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Summer Habitat Use by Columbia River Redband Trout in the Kootenai River Drainage, Montana

CLINT C. MUHLFELD*[1] AND DAVID H. BENNETT
Department of Fish and Wildlife Resources,
University of Idaho, Moscow, Idaho 83844, USA

BRIAN MAROTZ
Montana Department of Fish, Wildlife, and Parks,
490 North Meridian Road, Kalispell, Montana 59901-3854, USA

Abstract.—The reported decline in the abundance, distribution, and genetic diversity of Columbia River redband trout *Oncorhynchus mykiss gairdneri* (a rainbow trout subspecies) has prompted fisheries managers to investigate their habitat requirements, identify critical habitat, and develop effective conservation and recovery programs. We analyzed the microhabitat, mesohabitat, and macrohabitat use and distribution of Columbia River redband trout by means of snorkel surveys in two watersheds in the Kootenai River drainage, Montana and Idaho, during the summers of 1997 and 1998. Juvenile (36–125 mm total length, TL) and adult (≥126 mm TL) fish preferred deep microhabitats (≥0.4 m) with low to moderate velocities (≤0.5 m/s) adjacent to the thalweg. Conversely, age-0 (≤35 mm) fish selected slow water (≤0.1 m/s) and shallow depths (≤0.2 m) located in lateral areas of the channel. Age-0, juvenile, and adult fish strongly selected pool mesohabitats and avoided riffles; juveniles and adults generally used runs in proportion to their availability. At the macrohabitat scale, density of Columbia River redband trout (>35 mm) was positively related to the abundance of pools and negatively related to stream gradient. The pool: riffle ratio, gradient, and stream size combined accounted for 80% of the variation in density among 23 stream reaches in five streams. Our results demonstrate that low-gradient, medium-elevation reaches with an abundance of complex pools are critical areas for the production of Columbia River redband trout. These data will be useful in assessing the impacts of land-use practices on the remaining populations and may assist with habitat restoration or enhancement efforts.

The Columbia River redband trout *Oncorhynchus mykiss gairdneri* (hereafter termed redband trout), a subspecies of rainbow trout *O. mykiss,* is native to the Fraser River and Columbia River drainages east of the Cascade Mountains as far as the barrier falls on the Pend Oreille, Spokane, Snake, and Kootenai rivers (Allendorf et al. 1980; Behnke 1992). Logging, mining, agriculture, grazing, dams, hybridization, and competition with nonnative fishes contributed to the decline of redband trout abundance, distribution, and genetic diversity in the Columbia River basin (Williams et al. 1989; Behnke 1992). Consequently, many populations are restricted to headwater streams that may serve as refugia until effective conservation and rehabilitation strategies are implemented. In response to the population declines, several state and federal agencies have classified redband trout as a sensitive species or a species of special concern. Concerns increased in 1994 when a petition to list the Kootenai River redband trout population in Montana as a threatened ‘‘species’’ under the Endangered Species Act was dismissed due to lack of information. Regardless of their legal classification, redband trout in Montana and the upper Columbia River basin are in immediate need of conservation that focuses on the identification of critical habitat.

Habitat use should be assessed at several spatial scales to fully understand the requirements of a species (Rabeni and Sowa 1996) because each spatial scale is considered to be nested within a hierarchical framework in which each scale influences the preceding one (Frissell et al. 1986). Microhabitat has been studied to identify specific habitat characteristics, such as water depth and focal velocity, that are selected by fish at a point within a hydraulic unit (Chapman and Bjornn 1969; Cunjak and Green 1983; Dolloff and Reeves 1990; Baltz et al. 1991). Microhabitat analyses are important because they identify specific focal-point locations in the stream that fish select based

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* Corresponding author: cmuhlfeld@state.mt.us

[1] Present address: Montana Department of Fish, Wildlife, and Parks, 490 North Meridian Road, Kalispell, Montana 59901-3854, USA

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on resource availability, competition, ontogeneity, predation, and optimal foraging opportunity (Everest and Chapman 1972; Fausch 1984; Schlosser 1987). Basinwide habitat inventories (Hankin and Reeves 1988) have identified habitat types (mesohabitats) such as pools and riffles that are important to fish and that influence the relative abundance of fish throughout a watershed (Hankin and Reeves 1988; Roper et al. 1994; Saffel and Scarnecchia 1995; Herger et al. 1996). Studies of stream reaches have related salmonid abundance to stream characteristics (macrohabitat) such as gradient (Chisholm and Hubert 1986), stream size (Kozel and Hubert 1989), and other geomorphic (Platts 1979; Fraley and Graham 1981; Lanka et al. 1987; Nelson et al. 1992; Kruse et al. 1997) and biotic (Binns and Eiserman 1979; Scarnecchia and Bergersen 1987) variables. Although each of these approaches provides valuable information, a single-scale approach may provide misleading and inadequate information on the requirements of a species because fish–habitat relations are complex and may differ depending on the scale of the analysis (Bozek and Rahel 1991).

The habitat requirements of redband trout in the upper Columbia River basin are not known. The Kootenai River drainage redband trout population may be at a high risk of extinction due to habitat fragmentation, stream habitat degradation, and hybridization with nonnative rainbow trout (Allendorf et al. 1980; Muhlfeld 1999). Identification of the factors that limit redband trout will provide resource managers with the appropriate information to develop biologically sound and effective conservation strategies for improving and protecting critical habitat. We evaluated the stream habitat use of redband trout at the microhabitat, mesohabitat, and macrohabitat scales in two watersheds in the Kootenai River drainage in Montana and Idaho. Our objectives were to (1) assess the patterns of microhabitat selection among size-classes of redband trout in the two drainages, (2) assess use of pools, riffles, and runs that differ in depth, velocity, and substrate, and (3) relate stream reach characteristics to the density of redband trout.

