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Spatial Variation in Spawning Habitat of Cutthroat Trout in a Sediment-Rich Stream Basin

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Abstract.—We examined distribution and habitat characteristics of spawning sites of cutthroat trout *Oncorhynchus clarki* at various spatial scales to assess effects of sedimentation within a large basin in Montana. Redd density varied widely across the basin; nearly all (99%) of the 362 redds observed occurred in two high-elevation headwater tributaries. Redd density at the reach scale was positively correlated ($r^2 = 0.72$, $P = 0.001$) with abundance of spawning gravels. Other habitat variables, such as gradient, width, depth, embeddedness, bank stability, and percent riffle, were not significantly correlated to redd density. Taylor Fork redds contained some of the highest proportions of fine sediments (<6.35 mm, mean = 41.6%; <0.85 mm, 17.9%) observed in egg pockets of salmonid redds in the Rocky Mountain region. Cache Creek, a highly disturbed subbasin, had significantly greater proportions of fine sediments smaller than 0.85 mm in redds than the undisturbed Wapiti Creek subbasin. High fine-sediment levels in redds led to very low estimated embryo survival (mean, 8.5%), but sedimentation did not appear to limit recruitment. Our data suggest that compensatory juvenile survival and high embryo survival in the small proportion of redds with good substrate quality may buffer the effects of the high sediment levels in the basin.

Predicting the effects of sedimentation resulting from land use activities has been a research priority for fishery biologists for the past 60 years (Chapman 1988). Much of the research has focused on effects of fine sediment on emergence success of salmonid fry (e.g., Chapman 1988; Young et al. 1991; Weaver and Fraley 1993). In their review of sediment studies, Everest et al. (1987) concluded that studies of population-level effects are needed to examine how sedimentation affects fish populations within entire drainage basins. However, we found few published studies that have adopted this approach. Exceptions are studies by Shepard et al. (1984a), Cederholm and Reid (1987), and Scrivener and Brownlee (1989) that assessed population effects of sedimentation by combining data on numbers of recruits, relations between fine sediments and egg-to-fry survival, and amount of fine sediments within redds contributed by land use activities.

Geologic characteristics of a drainage basin exert a strong influence on degree of sedimentation and sensitivity to land disturbance (Everest et al. 1987). Dominant geological formations in the range of cutthroat trout *Oncorhynchus clarki* in Montana include highly erosive granitic series of the Idaho Batholith, cobble-producing Belt series, and various fine silt-producing volcanic and sedimentary series (Alt and Hyndman 1986). Much of the research on sediment effects on salmonids in the Rocky Mountain region has focused on granitic soils and sand-sized particles of the Idaho Batholith (Bjornn et al. 1977; Platts et al. 1989). To evaluate the effects of smaller sediment particles, we sampled streams draining sedimentary geology.

Recent studies indicate that spawning habitat of stream-dwelling salmonids may be more spatially variable across drainage basins and may play a larger role in determining patterns of distribution of juveniles and adults than previously thought (Beard and Carline 1991; Bozek and Rahel 1991). To properly characterize such high spatial variability in habitat use and document population effects of habitat change, sampling designs that employ a hierarchial series of spatial scales ranging from the entire watershed to microhabitats are needed (Frissell et al. 1986).

The objectives of our study were to (1) characterize spawning habitats of cutthroat trout across a large sediment-rich drainage basin, (2) examine

