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[Article]

Complementation of Habitats for Bonneville Cutthroat Trout in Watersheds Influenced by Beavers, Livestock, and Drought

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Abstract.—Multiple age-classes of Bonneville cutthroat trout *Oncorhynchus clarkii utah* throughout two Rocky Mountain watersheds were influenced by interactions among geomorphology, land use, activity by beavers *Castor canadensis*, and drought. Age-0 trout were present in a limited portion of the watersheds, and their distribution became increasingly restricted as drought conditions developed over a 3-year period. The Coal Creek watershed (including Huff Creek) produced the most age-0 trout in the first 2 years of the drought, lacked beaver activity, and was affected by land use, suggesting that spawning habitat was determined by geomorphology rather than land use or beaver activity. However, the high abundance of age-0 cutthroat trout in Huff Creek did not result in a high abundance of juvenile and older age-classes of fish in subsequent years, most likely because of the lack of complementary habitats providing refuge for older fish. A nearby watershed and its major stream, Water Canyon, had less spawning habitat and produced fewer age-0 fish during the first 2 years of the study but had more trout in the juvenile and adult age-classes, most likely because of a higher degree of habitat complementation. In Water Canyon, less-intense livestock grazing and the presence of beavers allowed for the development of pools and woody riparian vegetation that provided cover for older trout. Water Canyon was also the only stream to produce age-0 trout during the most severe year of drought, suggesting that streams with more natural habitat may provide a spawning refuge during low-flow conditions that occur periodically in the region. These results demonstrate that habitat complementation is important for the coexistence of multiple age-classes of fish and that the adjacency of spawning habitat and refugia is crucial for the persistence of fish in the face of environmental stress associated with drought.

Habitat conditions that influence the distribution and abundance of stream fishes are often the result of interactions among geomorphologic processes, climatic events, and land use patterns. At large spatial scales, basin geomorphology and geochemistry determine the range of conditions possible for smaller scale factors such as gradient, substrate types, pool–riffle development, biological productivity, and temperature regimes (Modde et al. 1991; Baxter and Hauer 2000; Isaak and Hubert 2001a). Climate conditions, such as drought or prolonged cold periods, contribute to a natural range of stream temperature and flow variability that characterizes most stream systems (Poff et al. 1997). Land use practices often modify stream habitat conditions and, in extreme cases, may push streams beyond their range of natural variability (Magee and McMahon 1996; Isaak and Hubert 2001b; Marchetti and Moyle 2001). Understanding how basin geomorphology, land use patterns, and climatic conditions interact to influence stream habitat conditions is especially challenging for the management of fish populations in areas designated for multiple uses such as livestock grazing, timber harvest, mining, and recreation. Land use practices that have relatively minor impacts on stream habitats in some geomorphologic settings can be quite harmful in other settings (Nelson et al. 1992). Furthermore, efforts to improve habitat conditions by adding physical structures to streams or by altering grazing practices in the watershed may be confounded by natural climate fluctuations (Binns and Remmick 1994; Gowan and Fausch 1996).

Maintaining healthy fish populations requires maintaining access to the set of complementary habitats needed by various life history stages (Schlosser 1995; Rosenfeld et al. 2000). In a general sense, complementation can be thought of as the use of non-substitutable resources by individual organisms moving between habitat patches in a landscape (Dunning et al. 1992). Fish populations may be negatively affected by anthropogenic structures such as dams or road culverts that disrupt the connectivity between complementary habitats (e.g., Fausch et al. 2002; Schrank and Rahel 2004). Fish populations may also be negatively affected by land use activities that diminish the quality of habitats needed by particular life history stages, even if the habitats needed by other

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life stages remain unaffected. Examples include the loss of clean gravels needed for spawning, reduction of side channel habitats used by juvenile fish, and loss of pool habitats used by adult fish (Moore and Gregory 1988; Binns 1994; Merz and Setka 2004).

Habitat loss has been implicated in the decline of many subspecies of cutthroat trout *Oncorhynchus clarkii* throughout western North America (Budy et al. 2007), and, as a result, much effort has been directed toward habitat restoration and preservation for these taxa (Behnke 2002). The focus of our study was Bonneville cutthroat trout *O. c. utah*, which is native to the Bonneville Basin in Idaho, Wyoming, and Utah. This subspecies has declined throughout its native range and is the object of much conservation attention, including efforts to increase populations through habitat enhancement (Binns and Remmick 1994; Schrank and Rahel 2004). Habitat improvement efforts would benefit from an increased understanding of how geomorphology, climatic fluctuations, and land use practices interact to influence variation in the distribution of multiple age-classes of fishes.

Previous studies of age-specific mortality suggest that young age-classes of fish can experience high mortality rates (Knapp et al. 1998; Biro et al. 2004), and focusing conservation on those age-classes can potentially yield a high rate of return in terms of fish productivity gained versus effort invested. In addition, spawning habitat for salmonids can be rare and patchily distributed across a basin (Beard and Carline 1991; Baxter and Hauer 2000). Therefore, in order to gain a more complete understanding of the spatial distribution and occurrence of multiple age-classes of Bonneville cutthroat trout in successive years and adjacent watersheds, our first objective was to document basinwide patterns in the abundance of age-0 cutthroat trout in the headwaters of the Thomas Fork River, Wyoming. During the 3-year duration of our study, a progressively severe drought provided an opportunity to examine how increasing summer stream temperatures and decreasing streamflows were related to the spatial distribution of age-0 trout. Our second objective was to relate geomorphic and riparian habitat features to cutthroat trout distribution, and relate those habitat features to basin geomorphology, activity by beavers *Castor canadensis*, and livestock grazing impacts. Finally, field observations suggested that older age-classes of cutthroat trout may not necessarily be present in direct proportion to age-0 trout densities throughout the drainage, so our third objective was to contrast distributions and habitat associations between watersheds and among multiple age-classes of Bonneville cutthroat trout.

Study Area

The study area encompassed headwaters of the Thomas Fork drainage (584.2 km^2), a tributary of the Bear River in western Wyoming (Figure 1). Most headwater tributaries in this system contain populations of Bonneville cutthroat trout, and to date no nonnative fish species have become naturalized in the study area. Bonneville cutthroat trout spawn in spring, just after peak snowmelt runoff. Fry emerge from redds from July through early September.

Water Canyon, the highest-elevation tributary (2,542 m), is in the Bridger-Teton National Forest and is characterized by dense riparian willows *Salix* spp., extensive dam building and other channel-altering activity by beavers, and relatively cool summer water temperatures. Management objectives in the Bridger-Teton National Forest include meeting the needs of multiple uses (e.g., some grazing of livestock). Coal Creek and its tributaries (East Fork Coal, Huff, Stoner, and Little Muddy creeks; 2,311–2,369 m in elevation) are in drainages managed primarily for livestock grazing by the U.S. Bureau of Land Management (BLM). The Coal Creek drainage is characterized by the virtual absence of willows and the presence of heavily grazed riparian areas, eroded banks, and compacted soils. With a few exceptions, the Coal Creek drainage contains only remnant beaver dams that no longer impound water. Summer water temperatures are generally warmer in Coal Creek and its tributaries than in Water Canyon.

