Effects of Habitat Area and Complexity on Colorado River Cutthroat Trout Density in Uinta Mountain Streams

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Abstract.—Habitat degradation has reduced the complexity and connectivity of streams on the north slope of the Uinta Mountains in northeastern Utah. These changes have diminished the historical range of Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus,* isolated the populations of this subspecies, and perhaps increased its risk of extinction. We assessed the effects of fragment area and habitat complexity on Colorado River cutthroat trout density. We studied 88 reaches in 4 isolated stream fragments. At the fragment scale, both the density of adults and habitat complexity increased significantly as fragment size increased. In the smaller fragments, the density of adults was lower while that of juveniles was higher. Habitat differed substantially among fragments. At the reach scale, the density of adults was positively related to elevation, the percentage of undercut banks, and mean substrate particle size and negatively related to residual pool depth and the extent of large woody debris. The density of juveniles was positively related to the extent of large woody debris and negatively related to residual pool depth and stream width. The habitat complexity index was weakly related to adult density at the reach scale. We were not able to distinguish the influence of habitat area or complexity on the density of adults, but a population living in an isolated stream fragment with low habitat complexity probably requires more area to persist than a population of the same size living in a highly complex habitat.

Historically, Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus* were widely distributed among the coldwater tributaries of the Green and upper Colorado rivers (Behnke and Benson 1980). Currently, these trout occupy less than 1% of their historical range (Behnke 1992). Federal and state agencies have responded to the species' decline by granting it special status. Colorado River cutthroat trout were classified as a Category 2 species (i.e., a candidate species for listing under the U.S. Endangered Species Act) by the U.S. Fish and Wildlife Service until that classification code was abolished in 1996. The U.S. Forest Service (in Regions 2 and 4) and the states of Colorado, Utah, and Wyoming have granted Colorado River cutthroat trout special management status. A petition has also been filed to list the species under the U.S. Endangered Species Act.

Habitat degradation has contributed to the decline of many salmonids throughout the western United States (Williams et al. 1989; Frissell 1993; Young 1995; Lee et al. 1997). Degradation can include habitat fragmentation and loss of habitat complexity. Habitat fragmentation results when a large area of habitat is subdivided into smaller, isolated patches (Wilcove et al. 1986) and is perhaps the most important problem threatening the survival of many species (Wilcox and Murphy 1985). Logging, mining, overgrazing, dams, and irrigation diversions have degraded aquatic habitats, eliminated migratory corridors, and isolated fish populations on the north slope of the Uinta Mountains in northeastern Utah (Kershner et al. 1997). Loss of migratory corridors and reduced habitat area may lead to local extinctions of cutthroat trout (Dunham et al. 1997).

Habitat quality is also important to populations of aquatic animals. Complexity is one aspect of habitat quality that is thought to influence the size, structure, distribution, and stability of populations. Complexity has been described in terms of structural components (McMahon and Hartman 1989), hydraulic variation (Lamberti et al. 1989; Pearsons

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et al. 1992), and the diversity of depth, velocity, and substrate (Gorman and Karr 1978; Angermeier and Schlosser 1989). Cutthroat trout abundance has been positively associated with habitat complexity (Fausch and Northcote 1992). Complex habitats may be necessary to meet all life history needs of cutthroat trout as well as to provide refugia during extreme environmental events (Connell and Sousa 1983; Poff and Ward 1990; Sedell et al. 1990). Moreover, complex habitats may lessen predation risk by reducing predator efficiency (Crowder and Cooper 1982).

Human activities have contributed to the loss of habitat complexity in Uinta Mountain streams. In the early 1900s, some drainages were logged, and succeeding floods often scoured stream channels to bedrock. Some of these streams still lack deep pools and late successional riparian vegetation, and streambeds are dominated by large, armored particles. The north slope of the Uinta Mountains has an extensive road network that is used for recreation and resource extraction. Poorly designed roads can affect aquatic biota by increasing sediment delivery to the stream, and improperly placed culverts can interfere with fish migration (Furniss et al. 1991). Many stream reaches are grazed by sheep and cattle. Stream reaches in the High Uintas Wilderness, however, have been less degraded than the downstream reaches, although this wilderness supports recreation and livestock grazing (Kershner et al. 1997).

Management activities on the north slope of the Uinta Mountains have created a range of conditions within and among streams. Our aim was to study the role of habitat complexity and habitat area on Colorado River cutthroat trout (CRCT) populations in second- and third-order streams. We focused our analysis at two spatial scales, stream fragment and stream reach. Multiple-scale studies are important to better understand fish–habitat relations, as different spatial scales have unique physical and biological roles in the stream system (Frissell et al. 1986). Analyses that address both the stream and reach scales may also identify whether each scale affects a population independently or interactively (Dunham and Vinyard 1997).

A stream fragment was defined as all contiguous streams and tributaries in a watershed that are physically isolated from other streams. Stream fragments vary geomorphically and vegetatively from the headwaters to downstream areas, thereby influencing the physical and chemical components of instream habitats. Habitat diversity, which typically varies over the entire length of a stream, can affect the abundance, structure, and distribution of a population. Studies at the fragment scale are often a useful means of assessing basinwide changes.

Our first objective was to examine the relation of fragment area to the size and density of juvenile and adult CRCT. Many studies have looked at the effect of habitat area on animal density (Bender et al. 1998), but few have done so for fish (Lanka et al. 1987; Kozel and Hubert 1989). We also wished to test the merit of an index of habitat complexity in predicting adult density, describe habitat differences among study fragments, and evaluate fish–habitat relations.

We defined stream reaches within fragments as lengths of stream having homogeneous morphological features that we evaluated qualitatively. Analyses done at the reach scale are useful for describing population characteristics (e.g., juvenile and adult density) as well as the physical variation within the reach, which can affect the temporal and spatial condition of channel form and fish habitat. At the reach scale, our objectives were to determine the most important variables for juvenile and adult CRCT and to test the index of habitat complexity against adult density.

Study Area

The Uinta Mountains are an east-west range on the Utah–Wyoming border. This study included all of the streams on the north slope of these mountains within Wasatch-Cache National Forest that contained allopatric populations of CRCT (Utah Division of Wildlife Resources, unpublished data; K. Johnson, Wyoming Department of Fish and Game, personal communication). We limited our study to allopatric populations because the habitat use and growth of CRCT may be affected by nonnative trout (Thomas 1996). We located six streams that formed four isolated stream fragments (Kershner et al. 1997).