Study Area

We evaluated the stream characteristics and habitat use of redband trout in two mountain watersheds within the Kootenai River drainage in northwestern Montana during the summers of 1997 and 1998 (Figure 1). Callahan Creek, a fourth-order tributary of the Kootenai River, originates in the eastern slopes of the Cabinet Mountains in Idaho (Idaho Panhandle National Forest) and flows approximately 20.8 km east to its confluence with the Kootenai River in Troy, Montana. The drainage includes North Fork Callahan Creek, South Fork Callahan Creek, and the main-stem Callahan Creek. The entire watershed is in the Kootenai National Forest, with the exception of privately owned land in the lower 2 km of the drainage. Elevation ranges from 549 m at the Kootenai River to 1,897 m on Middle Mountain. Annual precipitation ranges from 63.5 to 274 cm (U.S. Forest Service, Three Rivers Ranger District, unpublished data). The drainage has been intensively managed for timber production and mining. Fish found in Callahan Creek include native redband trout, bull trout *Salvelinus confluentus*, and mountain whitefish *Prosopium williamsoni.* A potential barrier falls located 3.2 km upstream from the confluence with the Kootenai River may preclude genetic introgression with hybrids of coastal rainbow trout *O. mykiss irideus* and redband trout in the Kootenai River (Marotz and Fraley 1986).

Basin Creek, a third-order tributary of the East Fork Yaak River, originates in the northern slopes of the Purcell Mountains and flows north approximately 29.5 km to its confluence with the East Fork of the Yaak River approximately 45 km east of Yaak, Montana (Figure 1). This drainage includes the East Fork Basin Creek, the West Fork Basin Creek, the main-stem Basin Creek, and Porcupine Creek. The entire drainage is in the Kootenai National Forest, with the exception of a privately owned 2.5-km parcel located along the main stem. Annual precipitation ranges from 63.5 cm to 142 cm (U.S. Forest Service, Three Rivers Ranger District, unpublished data). Elevation ranges from 976 m at the confluence with the East Fork of the Yaak River to 2,095 m at the Purcell Divide. The Basin Creek drainage has been intensively managed for timber production. Redband trout is the only fish species found in the drainage. A potential barrier identified 3.6 km upstream from the confluence with the North Fork Yaak River may prevent genetic exchange with other hybridized assemblages in the Yaak River system.

Methods

Microhabitat.—We observed microhabitat use by redband trout in Basin and Callahan creeks during the low-flow period of 1998 by means of snorkeling and bank observation. Streams were stratified into reaches based on changes in gradient, sinuosity, valley bottom type, and the addition of

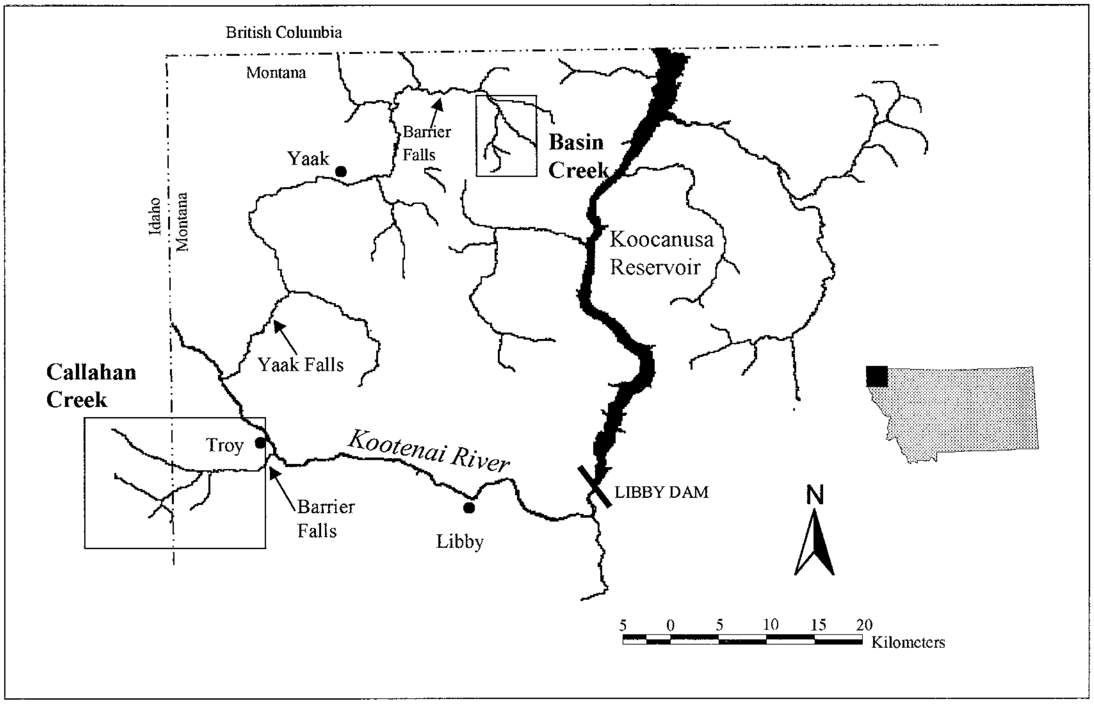

FIGURE 1.—Locations of Callahan and Basin creeks in the Kootenai River drainage, Montana and Idaho. Boxes mark study areas.

tributaries. Redband trout were randomly sampled in five reaches in Callahan Creek and three reaches in Basin Creek. Two randomly selected, 50-m sections within each study reach were examined by snorkeling between 1000 and 1600 hours to ensure optimal visibility. Each section contained pool and riffle habitats. The diver and bank observer entered the sample section from the lower boundary and simultaneously proceeded upstream, noting fish locations. A numbered, brightly colored washer was placed at the focal point of each fish. At each focal point, the species, total length (to the nearest cm) and elevation were recorded on a Plexiglas slate attached to the wrist of the diver. Total fish length and elevation were estimated to the nearest 5 mm with a ruler.