Methods

Climate conditions: streamflow and stream temperature.—For the purposes of this study, streamflow and stream temperature in the basin acted as surrogates for regional climate conditions. Stream temperatures were monitored in the upper and lower portions of Coal Creek and at the downstream end of Huff Creek and Water Canyon during 2000–2002. Temperature loggers were placed in pools and set to record temperature every 15 min during July of each year, the time of warmest stream temperatures based on previous research in the basin (Schrank et al. 2003). Mean annual streamflow data from 1955 to 1902 came from a U.S. Geological Survey (USGS) station on the Bear River upstream of the confluence with the Thomas Fork, the nearest operating stream gauging station with data that overlapped the study period (USGS 2008).

Objective 1: basinwide distribution of age-0 trout.—To describe the spatial distribution of age-0 Bonneville cutthroat trout, we conducted streamside visual surveys throughout the Coal Creek and Water Canyon drainages from late August through September of

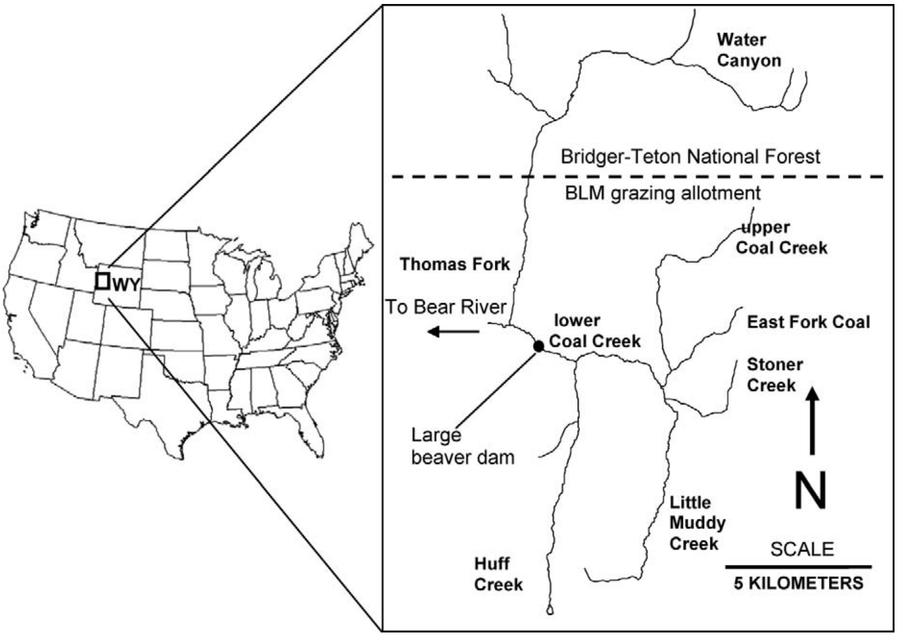

FIGURE 1.—Study area in the headwater streams of the Thomas Fork drainage of western Wyoming managed for multiple use by the U.S. Forest Service and the Bureau of Land Management.

2000–2002. We chose the late summer–early autumn sample period because it came after the emergence of fry from redds, according to intensive visual surveys in portions of the study area from July through mid-October (White 2003).

The streamside visual survey consisted of two observers walking on opposite sides of the streams, counting age-0 Bonneville cutthroat trout and communicating their findings with one another. When age-0 trout were present, we recorded the upstream and downstream endpoints of stream segments with homogeneous fish densities using a Garmin Etrex global positioning system unit (accuracy ≈7–15 m). We were confident in our ability to identify age-0 Bonneville cutthroat trout because no other trout species resided in the Thomas Fork basin and age-0 cutthroat trout were easy to distinguish from the other fish species encountered in the survey: longnose dace *Rhinichthys cataractae*, redside shiner *Richardsonius balteatus*, Utah sucker *Catostomus ardens*, and mottled sculpin *Cottus bairdii*. Using this approach, we generated continuous maps of age-0 trout distribution throughout the Water Canyon and Coal Creek drainages in multiple years.

To verify that visual estimates of age-0 Bonneville cutthroat trout abundance were a consistent indicator of population size, we conducted multiple-pass depletion electrofishing in twenty-one 100-m-long reaches distributed throughout the Thomas Fork headwaters. First, we conducted the streamside visual survey, waited 1 h, and then performed three electrofishing passes with the following exceptions: in cases where we did not catch age-0 Bonneville cutthroat trout in the first two passes, we ceased sampling; and in cases where we did not achieve a substantial reduction of age-0 cutthroat trout after three passes, we performed a fourth pass. A simple linear regression of log-transformed data (to meet the assumption of equal variances) revealed that the abundance estimates from visual surveys were positively correlated with depletion estimates ($\log_e[N] = 0.63 + 1.50 \times \log_e[V]$, where N is the population estimate of age-0 trout based on multiple-pass electrofishing and V is the visual estimate of age-0 trout abundance; $n = 21$, $P < 0.0001$, adjusted $r^2 = 0.66$). Because the intercept (0.63) was not significantly different than zero (P-value $= 0.12$), we were confident in our ability to identify reaches as having age-0 trout present or absent. Bozek and Rahel (1991a) found that a similar method was suitable for censusing age-0 cutthroat trout in small streams with clear water.

During the 2000 field season, we surveyed age-0 Bonneville cutthroat trout abundance in Coal Creek, Little Muddy Creek, Water Canyon, and Huff Creek (Figure 1). During the 2001 and 2002 field seasons, we extended the survey to include two tributaries of Coal Creek: East Fork Coal Creek and Stoner Creek. We conducted multiple surveys in selected years and drainages in order to verify that our estimates of age-0 trout occurrence were made after the time of peak age-0 trout emergence from redds. To assess whether or not age-0 trout were emigrating downstream out of Huff Creek after emergence from redds, we electrofished and visually surveyed a 300-m reach of Coal Creek below the Huff Creek confluence in September of 2002. The downstream end of this reach was marked by a large beaver dam that appeared to be a barrier to the downstream migration of young trout during low-streamflow conditions in late summer–autumn (Figure 1).

We created maps in a geographical information system (GIS) to examine how the spatial distribution of age-0 Bonneville cutthroat trout changed during the 3-year period of increasing severity of drought conditions. We plotted the distribution of age-0 trout on 1:100,000-scale hydrography maps using ArcView GIS software version 3.2 (Environmental Systems Research Institute, Inc., Redlands, California), then created routes of fish density for each segment of stream between geographic coordinates as described by Torgersen et al. (1999). The abundance of age-0 trout between coordinates was expressed as linear density (fish/m) to account for variance in segment length.

