

1 **A Study of the Spawning Ecology and**
2 **Early Life-History Survival of Bonneville Cutthroat Trout**

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

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

49

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

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

70 Isaak et al. 2007), significant gaps remain in our understanding of these life stages for Bonneville
71 cutthroat trout (*Oncorhynchus clarkii utah*; BCT), the focus of this study (*see also* Hilderbrand
72 2003). As with other spring-time spawners, cutthroat trout spawning is thought to be initiated in
73 response to seasonal changes, when environmental conditions reflect the transition from winter
74 to spring with increasing water temperatures, increasing day length and receding flows from
75 spring runoff (Behnke 1992). The environmental conditions that follow spring runoff (e.g.,
76 stable flows and warm water temperatures) are representative of high mountain rivers and
77 provide ideal conditions for embryo incubation, fry emergence, and the rearing of juveniles
78 (Behnke 1992; Kershner 1995).

79 While information describing the spawning ecology and early life-history of BCT is
80 limited, a considerable body of literature provides insight into this critical stage for other species
81 of cutthroat trout. Such studies include the description of physical characteristics of redds (e.g.,
82 Thurow and King 1994; Schmetterling 2000), the determination of age at maturity and fecundity
83 of females (e.g., Downs et al. 1997), and the characterization of the relationship of habitat
84 availability, habitat type, and substrate characteristics (e.g., percent fine sediment) to spawning
85 distribution, and redd composition and redd densities (e.g., Magee et al. 1996; Joyce and Hubert
86 2004). However, to our knowledge, there has been a paucity of research focused on the
87 spawning ecology of BCT, specifically, the quantification of the spawning distribution, spawning
88 duration and timing, fecundity, egg incubation period, emergence time, and egg-to-fry survival
89 of BCT. While restoring these imperiled cutthroat trout populations and protecting and
90 preserving remaining healthy populations remains a top priority and concern (Budy et al. 2007;
91 Williams et al. 2009), these data gaps challenge our ability to identify links between land

92 management and cutthroat trout viability and thus limit the effective prioritization of
93 conservation and recovery actions.

94 In addition to being difficult to quantify and sensitive, for most salmonids, these early life
95 stages typically exhibit high rates of natural mortality for both incubating embryos and emergent
96 fry (e.g., Knight et al. 1999; Kershner 1995). Furthermore, a wide suite of abiotic variables (e.g.,
97 water temperature, dissolved oxygen, water velocity, gravel size, percent fine sediment) can be
98 influential in determining early survival (Hickman and Raleigh 1982; Bjorn and Reiser 1991;
99 Kondolf 2000) and disturbances to habitat, via land-use activities, can alter these key physical
100 factors. Hickman and Raleigh (1982) suggest that suitable spawning criteria for cutthroat trout
101 in general include: 1) water temperatures between 6-17°C, with optimal embryo incubation at
102 10°C, 2) mean water column velocities suitable for embryo incubation between 0.11-0.90 m/sec,
103 with optimal velocities between 0.30-0.60 m/sec, and 3) a range of substrate sizes for embryo
104 incubation between 3-80 mm and optimal between 15-60 mm. The critical value for dissolved
105 oxygen is not known at this time for cutthroat trout embryos but is assumed to be similar to that
106 of adult cutthroat trout; optimal dissolved oxygen levels for adult cutthroat trout is >7mg/l at
107 $\leq 15^{\circ}\text{C}$ and ≥ 9 mg/l at $>15^{\circ}\text{C}$. (Hickman and Raleigh 1992). Overall, the abundance of spawning
108 gravel is perhaps one of the most critical and limiting factors for both successful redd
109 construction and embryo incubation (Kondolf et al. 1991). Despite these general criteria, we
110 know extremely little about how spawning criteria differ among the different species of cutthroat
111 trout, species that are adapted to very different environments.