After the entire section was snorkeled, microhabitat use data were recorded at each location. The total depth of the water column was measured (to the nearest 5 mm) at the focal point of the fish with a meter stick. Mean water column velocity (m/s) was measured at 0.6 of total water depth, and focal-point velocity (m/s) was measured at the depth of the focal point. Velocity measurements were taken with a Swoffer model 2100 electronic flowmeter attached to a wading rod. A single predominant substrate rank was visually estimated at the focal point according to the following modified Wentworth scale: sand−silt (<0.2 cm; rank = 1), small gravel (0.2–0.6 cm; rank = 2), large gravel (0.6–7.5 cm; rank = 3), cobble (7.5–30.0 cm; rank = 4), small boulders (30.0–60.0 cm; rank = 5), large boulders (>60 cm; rank = 6), and bedrock (rank = 7). Dominant cover type identified within a 0.5-m radius of the focal point was categorized as (1) woody debris, (2) undercut bank, (3) overhanging vegetation, or (4) turbulence.

We quantified resource availability in each of the two 50-m sections at 10 transects perpendicular to the stream, beginning with a random starting point and continuing at 5-m intervals throughout the section. The physical characteristics total depth, mean water column velocity, dominant substrate, and cover type (within a 0.5-m radius) were measured at 10 equally spaced point locations across each transect.

Fish were categorized into three size-classes based on a length frequency distribution that was used for all subsequent analyses (Muhlfeld 1999). The age composition of each size-class was estimated from existing length-at-age data (Montana Department of Fish, Wildlife, and Parks, Libby, unpublished data). Fish less than 35 mm in length were classified as age-0 fish, those between 36 and 125 mm were classified as juveniles (age 1 and age 2), and those longer than 125 mm were classified as adults (age 3 and older).

We used an aligned-rank procedure to test the null hypotheses that microhabitat use by size-class was the same as random availability (with reach as a blocking factor) and that microhabitat use based on total depth, mean velocity, focal depth, focal velocity, and relative depth was the same among size-classes (SAS Institute 1988). Linear contrasts were used for multiple comparisons. Jacobs' electivity index (1974) was used to portray microhabitat selection for total depth, mean velocity, and substrate. This index ranges from +1 to −1, where +1 indicates exclusive use of a defined microhabitat category, 0 indicates habitat use in proportion to availability, and −1 indicates avoidance of that microhabitat category. All cover types were assigned to one of two categories, no cover and cover. A chi-square goodness-of-fit test was used to test the null hypothesis that each size-class of redband trout used cover in proportion to availability. Some expected substrate categories (random availability) contained inadequate observations (<5), which precluded meaningful statistical comparisons (Zar 1996).

Mesohabitat.—Stream reach characteristics and redband trout habitat use and distribution were evaluated during the low-flow periods of July−September 1997 and August 1998 in Callahan Creek and July 1998 in Basin Creek. We used a modified Hankin and Reeves (1988) basinwide inventory to avoid the error of extrapolating from a few small sections of stream to the entire system (Hankin 1984). We first counted the number of habitat units that spanned the entire channel width throughout a series of contiguous stream reaches (defined above) in each watershed. Surveyors then proceeded upstream and measured the width and thalweg length of each habitat unit. Habitat units were classified as either a pool, riffle, or run based on channel characteristics and stream flow (Bisson et al. 1982). Reach gradient was measured every 100 m with a hand-held clinometer.

Juvenile and adult redband trout abundance (stratified by habitat type) was estimated by one or two independent divers snorkeling a random sample of at least 10 pools, 10 riffles, and 10 runs or at least 10% of the available habitat of each habitat type in each stream reach. Divers entered each habitat unit from the downstream end, then simultaneously proceeded upstream and independently estimated fish numbers.

Mean water depth, mean velocity, mean substrate size, and percent cover were estimated for each sample habitat. Three equidistant transects perpendicular to the stream flow and three equidistant point locations along each transect were established in each sample unit. Mean depth, mean velocity (taken at 0.6 of total depth), and a single substrate rank were measured at each point location. Mean depth was the sum of the nine depth measurements divided by 12 to account for zero depths at the shoreline (Platts et al. 1983). The proportion of the surface area covered by woody debris, undercut bank, turbulence, or overhanging vegetation was visually estimated in each habitat unit.

Chi-square goodness-of-fit tests were used to test the null hypothesis that the habitat use of each size-class of redband trout was proportional to the availability of a particular habitat type. Expected values were calculated as the total proportional area sampled in each habitat type multiplied by the total counts of each size-class. Observed habitat use was the total number of fish in that particular habitat type. Bonferroni confidence intervals were constructed to determine whether each size-class of redband trout selected, avoided, or used habitat types as expected (Neu et al. 1974). Differences in mean velocity, mean depth, cover, and substrate among habitat types were tested using a rank-based analysis of variance (ANOVA; Conover and Iman 1981). Post hoc comparisons were conducted using the Scheffé method. Because velocity and substrate measurements were unavailable for 1997, comparisons of habitat characteristics were restricted to 1998.

Macrohabitat.—We described the distribution of redband trout from surveys conducted in 23 reaches of 5 streams at elevations ranging from 595 m to 1,576 m during the summers of 1997 and 1998. Mean reach gradients ranged from 0.5% to 7.5%, and mean stream widths ranged from 2.6 m to 11.8 m. To identify the reach characteristics that were most related to the abundance and distribution of redband trout, four variables were measured in each study reach. Mean total redband trout density (of fish ≥35 mm) and mean water depth were determined by means of equations for stratified random sampling (Scheaffer et al. 1996). Mean gradient was the sum of the gradient measurements in each reach divided by the total number of measurements in each reach. Mean stream width and

TABLE 1.—Means (±SE) of microhabitat use and availability for age-0 (≤35 mm), juvenile (36–125 mm), and adult (≥126 mm) Columbia River redband trout in Callahan and Basin creeks during summer 1998. Values with the same small letters are not significantly different ($P > 0.05$); asterisks denote significant differences compared with random availability ($P < 0.001$).