Objective 2: habitat associations of age-0 trout.—Habitat associations of age-0 Bonneville cutthroat trout were examined in August–September of 2001 in Huff Creek and Water Canyon. We choose these two streams because they differed in the relative abundance of age-0 versus older age-classes of trout, and we were interested in whether differences in habitat features between the two streams might be contributing to this pattern. Estimates of age-0 trout abundance for this analysis came from the previously described, basin-wide visual surveys. After the visual surveys were completed, we randomly selected 33 reaches for habitat surveys (17 reaches in Huff Creek, 16 reaches in Water Canyon), using the lengths of stream with homogeneous age-0 trout density to guide our determination of sample reach lengths. The average length of sample reaches was 44 m (range = 30–170 m). We measured riparian and geomorphic habitat characteristics commonly used in fisheries studies and potentially relevant for both age-0 and older age-classes of cutthroat trout. At stations placed 10 m apart along the length of each sample reach, we measured wetted stream width and percent canopy cover, and classified channel unit type as pool, riffle, or glide. At five equidistant points across the stream at each station, we recorded stream depth, current velocity at 0.6 of depth, and the presence of gravel suitable for cutthroat trout spawning (2–64 mm in diameter). Along the length of the entire sample reach, we measured channel slope with an Abney level, total length of eroded bank, and total length of undercut bank overhanging the stream by at least 40 cm. We also measured the length of wetted channel having the following features present: large woody debris, overhanging woody vegetation, nonwoody vegetation overhanging the stream by 10 cm or more (based on BLM designation for allowable stubble heights in meeting range health standards, defined here as "grass overhang"), and margin habitat suitable for age-0 cutthroat trout. Margin habitat suitable for age-0 cutthroat trout was defined as water that was deeper than 3 cm (Bozek and Rahel 1991), shallower than 40 cm, and slower than 4.0 cm/s (Moore and Gregory 1988). The length of channel having the above features was divided by the total length of right and left streambanks to determine the percent of each feature within the sample reach. To determine if heterogeneity in stream depth, width, and velocity were associated with fish presence or absence, we calculated the coefficient of variation (CV = standard deviation/mean) for these variables for input into a discriminant analysis model as discussed below.

Objective 3: abundance, size-classes, and habitat associations of age-1 and older trout.—The original study was designed only to assess the distribution and habitat associations of age-0 Bonneville cutthroat trout. However, after our field observations in 2001, we recognized the possibility that areas of high age-0 production might not correspond with areas having abundant older trout. In 2002, we compared the abundance and size distribution of Bonneville cutthroat trout in age-classes 1 year and older in Huff Creek and Water Canyon. We assessed the relative abundance of age-1 and older trout using single-pass electrofishing at 20 random locations in each of the two streams, for a total of 40 sample reaches. At each location, we installed upstream and downstream block nets and used single-pass electrofishing in each 50-m reach, followed by subsequent electrofishing passes in each randomly selected reach. The number of trout and individual fish lengths were recorded. Single-pass electrofishing has been highly effective for sampling trout in small streams (Kruse et al. 1998), with a catch of zero indicating trout were absent or present in extremely low abundance. To further increase our confidence in the efficiency of single-pass electrofishing for capturing age-1 and older trout, we conducted multiple-pass, depletion electrofishing in 26 of the 40 reaches, and found that the probability of capture was uniformly high (mean = 0.90; SD = 0.15) and not statistically different between the two streams, based on a two-sample t-test of pooled group differences with equal variances ($P = 0.47$). This indicated we were efficient in capturing age-1 and older trout and that single-pass electrofishing was a good measure of relative fish abundance among reaches.

In the same streams where we analyzed habitat associations for age-0 trout in the 2001 season, we examined habitat associations of age-1 and older Bonneville cutthroat trout (presumed to be the combination of surviving age-0 trout from the previous season, resident trout of older age-classes, and immigrants) in July–August 2002 prior to the peak emergence of age-0 trout from redds. Habitat surveys were conducted for the same 40 sample reaches that were used to assess the abundance and size distribution of age-1 and older trout. Immediately after electrofishing each reach, we measured the same habitat features described above for the analysis of habitat associations of age-0 trout.

Statistical analysis of habitat associations.—We used linear discriminant analysis to explore the relationship between trout distributions and riparian and geomorphic conditions. Discriminant analysis is somewhat analogous to logistic regression but predicts membership of data into predefined groups based on multivariate functions. The procedure maximizes variation in among-group variables relative to within-group variables, and results in the use of only significant variables in functions that differentiate the predefined groups (McCune and Grace 2002). Discriminant analysis has been used for elucidating the habitat associations of birds (Harner and Whitmore 1980; Rice et al. 1980), mammals (Cavallaro et al. 1980), and fish (reviewed in Paukert and Wittig 2002). We felt discriminant analysis was an appropriate procedure for analyzing fish–habitat associations in our system because (1) fish densities tended to have a binomial distribution (i.e., fish were either present in significant quantities or not at all), (2) we wanted to predict group membership into more than two categories, and (3) the nature of the riparian and geomorphic characteristics called for a perspective capitalizing on the multivariate correlation structure of the data set.

We defined four a priori groups of stream reaches based on stream identity and Bonneville cutthroat trout presence or absence: (1) Huff Creek–trout present, (2) Huff Creek–trout absent, (3) Water Canyon–trout present, and (4) Water Canyon–trout absent.

In our analysis, Huff Creek and Water Canyon were considered to represent degraded and relatively pristine stream characteristics, respectively. A separate discriminant analysis was conducted for age-0 Bonneville cutthroat trout and for age-1 and older trout. Comparisons of the discriminant functions from the two analyses provided insight into how habitat associations differed between the two age-groups. Results were interpreted by analyzing structure loadings of habitat variables onto discriminant functions and by comparing mean scores of the a priori groups along the discriminant functions. Structure loadings indicate the importance of each variable in composing the discriminant function; structure loadings having an absolute value near 1.0 indicate a strong correlation, while values near zero represent weak correlations. After discerning associations between stream characteristics and trout distributions, we used classification analysis to calculate the success rate for identifying stream reaches into the a priori groups based on discriminant functions. Classification analysis is an indicator of how well the discriminant functions parse out the entire set of sample units into the a priori groups and is conceptually similar to a goodness-of-fit test. Discriminant and classification analyses were performed with SPSS statistical software (SPSS 1997).

For both the age-0 and age-1 and older Bonneville cutthroat trout habitat analyses, the assumption of equal population covariance matrices (Box's M) was not met, which can lead to distorted distances among groups along the discriminant function. However, discriminant analysis is generally robust to this and other violations of assumptions, especially if the number of observations is at least three times the number of discriminating variables (Paukert and Wittig 2002). In our analyses, the number of observations was always at least six times the number of discriminating variables.