The largest fragment, East Fork Blacks Fork (EFBF), contained the East Fork and the Little East Fork Blacks Fork, which are third-order streams. Meeks Cabin Reservoir is downstream of the confluence of these two streams, and the dam that forms the reservoir is a barrier to migration. We sampled these streams and their tributaries from the headwaters to their confluence, at which time the stream was fourth-order and too large to sample with the available crew and equipment. Archie Creek and West Fork Smiths Fork (WFSF) formed the second-largest fragment. The CRCT populations in these second-order streams are isolated from other CRCT populations as a result of down-

TABLE 1.—Range of means for measured variables at study sites in the Uinta Mountains, Utah. Six variables (indicated by asterisks) were selected a priori to test the hypothesis that these attributes are important to Colorado River cutthroat trout. One of these, hydraulic retention, was later dropped.

Variable	Range of means
Bank stability (%)	8–100
Channel classification type[a]	A1–C5
Channel depth (m)	0.07–0.49
Elevation (m)	2,591–3,340
Gradient (%)	0–15
Hydraulic retention* (s/m)	3.7–137.0
Large woody debris, aggregates (m^3)	0.0–165.8
Large woody debris, single logs* (pieces)	0–23
Residual pool depth* (m)	0.12–0.54
Pool habitat* (%)	3–75
Riffle–run habitat (%)	25–97
Particle size* (mm)	1–2,899
Undercut bank* (%)	0–100
Wetted width (m)	1.1–8.3

[a] Based on Rosgen scale (Rosgen 1985).

stream dewatering on private land. We sampled WFSF from the headwaters to the U.S. Forest Service property line. Willow Creek, the smallest fragment, is also a second-order tributary to West Fork Smiths Fork. We sampled Willow Creek from the headwaters to the U.S. Forest Service property line. Willow Creek becomes uninhabitable to fish below the property line owing to dewatering on private land (private landowner, personal communication). Dahlgreen Creek, the fourth fragment, is a second-order tributary to the Henrys Fork drainage. We sampled Dahlgreen Creek from its headwaters to a point above its confluence with Henrys Fork River, where the channel goes subsurface for 2.4 km. The Henrys Fork River drains into Flaming Gorge Reservoir. Two reaches (totaling 1.7 km) in Dahlgreen Creek could not be

sampled because beavers *Castor canadensis* had dammed the stream and turned the channel into a deep, silty run. Other native fish present in the study streams included mountain whitefish *Prosopium williamsoni,* mottled sculpin *Cottus bairdi,* mountain sucker *Catostomus platyrhynchus,* and longnose dace *Rhinichthys cataractae.*

Methods

Habitat survey.—We conducted habitat surveys during summer base flows on the lower half of WFSF in 1992. We sampled Dahlgreen Creek and the upper half of WFSF in 1993 and Willow Creek and EFBF in 1994. We walked each stream and delineated reaches based on qualitative changes in the following geomorphic variables: gradient, substrate particle size, sinuosity, and valley confinement (Rosgen 1985). Within each of the 88 reaches, we randomly chose a 100-m site to represent the reach. For reaches longer than 1 km, we randomly chose additional sites to ensure that at least 10% of the stream length was sampled. We measured several habitat variables at each site (Table 1) and determined the elevation and gradient of each reach with U.S. Geological Survey 1:24,000 maps.

Six habitat variables were chosen a priori to measure habitat quality: percent of pool habitat (based on surface area), residual pool depth, percentage of undercut bank, extent of large woody debris (pieces), particle size, and hydraulic retention. We chose these six variables because reports in the literature described their importance to fish abundance and life history. We partitioned each 100-m site into discrete habitat units of pool, riffle, or run (Hawkins et al. 1993). These habitat types differed in velocity, depth, and substrate particle size, thereby affecting the suitability of the habitat

TABLE 2.—Pearson correlation coefficients for 11 habitat variables at study sites in the Uinta Mountains, Utah. Values in bold italic indicate correlated variables. Asterisks denote significance ($P < 0.05$); LWD = large woody debris.

Variable	N	Variable						
		1	2	3	4	5	6	7
1 Undercut bank (%)	88							
2 Pool habitat (%)	88	0.46*						
3 Particle size (cm)	88	0.10	−0.11					
4 Hydraulic retention (s/m)	76	−0.29*	−0.14	*−0.50**				
5 LWD, pieces	88	−0.21*	−0.21*	0.03	0.14			
6 Residual pool depth (m)	83	0.22*	0.07	0.07	−0.19	−0.25*		
7 Mean depth (m)	88	0.45*	0.41*	−0.03	−0.31*	−0.35*	0.45*	
8 Elevation (m)	88	0.34*	0.20	0.15	−0.36*	−0.42*	−0.15	0.46*
9 Gradient (%)	88	−0.17	−0.20	0.16	−0.02	0.22*	−0.27*	−0.29*
10 LWD, aggregates (m^3)	87	0.14	0.09	0.20	−0.23*	0.38*	−0.11	0.04
11 Wetted width (m)	88	0.27*	0.18	0.43*	*−0.68**	−0.12	0.23*	0.27*

for different life stages of salmonids. Maximum and tail depths of pools were measured to calculate residual pool depth (maximum depth less tail depth; Lisle 1987). Residual pool depth is a useful measure because it is independent of discharge and thus allows comparisons of depth among streams of different sizes. Fausch and Northcote (1992) found that yearling and adult salmonid biomass was most strongly correlated with pool volume and depth. Heggenes et al. (1991) found that larger cutthroat trout used deeper water. In four streams in western Washington, Bisson et al. (1982) reported that older trout preferred deeper water, whereas juveniles avoided it.

We measured the total length of undercut bank (≥10 cm horizontally undercut) of each habitat unit. Undercut banks are an important cover type in streams, and studies have shown that increases in cover can yield an increase in salmonid abundance (Boussu 1954; McMahon and Hartman 1989). Heggenes et al. (1991) reported that coastal cutthroat trout *Oncorhynchus clarki clarki* used overhead cover more frequently than instream cover, and undercut banks were the preferred overhead cover type.

We counted and measured large woody debris (LWD) within the bank-full channel. Single pieces of LWD were at least 10 cm in diameter and more than 3 m long. The various functions of woody debris make it an important component of aquatic systems. Instream wood provides cover for fish as well as a substrate for macroinvertebrate colonization, which provides a food source for fish. It also affects channel morphology and in some streams is the dominant pool-forming structure (Andrus et al. 1988; Fausch and Northcote 1992).