Sample size and microhabitat variable	Columbia River redband trout size-class			Resource availability
	Age-0	Juvenile	Adult	
Callahan Creek				
Sample size	106	135	186	1,000
Total depth (m)	0.132 ± 0.006 z*	0.360 ± 0.012 y*	0.449 ± 0.011 x*	0.225 ± 0.004
Focal elevation (m)	0.018 ± 0.001 z	0.042 ± 0.003 y	0.092 ± 0.006 x	
Relative depth (m)	0.804 ± 0.030 z	0.875 ± 0.008 z	0.802 ± 0.011 z	
Focal velocity (m/s)	0.008 ± 0.001 z	0.051 ± 0.006 y	0.061 ± 0.005 x	
Mean velocity (m/s)	0.018 ± 0.003 z*	0.144 ± 0.013 y*	0.126 ± 0.009 y*	0.224 ± 0.007
Basin Creek				
Sample size		307	146	600
Total depth (m)		0.433 ± 0.010 z*	0.5094 ± 0.03 y*	0.327 ± 0.007
Focal elevation (m)		0.041 ± 0.002 z	0.1149 ± 0.007 y	
Relative depth (m)		0.900 ± 0.004 z	0.785 ± 0.010 y	
Focal velocity (m/s)		0.111 ± 0.007 z	0.132 ± 0.009 y	
Mean velocity (m/s)		0.264 ± 0.012 z*	0.250 ± 0.013 z*	0.398 ± 0.012

pool−riffle ratio were determined from the basinwide availability survey.

Redband trout densities were related to the gradient, pool−riffle ratio, mean depth, and mean width using simple linear regression and multiple regression (Norusis 1990). For each regression analysis, the density of redband trout was the dependent variable and the four physical habitat characteristics were the independent variables. A *k*-means cluster analysis with three clusters was used to group stream reaches based on mean depth, mean width, gradient, and dominant and subdominant substrate types. Reach 1 in Callahan Creek was excluded from all analyses because hybridized rainbow trout from the Kootenai River could have been mistaken for redband trout during snorkel surveys.

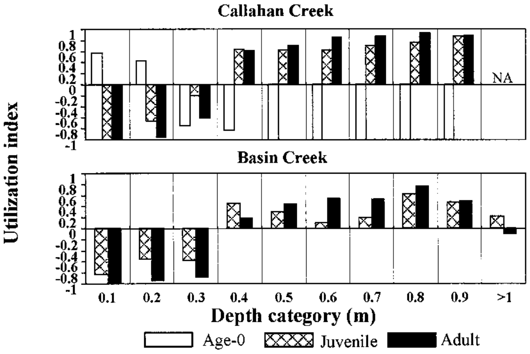

FIGURE 2.—Depth selection by age-0, juvenile, and adult redband trout in Callahan and Basin creeks during the summer of 1998. The utilization index ranges from +1 (exclusive selection of a particular depth) to −1 (complete avoidance of a particular depth). Age-0 redband trout were not available in Basin Creek when the surveys were conducted.

Results

Microhabitat

We made direct observations of microhabitat use on 106 age-0, 135 juvenile, and 186 adult redband trout in Callahan Creek and on 307 juvenile and 146 adult redband trout in Basin Creek (Table 1). As the emergence of age-0 redband trout in Basin Creek began during the latter part of July, they were not included in the analyses. We sampled 1,000 random resource availability locations from Callahan Creek and 600 from Basin Creek for each variable.

No size-classes of redband trout used water depth in proportion to availability. In both streams, juvenile and adult fish utilized significantly ($P < 0.001$) deeper water than the mean, whereas age-0 fish occupied shallower areas than the mean (Table 1). Juvenile and adult fish selected water depths between 0.4 and 0.9 m and avoided depths less than 0.3 m; age-0 fish selected depths less than 0.2 m along the channel margins and avoided areas deeper than 0.3 m (Figure 2).

Mean depths and focal elevations increased with fish size (Table 1). Adults occupied the deepest water along the thalweg and held positions significantly ($P < 0.001$) farther from the streambed than juvenile and age-0 fish. Juvenile redband trout used deeper water and higher focal elevations than age-0 trout. Juvenile and adult fish generally main-

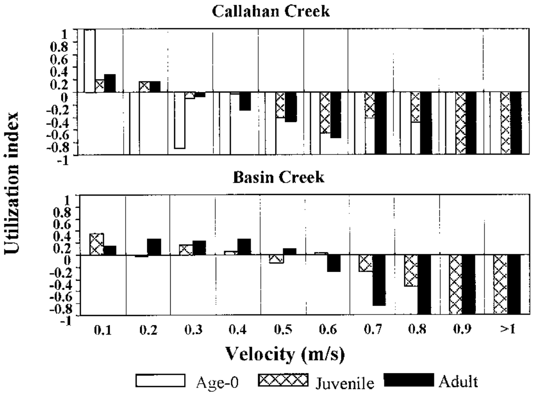

FIGURE 3.—Velocity selection by age-0, juvenile, and adult redband trout in Callahan and Basin creeks during the summer of 1998. The utilization index ranges from +1 (exclusive selection of a particular velocity) to −1 (complete avoidance of a particular velocity). Age-0 redband trout were not available in Basin Creek when the surveys were conducted.

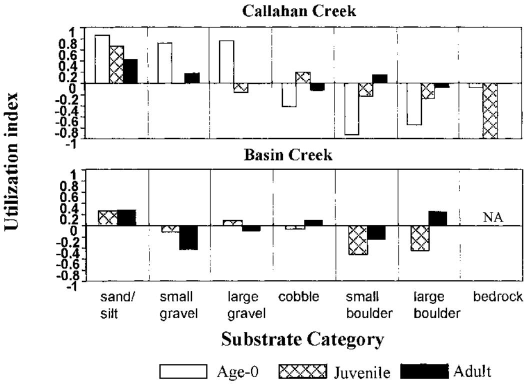

FIGURE 4.—Substrate selection by age-0, juvenile, and adult redband trout in Callahan and Basin creeks during the summer of 1998. Except for bedrock, substrate categories are defined by particle diameter as follows: sand−silt, ≤ 0.2 cm; small gravel = 0.2−0.6 cm; large gravel = 0.6−7.5 cm; cobble = 7.5−30.0 cm; small boulders = 30.0−60.0 cm; and large boulders, > 60.0 cm. The utilization index ranges from +1 (exclusive selection of a particular substrate) to −1 (complete avoidance of a particular substrate). Age-0 redband trout were not available in Basin Creek when the surveys were conducted.

tained deep positions relatively close to the streambed and occasionally left their focal points to ward off competitors.