Results

Climate Conditions

Based on USGS streamflow data, our study spanned three seasons in the midst of a dry period for the basin (Figure 2). Anecdotal information from local land managers and the cattle association rider indicated water levels were much lower and stream temperatures were much higher than usual. However, it should be noted that low streamflows of similar magnitude have been observed several times during the last 50 years. Mean July stream temperatures increased throughout the study and were approximately 1.5°C warmer in 2002 relative to 2000 (Figure 3).

Objective 1: Basinwide Distribution of Age-0 Trout

Relative to the overall length of stream surveyed, age-0 Bonneville cutthroat trout were present in only a small portion of the drainage (Figure 4). Age-0 trout were primarily found in Huff Creek, upper Coal Creek, and Water Canyon in 2000–2001 but were found only in Water Canyon in 2002. The overall distribution of age-0 trout encompassed approximately 45% of the

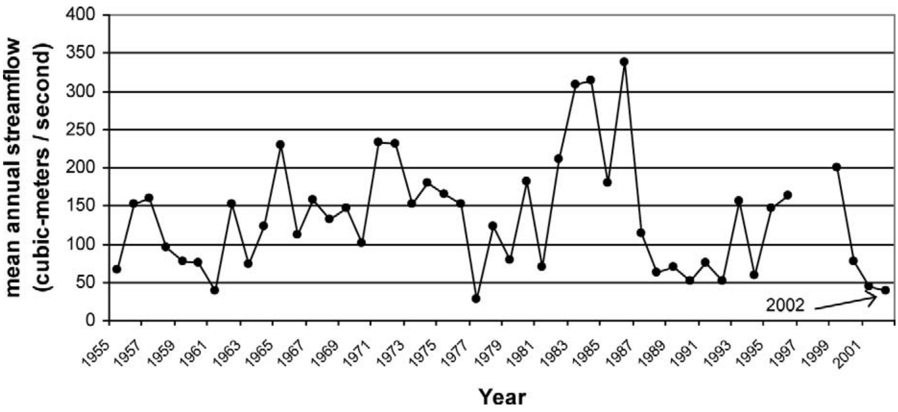

FIGURE 2.—Mean annual streamflow in the Bear River upstream from its confluence with the Thomas Fork, 1955–2002, showing the increasing drought conditions during the study period. No data were collected in 1997 or 1998.

total length of streams surveyed in 2000, 13% in 2001, and less than 1% in 2002.

Age-0 Bonneville cutthroat trout abundance decreased in each stream through the 3 years of study. From 2000 through 2002, the numbers of age-0 trout observed in Huff Creek were 3,720, 226, and 0, respectively. During this same period, the numbers of age-0 trout observed in upper Coal Creek were 1,164, 309, and 0. In Water Canyon, the numbers of age-0 trout observed during this period were 1,365, 95, and 10. It is noteworthy that during the most severe year of drought (2002), age-0 trout were present only in Water Canyon, the drainage with the least apparent effects of livestock grazing.

Objective 2: Habitat Associations of Age-0 Trout

Three significant discriminant functions separated the four groups based on fish presence or absence in Water Canyon versus Huff Creek (Tables 1, 2). The first discriminant function described the meadowlike qualities of a reach. High scores on this function distinguished meadow reaches with sparse overhanging woody vegetation, abundant spawning gravel, and some overhanging grass from reaches that were not meadowlike. The second discriminant function primarily distinguished reaches with high variation in current velocity from reaches with more uniform velocity. The third discriminant function represented the extent of exposed stream margins and spawning habitat in the reach. High scores on this function distinguished reaches having exposed stream margins and abundant spawning gravel from reaches that were not exposed and spawnable.

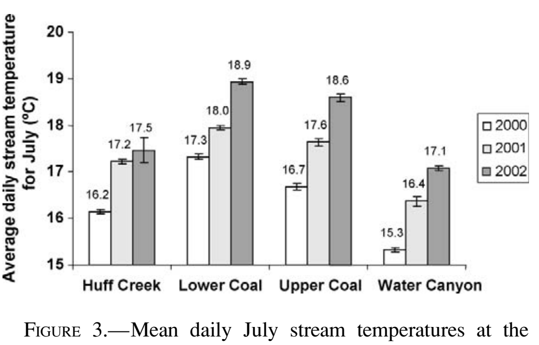

FIGURE 3.—Mean daily July stream temperatures at the mouths of Huff Creek, the lower and upper portions of Coal Creek, and Water Canyon during 2000–2002. The thin vertical lines indicate SEs.

The first and third discriminant functions provided the most biological insight regarding the habitat conditions associated with the presence and absence of age-0 Bonneville cutthroat trout in the two streams. The first discriminant function distinguished Huff Creek, which had riparian areas that were grassy or bare, from Water Canyon, which had riparian areas with overhanging woody vegetation (Tables 1, 2; Figure 5). The third discriminant function indicated that reaches with age-0 trout contained abundant spawning gravel and little grass in the riparian area, whereas reaches without age-0 trout did not have abundant spawning gravel but had grassy riparian areas, suggesting that age-0 trout were less associated with riparian habitat features and more associated with the spawning locations of their parents. The overall correct classification rate was 87.9%, as compared with a probability of correct classification by chance of 27.5% (only 4 of 33 reaches were misclassified).

Objective 3: Abundance, Size-Classes, and Habitat Associations of Age-1 and Older Trout

The abundance and length-frequency distributions of age-1 and older Bonneville cutthroat trout were