We measured substrate particle size in two randomly chosen slow units (pools) and two fast units

(riffles or runs) at each site. Each of these habitat units was divided into thirds by two transects perpendicular to stream flow. We selected 20 particles along each transect and measured the longest axes to the nearest 0.5 cm. Salmonids use substrate particles as cover and as locations for feeding and spawning.

We measured hydraulic retention in the same four units by introducing fluorescent dye at the upstream end of the habitat unit (Lamberti et al. 1989). Dye was continually applied until it visibly extended throughout the unit. We defined hydraulic retention as the time it took the thalweg to be visually clear of dye divided by the length of the unit. High retention rates are one measure of channel complexity because high rates may indicate variable stream hydraulics and channel shape, along with the presence of boulders or woody debris (Lamberti et al. 1989). Hydraulic retention was not measured in the lower WFSF.

We also measured the length, wetted width, and depth of each habitat unit within the site. Bank stability within the site was qualitatively evaluated and measured. We measured aggregates of LWD, which we defined as two or more single pieces of LWD that were in contact and trapping instream debris. Water temperature was measured in Willow Creek and EFBF only.

Habitat complexity.—We developed a habitat complexity index to quantify habitat quality within each site (see Kershner et al. 1997). We calculated the mean complexity of each site and then computed an overall mean for all reaches within each fragment. In our model, we assumed that all variables were equally weighted and independent. We tested for variable independence with correlation analysis. Variables that had a correlation coefficient less than 0.50 were considered independent (Table 2). Because hydraulic retention was correlated with particle size, it was omitted from the model. We chose to eliminate hydraulic retention and not particle size because hydraulic retention was measured over a relatively short distance (the habitat unit) and probably did not provide a good estimate of retention time over a long area, such as the reach. Because hydraulic retention was also correlated with wetted width, we eliminated hydraulic retention from all further analyses.

In previous work, we created a single model for both juvenile and adult cutthroat trout (Kershner et al. 1997). Because juveniles and adults often require different habitat conditions (Cunjak and Power 1986; Moore and Gregory 1988; Bozek and Rahel 1991; Fausch and Northcote 1992; Nickel-

TABLE 2.—Extended.

Variable	Variable		
	8	9	10
1 Undercut bank (%)			
2 Pool habitat (%)			
3 Particle size (cm)			
4 Hydraulic retention (s/m)			
5 LWD, pieces			
6 Residual pool depth (m)			
7 Mean depth (m)			
8 Elevation (m)			
9 Gradient (%)	0.25*		
10 LWD, aggregates (m^3)	−0.04	−0.07	
11 Wetted width (m)	0.11	−0.21	0.30*

son et al. 1992), we revised the complexity index to model only adult density. Our assumption in the original model was that more complex habitats would have higher values for each habitat variable (i.e., that more would be better). Upon further review, we hypothesized that less of some attributes would be more favorable. As a result, we modified the model as follows: Variables that were expected to be positively related to fish density were given a maximum scaled value of 100 (Kershner et al. 1997), whereas the values of variables that were expected to be negatively related were subtracted from 100.

Colorado River cutthroat trout.—We sampled CRCT at each site with a backpack electroshocker. We used nets to block the upstream and downstream ends of the site to prevent fish from entering or leaving and made a minimum of three passes. In 1994 we recorded the number of CRCT captured during each electrofishing pass, but in previous years we did not separate them by pass. We weighed each fish to the nearest gram and measured fork length to the nearest millimeter. Young –of –the year (<40 mm) were not collected. Other fish species were identified and counted.

We used two life stage classes based on a length-frequency histogram of all CRCT captured: Juveniles ($N = 819$) were 125 mm long or less, and adults ($N = 1,148$) were more than 125 mm long. Juvenile and adult densities (number per 100 m^2) were calculated for each site. We assumed total depletion due to the lack of information on fish captured per pass at all sites. Fragment density was estimated by averaging densities of all sites within the fragment.

Data Analysis

Fragment Scale

We used correlation analysis to test the relation between fragment size (i.e., wetted stream area) and fish size and density as well as to test the association between habitat complexity and adult density. We used analysis of variance (ANOVA) to test for habitat differences among fragments, and we used the Tukey–Kramer multiple-comparisons method to control the experimentwise error rate because that method is robust for unequal sample sizes (SAS Institute 1993). We used analysis of covariance (ANCOVA) to test whether relations between site-scale habitat variables, including the habitat complexity index, and juvenile and adult CRCT density differed among fragments. The advantage of ANCOVA is that it considers site-scale and fragment-scale variability

within the same analysis (Dunham and Vinyard 1997) by simultaneously comparing simple linear regression equations among the four fragments and by providing hypothesis tests for differences in slope and intercepts among the fragments (Hamilton 1992). First, ANCOVA was run with the interaction term, which tested for fragment × site interactions. Models that had statistically significant interaction terms indicated that there was an interaction between fragment and site. In those cases we ran simple linear regression models for each fragment separately to identify which fragments were different. Next, significant ANCOVA models that had insignificant interaction terms were rerun without the interaction terms to test for fragment-scale effects. A rerun model that was not significant implied that the regression lines of the four fragments were identical; a model that was significant implied that there was a difference among the intercepts. Owing to our small sample size, significance for all results at the fragment scale is defined as $\alpha \leq 0.10$ unless otherwise indicated. Statistical analyses were conducted with SAS for Microsoft Windows, version 6.1 (SAS Institute 1993).

Reach Scale

We developed a multiple-regression model to predict juvenile and adult CRCT trout density from five habitat variables (Table 1). Several variables had to be transformed ($\log_{10}[x + 1]$) to correct for nonnormality (Zar 1984): juvenile and adult density, percent of undercut bank, pool habitat, and LWD. Diagnostic tests indicated that one site in Willow Creek was an influential outlier (Figure 1). After that site was removed, diagnostic tests revealed no statistical problems with the model (e.g., autocorrelation, heteroscedasticity, multicollinearity, or outliers). We compared the results of the multiple-regression model to a stepwise regression model with forward selection and five additional habitat variables (gradient, elevation, LWD aggregates, mean depth, and wetted width). We used simple linear regression to test whether the habitat complexity index could predict adult density. Significance for all results at the reach scale is defined as $\alpha \leq 0.05$ unless otherwise indicated.