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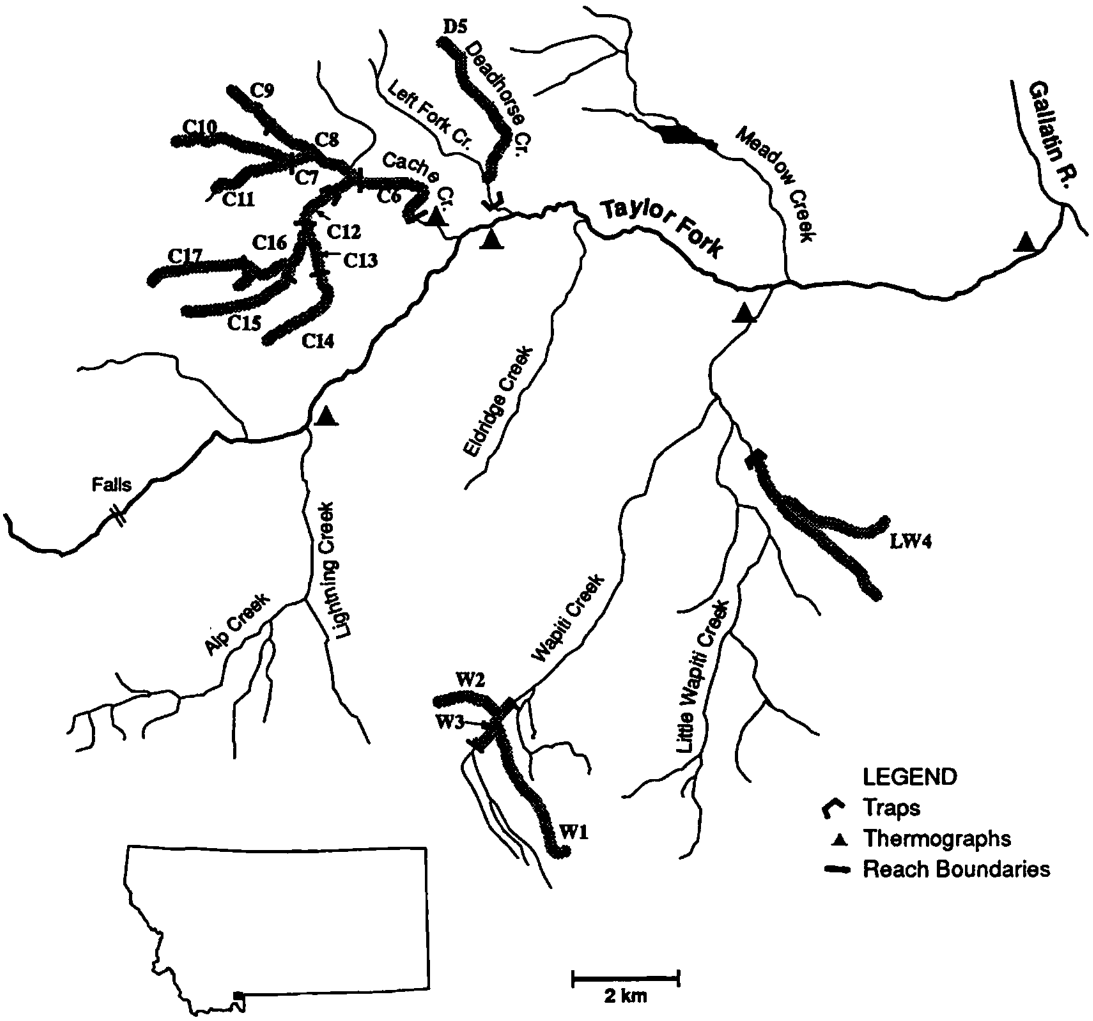

FIGURE 1.—Locations of spawning reaches (stippled and coded areas), weirs, and thermographs in Taylor Fork basin, Montana.

factors influencing redd distribution at different spatial scales (basin, subbasin, and reach), and (3) evaluate effects of sedimentation on redd substrate composition and estimated emergence success. We use the data to address the question, Is fine sediment limiting recruitment of the cutthroat trout population in the Taylor Fork basin?

Study Area

Taylor Fork is a fourth-order tributary to the upper Gallatin River in southwest Montana (Figure 1). The drainage encompasses 161 km^2 and contains about 100 stream kilometers. Peak flows occur from snowmelt during late May to mid-June. Three major elevational land types exist in the drainage. Headwater sections (above 2,300 m) of the major third-order tributaries (Cache, Wapiti, and Lightning creeks) meander through alpine meadows. Midelevation sections (2,100–2,300 m) have steeper gradients, more constrained valley floors, and are bordered by coniferous forest. Lower sections (below 2,100 m) and the main-stem Taylor Fork drain wide valley floors vegetated by sagebrush *Artemisia* spp. and willow *Salix* spp.

Taylor Fork drains sedimentary soils predominantly consisting of fine silt (Snyder et al. 1978). This material is highly erosive and produces large quantities of fine sediment; many of the streambanks in the basin were rated unstable by Snyder et al. (1978). Habitat conditions in the basin range

TABLE 1.—Genetic status of Taylor Fork cutthroat trout as determined by protein electrophoresis (R. Leary, University of Montana, personal communication).

	Percent genetic composition of:		
Location	Westslope cutthroat trout	Rainbow trout	Yellowstone cutthroat trout
Cache Creek	87	11	2
Upper Wapiti Creek	57		43
Deadhorse Creek	85	10	5
Upper Taylor Fork[a]	93	2	5

[a] Near Lightning Creek.

from pristine to highly altered. Splash dams were operated in the late 1800s on the main-stem Taylor Fork to transport logs downstream (Snyder et al. 1978). Livestock graze allotments in upper Cache and middle Wapiti creeks, and areas of the Cache Creek drainage have been recently logged. In the Cache Creek subbasin, there is a predominance of bare, unstable banks and the incised channels and encroachment of sagebrush characteristic of heavily grazed riparian zones (Snyder et al. 1978). In contrast, upper Wapiti Creek, which is similar in size, elevation, and geomorphology to upper Cache Creek, has no known history of logging, grazing, or road building.