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

115 2009). Anthropogenic activities such as road construction and irrigation diversions also have the
116 potential to negatively affect spawning either by fine sediment increases or redd dewatering
117 (Hickman and Duff 1978; Kershner 1995). The effects of fine sediment accumulation can be
118 significant, as sediment caps can form over redds and smother or suffocate incubating embryos
119 and prevent fry emergence (Tappel and Bjornn 1983; Lisle 1989). Given the challenges of
120 quantifying early life-history survival in the wild, lab-based studies have evaluated the
121 relationship between some of these key abiotic variables and cutthroat trout survival at the early
122 life stage in controlled laboratory settings. Young (1991), for example, used Colorado River
123 cutthroat trout (*O. c. pleuriticus*) eggs in a lab setting to assess the degree to which different
124 proportions of sediment impacted early survival and concluded that egg-to-fry survival declined
125 in respect to the percent fine sediment 13.8 mm and greater in size. Similarly, while studying the
126 effects of water temperature reduction on survival of cutthroat trout embryos fertilized at 7°C,
127 Hubert and Gern (1995) found survival to the hatching stage to be lower for those embryos that
128 were at an earlier development stage when water temperatures were reduced to 3°C. While these
129 studies have advanced our knowledge of the early life stages of cutthroat trout in general, they
130 have not identified mechanistic linkages between habitat quality and quantity, and survival as
131 they occur in nature.

132 Within the context of native trout conservation and recovery, the overall goal of our
133 research was to gain a better understanding of, and to identify, the underlying factors controlling
134 the spawning ecology and early life stage survival of BCT. To meet that goal, we selected four
135 study streams that captured the natural range of habitat characteristics and BCT redd densities,
136 and focused our research on three primary objectives: 1) documenting the spatial and temporal
137 distribution of BCT spawning among four study streams in the Logan River drainage, 2)

138 quantifying substrate use versus substrate availability in four study areas in the Logan River
139 drainage, and 3) evaluating differences in hatch and emergence fry success among and within
140 study areas as a function of variation in habitat quality and quantity.

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Methods

143 *Study Area.*--Our study area is located within the Logan River drainage, in northern Utah. The
144 headwaters of the Logan River (2,600 m elevation) originate in the Bear River Mountains of
145 southeastern Idaho, flowing approximately 64 river km southwest into the Logan Canyon of
146 northern Utah, eventually draining into the Little Bear River in Cache Valley (see Budy et al.
147 2007 for a more detailed site description; Figure 1). The upper Logan River is characterized by a
148 fairly unconfined valley, with moderate to steep gradient channels, coarse sediment loads, and
149 discharge ranging from 0.24 to 7.57 m³/s. The lower reaches of the river are typified by a
150 dissected canyon, with lower gradient channels, smaller substrate, and fluctuations in discharge
151 from 1.41 to 29.03 m³/s. The Logan River's hydrograph is dominated by seasonal variation in
152 flow, with snowmelt-driven high flows in the spring (April-May) followed by relatively stable
153 base-flow conditions throughout the remainder of the year. As is typical across the
154 Intermountain West, anthropogenic activities that potentially affect in-stream and riparian habitat
155 in this area are concentrated over summer and early autumn seasons (June-October) and include
156 livestock grazing, horseback riding, dispersed camping, and off-road motorized vehicle use. The
157 Logan River drainage is home to one of the largest remaining metapopulations of imperiled BCT.
158 Densities in the Logan River drainage currently far exceed those documented for any other BCT
159 population throughout the Bonneville Basin (Budy et al. 2007), making this population ideal for
160 ecological research and also a conservation priority.

161 Based on a pilot study of all tributaries and a subset of mainstem areas in 2007, we *a*
162 *priori* chose four study streams within the Logan River drainage to conduct our research (Table
163 1; Figure 1). Spawn Creek (1800 m in elevation) is a small, spring-fed, 1st-order tributary to
164 Temple Fork, with perennial flows largely controlled by groundwater input, and mean

165 summertime water temperatures of 9°C. Temple Fork (1745 m in elevation), also a perennial
166 creek and a tributary to the mainstem of the Logan River, originates from Temple Springs with
167 stream flow largely driven by spring runoff, with mean summertime temperatures of 10°C.
168 Beaver Creek (2000 m in elevation) and Franklin Basin (2052 m in elevation) each originate
169 from headwater springs in southern Idaho, with perennial stream flows dominated by spring-
170 runoff, and mean summer water temperatures of 10°C and 8°C, respectively. Franklin Basin and
171 Beaver Creek join to form the mainstem of the Logan River. We chose these sites because they
172 represented a wide range of redd densities and habitat characteristics. In addition, Spawn Creek,
173 anecdotally known as a primary area for BCT spawning (Fleener 1951; Bernard and Israelsen
174 1982), was the site of a recent restoration project, where a fenced enclosure was constructed to
175 prevent cattle access to the entirety of the stream, except for the first 200 meters (Hansen and
176 Budy 2011). In contrast, Temple Fork is susceptible to livestock grazing and the associated
177 impacts of riparian grazing during the spring and summer months.

