. 2002). The Logan River, in northern Utah, serves as a conservation priority, as well as an ideal system for studying the different life-stages of the endemic BCT, as this system supports one of the largest remaining known metapopulations of this sub-species (Budy et al. 2007). Within the context of BCT conservation, previous research in this system has investigated the interaction of BCT and exotic brown trout (Salmo trutta), (e.g., de la Hoz Franco and Budy 2005; McHugh and Budy 2005; McHugh and Budy 2006), quantified the vital rates and population trends of adult and juvenile BCT (Budy et al. 2007); and evaluated the effectiveness of passive stream restoration on ecosystem health and disease (Hansen 2007), providing a template for conservation and recovery planning range-wide.

However, BCT spawning ecology and early life history represents a critical gap in our knowledge and limits our ability to prioritize conservation efforts for BCT. Thus, the goal of our research was to document the spatial and temporal distribution of BCT spawning and identify key abiotic variables driving both spawning, and egg-to-fry survival within the Logan River Watershed. We documented BCT spawning over a large spatial scale, from mid-to-high elevation tributaries, and observed large variability in the timing, magnitude and duration of spawning in response to, in part, the unique, multi-peaked hydrograph of 2008. We also observed considerable variability in both egg-to-fry survival and developmental time to the hatch and emergence stages, suggesting the
significant role of abiotic variables at the microhabitat scale, such as water temperature and fine sediment, in determining the success of BCT early life stages.

Cutthroat trout have adapted life-history strategies at the spawning stage, as to maximize the fitness and survival of young in challenging mountain environments (Behnke 1992). This adaption is perhaps best demonstrated by their strategy of 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). Thurow and King (1994) observed Yellowstone cutthroat trout (YCT; Oncorhynchus clarkii 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; Oncorhynchus clarkii lewisi) in four tributaries in western Montana occurred after a single peak flow event in May. While we observed BCT spawning during a similar time frame as for other cutthroat trout sub-species (e.g., May-August; Magee et al. 1996; Knight et al. 1999; Meyer et al. 2003), the variability in the timing, magnitude, and duration of spawning was pronounced between our mid-elevation and high-elevation tributaries.

The among-site variation we observed in the timing of BCT spawning may be explained, in part, by significant differences in discharge during the spring and summer seasons. The spring and summer of 2008 represented a unique year for the Logan River, both spatially and temporally, with three peak flow events occurring from May-July (http://waterdata.usgs.gov/nwis/rt). In our high-elevation tributaries, discharge remained high and variable into late-June, with redd densities consistently low; in contrast, at our
mid-elevation tributary sites, peak flow events were smaller in magnitude, redd densities were higher, and flows started to recede and stabilize earlier in June. This variability in spawning, as the result of a dynamic hydrograph, has been observed for other cutthroat trout sub-species (e.g., Humboldt cutthroat trout (Oncorhynchus clarki sub-species); a sub-species of the Lahontan cutthroat trout (Oncorhynchus clarkii henshawi) in Nevada, Nelson et al. (1987)). In the latter, Nelson et al. 1987 hypothesized two discrete spawning periods occurred during 1938, following peak flow events in April and May, respectively. In the Logan River, while we did observe spawning starting 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 were most optimal. One important exception to this pattern occurred at our tributary study stream, Spawn Creek, a small, spring-fed tributary, demonstrating only a minor spring-runoff spate. We hypothesize that BCT are cueing into flows at Temple Fork and/or the mainstem of the Logan River, and by the time BCT reach Spawn Creek, these fish have already made a decision to spawn, despite the flow conditions at Spawn Creek (Homel and Budy 2008).