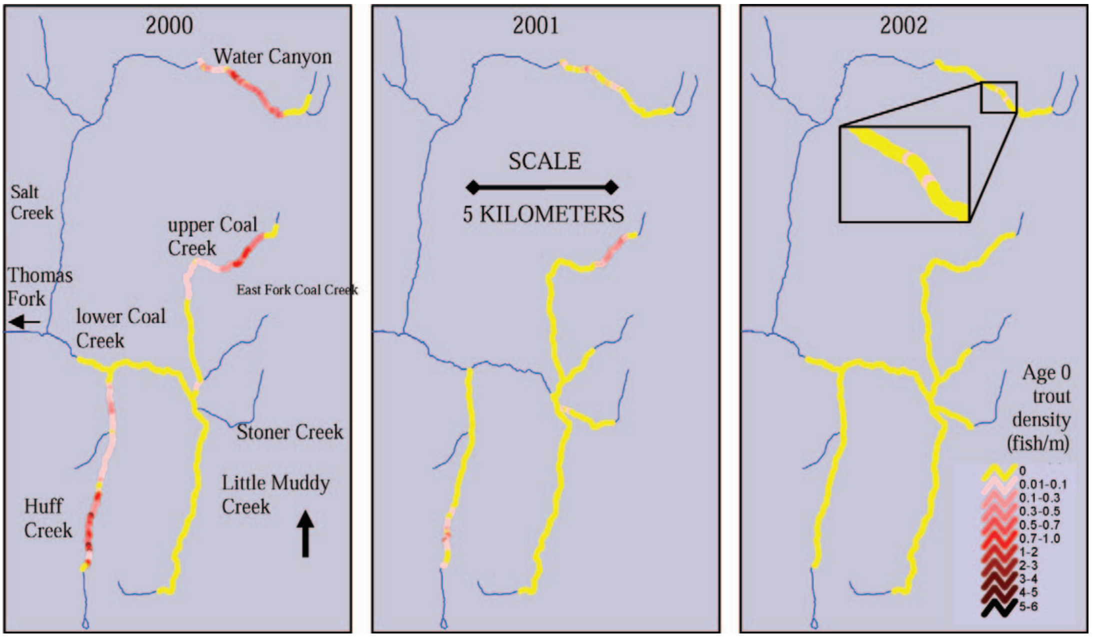

FIGURE 4.—The distribution of age-0 Bonneville cutthroat trout over 3 years, based on streamside visual surveys. The thin dark lines represent stream reaches that were not surveyed. The white segments represent reaches that were surveyed but in which no age-0 trout were found. The degree of shading in the other segments represents reaches with various fish densities. Each stream was surveyed upstream to the point of intermittency. In 2002, age-0 trout were only found in small portions of Water Canyon (inset).

markedly different between Huff Creek and Water Canyon. Based on single-pass electrofishing estimates of relative abundance in the randomly selected reaches, the density of age-1 and older trout was higher in Water Canyon (0.14 fish/m) than in Huff Creek (0.04 fish/m) in 2002. The few trout present in Huff Creek tended to be relatively large (>150-mm total length), whereas fish having a total length between 100 and 210 mm comprised the majority of trout in Water Canyon (Figure 6). In Huff Creek, the smallest trout captured was 125 mm, whereas in Water Canyon we captured 18 trout of 125 mm or less. No age-0 or age-1 and older trout were captured in the 300 m of Coal Creek between the large beaver dam and the Huff Creek confluence (Figure 1), suggesting that age-0 trout did not migrate downstream out of Huff Creek. If a large-scale emigration had occurred, we would have expected to capture at least a few young trout in the Coal Creek beaver pond.

Analysis of age-1 and older Bonneville cutthroat trout presence or absence and habitat features produced three significant discriminant functions separating the four groups from one another. There was little overlap

TABLE 1.—Discriminant function structure loadings for habitat variables for age-0 Bonneville cutthroat trout. Function 1 pertained to the extent of meadowlike conditions, function 2 to the heterogeneity of water velocity, and function 3 to the suitability of spawning habitat. The test of functions 1–3 was significant (Wilk's lambda = 0.08; $\chi^2 = 71.07$, df = 12, $P < 0.001$), as were the tests of functions 2–3 (Wilk's lambda = 0.30; $\chi^2 = 33.58$, df = 6, $P < 0.001$) and function 3 (Wilk's lambda = 0.58; $\chi^2 = 15.46$, df = 2, $P < 0.001$).

	Discriminant function		
Variable	1	2	3
Percent overhanging woody vegetation	−0.73	−0.07	0.13
Percent grass overhang	0.26	0.03	−0.81
Velocity CV	−0.01	0.87	0.46
Percent spawning gravel	0.51	−0.21	0.79

TABLE 2.—Mean group scores along each discriminant function for age-0 Bonneville cutthroat trout. The number of sites in each group is given by n. See Table 1 for further details.

	Discriminant function		
Group (n)	1	2	3
Huff Creek–age-0 trout present (n = 6)	1.93	−0.78	1.2
Huff Creek–age-0 trout absent (n = 11)	1.28	0.54	−0.8
Water Canyon–age-0 trout present (n = 5)	−1.64	1.56	0.98
Water Canyon–age-0 trout absent (n = 11)	−1.59	−0.82	−0.3

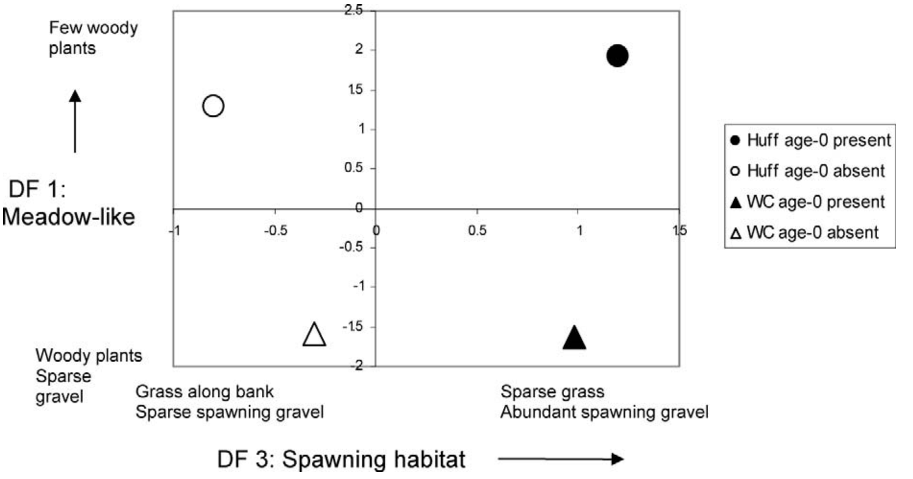

FIGURE 5.—Results of discriminant analysis for age-0 Bonneville cutthroat trout. Mean group scores are plotted against discriminant functions (DFs) 1 and 3, representing the extent of meadowlike conditions and the amount of habitat suitable for spawning, respectively. The first function discriminates Huff Creek from Water Canyon (WC), the second sites with age-0 trout from sites without age-0 trout.