Results

Fragment size was positively correlated with juvenile length ($r = 0.95$, $P = 0.05$), adult length ($r = 0.99$, $P = 0.01$), and adult density ($r = 0.92$, $P = 0.08$), but it was not related to juvenile density. The lengths and weights of juveniles were significantly correlated with one another ($r = 0.92$,
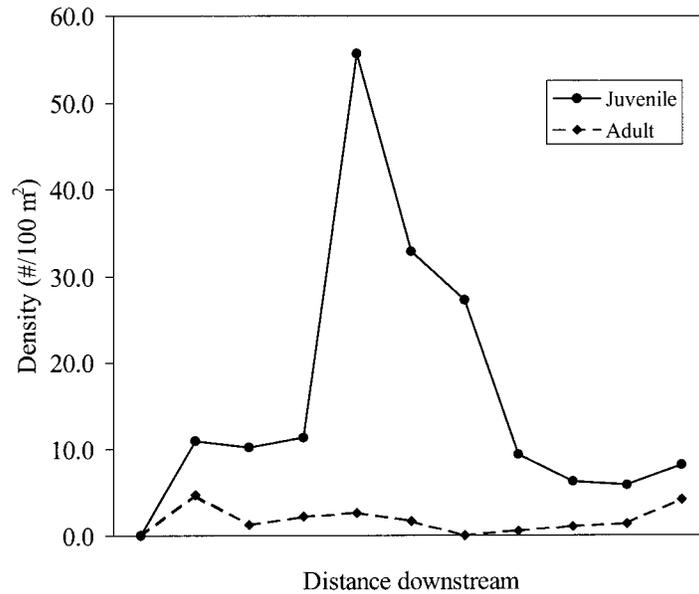
FIGURE 1.—Density of juvenile and adult Colorado River cutthroat trout in Willow Creek, Utah. Each point represents a 100-m sample site. Site 5 was immediately upstream of a beaver pond and was eliminated from all analyses after statistical diagnostic tests identified it as an influential outlier.

$P = 0.08$), as were the lengths and weights of adults ($r = 0.99$, $P = 0.005$). Juvenile density was significantly greater in Willow Creek than in other areas, and adult density was significantly greater in EFBF ($P \leq 0.10$; Table 3). Adult density was correlated with the complexity index at the fragment scale, but the relation was not significant ($r = 0.89$, $P = 0.108$).

All habitat variables except gradient were significantly ($P < 0.05$) different among fragments (Table 4). The largest fragment, EFBF, had nearly 50% more undercut bank, 17% more pools, and 29% larger mean particle size, but 20% fewer pieces of large woody debris per site than any other fragment (Table 5). Willow Creek, the smallest fragment, had 130% more LWD than the fragment with the next largest quantity but less undercut bank and pool habitat and a smaller mean particle size than any of the other fragments. The complexity index score was highest for EFBF and lowest for Willow Creek. Habitat complexity was highly correlated with fragment size ($r = 0.97$, $P = 0.01$). Water temperatures ranged from 8.5°C to 22.5°C in Willow Creek, which was sampled the last week in June. East Fork Blacks Fork was sampled in July and August, and temperatures ranged from 4.0°C to 19.5°C.

Cutthroat trout and habitat relations were, for

TABLE 3.—Mean length, weight, and density of Colorado River cutthroat trout in four fragmented stream systems: Willow Creek (WILL), Dahlgreen Creek (DAHL), West Fork Smiths Fork (WFSF), and East Fork Blacks Fork (EFBF). Standard errors are in parentheses; density values within an age-class that are followed by the same letter are not significantly different ($P > 0.10$).

Frag-ment	N	Juveniles			Adults		
		Length (mm)	Weight (g)	Density (fish/100 m^2)	Length (mm)	Weight (g)	Density (fish/100 m^2)
WILL	10	86.4	8.56	12.2 y	145.4	36.6	1.7 y
		(4.0)	(0.9)	(3.2)	(3.3)	(2.2)	(0.5)
DAHL	7	91.2	9.0	5.3 y	149.3	37.1	0.9 y
		(5.1)	(1.6)	(2.3)	(4.4)	(2.8)	(0.4)
WFSF	41	95.4	10.0	1.7 x	171.1	56.6	2.1 y
		(2.3)	(0.6)	(0.3)	(2.8)	(2.9)	(0.4)
EFBF	30	100.7	13.7	1.5 x	183.7	70.4	6.0 z
		(2.1)	(0.5)	(0.2)	(2.5)	(2.8)	(0.8)

TABLE 4.—Results of analysis of variance for differences in habitat variables among stream fragments in the Uinta Mountains, Utah (df = 3). Values are F-statistics; all variables except gradient show significant ($P < 0.05$) differences across fragments; LWD = large woody debris.

Variable	F
Undercut bank	5.3
Pool habitat	3.5
Particle size	5.6
LWD, pieces	5.1
Residual pool depth	6.9
Mean depth	12.3
Gradient	1.7
LWD, aggregates	2.8
Wetted width	18.3
Complexity index	18.1

TABLE 6.—Significance values for analyses of covariance that did not reveal significant reach × fragment interactions. Asterisks denote significant ($P < 0.10$) interactions between reach and fragment. The symbol n/a means not applicable; LWD = large woody debris.

	Adult density		Juvenile density	
	Site effect	Fragment effect	Site effect	Fragment effect
Undercut bank	*	*	0.97	0.0001
Pool habitat	0.01	0.0001	0.97	0.0001
Particle size	0.95	0.0001	0.48	0.0001
LWD, pieces	0.0001	0.0001	0.02	0.0001
Residual pool depth	*	*	0.25	0.0001
Complexity index	0.0007	0.0002	n/a	n/a

the most part, influenced by fragment effects. Only two ANCOVA models showed significant reach × fragment interactions: adult density with undercut bank and adult density with residual pool depth (Table 6). We examined plots of adult density versus undercut bank and residual pool depth and noted that in EFBF the density of adult CRCT was negatively related to percentage of undercut banks whereas there were strong positive associations in the other three fragments. The plot of adult density versus residual pool depth indicated that there were negative correlations in both EFBF and WFBF. We eliminated the EFBF data and reran the ANCOVA models that had reach × fragment interactions. In the model of adult density versus undercut banks, the interaction became insignificant, but in the model of adults versus residual pool depth the significant interaction remained. Because EFBF showed a strong effect in these two analyses, we decided to rerun the other models

without EFBF data. Except for the complexity index, each of the adult models changed from having significant to having insignificant fragment effects, whereas the juvenile models remained unchanged.