Discharge serves as only one environmental cue for the onset of salmonid spawning. Additional environmental cues, such as, water temperature and photoperiod (i.e., day length), are known to play important roles in the onset of cutthroat trout spawning (Behnke 2002). In contrast to other studies examining the relationship between water temperature and cutthroat trout spawning (e.g., Thurow and King 1994), temperature did not appear to be a strong environmental cue for the onset of BCT spawning in our four study streams; temperature likely served as a weaker cue due to the
multipeaked, protracted hydrograph in 2008 and/or the spring-fed nature of our study streams. Furthermore, temperature may simply not be as important a cue for BCT spawning in the Logan River, relative to other systems and other sub-species of cutthroat trout, as discharge and photoperiod are.

In 2008, BCT spawning in the Logan River appeared to be most largely initiated and controlled by discharge and photoperiod. In high-elevation tributaries, Franklin Basin and Beaver Creek, spawning was delayed, likely in response to high and variable flows, with the majority of spawning occurring after each tributary’s final peak flow event. When relating discharge in these high-elevation tributaries to the photoperiod, we observed the final peak flow event in each tributary occurring when day length was at its greatest. Spawning in these high-elevation tributaries was likely initiated in response to increasing day length, but on a very small scale, with very few redds observed; the majority of spawning was delayed until after the final peak flow event, when day length was actually decreasing, not increasing. In mid-elevation tributaries, Spawn Creek and Temple Fork, spawning appears to have also been initiated in response to increasing day length. In Temple Fork, spawning was largely controlled by both discharge and photoperiod, with spawning initiated as day length was increasing, and flows receding from the tributary’s first peak flow event. In both Spawn Creek and Temple Fork, the majority of spawning occurred as day length was increasing, with a relatively small degree of late spawning activity as day length was decreasing. While our findings suggest that discharge and photoperiod are indeed important cues for spawning, it is possible, as we observed in Franklin Basin and Beaver Creek, that spawning may be delayed beyond the time period in which day length is increasing and at its greatest, and
that the duration of spawning may be shorter, in response to high and variable flows, especially in high-elevation tributaries.

In addition to the differences we observed in the timing, duration, and density of BCT spawning, fundamental differences in habitat type do exist between our mid-elevation tributaries and high-elevation tributary, Franklin Basin and may explain the disparity we observed in redd densities. Tributaries often represent ideal conditions for spawning cutthroat trout, with a high availability of suitable sized gravels (Bjornn and Reiser 1991), and the use of tributaries for spawning has been well documented for many salmonids (e.g., Knapp and Vredenburg 1996; Magee et al. 1996; Schmetterling 2000). In the Logan River, however, high-elevation tributary, Franklin Basin, is dominated by cobble and boulder-type substrate, with a naturally low availability of suitable spawning habitat; the spawning habitat that is available is sub-optimal, restricted to marginal areas along the bank, and silty in composition, with these areas along the bank highly susceptible to cattle intrusion during the spring and summer months (personal observation). Beaver Creek is also a high-elevation tributary, but in contrast to Franklin Basin, contains a higher percentage of suitable sized spawning gravels for cutthroat trout (this study). Despite this high abundance of spawning gravels, BCT redd densities were lower during 2008 in Beaver Creek than observed during our pilot study in 2007; such year-to-year variability in redd densities in Beaver Creek appears to be a function of the significantly different hydrograph in 2007 relative to 2008. We found that despite a high abundance of suitable spawning gravels in Beaver Creek, BCT spawning activity in 2008 was significantly lower, as compared to our two mid-elevation tributaries, where in-stream flow conditions were more suited for successful spawning and a longer spawning
season. Our documentation of the temporal and spatial distribution of BCT spawning in the Logan River highlights the importance of discharge as a key abiotic variable and as an important ecological driver in the control and/or limitation of BCT spawning, as well as in the variability of spawning characteristics across mid and high elevation tributaries. The persistence of self-sustaining populations of spring-spawning salmonids in other watersheds may be limited at the reproductive stage, where spawning habitat availability is low, and flow conditions are unsuitable for the successful spawning and rearing of young (Magee et al. 1996; Knapp et al. 1998).