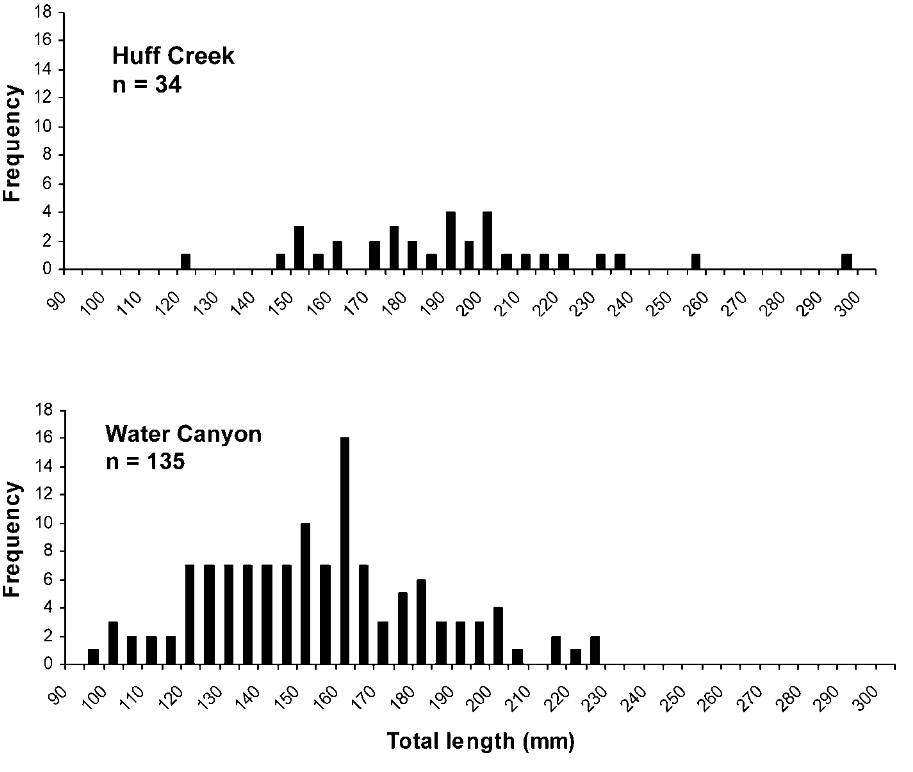

FIGURE 6.—Length-frequency distributions of age-1 and older Bonneville cutthroat trout in Huff Creek and Water Canyon in 2002.

TABLE 3.—Discriminant function structure loadings for variables for age-1 and older Bonneville cutthroat trout habitat analysis. Function 1 pertained to the extent of meadowlike conditions, function 2 to the extent of canyonlike conditions, and function 3 to the suitability of refuge habitat. Structure loadings of 0.20 or more (asterisks) were used to name functions. The test of functions 1–3 was significant (Wilk's lambda = 0.02; $\chi^2 = 125.09$, df = 24, $P < 0.001$), as were the tests of functions 2–3 (Wilk's lambda = 0.26; $\chi^2 = 44.04$, df = 14, $P < 0.001$) and function 3 (Wilk's lambda = 0.64; $\chi^2 = 14.83$, df = 6, $P < 0.001$).

Variable	Discriminant function 1	2	3
Percent grass overhang	0.35*	−0.03	−0.18
Percent overhanging woody vegetation	−0.27*	0.36*	0.26*
Velocity	0.24*	0.35*	0.003
Slope	−0.16	0.44*	0.22*
Pool–riffle ratio	−0.16	−0.39*	0.62*
Percent undercut bank	0.13	0.005	0.49*

TABLE 4.—Mean group scores along each discriminant function for age-1 and older Bonneville cutthroat trout. The number of sites in each group is given by *n*. See Table 3 for further details.

Group (*n*)	Discriminant function 1	2	3
Huff Creek–age-1 and older trout present (*n* = 13)	3.82	0.3	0.5
Huff Creek–age-1 and older trout absent (*n* = 7)	1.42	−0.52	−1.48
Water Canyon–age-1 and older trout present (*n* = 17)	−2.84	−0.67	0.29
Water Canyon–age-1 and older trout absent (*n* = 3)	−3.8	3.68	−0.36

among the variables dominating each of the discriminant functions, so in order to simplify the analysis and produce ecologically interpretable results, we chose structure loadings with a minimum value of 0.20 when naming functions (Tables 3, 4). The three discriminant functions were composed of the following variables: percent overhanging woody vegetation, grass overhang, and undercut bank along the streambank; percent slope; velocity; and pool–riffle ratio. The first function was nearly identical to the "meadowlike" function in the age-0 trout habitat analysis. This function discriminated meadow reaches having abundant overhanging grass, sparse overhanging woody vegetation, and moderately fast water velocities from reaches that were not meadowlike. The second discriminant function was an indicator of the canyonlike quality of reaches. This function discriminated reaches with steep slopes, low pool–riffle ratios, abundant overhanging woody vegetation, and fast water velocities from reaches that were not canyonlike (field observations indicated that woody plant species were abundant in canyons where access to the riparian zone was limited for livestock). The third discriminant function was an indicator of the refuge qualities of the reach as previously described for critical landscape features for fish in headwater streams (Schlosser 1995). High scores on this function discriminated reaches having refuge from predators or harsh environmental conditions in the form of high pool–riffle ratios, abundant undercut banks, and overhanging woody vegetation from reaches that did not have such habitat characteristics.

Each function discriminated two groups from the others (Tables 3, 4). Just as in the age-0 Bonneville cutthroat trout habitat analysis, reaches in Huff Creek were more meadowlike and reaches in Water Canyon were less meadowlike (Figure 7). Huff Creek reaches without age-1 and older trout and Water Canyon reaches with age-1 and older trout were canyonlike, whereas Huff Creek reaches with age-1 and older trout and Water Canyon reaches without age-1 and older trout were not canyonlike. For both streams, reaches with age-1 and older trout present provided more refuge habitat than reaches without age-1 and older trout (Figure 7). The overall correct classification rate was 97.5%, as compared with a probability of correct classification by chance of 32.8% (1 out of 40 reaches was misclassified).

To better understand the reasons for the differences in the abundance of age-1 and older Bonneville cutthroat trout between Water Canyon and Huff Creek, we performed an ad hoc comparison of the refuge habitat characteristics (based on characteristics from the discriminant analysis) of these two streams for the reaches sampled in 2001 and 2002. Huff Creek, where age-1 and older trout were less abundant, had much less overhanging woody vegetation and pool habitat than Water Canyon, where age-1 and older trout were more abundant (Figure 8). The two streams had similar levels of undercut bank and similar channel slopes.

Discussion

Age-0 Bonneville cutthroat trout were present in only a limited portion of the Coal Creek drainage across all 3 years of the study. We believe that the locations of trout fry in the drainage were determined by where spawning occurred and were not due to postemergence migration of fry to rearing areas. Three lines of reasoning support this idea. First, age-0 trout were primarily found in areas associated with spawning habitat. Second, cutthroat trout fry have a preference for low water velocities and are not strong swimmers (Moore and Gregory 1988; Bozek and Rahel 1991b); hence it is unlikely they could disperse upstream given