All size-classes of redband trout in both streams utilized areas with lower velocities than the mean velocity available (Table 1). Age-0 fish selected velocities less than 0.1 m/s and avoided velocities faster than that (Figure 3). In Callahan Creek, juvenile and adult fish selected velocities less than 0.2 m/s and avoided velocities higher than 0.5 m/s, whereas in Basin Creek, juveniles and adults selected all velocities less than 0.5 m/s (Figure 3).

With a few exceptions, the use of water column and focal velocities increased with redband trout size (Table 1). In both streams, adult trout held their position in faster focal velocities than juvenile and age-0 fish; age-0 fish occupied focal velocities lower than those of juvenile fish. The mean water column velocities used by adults and juveniles differed significantly ($P < 0.001$) from those used by age-0 fish but not from each other.

Use of substrate by juvenile and adult redband trout did not appear to differ from what was available (Figure 4). The high preference for fine substrate by juvenile and adult fish was probably an anomaly resulting from the small sample sizes. In contrast, age-0 redband trout appeared to maintain positions over fine, small, and large gravel substrates and avoided larger substrate categories (Figure 4).

Use of cover varied among streams and size-classes of redband trout. Adult redband trout used cover more than expected in Callahan Creek ($\chi^2 = 25.56$; df = 1; $P < 0.05$) but not in Basin Creek ($\chi^2 = 0.071$; df = 1; $P > 0.05$). In Callahan Creek, juvenile redband trout used cover in proportion to its availability ($\chi^2 = 1.24$; df = 1; $P > 0.05$), whereas in Basin Creek, juveniles used cover more than expected ($\chi^2 = 49.105$; df = 1; $P < 0.05$). In Callahan Creek, age-0 redband trout were found exclusively along stream margins without cover; hence, they used cover less than expected ($\chi^2 = 8.97$; df = 1; $P < 0.05$).

Mesohabitat

In 1997, we sampled 170 pools, 180 riffles, and 171 runs (29.5% of the available habitat) in 19 reaches of Callahan Creek. In 1998, we sampled 38 pools, 32 riffles, and 29 runs (13.3% of the available habitat) in 5 reaches of Basin Creek and 27 pools, 28 riffles, and 22 runs in 3 reaches of South Fork Callahan Creek (Table 2).

Habitat types were unevenly distributed throughout each stream and differed in depth, velocity, substrate, and cover (Figure 5). In Callahan Creek, riffles were the most abundant habitat type (81.1%), followed by runs (9.9%) and pools (8.9%); in Basin Creek, riffle habitat was most abundant (64%), followed by pools (20.5%) and runs (15.5%). In both streams, pools were deeper

TABLE 2.—Expected and observed mesohabitat use by age-0 ($\leq$35 mm), juvenile (36–125 mm), and adult ($\geq$126 mm) Columbia River redband trout in pools, riffles, and runs in Callahan and Basin creeks, Montana. Asterisks denote habitats where use was significantly ($P < 0.05$) different from availability. Bonferroni confidence intervals were used for multiple comparisons. There are three degrees of freedom for each chi-square test.

	Habitat type				
	Pool	Riffle	Run	χ^2	*P*-value
Callahan Creek, 1997					
Expected use	19.1%	61.4%	19.5%		
Observed use					
Juveniles	33.6%*	43.4%*	23.0%*	348.16	<0.001
Adults	41.8%*	32.0%*	26.1%*	1,530.30	<0.001
Basin Creek, 1998					
Expected use	28.9%	43.1%	27.9%		
Observed use					
Juveniles	42.7%*	22.5%*	34.8%*	214.23	<0.001
Adults	51.9%*	19.1%*	29.0%	200.20	<0.001
South Fork Callahan Creek, 1998					
Expected use	16.7%	66.2%	17.2%		
Observed use					
Age-0 fish	35.2%*	37.3%*	27.5%*	162.82	<0.001
Juveniles	37.6%*	43.2%*	19.1%	201.18	<0.001
Adults	32.2%*	50.8%*	17.0%	66.28	<0.001

and slower and contained more total cover (Scheffé post hoc comparison; $P < 0.05$) than runs or riffles; runs had intermediate depths and velocities ($P < 0.05$), and riffles were shallower with higher velocities ($P < 0.05$). Pool substrate scores were significantly ($P < 0.05$) lower than those for riffles in both streams.

Redband trout of all size-classes failed to use habitat types in proportion to availability (Table 2). All size-classes of redband trout were found significantly more often than expected in pools and less often than expected in riffles (Scheffé post hoc comparison; $P < 0.05$). Juvenile and adult fish used runs more than expected in Callahan Creek ($P < 0.05$) and as expected in South Fork Callahan Creek; adults in Basin Creek also used runs as expected. Therefore, juvenile and adult redband trout were observed more often than expected in deeper, slower habitats with more cover and smaller substrates (e.g., pools) and less often than expected in shallower water with higher velocities and larger substrate (e.g., riffles). Larger redband trout generally used habitats with moderate velocities and depths (e.g., runs) in proportion to availability, while age-0 fish used them more than expected.

Macrohabitat

Densities of redband trout at least 35 mm in length ranged from 0.018 to 0.480 fish/m^2 (Table 3). Redband trout were present in all of the stream reaches sampled, although the distribution was uneven in each watershed. No redband trout were observed in headwater stream reaches with gradients steeper than 10% due to barriers to fish migration or inadequate habitat conditions.