178

179 *Redd Counts.*--We refer to the sample areas within which we surveyed for redds, within each
180 study stream, as “study areas.” We initiated biweekly redd counts during the last week of April
181 (2008) in each of our four study areas to document the spatial and temporal distribution of BCT
182 spawning, and continued until spawning activity ceased in July (2008). These study areas
183 constituted the majority of spawning activity as observed during the pilot study of 2007; redd
184 counts were conducted throughout approximately 2.5 km of each stream, depending on stream
185 topography. In each study area, we identified the presence and location of new redds and
186 classified a redd as an area of cleaned gravel with a characteristic pocket and pillow shape
187 (Hassemer 1993) and recorded the location of each redd using a hand-held Global Position

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

191
192 *Discharge and Water Temperature.*--We used a combination of stage-height recorders and
193 discharge measurements to project an hourly discharge value throughout spawning in each of our
194 four study areas. In addition, we installed temperature data loggers in each of our four study
195 areas; each logger was set to record temperature every hour.

196
197 *Spawning Substrate Use and Availability.*--To describe the physical characteristics of spawning
198 substrate used by BCT in our four study areas, we measured the gravel composition along the
199 width of each redd via 100-count Wolman pebble surveys (Wolman 1954). Given the
200 conservation status of BCT and our desire to not disturb any redds, the gravel immediately
201 adjacent to each redd was assumed to be of a similar composition to the gravel that was
202 encountered by the spawning female prior to redd construction (Thurow and King 1994). To
203 avoid bias, we measured a randomly selected subset of redds during different times (every one to
204 two weeks as based on new redd activity) throughout the spawning season in each of our four
205 study areas. All attempts were made to measure the gravel composition of an arbitrary but
206 logistically feasible minimum of 30% of the total redds per study area.

207 We conducted 55 Wolman pebble surveys in each of our four study areas to characterize
208 substrate availability (Wolman 1954). We delineated each study area (~2.5 km) into eleven 200-
209 m reaches. Within each 200 m reach, we then defined twenty 10-m segments, parallel to stream
210 flow. We then randomly selected five of the twenty transects in each reach to conduct a 100-
211 count pebble survey. We assessed the distribution of available substrate in each study area

212 within the range recommended for cutthroat trout spawning (i.e., 3-80mm; Hickman and Raleigh
213 1982), and calculated the proportion of substrate used versus the proportion available for each
214 substrate size category.

215 *Egg-to-Fry Survival Experiment*

216 In order to assess differences in fry hatch and emergence success of BCT, we placed
217 hatchery (local fluvial Bear Lake strain) brood-stock, eyed eggs (i.e., day 20 of development at
218 time of installation) into slotted egg incubation boxes and buried the boxes in locations
219 throughout the Logan River drainage on 1 July 2008. Mean daily water temperatures at the time
220 of installation as recorded by the temperature loggers at the egg-box level were 11.4 °C in Spawn
221 Creek, 9.1 °C in Temple Fork, 7.2 °C in Franklin Basin and 10.4 °C in Beaver Creek. Our
222 primary goal was to install egg boxes in sites where spawning had been observed during the
223 2008 redd counts. Sites in which egg boxes were installed are referred to hereafter as “study
224 sites.” To determine appropriate sites for egg box installation, we randomly selected a subset of
225 redds in each of our four study areas, and selected nearby sites for our egg boxes, after assessing
226 flow and substrate characteristics via a Wolman pebble survey.

227 In total, we installed 96 egg boxes throughout our four study areas, with 24 egg boxes
228 installed in each study area; these 24 egg boxes were separated into 4 study sites, with 6 egg
229 boxes installed per study site. We used an egg box design based on Harris (1973) and modified
230 according to Wood and Budy (2009). Each egg box (tubular in shape) was 10 cm long by 10 cm
231 wide, and constructed of rigid, tubular polypropylene, with an approximate slot size of 1 mm by
232 5 mm to allow adequate delivery of water and oxygen, while still preventing the escape of sac fry
233 and emergent fry. We equipped each egg box with lightweight, flexible polyethylene caps
234 perforated with small holes (1.5 mm). Each egg box was filled with spawning sized gravel and
235 100 eyed, hatchery-fertilized BCT eggs (Utah Division of Wildlife Resources, Mantua Fish