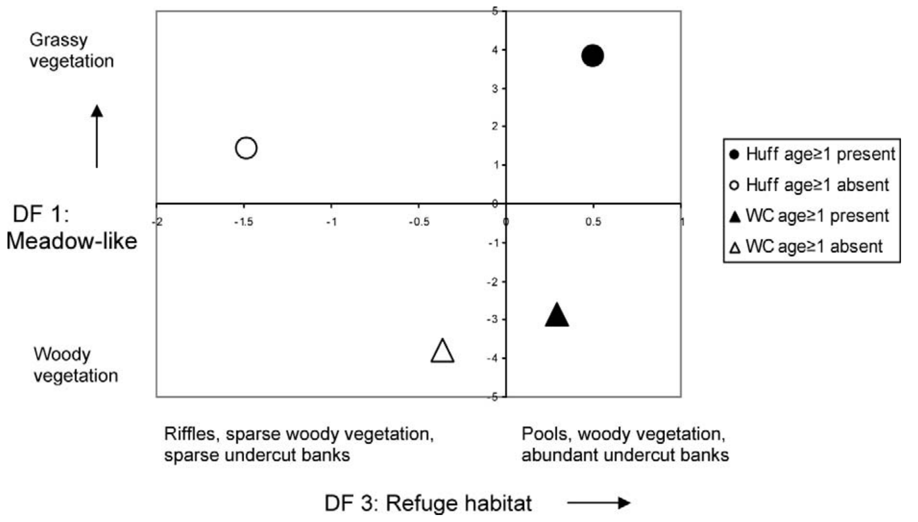

FIGURE 7.—Results of discriminant analysis for age-1 and older Bonneville cutthroat trout. Mean group scores are plotted against discriminant functions (DFs) 1 and 3, representing the extent of meadowlike conditions and the amount of refuge habitat, respectively. The first function discriminates Huff Creek from Water Canyon (WC), the second sites with age-1 and older trout from sites without such trout.

the generally high stream gradients in these mountain streams. Third, if fry had drifted downstream, we would have expected to find them in greater abundance in the downstream portions of Huff Creek, near the Coal Creek confluence, especially in 2000 which was a year of high fry abundance in headwater reaches. Instead, fry were present in low abundance in the lower portions of Huff Creek and absent in downstream reaches of the drainage.

Although salmonid redds are located in riffle areas, young trout require areas of slow current (Bozek and Rahel 1991b). Thus, the distribution of age-0 Bonneville cutthroat cutthroat trout in the Coal Creek watershed reflected the spatial juxtaposition of spawning habitat (fast velocity, gravel–cobble substrate) and fry habitat (slow velocity, shallow depths). Bozek and Rahel (1991b) reported that the distribution of age-0

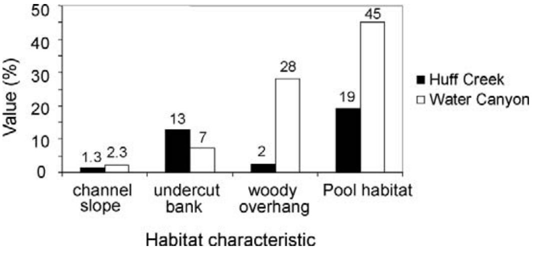

FIGURE 8.—Comparison of refuge habitat characteristics at Huff Creek (n = 20 reaches) and Water Canyon (n = 20 reaches).

Colorado River cutthroat trout *O. c. pleuriticus* in southern Wyoming streams was dependent on a similar juxtaposition of habitat types. Some areas with suitable fry habitat lacked age-0 cutthroat trout, which the authors attributed to the absence of suitable spawning gravels nearby.

If spawning and rearing habitats are rare in a watershed, then management strategies can be streamlined by focusing efforts there. In our case, areas with age-0 Bonneville cutthroat trout represented only 45, 13, and 0.4% percent of the total stream length surveyed in 2000, 2001, and 2002, respectively. In southwestern Montana, cutthroat trout spawning locations were also limited to a small portion of the stream network, as 99% of redds in a 161-km^2 drainage occurred in two high-elevation tributaries (Magee and McMahon 1996). Spawning and rearing areas can be identified by aerial surveys of redds (Isaak et al. 2003) or by ground-based visual surveys of age-0 fish as in the present study. Once located, these rare habitats can be targeted for protection or enhancement. However, as discussed below, it is also important to consider the spatial juxtaposition of habitats required for older age-classes of fish.

The abundance of age-0 Bonneville cutthroat trout declined during the 3 years of our study in concert with increasing water temperatures and decreasing water levels in the Thomas Fork drainage. Climate fluctuations can influence trout reproductive success over large geographic areas (Gowan and Fausch 1996; Isaak et al. 2003). What was notable in the Thomas Fork drainage was that areas of reproduction became more restricted as the drought increased in magnitude. In 2001, reproductive success, as established by the presence of age-0 cutthroat trout, was restricted to a subset of the reaches that produced trout fry in 2000. By 2002, reproductive success was restricted even further to just a few reaches in Water Canyon. Interestingly, Water Canyon did not consistently produce the greatest number of trout fry, but it appeared that when drought conditions were most pronounced in 2002 Water Canyon served as a buffer from environmental extremes. The importance of Water Canyon as a refuge for reproduction during environmental extremes would not have been apparent had we surveyed age-0 cutthroat trout only in 2000 and 2001. In those years, age-0 trout were more abundant in upper Coal Creek and Huff Creek. Geomorphic features and riparian shading provide likely explanations as to why cutthroat trout were able to spawn successfully in Water Canyon during even the most severe conditions. Water Canyon was at the highest elevation of all the study streams and had abundant willows to provide riparian shading, resulting in cool water temperatures. Streams like Water Canyon having relatively natural habitat can provide a refuge for fish populations during environmental extremes. Such refuges are likely important for the long-term persistence of cutthroat trout populations since the drought conditions experienced in 2002 have occurred periodically in this region. Global warming may further increase the incidence and severity of drought conditions in Rocky Mountain streams (Hauer et al. 1997).

Contrasting habitat features were associated with the occurrence of age-0 versus older Bonneville cutthroat trout. Abundant spawning gravel and sparse overhanging grass were the major factors distinguishing reaches with age-0 trout from reaches without, in both Huff Creek and Water Canyon. By contrast, the major factor distinguishing reaches with age-1 and older trout from reaches without was the presence of cover in the form of pools, overhanging woody vegetation, and undercut banks. Whereas younger age-classes of cutthroat trout tend to be found in shallow habitats along the stream margin (Moore and Gregory 1988; Bozek and Rahel 1991b), older age-classes move to progressively deeper water and seek cover from predators or fast current speeds (Rosenfeld and Boss 2001). Such refuge habitat can be provided by deep water, woody debris, large boulders, or undercut banks (Heggenes et al. 1991; Binns 1994). Harig and Fausch (2002) found that streams having sufficient deep-pool habitat facilitated the success of cutthroat trout translocations.

Although Huff Creek was capable of producing many age-0 Bonneville cutthroat trout in some years, few age-1 and older fish were present in this stream. By contrast, Water Canyon generally produced fewer age-0 fish but contained more age-1 and older fish. This pattern was likely due to the fact that whereas both Huff Creek and Water Canyon contained areas suitable for spawning, refuge cover needed by older age-classes of cutthroat trout was scarce in Huff Creek. This finding is similar to that of Petty et al. (2005) who reported that large brook trout *Salvelinus fontinalis* in Appalachian streams were associated with instream cover, deep water, and riparian canopy cover, whereas age-0 and juvenile brook trout were primarily found adjacent to spawning areas.