Of the four habitat characteristics measured in each stream reach, only the pool−riffle ratio and stream gradient were significantly related to the abundance of redband trout. The density of redband trout increased with an increase in the pool−riffle ratio ($Y = 0.07 + 0.05\text{PR}$, where Y represents density and PR the pool−riffle ratio; $R^2 = 0.45$; df = 22; $P < 0.0001$). The density of redband trout was negatively related to stream gradient ($Y = 0.22 - 0.03G$, where G represents the gradient; $R^2 = 0.28$; df = 22; $P = 0.01$). The densities found in moderately sloped box canyons and wide, boulder-dominated reaches in the main stem and North Fork Callahan Creek were poorly described by the model (i.e., outliers). These reaches were identified as a distinct group based on the results of a *k*-means cluster analysis with three clusters (Muhlfeld 1999). Removal of these reaches from the regression analysis substantially increased the amount of variability explained by the linear model ($R^2 = 0.59$; df = 14; $P = 0.001$).

In general, low-gradient, medium-size reaches with abundant pools had higher densities of redband trout. Redband trout density was best predicted by the pool−riffle ratio, stream gradient, and mean stream width (W): $Y = 0.435 +$

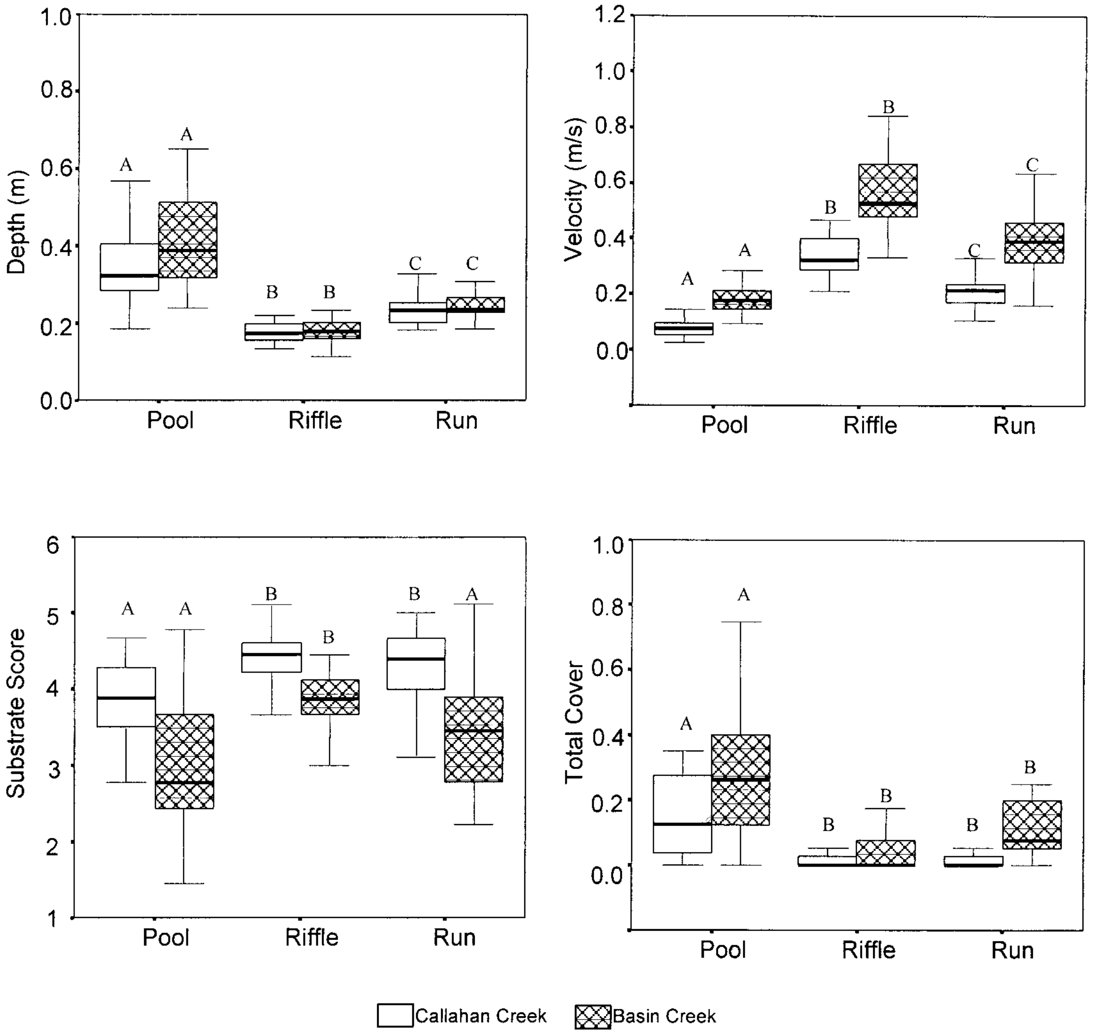

FIGURE 5.—Boxplots of the 10th, 25th, 75th, and 90th percentiles for depth, velocity, substrate, and cover by habitat type (pool, riffle, or run) in Callahan and Basin creeks during the summer of 1998. Different letters indicate significant ($P < 0.05$) differences in a given habitat characteristic among habitat types.

$0.027\text{PR}–0.046G − 0.029W$ ($F = 24.94$; df = 22; $P < 0.0001$). The pool−riffle ratio alone accounted for 45% of the variation in the density of redband trout among 23 stream reaches; with the addition of the gradient, the model accounted for 56% of the variation, and with the further addition of width it accounted for 80% of the total variation. Examination of the univariate relationship of stream width to density revealed that it was quadratic rather than linear. However, addition of a quadratic term to the multiple-regression model did not substantially increase the amount of variation explained, so no such term was included in the final model.

Discussion

Microhabitat Scale

Summer microhabitat use differed among size-classes of redband trout in the small headwater streams we studied in the Kootenai River drainage. Age-0 fish inhabited shallow, low-velocity areas along the stream margins, whereas juvenile and adult trout occupied deeper, faster locations with higher focal points in the water column. Our results are consistent with those of other studies that reported size-specific segregation of microhabitats along depth and velocity gradients for other stocks of redband trout (Hirsch 1995), coastal rainbow

TABLE 3.—Characteristics of 24 reaches sampled in Callahan and Basin creeks during summer 1997 and 1998. Abbreviations are as follows: CB = cobble; SB = small boulders; LG = large gravel; and SG = small gravel; CI = 95% confidence interval.