In addition to differences in the timing of spawning and density of redds, we also observed significant differences in redd characteristics (e.g., velocity, water depth) among redds within tributaries, Temple Fork and Spawn Creek. Notably, water depths were deeper and average water velocities were higher, both above and adjacent to redd pockets in Temple Fork. Average water velocities in both tributaries were within the range recommended for cutthroat trout spawning (Hickman and Raleigh 1982), but BCT in Spawn Creek spawned in average water velocities and water depths slightly lower than observed for both YCT (Thurow and King 1996), and WSCT (Schmetterling 2000), while still utilizing a similar range in substrate sizes. In contrast, average water velocities, water depths, and substrate used in Temple Fork were similar to those selected by other spawning cutthroat trout, with one notable exception. Thurow and King (1994) documented YCT spawning in deeper water depths, a disparity that may be explained by differences in available flow conditions and/or body size between BCT and YCT. By quantifying the microhabitat characteristics of redds for native, imperiled salmonid species, such as BCT, we can determine the need for restoration and/or stream
improvement projects aimed at increasing the amount of in-stream spawning habitat, and ultimately, the survival of embryos and fry throughout the early life-history stage.

Prior to this study, our knowledge of the early life-history stages of BCT, and our ability to obtain empirical estimates of survival, was limited. With our egg-to-fry survival experiments, we observed among and within site variability in hatch and emergence survival rates throughout 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 fine sediment that may be occurring naturally and/or as a result of anthropogenic impacts (Bjorn and Reiser 1991). The relationship between salmonid early life-stage survival and fine sediment has been firmly documented in the literature (e.g., Chapman 1988; Kondolf 2000; Julien and Bergeron 2006), identifying the mechanistic links of fine sediment to hatch and emergence survival. However, it is important to note here that the level of fine sediment we observed in experimental egg boxes may be a function of natural conditions, anthropogenic conditions, our egg box design, or some combination of all. While Harris (1973) noted that these types of egg boxes were sufficient in allowing adequate passage of fine sediment, in areas such as Franklin Basin and Spawn Creek, these boxes may serve as potential sediment traps. The notably lower levels of fine sediments in egg boxes in Temple Fork and Beaver Creek, though, suggest the high levels of fines we observed elsewhere was a function of site-specific natural and/or anthropogenic variation, not our egg box design. For example, the restriction of spawning habitat to areas naturally-silty in composition may explain why we observed such high levels of fines in study sites in Franklin Basin. In addition, while studying brown trout early life-stage survival in the
Logan River Watershed, Wood and Budy (in press) observed elevated levels of fines, with high box-to-box variability, within egg boxes at a single study site in Spawn Creek. Further, the level of fine sediment naturally occurring in Franklin Basin and Spawn Creek may further be amplified by anthropogenic activities. Regardless of the ultimate determinate of percent fines, the negative relationship we observed between fine sediment and hatch and emergence survival rates has important implications for the management of anthropogenic activities that may elevate the level of fine sediment entering a system (McHugh et al. 2004).

In addition to fine sediment, water temperature also serves as a key abiotic variable influencing salmonid early life-stage survival and embryo development. By monitoring temperature during the course of our egg-to-fry survival experiments, we were able to examine the effect of temperature on hatch and emergence times, as well as survival rates. While we did observe a statistically significant relationship between temperature and hatch survival rates, this relationship did not hold a large ecological significance. Conversely, water temperature appeared to have a large ecological significance on hatch and emergence times; we observed a considerable delay in embryo development in high-elevation tributary, Franklin Basin, as compared to our three other study streams. In particular, fry emerged approximately 10 days later in Franklin Basin than in Temple Fork, Spawn Creek, and Beaver Creek. The relationship between cooler water temperatures and delayed cutthroat trout embryo development has been studied extensively in the lab (e.g., Merriman 1935; Stonecypher et al. 1994; Hubert and Gem 1995), with Hickman and Raleigh (1982) recommending optimal water temperatures for cutthroat trout embryo incubation at 10°C. Mean daily water temperatures (°C) in study
sites within Temple Fork, Spawn Creek, and Beaver Creek were close to the optimal temperature for embryo incubation, suggesting that temperature is not limiting embryo development in these three study streams. In contrast, mean daily temperatures observed in study sites in Franklin Basin were on average at least 2°C cooler during the course of the experiment (e.g., ~7°C). The delay in embryo development we observed at Franklin Basin may have important implications for the ability of fry in this high-elevation tributary to reach the body size needed to successfully survive the overwintering stage. 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 (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, as relative to the conditions observed in Temple Fork, Spawn Creek, and Beaver Creek, an important implication consideration for prioritizing conservation actions.