At the reach scale, estimated densities of adult CRCT ranged from 0.0 to 17.7/100 m². Adult density was positively related to undercut bank and mean particle size, and negatively related to residual pool depth and LWD (Table 7). The model explained 46% of the variation in adult density. The stepwise model explained more of the variation in adult density ($R^2 = 0.61$); adult density increased with increases in elevation, percent of undercut bank, and particle size and with decreases in channel depth and LWD (Table 8). Further analysis indicated a significant correlation between elevation and adult density ($r = 0.71$, $P = 0.0001$). The habitat complexity index was positively related to adult CRCT density (Figure 2), but it was not a strong predictor of adult density ($r = 0.29$, $P < 0.0001$).

TABLE 5.—Physical characteristics of four fragmented stream systems: Willow Creek (WILL), Dahlgreen Creek (DAHL), West Fork Smiths Fork (WFSF), and East Fork Blacks Fork (EFBF). The symbol N represents the number of sections sampled in each fragment. Elevation is the range in which sampling was done. Habitat complexity is based on a five-variable model. Standard errors for mean values are in parentheses; LWD = large woody debris.

	WILL	DAHL	WFSF	EFBF
N	10	7	41	30
Total area (m²)	13,570	14,276	79,675	136,558
Total length (km)	7.4	6.6	23.0	27.3
Elevation (m)	2,591–2,908	2,713–2,926	2,633–3,276	2,865–3,340
Mean gradient (%)	6 (0.6)	3 (0.6)	4 (0.4)	4 (0.6)
Mean width (m)	1.8 (0.1)	2.2 (0.1)	3.5 (0.2)	5.0 (0.3)
Mean depth (m)	0.10 (0.01)	0.14 (0.01)	0.18 (0.01)	0.21 (0.01)
Mean residual pool depth (m)	0.18 (0.01)	0.21 (0.02)	0.30 (0.02)	0.26 (0.01)
Mean undercut bank (%)	5 (0.7)	8 (2.2)	10 (2.3)	15 (1.7)
Mean pool habitat (%)	21 (2.5)	26 (6.0)	22 (1.7)	31 (2.6)
Mean particle size (cm)	10.8 (1.4)	12.6 (1.3)	13.5 (0.7)	17.4 (1.2)
Mean LWD (pieces/100 m)	11.5 (2.8)	5.0 (1.9)	3.6 (0.7)	3.0 (0.7)
Habitat complexity	34 (3.4)	40 (4.5)	50 (1.8)	63 (1.6)

TABLE 7.—Results of regression analyses testing five habitat variables related to Colorado River cutthroat trout density at the reach scale. All regression coefficients are statistically significant ($P < 0.05$); LWD = large woody debris.

Response variable	Explanatory variables	df	Coefficients	R^2
Adult density	Intercept	70	0.63	0.46
	Undercut bank		0.39	
	Particle size		0.02	
	Residual pool depth		−0.84	
	LWD, pieces		−0.24	
Juvenile density	Intercept	82	0.79	0.12
	Residual pool depth		−1.27	

Juvenile CRCT densities ranged from 0.0 to 32.8/100 m². The best multiple-regression model for juveniles had one significant variable, residual pool depth, and only explained 12% of the variation in juvenile density. In the stepwise model, juvenile CRCT density was related positively to LWD and negatively related to residual pool depth and channel width. The stepwise model for juvenile density was slightly better than the multiple-regression model, explaining 20% of the variation in juvenile density.

Discussion

Fragment Scale

Both adult CRCT density and habitat complexity increased significantly as fragment size increased. Although this pattern has been noted in studies of insects and birds (see Connor et al. 2000), some aquatic studies have shown a decrease in trout density as stream size increased. In systems where interspecific predation was not a causal factor, the decrease in density was explained by either reduced riparian cover and increased human disturbance (Lanka et al. 1987) or a decline in habitat quality (Kozel and Hubert 1989). Poor habitat quality was not a characteristic of the largest fragment, EFBF, which had the best adult habitat,

highest adult densities, and the highest complexity score.

There are several possible explanations for the significantly higher adult densities in EFBF. First, the EFBF drainage is a large, well-connected stream system that becomes fourth order before flowing into Meeks Cabin Reservoir. Large habitat areas can provide a population with more habitat diversity and more food resources, thereby supporting more individuals (Williams 1964). Second, the streams and tributaries in this fragment have higher-quality habitat than those in the lower-elevation fragments, which have been subjected to more intense management activities (Kershner et al. 1997). High-quality habitats may increase survival rates for salmonids. Finally, there is evidence that resident CRCT may move large distances, often to deeper water (Young 1996), to maximize survival (Fausch and Young 1995); hence, Meeks Cabin Reservoir may function as a winter refugium.

East Fork Blacks Fork had a significant effect on our analyses of fish–habitat relations with adult CRCT. Adult CRCT responded differently to habitat attributes in EFBF than they did in other fragments. Unfortunately, our fragment-scale analyses were handicapped by a small sample size and the

TABLE 8.—Results of stepwise regression analyses of Colorado River cutthroat trout density on eight habitat variables at the reach scale. Variables are listed in the order in which they entered the model. Asterisks denote significance ($P < 0.05$); LWD = large woody debris.

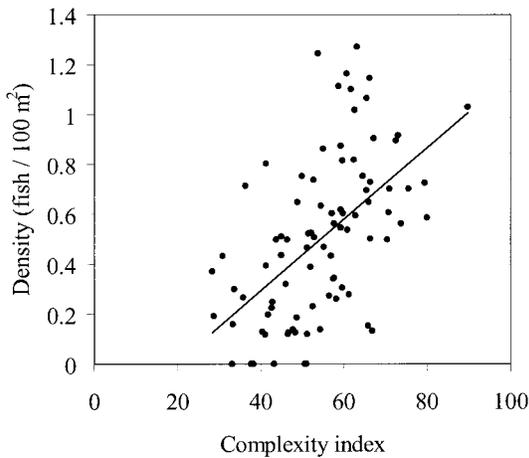| Response variable	Explanatory variables	df	Coefficients	Model R^2	Partial R^2
Adult density	Intercept	80	−2.52*	0.61	0.48
	Elevation		0.0003*		0.07
	Undercut bank		0.34*		0.015
	LWD, pieces		−1.12*		0.015
	Particle size		0.02*		0.03
	Mean depth		−1.87		
Juvenile density	Intercept	80	0.75*	0.20	
	Residual pool depth		−0.85*		0.12
	Mean width		−0.04*		0.05
	LWD, pieces		0.16*		0.03

FIGURE 2.—Density of adult Colorado River cutthroat trout ($\log_{10}[x + 1]$ transformed) plotted against the habitat complexity index at the reach scale.

significant influence of EFBF. The inclusion of EFBF in this study is critical, however, because it highlights the contrasting conditions that exist among habitat fragments in the study area.