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

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

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

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

260 *Statistical Analysis*

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

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

277
278

278 **Results**

279 *Redd Counts.*--We observed substantial variability in the timing, magnitude, and duration of
280 BCT spawning among our four study areas during the 2008 spawning season. Notably, the onset
281 of spawning in our two mid-elevation tributaries occurred a month earlier (mid-May) than in our

282 high-elevation tributaries (mid-June; Figure 2). We identified the onset of spawning in our mid-
283 elevation tributaries during May 2008 and first counted redds on 13 May at Spawn Creek and 15
284 May at Temple Fork (Figure 2). In Spawn Creek, spawning peaked on 19 May; we observed
285 two peaks in spawning in Temple Fork, with the first peak occurring on 9 June and the second
286 peak occurring on 23 June. In these stream areas, spawning continued through to the first week
287 of July 2008, commencing on 7 July, with 128 and 213 redds counted in Spawn Creek and
288 Temple Fork, respectively. In the high-elevation streams, the first redds were identified on 10
289 June and 16 June, respectively, at Franklin Basin and Beaver Creek (Figure 2), and spawning
290 peaked in early July and was completed 15 July and 23 July for Beaver Creek, and Franklin
291 Basin, respectively.

292 In total, from May to July 2008, we counted 388 BCT redds throughout tributaries:
293 Temple Fork (85.2 redds/km), Spawn Creek (58.2 redds/km), Beaver Creek (7.6 redds/km), and
294 Franklin Basin (8.0 redds/km). Redds identified in Beaver Creek and Franklin Basin contributed
295 12% to the total number of redds counted, whereas Temple Fork and Spawn Creek contributed
296 55% and 33%, respectively.

297

298 *Discharge and Water Temperature*

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

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

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

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

323 Franklin Basin also experienced its first peak in discharge on 20 May, but with a
324 considerably higher discharge (Figure 2), as compared to Beaver Creek. Spawning started on the
325 descending limb of the hydrograph's second peak, at a discharge of $10.2 \text{ m}^3/\text{s}$, with one redd
326 identified (Figure 2). As discharge increased to a third peak, spawning started to increase
327 slightly, and six redds were observed before the peak. We counted zero redds during a redd

328 count on 19 June, four days before the third and final peak. Seventy one percent of the total
329 redds counted were identified after the last peak.

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

336 *Substrate Use and Availability*

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

344 *Egg-to-Fry Survival Experiments*

345 Egg-to-hatch survival (i.e., hatch survival rate) varied substantially both among and
346 within our four study areas (Figure 5; Table 2). Egg boxes in Temple Fork and Beaver Creek
347 supported high rates of hatch survival, with mean hatch survival rates of 77% and 74%,
348 respectively. In contrast, mean hatch survival rates were lower in Spawn Creek and Franklin
349 Basin, with 43% and 60% of eggs hatching, respectively (Table 2). Hatch survival rates were

350 variable across our four study areas ($P=0.12$; Table 3). We also observed a large degree of
351 spatial variability in hatch survival across sites within some, but not all, study areas (e.g.,
352 Franklin Basin ($P=0.06$; Table 3) and Spawn Creek ($P=0.03$; Table 3).

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

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

368 Mean daily water temperatures during the course of the experiment were similar and
369 close to the optimal temperature for cutthroat trout embryo incubation in all study areas except
370 Franklin Basin. Mean daily water temperatures during the course of the experiment were 9.0 °C
371 and 10.7 °C in mid-elevation tributaries, Temple Fork and Spawn Creek, respectively and 10.2
372 °C and 7.2 °C in high-elevation tributaries, Beaver Creek and Franklin Basin, respectively

373 (Figure 7). Mean daily stream discharge in general during the course of the egg-to-fry
374 experiment was 0.3 m³/s in Temple Fork, 3.7 m³/s in Franklin Basin, 0.1 m³/s in Spawn Creek,
375 and 0.38 m³/s in Beaver Creek.