It is important to realize that our estimates of hatch and emergence survival were estimated from a field experiment, where conditions were manipulated as a function of our experimental design. Our estimates of survival, therefore, 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., sculpin), and to a certain degree, anthropogenic impacts (e.g., trampling from recreationists and/or grazing livestock) (Kershner 1995;
DeVries 1997). As mentioned before, a few eggs boxes were impacted by cattle, and while these boxes were cracked and/or destroyed, hatch survival did not appear to be largely impacted. The egg boxes likely served as shield, sustaining the impacts from anthropogenic activities that an egg pocket would sustain in a natural redd. We did not observe any evidence of egg box destruction for boxes pulled at the emergence stage, and therefore, we do not suspect any escapement of emergent fry from our egg boxes.

Obtaining quantitative estimates of hatch and emergence survival, under natural conditions, is particularly challenging for researchers studying the vulnerable early life-history stage of fish. Specifically, it can be extremely difficult, if not impossible, to quantity the exact number of egg deposited per-redd, and the protected status of many salmonids prohibits disturbance of redds. Biologists often rely on length-fecundity relationships in predicting estimates of eggs-per-redd; developing a reliable model of length-fecundity, though, requires a large sample size, targeting a wide range of body lengths (Downs et al. 1997). If one wanted to evaluate sac fry and emergent fry survival from a natural redd, they would need to know (or have a good estimate) of the length of the female who created the redd, and for many studies, such data is not available. Furthermore, in order to assess emergence survival in particular, one must not only have a good estimate of the starting number of eggs, but also, a way to capture emerging fry. In recent years, various emergence traps have been developed for evaluating survival in artificial redds, with potential for such traps to be used on natural redds (e.g., Radtke 2008), but egg boxes buried within artificial redds serve as a more reliable method of evaluating survival in response to different abiotic variables (e.g., sediment, water temperature, dissolved oxygen, flow). By monitoring egg-to-fry survival via an egg box
experiment (lab or field), biologists can obtain critical data on the survival and
developmental rates of embryo and fry in response to varying levels of abiotic variables,
as well as in response to land-use activities.

Like many places in the Intermountain West, the potential for land-use activities,
such as cattle grazing, to negatively impact the vulnerable early life-stage survival of
BCT is substantial in the Logan River Watershed. During the spring and summer
months, anthropogenic activity is particularly high, with livestock grazing, horseback
riding, and ATV use often at their highest intensity during the same time periods of early
life-stages of BCT (personal observation). In particular, tributary Temple Fork is a
popular destination for summer recreational enthusiasts, as well as a primary grazing
allotment for cattle in the Logan River Watershed. While the time-frame over which
cattle are grazed on Temple Fork is actually very short (i.e., ~2 weeks), in 2008, cattle
grazing coincided directly with the spawning period, as well as the early hatch and
emergence periods of BCT. In fact, during the course of our egg-to-fry experiments,
some egg boxes were destroyed by cattle in Temple Fork. This overlap of anthropogenic
activity and BCT spawning and early life history has obvious and important implications
for population viability and persistence.