One of the major findings of the present study was that the spatial patterns in the abundance of age-0 fish were not strongly related to those in the abundance of older age-classes of fish. This suggests that failure to survive through the first winter of life may be limiting production of adult Bonneville cutthroat trout. Thus, management actions aimed at improving spawning habitat may not result in increased adult fish if habitats needed by fry and older age-classes are missing or not in close proximity.

The differences in the amount of refuge cover between Huff Creek and Water Canyon appeared to reflect interactions among basin geomorphology, beaver activity, and land use. From a geomorphologic perspective, Huff Creek has a wider valley floor that promotes development of wet meadow areas, whereas Water Canyon, as its name suggests, has a narrow valley floor allowing for the growth of large conifers near the stream channel. These trees eventually fall into the channel, create pools, and provide refuge cover for fish. The two streams also differed greatly in beaver activity. In Water Canyon, we counted 7.4 active beaver dams per kilometer of stream in 2001, and these dams resulted in numerous deepwater habitats that were used by juvenile and larger size-classes of Bonneville cutthroat trout. By contrast, there were no active beaver dams on Huff Creek, most likely because of the absence of willows and cottonwood trees along the stream.

The primary land use in the study area was livestock grazing, which appeared to have a more detrimental effect on riparian vegetation along Huff Creek than along Water Canyon. This was likely the result of differences in grazing intensity, timing of grazing, and potentially the historical effects of land use and beaver activity in the drainage. Although grazing intensity was only slightly higher in the Huff Creek watershed than in the Water Canyon watershed (0.10 versus 0.08 animal unit months per acre, respectively), most of the grazing was done by cattle *Bos taurus* in the Huff

Creek watershed, whereas most grazing was done by sheep *Ovis aries* in the Water Canyon watershed. For behavioral reasons, cattle are thought to be more detrimental to riparian habitat than sheep (May and Somes 1982). Livestock grazing began in late May in the Huff Creek watershed but not until early July in the Water Canyon watershed. Delaying grazing by more than a month may reduce the negative effects on riparian vegetation by allowing sensitive riparian soils to dry and become more stable before trampling by livestock occurs (Marlow and Pogacnik 1985). Finally, historic patterns of land use can greatly influence current ecological patterns, as in the study by Harding et al. (1998) who correlated current patterns of fish and invertebrate community structure to land use from 50 years prior. In the case of the present study, applications of herbicides in the Coal Creek drainage (including Huff Creek) through the 1970s to reduce riparian vegetation, the lack of regeneration of riparian willows, and the subsequent local extirpation of beavers have likely contributed to the decreased resilience of livestock-influenced watersheds.

In the streams we studied, spawning habitat appeared to be less sensitive to grazing than habitat for age-1 and older trout. In 2 of the 3 years of our study, the more intensively grazed watershed (Coal Creek and tributaries) produced higher abundances and densities of age-0 trout than the less intensively grazed watershed (Water Canyon). This was likely because spawning habitat was controlled by geomorphic processes producing low-gradient reaches with appropriate size gravels in Huff Creek, a stream within a broad alluvial valley. Baxter and Hauer (2000) noted that spawning habitat for bull trout *S. confluentus* was also determined by basin geomorphology, especially by groundwater inputs. In contrast, habitat for older age-classes of fish consisted of refuge areas formed by woody debris, overhanging vegetation, undercut banks, and beaver impoundments. Livestock reduce such habitat directly by removing overhanging vegetation or by sloughing streambanks, or indirectly through cascading effects on beavers, which are unable to survive because of the lack of riparian trees. Without beavers and their impoundments, there are few opportunities for the formation of pool habitat in these headwater streams. In their analysis of cutthroat trout translocation success in Colorado and New Mexico, Harig and Fausch (2002) implicated beaver ponds in generating critical habitat features, namely, deep water that could be used as refuge by adult trout. Our results suggest that geomorphology, land use, and beaver activity interact to produce the patterns of fish abundance across multiple age-classes that are evident in the Thomas Fork drainage.

Given the patchy distributions of multiple age-classes through time and a heterogeneous distribution of habitats, it is tempting to consider whether Bonneville cutthroat trout in the study system exhibit the source–sink dynamics characteristic of a metapopulation. The existence of a metapopulation structure would mean that local extinctions in tributary streams could be balanced by immigration from nearby populations (Hanski and Simberloff 1996; Rieman and Dunham 2000). However, there appears to be sufficient movement of adult fish throughout the entire Thomas Fork drainage to preclude development of relatively isolated local populations (Schrank and Rahel 2004; Colyer et al. 2005).

Fausch et al. (2002) urged natural resource managers to adopt a riverscape perspective in managing stream fish assemblages. A major aspect of managing at larger spatial scales is recognizing that many stream fishes require access to a variety of habitat conditions to fulfill their life history requirements, a phenomenon known as habitat complementation (Schlosser 1995). The effects of complementary habitats were evident in our study, where the stream having the presence of both spawning areas and adult refuge habitat (Water Canyon) contained a higher abundance and broader size distribution of Bonneville cutthroat trout compared with the stream with spawning habitat present, but few pools and little riparian cover (Huff Creek). Management efforts will need to consider providing the full range of habitats needed by all life history stages if populations are to thrive. This can be achieved by ensuring that spawning and larval rearing habitat are adjacent to one another when implementing stream restoration projects or protection efforts. Alternatively, if complementary habitats are not in close spatial proximity—such as when adults reside primarily in the larger, downstream portions of rivers but migrate to spawn in small headwater tributaries—managers should strive to maintain migration corridors between habitats needed by different life history stages (Schlosser 1995; Schrank and Rahel 2004).

Our conclusions are tempered by the fact that our study consisted of only two adjacent watersheds, whereas the most appropriate spatial scale for examining the effects of land use and larger-scale geomorphology most likely consists of larger geographic regions and encompasses multiple populations of fish (e.g., Rahel and Nibbelink 1999). However, fish–habitat associations at the stream or patch scale—as examined in the present study—can further elucidate patterns of survival, reproduction, and persistence that are relevant to managers. Using model selection techniques to determine the appropriate spatial scale of measurement to predict cutthroat trout translocation success, Harig and Fausch (2002) found that the patch scale was most appropriate and that their finding corroborated the conclusions of studies of other salmonids and vertebrate taxa. Therefore, although our most conservative scope of inference involves only the Water Canyon and Coal Creek watersheds, interactions among geomorphology, land use, and beaver activity are likely to affect trout populations in other watersheds in the Rocky Mountain region.

Another aspect of managing from a riverscape perspective is recognizing the importance of refuge habitats during extreme environmental conditions. In our study, the watershed with less grazing intensity (Water Canyon) did not produce the highest numbers of age-0 Bonneville cutthroat trout each year, but it appeared that beaver activity and less-intense livestock grazing created a buffer from the effects of drought, allowing for age-0 trout production in years when other tributaries (Huff and Coal creeks) lack such production. If we are to manage for the long-term persistence of fish populations at the landscape scale, complementary habitats should be identified and given high priority for protection.

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