Adult habitat appeared to be limiting in the smaller fragments, Willow and Dahlgreen creeks, based on measured habitat attributes and what we thought determined habitat complexity. Willow Creek is a comparatively small stream that may lack adequate cover for adult fish within most of the channel. It is relatively shallow, has a small-particle substrate, and lacks stable, vegetated undercut banks. Bank collapse and sloughing within Willow Creek is partly the result of the logging and cattle grazing that have occurred in the drainage.

There are active and remnant beaver complexes in the lower-elevation sites of Willow Creek. Landowners who required water for irrigation routinely destroyed beaver dams 20–30 years ago to increase downstream flows (private landowner, personal communication). Fines continue to erode into the stream even though many of these decadent complexes are now well vegetated. The percentage of fines was not estimated as a habitat variable, but our field books describe the excess of silt that covers the substrate. Although spawning adults are able to remove fine sediments from the egg pocket during redd construction (Young et al. 1989), emergence success may be compromised by the amount of fine sediments (Weaver and Fraley 1993) that settle onto redds during base flows.

Water temperatures in Willow Creek approached lethal limits for fish during late-June sampling.

Most salmonids are in danger at temperatures above 23–25°C (Bjornn and Reiser 1991), and we observed temperatures as high as 22.5°C. A rise in temperature stimulates fish metabolism and has a negative effect on swimming performance and feeding rate (Wootton 1990; Meeuwig 2000). Fish sampling had to be restricted to early morning to ease the stress compounded by electrofishing and high temperatures.

In spite of the poor habitat conditions that we observed in Willow Creek, it had significantly higher juvenile densities than any other fragment. There are several explanations for this pattern, some of which are contradictory. First, it is possible that Willow Creek is not limited in terms of juvenile habitat. Studies of salmonids indicate that young fish prefer slow, shallow water (Bozek and Rahel 1991), and these qualities are characteristic of Willow Creek. The small pools in Willow Creek may provide key habitat for small fish because they are undisturbed by competition from the larger, seemingly absent, adults. Second, it is conceivable that a large population of adult CRCT resides in beaver ponds in Willow Creek, and these adults produce large numbers of juvenile fish (see Schlosser 1995). Third, we may have overestimated the minimum size of adult fish; some fish that we thought were juveniles may actually be mature, spawning adults. Fourth, it is possible that the high densities of juveniles are not related to habitat quality in Willow Creek (e.g., Van Horne 1983). Small, isolated populations are able to persist for extended periods for reasons we do not understand (Stacey and Taper 1992). Lacking long-term demographic data, we cannot know how variable the population size and structure in Willow Creek are (Platts and Nelson 1988).

Dahlgreen Creek had the lowest density of adult trout in the study, and fewer juveniles than were observed in Willow Creek. Beavers lived in the lower sites of Dahlgreen Creek, and we were unable to sample fish in two sites because their entire lengths (totaling 1.7 km) consisted of deep, silty runs created by beaver dams. Our estimate of fish density in Dahlgreen Creek might have been higher if we had included fish living in those two sites. Because we could not collect fish from those sites, we also did not measure habitat variables. Dahlgreen Creek had low mean values for pool depth and undercut bank and a low complexity index score. Mean values of depth, pool depth, and undercut bank would have been higher had we measured habitat in the long beaver runs.

West Fork Smiths Fork was a fragment that had

properties similar to the other fragments: higher-quality habitat in the upstream sites and visible effects of land use in the lower sites. The wilderness sites of WFSF had high-quality habitat, and we observed the highest densities of adults in two meadow sites with deep, stable undercut banks (Kershner et al. 1997). Except for these two sites, juvenile trout density was greater in almost every other site within the wilderness. Because the spatial distribution of juvenile trout is often related to the availability of spawning and rearing habitats (Beard and Carline 1991), we assume that the upstream sites of WFSF provided high-quality habitat for the juveniles and adults of this population. Habitat quality in WFSF is dramatically reduced below the wilderness boundary, which is probably the result of historical tie-drive logging, grazing, and riparian road construction.

Reach Scale

Adult CRCT densities were highest in sites that had large substrate particles and a high percentage of undercut bank. Boulders and undercut banks are important cover types (Behnke and Zarn 1976), and previous studies have shown increases in salmonid abundance with increased cover (Boussu 1954; McMahon and Hartman 1989). Heggenes et al. (1991) reported that cutthroat trout in a small, coastal stream in British Columbia used overhead cover more frequently than instream cover and that undercut banks were the preferred overhead cover type. In contrast, Young (1996) reported that CRCT in south-central Wyoming appeared to use cover infrequently, and Wilzbach (1985) observed that cover was less important than prey availability to adult cutthroat trout in Oregon. Adults in the upper sites of WFSF were especially influenced by undercut banks in low-gradient, meadow sites (Kershner et al. 1997).

Adult CRCT density was positively related to elevation, as indicated by the stepwise regression model. In a study comparing wilderness and nonwilderness sites, Kershner et al. (1997) reported significantly more adult fish in the high-elevation, wilderness sites. There are many explanations for the positive effect of elevation on density. First, the high-elevation sites in our study area were of higher quality and had been less exposed to habitat degradation from management activities than the lower sites (Kershner et al. 1997). Second, cutthroat trout are vulnerable to angling (Behnke and Zarn 1976), and the larger fish may have been removed from the more accessible, low-elevation sites (Thurow and Bjornn 1978). Third, water temperature, an important abiotic factor for salmonids, typically decreases as elevation increases. Rieman and McIntyre (1995) found that the presence of bull trout *Salvelinus confluentus* was related to elevation because of a presumed restriction of stream temperature on local populations.