376 Embryo developmental rates in study sites within the high-elevation tributary, Franklin
377 Basin, were considerably later in comparison to our other study sites. Embryo development
378 progressed rapidly in study sites at Spawn Creek and Beaver Creek, with hatching completed on
379 12 July, only 12 days after installation. Stream conditions in Temple Fork also supported rapid
380 development, with hatching completed at 14 days after installation. In contrast, fry in Franklin
381 Basin finished hatching 22 days after installation. Fry completed emergence on 28 July in
382 Temple Fork, Spawn Creek, and Beaver Creek, only 28 days after installation, and a full 11 days
383 before emergence completed in Franklin Basin (7 August).

384

385

Discussion

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

395 (2000) noted that the spawning period of Westslope cutthroat trout (WSCT; *O. c. lewisi*) in four
396 tributaries in western Montana occurred after a single peak flow event in May.

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

417 and migrate through to Spawn Creek (Figure 1) and/ or stream water temperature (e.g., Homel
418 and Budy 2008; Seidel 2009).

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

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

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

456 Despite differences in the amount of available spawning substrate among our four study
457 areas, BCT appeared to primarily utilize substrate within the range recommended for cutthroat
458 trout spawning in all four study areas (e.g., 3 - 80mm, Hickman and Raleigh 1982). BCT used
459 substrate similar to that of WSCT (e.g., 0.07 - 50.8 mm, Magee et al. 1994; 6 – 110 mm,
460 Schmetterling 2000) but of sizes greater than the range observed for Snake River spotted
461 cutthroat trout (*O. c. [proposed] behnkei*; 2 – 20 mm; Joyce and Hubert 2004). The variability

462 observed in spawning substrate use among subspecies of cutthroat trout may simply be a
463 function of fish size (i.e., larger fish utilize large substrate) and/or available substrate.

464 While we made every effort to accurately identify the onset of spawning and the presence
465 of redds, our study did have important and obvious limitations and constraints. Observer error
466 can limit the accuracy and precision of redd counts, when counts are used as a technique to
467 monitor adult fish populations (Dunham et al. 2001; Al-Chokhachy et. al 2005; Muhlfeld et al.
468 2006). The purpose of our redd counts, though, was not to monitor and/or estimate adult BCT
469 populations, but rather, to provide critical information in furthering our understanding of the
470 temporal and spatial distribution of BCT throughout the Logan River drainage. Nevertheless,
471 observers may have underestimated the number of redds and/or the date of the onset of
472 spawning, especially in our high-elevation study streams, where flow conditions were high and
473 turbid into late June. However, we might expect that in years when the magnitude, frequency,
474 and duration of peak flows events is smaller, flow and water conditions (i.e., turbidity levels)
475 could potentially be suitable for spawning earlier in the spring and summer than what we
476 observed in 2008. As such, our identification of the onset of BCT spawning in our four study
477 areas may have been accurate, and the low density of redds observed in Franklin Basin and
478 Beaver Creek may simply be a function of a shorter available spawning season, due to
479 hydrologic stream conditions (e.g., Hickman and Raleigh 1982; Thurow and King 1994).

480 In addition to the constraints on our ability to identify the onset of spawning, it is
481 important to understand the somewhat unavoidable limitations of estimating hatch and
482 emergence survival even with a large-scale field experiment and substantial degree of effort.
483 Our estimates of survival are likely an overestimation of survival under natural conditions.
484 Incubating embryos, sac fry and emergent fry were protected, by a large degree, from both

485 abiotic and biotic factors, such as scouring flows, predation (e.g., by sculpin, *Cottus bairdii*), and
486 to a certain degree, anthropogenic impacts (e.g., trampling from recreationists and/or grazing
487 livestock; Kershner 1995; DeVries 1997; Gregory and Gamett 2009). In contrast, some boxes
488 may have experienced artificially high sediment accumulation based simply on small
489 microhabitat differences in location within the artificial redd (see further discussion below).
490 Despite these potential limitations, our estimates of BCT hatch and emergence survival provided
491 an excellent description of the relative variability in early survival among a wide range of habitat
492 conditions and provides novel information on a life stage for which there was little previously
493 known.