Population models can be an important management tool in simulating the effects
of natural and/or anthropogenic variation on near-and- long-term population trends for
fish species, especially those that are a conservation priority, such as many native
salmonids (Lande 1993). For example, in our study we manipulated the population
model in Hilderbrand (2003) as to model the impacts of BCT redd destruction via
hypothetical habitat degradation on the near-term population trend in tributary study
stream, Temple Fork, as well as the subsequent number of new reproductively mature BCT required to immigrate into Temple Fork. Due to our model design, there was a constant source of redd destruction, year-to-year; our model, therefore, functioned as an extreme sink for population growth. By simulating a constant source of redd degradation, our model projected near-term increases in growth, but in the long-term, growth will actually stabilize near 1, despite the number of new immigrants added. Nonetheless, we observed a strong, positive relationship between the number of reds destroyed and the number of new, reproductively mature BCT required to immigrate into Temple Fork and a strong, negative relationship between the number of reds destroyed and lambda (λ). Hilderbrand (2003) likewise determined that immigration, albeit only a small degree, was required to prevent population extinction of cutthroat trout, in light of environmental stochasticity. The results of our model were not surprising, given the documented vulnerability and sensitivity of type-III organisms, such as fish, to perturbation at the early life stages (Roberts and White 1992). Nevertheless, a key component to maintaining population persistence within a watershed network is network connectivity (Hilderbrand 2003), where the immigration of fish from a core population (e.g., mainstem of a river), to peripheral populations (e.g., tributaries), can supplement declining fish abundance or in the case of this study, stabilize the long-term population trend in light of decreased egg-to-fry survival. In many watersheds in the Intermountain West, immigration may be restricted due to the fragmented, isolated nature of many salmonid populations; in cases such as this, active measures may need to be taken to supplement declining populations in which immigration is prevented due to a lack of connectivity (e.g., translocation, reintroduction, habitat restoration, exotic species
removal). Such measures may also be appropriate in systems in which connectivity appears high, but immigration fails to be sufficient in stabilizing long-term population trends. While our simple population model does have limitations, as with any model, this approach does provide an important tool to aide in the management and prioritization of conservation efforts for species such as BCT.

Management Implications

The conservation and recovery of imperiled, native fish species poses several significant recovery challenges. Specifically, it can be extremely difficult to identify the limiting life stage for a given fish species and then prioritize conservation efforts accordingly (e.g., Budy and Schaller 2007). Our study is one of few to quantify both the spawning ecology and early life-history survival of cutthroat trout via a large-scale field study. The variability we observed in the timing of BCT spawning, redd densities, and redd characteristics appeared to be strongly linked to variation in the in-stream habitat conditions (e.g., discharge, substrate), and as such, has important implications for the future conservation and possible 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, as well as the potential for anthropogenic activities, such as livestock grazing, to directly (e.g., destruction of reds, increased mortality of embryos and/or fry) or indirectly (e.g., collapsed banks, increased fine sediment input) affect survival of cutthroat trout at the early life stage. Further conservation efforts for BCT at this early life stage may include implementing a delayed grazing schedule or constructing a cattle exclosure. By studying
the spawning ecology and early life history of BCT in a system where the quality and connectivity of habitat supports a very large metapopulation of BCT, our research provides critical information for aiding in the development of benchmarks for the recovery and persistence of BCT in other systems. In order to conserve and manage for self-sustaining populations of BCT range-wide, conservation efforts need to minimize anthropogenic activity during the critical timing of the spawning and vulnerable hatch and emergence periods of this important, endemic species.

The implications of this research are not limited to the management of BCT in the Intermountain West, but have much broader implications for the management and conservation of fish species worldwide. For example, we know that reproductive success is critical in maintaining population persistence, and by identifying key spawning areas, biologists can gain a greater ecological understanding of what factors are important for reproductive success, and ultimately, target and prioritize restoration activities accordingly. In addition, by locating key spawning areas, biologists can identify factors potentially limiting reproductive success (e.g., natural variation, anthropogenic variation, variability in spawning cues, variation in spawning habitat) and determine the relative contribution of such factors to both the spawning stage and early life-history stage. Ultimately, by evaluating the spawning and early life-history stages of a given fish species, biologists can prioritize conservation efforts to target the most limiting life stage or conversely, those life stages which contribute the greatest to the total fitness of the species.
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