Adult density was negatively related to woody debris and residual pool depth. The smaller, low-elevation sites had the most woody debris and lower adult densities. Woody debris did not form pools at low flows because most of the wood was outside the wetted channel. In sites where adult densities were high and wood was absent, other stream features provided good habitat. Although channels tend to scour during high flows, some channels change very little during flooding periods (Leopold et al. 1964). Channel scour can be influenced by roughness elements within and across the channel, such as wood and large boulders. In EFBF, where the channel had a large mean particle size, the bed may have been more resistant to forming deep, scoured pools.

Juvenile trout density was negatively related to residual pool depth and mean width. Young trout often occupy habitats in slow, shallow stream sections (Griffith 1972; Cunjak and Power 1986), and we found the highest densities of juvenile CRCT in sites with narrow channels and low mean depth. There were significantly fewer juveniles in WFSF and EFBF than in the other fragments. The sites in EFBF had the highest mean width and depth in the study. The low densities in EFBF may be explained by the difficulty inherent in sampling wide, deep streams (Rodgers et al. 1992) or by the possibility that young fish were in the small tributaries to EFBF that we assumed were fishless.

We observed a weak positive association between juveniles and LWD. We measured wood in the bank-full channel and noted that most pieces were outside the wetted channel. Large wood that is in contact with the channel during high spring flows can have a substantial influence on base flow habitats. Large wood reduces currents (Moore and Gregory 1988; McMahon and Hartman 1989); affects sediment routing, scour, and deposit (Beschta and Platts 1986); and may channel water toward the banks, creating lateral habitats (Carlson et al. 1990; Bozek and Rahel 1991). In EFBF, where juvenile density was the lowest, woody debris was least abundant and most trees spanned the channel upon falling. Had these logs entered the channel, they may have been more effective in creating juvenile habitat.

Complexity Index

The habitat complexity index was not related to adult density at the reach scale. Several interpretations of these data are possible. First, habitat complexity may be important to CRCT, but we failed to adequately describe it. We chose a suite of variables that, based on previous studies, appeared important to salmonids. Although each of the variables in the complexity index was related to density, there was an increase in density with some variables and a decrease with others. Even though we tried to correct for them, these offsetting tendencies may have been partly responsible for the lack of a relation between density and habitat complexity. In addition, variables not measured in this study (e.g., velocity, prey availability, and spawning habitat) may have been more useful in predicting adult density.

Second, electrofishing sampling efficiency is affected by habitat complexity and stream size (Heggenes et al. 1990). In complex pools, for instance, fish not captured on the first pass may hide under deep-cut banks or within rootwads and thereby avoid capture on subsequent passes (Rodgers et al. 1992). Wide, deep streams allow fish an even greater chance to escape capture and detection. It is probable that we underestimated trout density, especially within the most complex sites.

Third, habitat complexity may not be the most important factor influencing fish density. We assumed that high-quality, complex habitat was the most important factor affecting density. In a Minnesota stream, Schlosser (1995), found less than 5% of the variation in fish abundance in pools and riffles (microhabitat scale) was explained by habitat complexity. He reported that seasonal and annual environmental variation was more important in influencing fish abundance. Factors that we did not measure, such as food (Wilzbach 1985), may be more important to fish at finer scales.

At a larger scale, CRCT density may be determined by landscape features such as channel type, elevation, or stream order. Each of those factors may affect density because of the biological and physical differences associated with it. We might have seen a better relation between density and the complexity index if we had stratified our analyses by those features.

Summary

At the large scale, both habitat area and complexity appeared to be important to CRCT. However, the combination of area and complexity may

be more important to a population than either factor alone (Boecklen 1986; Angermeier and Schlosser 1989). A population living in a stream fragment with low habitat complexity may require more area to persist than a population of the same size living in a highly complex habitat. When a population encounters both reduced habitat area and less complexity, it may undergo losses in life history strategies, genetic variation, and population size, all of which may lead it to extinction (Dunham et al. 1997). Because extinction risk is assumed to be inversely related to population size (Connor and McCoy 1979), these small, closed populations will be under increased risk if they are subjected to even moderate levels of environmental stochasticity (Stacey and Taper 1992). A large range of fragment sizes at varying degrees of complexity are needed to test the hypothesis that habitat complexity compensates for small fragment size. Unfortunately, there were a limited number of allopatric populations of CRCT in our study area. Not only were we restricted to four fragments with widely differing stream sizes, there was considerable disparity in the number of sites within each fragment.

Habitat fragmentation compounds the threat to populations that have experienced losses in habitat area and complexity. Historically, CRCT populations were not restricted to small, headwater streams such as Willow and Dahlgreen creeks, and fish could move within and among drainages such as WFSF and EFBF. Adult fish, especially the larger, fluvial forms, often use small headwater tributaries for spawning and move downstream to deeper waters as flows recede (Reice et al. 1990; Rieman and McIntyre 1993). There is evidence that salmonids can move great distances (Fausch and Young 1995), and when we eliminate migration corridors, dispersal, and recolonization for migratory life histories, the effects of habitat fragmentation can be severe. Dunham et al. (1997) found that stream connectivity was the most important factor affecting the presence of Lahontan cutthroat trout *Oncorhynchus clarki henshawi*. Bull trout also appear to be sensitive to fragment size and will be vulnerable to extinction if fragmentation continues to limit their range, especially in small headwater streams (Rieman and McIntyre 1995).

Populations that have resident and migratory forms may have a greater chance at long-term persistence (Northcote 1992), but as fragmentation increases, a resident population may suffer more of a decline than one with a migratory life history

strategy (Doak et al. 1992). It is unknown whether the CRCT in this study have a migratory life history form and, if so, how far they may have moved. Nonetheless, juveniles and adults in Willow and Dahlgreen creeks are now confined to a smaller area than their historical range and must meet all of their life history requirements within the same restricted area. We need to know how mobile these populations previously were before we assess the effects of fragmentation in the Uinta Mountains (Doak et al. 1992), as isolation alone will not lead to extinction (Dunham et al. 1997). Residency is an important life history strategy, and isolated populations that exist in marginal habitat need protection because they may provide a valuable source of genetic diversity (Northcote 1992).

Acknowledgments

References

Andrus, C. W., B. A. Long, and H. A. Froehlich. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. Canadian Journal of Fisheries and Aquatic Sciences 45:2080–2086.

Angermeier, P. L., and I. J. Schlosser. 1989. Species–area relationships for stream fishes. Ecology 70:1450–1462.

Beard, T. D., and R. F. Carline. 1991. Influence of spawning and other stream habitat features on spatial variability of wild brown trout. Transactions of the American Fisheries Society 120:711–722.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Behnke, R. J., and D. E. Benson. 1980. Endangered and threatened fishes of the upper Colorado River basin. Colorado State University, Cooperative Extension Service, Bulletin 503A, Fort Collins.