494 In our experiments, we observed variability in hatch and emergence survival rates both
495 among but also within our four study areas, especially throughout study sites in tributaries,
496 Spawn Creek and Franklin Basin. Such variability is likely driven by important microhabitat site
497 differences in intragravel conditions such as the proportion of fine sediment and other substrate
498 characteristics (Bjorn and Reiser 1991). The negative relationship between salmonid early life-
499 stage survival and fine sediment we observed herein has been firmly and mechanistically
500 documented in the literature (e.g., Chapman 1988; Julien and Bergeron 2006). Further, using
501 Colorado River cutthroat trout (*O. c. pleuriticus*) eggs in a lab setting, Young (1991) assessed the
502 degree to which different proportions of sediment impacted early survival, concluding that egg-
503 to-fry survival was highest with geometric mean particle sizes 13.8 mm and greater. Kondolf
504 (2000) similarly highlights the importance of water flow through redds for the delivery of
505 dissolved oxygen and the removal of metabolic waste. Fine sediment accumulation within the
506 incubation gravel can greatly impede these critical and necessary processes and may explain the
507 differences we observed in hatch survival in emergence survival in Franklin Basin. In contrast,

508 in Spawn Creek, we actually observed a low mean hatch survival and a low mean amount of fine
509 sediment in one of our four study sites, highlighting the role of other environmental conditions,
510 perhaps outside of the egg boxes. Further, it is also important to note that the level of fine
511 sediment we observed in our egg boxes may be a function of natural conditions, anthropogenic
512 conditions, our egg box design, or some combination of the three. Regardless of the ultimate
513 determinate of the proportion fines, the negative relationship we observed between fine sediment
514 and hatch and emergence survival rates has important and obvious implications for land-use
515 management and BCT conservation (e.g., McHugh et al. 2004). In systems or areas that are
516 naturally near the upper limits for fine sediments, even a small degree of increase in
517 sedimentation can have large effects on early survival. Based on these results, if protection of
518 BCT is a management priority, efforts should be made to prevent excessive sedimentation in
519 critical spawning streams.

520 In addition to fine sediment, water temperature also serves as a key physical factor that
521 has a strong, mechanistic influence on salmonid early life-stage survival and embryo
522 development. In our study, embryo development was delayed in the cold, high-elevation
523 tributary, Franklin Basin, and fry emerged approximately 10 days later in Franklin Basin than in
524 Temple Fork, Spawn Creek, and Beaver Creek. The relationship between delayed cutthroat trout
525 embryo development and cooler and/or decreasing water temperatures has been documented
526 extensively in the lab (e.g., Merriman 1935; Stonecypher et al. 1994; Hubert and Gern 1995),
527 with Hickman and Raleigh (1982) recommending optimal water temperatures for cutthroat trout
528 embryo incubation at 10 °C. Mean daily water temperatures in all study sites except Franklin
529 Basin were close to the optimal temperature for embryo incubation, while in contrast, mean daily
530 temperatures observed in study sites in Franklin Basin were on average at least 2 °C cooler over

531 the course of the experiment (e.g., ~ 7 °C). Fry that emerge earlier in the summer may have a
532 greater potential to reach the critical body size need to successfully survive winter, as opposed to
533 fry that emerge later in the season and lack the body size and mass needed to endure the harsh
534 winter conditions common in the Logan River drainage (Cerven 1973; Smith and Griffith 1994).
535 Based on the results of our spawning surveys, as well as our egg-to-fry survival experiments,
536 high-elevation tributary, Franklin Basin appears to be naturally less suited for both spawning and
537 embryo incubation, relative to the conditions observed in the other three tributaries. These
538 results have important implications for local restoration activities (Budy et al. 2007) and
539 demonstrate a template for prioritizing conservation actions more broadly.

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

553 information for aiding in the development of benchmarks for the recovery and persistence of
554 BCT in this as well as other systems.

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

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

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

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

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

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

802

803

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

807

808 Figure 2. Number of BCT redds counted (bars) and average daily discharge (line; m³/s) during
809 the 2008 BCT spawning season in Beaver Creek, Franklin Basin, Spawn Creek, and Temple
810 Fork, from top to bottom.

811

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

815

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

819

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

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

828

829 Figure 6. Relationship between level of fine sediment, calculated as proportion of fines,
830 standardized by the maximum weight of fines, and (A) percent hatch survival ($\text{logit}(\text{hatch}$
831 $\text{probability}) = -0.0110 * \text{fine sediment} + 1.220$; Wald chi-square for slope = 86.1594, $P < 0.001$)
832 and (B) percent emergence survival ($\text{logit}[\text{emergence}] = -0.0128 * \text{fine sediment} + 1.0647$;
833 Wald chi-square for slope = 151.5350, $P < 0.001$).

834

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