Reach	Elevation (m)	Reach length (m)	Grad-ient (%)	Mean stream width (m)	Mean depth (m)	Dominant/ subdominant substrate	Pool–riffle ratio	Fish > 35 mm	
								Number/m^2	± CI
Main-stem Callahan Creek									
1	595–631	1,363	2.6	7.7	0.55	CB/SB	0.880	0.0971	0.0369
2	631–668	1,791	2.1	9.0	0.50	CB/SB	0.370	0.0407	0.0088
3	668–716	2,091	2.3	9.9	0.44	CB/SB	0.064	0.0415	0.0099
4	716–825	5,352	2.0	11.8	0.38	CB/LG	0.087	0.0212	0.0073
North Fork Callahan Creek									
1	825–898	3,000	2.4	10.5	0.32	CB/SB	0.064	0.0296	0.0090
2	898–930	1,695	2.0	9.8	0.31	CB/SB	0.083	0.0181	0.0075
3	930–967	1,183	3.1	8.5	0.28	CB/SB	0.064	0.0282	0.0071
4[a]	967–997	465	6.5	6.3	0.62	CB/SB	1.090	0.0708	0.0341
5	997–1,070	2,460	3.0	9.9	0.31	CB/SB	0.034	0.0449	0.0105
6[a]	1,070–1,205	4,338	3.1	7.3	0.25	CB/LG	0.096	0.1014	0.0248
7	1,205–1,278	2,440	3.0	6.1	0.24	CB/LG	0.055	0.0860	0.0234
8	1,278–1,294	1,324	2.5	4.3	0.18	CB/LG	0.144	0.0641	0.0180
9	1,294–1,310	255	6.3	2.8	0.16	CB/SB	0.090	0.0348	0.0117
10	1,310–1,325	1,976	4.3	3.0	0.17	CB/LG	0.100	0.0943	0.0397
South Fork Callahan Creek									
1	825–876	141	3.6	7.8	0.30	CB/SB	0.090	0.0756	0.0222
2[a]	876–970	4,085	2.3	7.3	0.22	CB/LG	0.080	0.0891	0.0197
3[a]	970–1,072	2,766	3.7	7.0	0.23	CB/SB	0.030	0.0441	0.0100
4[a]	1,072–1,316	5,138	6.1	3.6	0.20	CB/SB	0.124	0.0235	0.0098
5	1,316–1,383	3,237	7.5	2.6	0.22	CB/SB	0.123	0.0200	0.0057
Basin Creek									
1[a]	1,150–1,199	2,712	1.8	5.8	0.26	CB/LG	0.502	0.2572	0.0028
2[a]	1,199–1,203	635	0.5	4.8	0.40	LG/SG	7.740	0.4559	0.6596
3	1,203–1,207	784	0.5	4.1	0.27	LG/SG	0.970	0.4796	0.1026
4[a]	1,207–1,333	4,985	2.8	4.6	0.23	CB/LG	0.292	0.2290	0.0466
East Fork Basin Creek									
1	1,333–1,576	2,961	6.9	4.1	0.17	CB/SB	0.045	0.0431	0.0044

[a] Reach sampled for microhabitat analyses.

trout (Baltz and Moyle 1984; Moyle and Baltz 1985), cutthroat trout *Oncorhynchus clarki* (Heggenes et al. 1991), bull trout (Saffel and Scarnecchia 1995), and different species of salmon (Chapman and Bjornn 1969; Everest and Chapman 1972; Dolloff and Reeves 1990; Bugert et al. 1991). Hirsch (1995) reported that microhabitat was partitioned among fry and older redband trout during the summer in three central Oregon streams; fry generally used stream margins, backwaters, and shallow areas, whereas older fish (≥1 year) occupied deeper areas of the channel. Moyle and Baltz (1985) found that as rainbow trout increased in size they preferred deeper and faster water. Baltz and Moyle (1984) found that age-0 and adult rainbow trout did not exhibit a high niche overlap in two California streams due to ontogenetic shifts in space utilization. We also found that ontogenetic shifts in microhabitat use were proportional to body size; as fish grow, they move into deeper, faster microhabitats, which probably reduces intraspecific interactions (Chapman and Bjornn 1969; Everest and Chapman 1972) or reduces susceptibility to predation by larger fishes (Harvey 1991).

Our data suggest that the microhabitats used by different size-classes of redband trout were related to availability. Water depth was an important microhabitat factor for older fish in Callahan and Basin creeks, probably because these creeks are small headwater streams with limited availability of water deeper than 1 m (3% of the total availability in Callahan Creek and 14% in Basin Creek). Similarly, Moyle and Baltz (1985) found that age-0 (≤50 mm), juvenile (51–119 mm), and adult (≥120 mm) rainbow trout were highly selective as to the microhabitats they occupied, with selection based primarily on depth and velocity. In different stream systems, factors other than resource availability, such as stream temperature, food supply, and the presence of other species may also influence habitat and microhabitat use (Moyle and Baltz 1985). Redband trout probably occupied focal positions with low water velocities that minimized energy expenditure yet were close to faster water that maximized access to invertebrate drift (Fausch 1984).

Our results suggest that water depth may influence microhabitat selection by juvenile and adult redband trout more than water velocity does. This observation differs from those of studies that have identified water velocity as the most important microhabitat variable for rainbow trout (Lewis 1969; Gatz et al. 1987). Juvenile and adult redband trout selected higher-velocity microhabitat (≤0.5 m/s) in Basin Creek than in Callahan Creek (≤0.2 m/s), which had lower available velocities. In both streams the deepest water (≥0.4 m) was consistently selected. In Basin Creek, however, juvenile and adult redband trout continued to maintain positions in deeper areas even though velocities were higher. Discharge was relatively higher in Basin Creek because we sampled there earlier in the field season than at Callahan Creek. This indicates that redband trout need deeper water and that depth may be a key factor affecting density. Similarly, in Sierra Nevada streams, Pert and Erman (1994) found that the focal-point and mean water velocities occupied by adult rainbow trout increased with increasing discharge but that the fish still occupied deep water under both flow regimes. Selection of deeper water by larger redband trout may also be related to the greater overhead security and protection from avian or terrestrial predators that such areas offer (Everest and Chapman 1972).