Behnke, R. J., and M. Zarn. 1976. Biology and management of threatened and endangered Western trouts. U.S. Forest Service General Technical Report RM-28.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533.

Beschta, R. L., and W. S. Platts. 1986. Morphological features of small streams: significance and function. Water Resources Bulletin 22:369–379.

Bisson, P. A., J. L. Nielsen, R. A. Ralmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62–73 in N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Boecklen, W. J. 1986. Effects of habitat heterogeneity on the species–area relationships of forest birds. Journal of Biogeography 13:59–68.

Boussu, M. F. 1954. Relationship between trout populations and cover in a small stream. Journal of Wildlife Management 18:229–239.

Bozek, M. A., and F. J. Rahel. 1991. Assessing habitat requirements of young Colorado River cutthroat trout by use of macrohabitat and microhabitat analyses. Transactions of the American Fisheries Society 120:571–581.

Carlson, J. Y., C. W. Andrus, and H. A. Froehlich. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 47:1103–1111.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 125:789–824.

Connor, E. F., A. C. Courtney, and J. M. Yoder. 2000. Individuals–area relationships: the relationship between animal population density, and area. Ecology 81:734–748.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species–area relationship. American Naturalist 113:791–833.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802–1813.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 43:1970–1981.

Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for

conservation. Theoretical Population Biology 41: 315–336.

Dunham, J. B., and G. L. Vinyard. 1997. Incorporating stream level variability into analyses of site level fish habitat relationships: some cautionary examples. Transactions of the American Fisheries Society 126:323–329.

Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North American Journal of Fisheries Management 17:1126–1133.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682–693.

Fausch, K. D., and M. K. Young. 1995. Evolutionarily significant units and movement of resident stream fishes: a cautionary tale. Pages 360–370 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem; defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Frissell, C. A. 1993. Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (U.S.A.). Conservation Biology 7: 342–354.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Furniss, M. J., T. D. Roelofs, and C. S. Yee. 1991. Road construction and maintenance. Pages 297–323 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59:507–515.

Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho. Journal of the Fisheries Research Board of Canada 29:265–273.

Hamilton, L. C. 1992. Regression with graphics: a second course in applied statistics. Duxbury Press, Belmont, California.

Hawkins, C. P., and ten coauthors. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18(6):3–12.

Heggenes, J., A. Brabrand, and S. J. Saltveit. 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. Transactions of the American Fisheries Society 119:101–111.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48:757–762.

Kershner, J. L., C. M. Bischoff, and D. L. Horan. 1997. Population, habitat, and genetic characteristics of Colorado River cutthroat trout in wilderness and nonwilderness stream sections in the Uinta Mountains of Utah and Wyoming. North American Journal of Fisheries Management 17:1134–1143.

Kozel, S. J., and W. A. Hubert. 1989. Factors influencing the abundance of brook trout (*Salvelinus fontinalis*) in forested mountain streams. Journal of Freshwater Ecology 5:113–122.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and A. D. Steinman. 1989. Influence of channel geomorphology on retention of dissolved and particulate matter in a Cascade Mountain stream. U.S. Forest Service General Technical Report PSW-110.

Lanka, R. P., W. A. Hubert, and T. A. Wesche. 1987. Relations of geomorphology to stream habitat and trout standing stock in small Rocky Mountain streams. Transactions of the American Fisheries Society 116:21–28.

Lee, D. C., J. R. Sedell, B. E. Rieman, R. F. Thurow, and J. E. Williams. 1997. Broadscale assessment of aquatic species and habitats. Pages 1057–1496 *in* T. M. Quigley and S. J. Arbelbide, editors. An assessment of ecosystem components in the interior Columbia Basin. U.S. Forest Service General Technical Report PNW-405.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman, San Francisco.

Lisle, T. E. 1987. Using ''residual depths'' to monitor pool depths independently of discharge. U.S. Forest Service, Research Note PSW-394.

McMahon, T. E., and G. F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46:1551–1557.

Meeuwig, M. H. 2000. Effects of constant, and cyclical thermal regimes on growth, feeding, and swimming performance of cutthroat trout of variable sizes. Master's thesis. University of Nevada, Reno.

Moore, K. M. S., and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 45:1921–1930.

Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.

Northcote, T. G. 1992. Migration and residency in stream salmonids—some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research 67:5–17.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society 121: 427–436.

Platts, W. S., and R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land-

use evaluation. North American Journal of Fisheries Management 8:333–345.

Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environmental Management 14:629–645.

Reice, S. R., R. C. Wissmar, and R. J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14:647–659.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements of conservation of bull trout. U.S. Forest Service General Technical Report INT-302.

Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285–296.

Rodgers, J. D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. North American Journal of Fisheries Management 12:79–86.

Rosgen, D. L. 1985. A stream classification system. Pages 91–95 in R. R. Johnson, C. D. Ziebell, D. R. Palton, P. F. Folliott, and R. H. Hamre, editors. Riparian ecosystems and their management: reconciling conflicting uses. U.S. Forest Service General Technical Report RM-120.

SAS Institute. 1993. SAS procedures guide, volume 6. SAS Institute, Cary, North Carolina.

Schlosser, I. J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology 76:908–925.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711–724.

Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18–29.

Thomas, H. M. 1996. Competitive interactions between a native and exotic trout species in high mountain streams. Master's thesis. Utah State University, Logan.

Thurow, R. F., and T. C. Bjornn. 1978. Response of cutthroat trout populations to the cessation of fishing in St. Joe River tributaries. University of Idaho, Idaho Cooperative Fishery Research Unit, Bulletin 25, Moscow.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Weaver, T. M., and J. J. Fraley. 1993. A method to measure emergence success of westslope cutthroat trout fry from varying substrate compositions in a natural stream channel. North American Journal of Fisheries Management 13:817–822.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125:879–887.

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, London.

Williams, J. E., and seven coauthors. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. Fisheries 14(6):2–21.

Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Canadian Journal of Fisheries and Aquatic Sciences 42:1668–1672.

Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, London.

Young, M. K. 1995. Colorado River cutthroat trout. Pages 16–23 in M. K. Young, editor. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-256.

Young, M. K. 1996. Summer movements and habitat use by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences 53:1403–1408.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. Transactions of the American Fisheries Society 118:379–385.

Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.