Microhabitat analyses clearly demonstrated that age-0 redband trout selected shallow, low-velocity areas along channel margins. Moore and Gregory (1988) found the highest abundance of cutthroat trout fry in lateral habitats that provided shallow, low-velocity areas with abundant food. Channel margin habitats also reduce the likelihood of displacement by faster water in the main channel (Moore and Gregory 1988) and provide visual isolation from aquatic predators (Bugert and Bjornn 1991; Harvey 1991). In Callahan Creek, bull trout may preclude age-0 redband trout from maintaining positions in deeper water (Shepard et al. 1984).

Mesohabitat Scale

Redband trout of all ages selected deep, slow pool habitats with relatively abundant cover and avoided shallow, high-velocity riffle habitats. Selection of the lateral margins of pools as rearing habitat by age-0 redband trout is consistent with the behavior of other salmonid species (Bisson et al. 1988; Bozek and Rahel 1991). Similarly, other studies have demonstrated a higher abundance of older trout in pools (Lewis 1969; Hankin and Reeves 1988; Roper et al. 1994; Herger et al. 1996). In a Montana stream, Lewis (1969) found that large, deep, slow pools with extensive cover had the most stable populations of rainbow trout. However, our results differ from those of studies that reported that rainbow trout occupy faster riffle and run habitat in sympatric situations (Hartman 1965; Cunjak and Green 1984).

Macrohabitat Scale

Our results suggest that the distribution of redband trout was related to a combination of physical stream habitat variables. In general, low-gradient, medium-size reaches with abundant pools had higher densities of redband trout. Several studies have also related trout abundance to a combination of physical and biological factors in western streams (Binns and Eiserman 1979; Lanka et al. 1987; Scarnecchia and Bergersen 1987; Kozel and Hubert 1989). Other studies indicate that the spatial variation in the distribution of stream-dwelling salmonids may be largely attributed to the availability of spawning habitat within a drainage basin (Bozek and Rahel 1991; Magee et al. 1996). If juvenile redband trout do not disperse far from their natal incubation sites, this may also account for the observed spatial patchiness in the distribution of juvenile and adult redband trout throughout both watersheds.

Our results indicate that gradient influences the distribution and abundance of redband trout; as gradient increased, the density of redband trout generally decreased. Redband trout were most abundant in low-gradient reaches located in alluviated valley bottom types with well-defined floodplains and meandering plan-view geometries. We found that densities were lowest in steep headwater stream reaches (>4%), and no redband trout were observed in headwater streams with gradients greater than 10% (possibly because of barriers to fish migration or inadequate habitat conditions). Similarly, Kruse et al. (1997) reported that channel gradients greater than 10% limited the distribution of Yellowstone cutthroat trout *O. c. bouvieri* in the Greybull−Wood River drainage in Wyoming. In high-elevation streams in Wyoming, Chisholm and Hubert (1986) demonstrated that increased stream gradient had a negative influence on the abundance of brook trout *Salvelinus fontinalis.* Bozek and

Hubert (1992) also found that cutthroat trout did not occupy streams with channel slopes greater than 8%. In moderate-gradient reaches, our results revealed high variation in the abundance of redband trout, which suggests that factors other than gradient (i.e., channel entrenchment, substrate size, and stream width) influenced standing stocks of redband trout. Furthermore, the highest densities of redband trout occurred in medium-size streams. Platts (1979) and Lanka et al. (1987) also observed optimal trout habitat in the transitional reaches between high-gradient headwaters and lower-basin streams. Channel gradient and stream size influence stream habitat characteristics (Platts 1979; Bowlby and Roff 1986; Chisholm and Hubert 1986), which in turn influence the distribution (Bozek and Hubert 1992; Kruse et al. 1997) and abundance (Platts 1979; Chisholm and Hubert 1986) of trout.

Management Implications

We found that a hierarchical assessment of habitat use and distribution was useful for identifying the summer habitat requirements of redband trout in the Kootenai River drainage. At the microhabitat scale, depth and velocity were the most important factors associated with redband trout habitat use and size-class distribution. The mesohabitat analysis identified selection for pool habitats by all size-classes of redband trout. The macrohabitat scale revealed that gradient, stream size, and the abundance of pools were important factors influencing redband trout densities and distribution in stream reaches within the watershed; higher densities of redband trout are associated with low-gradient channels with abundant pool habitat. Finally, stream habitat inventories suggested that geologic barriers are important mechanisms for isolating genetically pure redband trout in the Kootenai River drainage. No single analysis would provide managers with such a comprehensive view of the importance of physical and biological factors at different spatial scales.

A modified basinwide inventory and microhabitat analysis were complementary methodologies for identifying fish−habitat relations. If habitat use had only been analyzed at the microhabitat and mesohabitat scales, the factors influencing the distribution of redband trout at the watershed level would have been missed. If abundance had only been estimated in one section of stream and then extrapolated to the basin level, estimates of densities may have differed by as much as a factor of 11 for Basin Creek and by more than a factor of 5 for Callahan Creek. Therefore, extrapolating to the stream or watershed level from one representative reach may produce misleading and inadequate information on the ecological requirements and distribution of salmonids within a basin (Roper et al. 1994).

Our findings at several spatial scales suggest the importance of maintaining channel complexity and quality pool habitat for redband trout throughout their limited range. Land development activities such as road construction, logging, and grazing can alter substrate composition and reduce the frequency and area of pools (Burns 1972; Heifetz et al. 1986; Hartman et al. 1996). Our results suggest that decreased pool habitat could have deleterious effects on the abundance and distribution of redband trout. Although supplementation efforts within the redband trout's historic range may be desired by state and federal agencies, introductions of species to any aquatic habitat requires careful consideration because species interactions are complex and difficult to predict (Li and Moyle 1981). The information gained from this study may be used to ascertain and predict how land-use alterations will affect these populations as well as helping to inform habitat enhancement or restoration decisions.

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