The basin contains one of the few remaining populations of westslope cutthroat trout *O. clarki lewisi* in the Gallatin River drainage (Liknes 1984). Other fishes inhabiting the basin include mountain whitefish *Prosopium williamsoni*, mottled sculpin *Cottus bairdi*, nonnative rainbow trout *O. mykiss*, brown trout *Salmo trutta*, and Yellowstone cutthroat trout *O. c. bouvieri*. Rainbow trout were stocked in Taylor Fork from 1928 to the late 1980s. Yellowstone cutthroat trout were stocked in small headwater lakes and subsequently invaded downstream reaches. As a result, westslope cutthroat trout are introgressed with rainbow trout and Yellowstone cutthroat trout to varying degrees throughout the basin (Table 1). We assume a negligible influence of this introgression on the effects of sedimentation.

Methods

Spawner and redd distribution.—The entire basin was surveyed in summer 1991 to identify potential spawning sites by the presence of redds, suitable spawning gravel, and newly emerged fry. Potential spawning sites were then stratified into 17 reaches (Figure 1), ranging in length from 324 to 3,020 m (mean length, 914 m). Reach boundaries were delineated by changes in gradient, geomorphology, or the presence of a tributary junction (Frissell et al. 1986). In 1992 we counted redds in each reach every 3–4 d from 25 May to 1 July. We counted a redd only if we observed fish spawning; cleaned gravel sites could not be reliably identified as redds because of their small size, lack of periphyton, and the high fine-sediment load in the stream. We marked individual redds by placing numbered stakes on the streambank and mapped probable egg pocket locations by observing where fish spawned. Redd density per reach was expressed as number of redds/100 m^2 of wetted stream area. Thermographs recorded hourly temperature at five locations in the basin (Figure 1).

We also employed weirs in the lower (Little Wapiti Creek), middle (Deadhorse Creek), and upper (Cache Creek) portions of the basin (Figure 1) to assess when and where spawning occurred. Weirs spanned the stream channel and captured upstream and downstream migrants. Weirs were checked twice daily from 19 May to 1 July 1992. Fish were weighed, measured for fork length, and tagged with a visible implant tag behind the left eye. Species, sex, and spawning condition were also noted.

Spawning habitat.—Habitat features were measured in 11 of the 17 spawning reaches to evaluate potential physical factors associated with variation in redd density. We were unable to measure habitat features in the other six spawning reaches as a result of early ice cover. Sampled reaches represented the full range of observed habitat conditions and redd densities. We measured habitat according to the procedure of Overton et al. (in press), a modification of the systematic habitat-sampling procedure described by Hankin and Reeves (1988). Proceeding upstream, we described each channel unit (pool, riffle, etc.) and measured its length, mean wetted width, and mean and maximum depths. The area of potential spawning gravel was measured with a meter stick and expressed as percent of total reach surface area. Based on observations of 362 completed redds, we defined potential spawning gravel as patches of substrate at least 0.25 m^2 in area with particles 2–35 mm in diameter. The same observer made all estimates of spawning gravel to reduce bias. At every 10th channel unit, we measured gradient with a clinometer and visually estimated percent bank stability and substrate embeddedness, using rating criteria described by Platts et al. (1983). In pool tailouts and riffles, we measured substrate composition with the pebble count technique (Wolman 1954), using 100 data points at each site in streams wider than 1 m and 50 data points in streams narrower than 1 m. We classified substrate size as sand–silt (<2 mm in diameter), pea gravel (2–16 mm), gravel (17–75 mm), rubble (76–150 mm), cobble (151–300 mm), or boulder (>300 mm). We used Spearman's rank correlation and simple linear regression (Zar 1984) to assess associations between redd density and reach habitat features. We were unable to statistically compare habitat features among subbasins because only one reach was sampled in two of the three subbasins.

Redd substrate composition.—We used a McNeil hollow-core sampler (Platts et al. 1983) to excavate substrate from 21 redds in upper Cache Creek (five reaches or reach groups) and 15 redds in upper Wapiti Creek (three reaches). In Cache Creek, we grouped north fork (reaches 8–11) and south fork (reaches 13–17) spawning reaches together for ease of sampling. Three to seven redds were randomly chosen for coring in each of these eight designated reaches or reach groups. To quantify substrate conditions near time of emergence, we collected cores during a 2-week period (23 July to 6 August) following our first sighting of emergent fry (22 July). We used the redd maps to position cores over egg pockets. Cores were taken to a depth of 10 cm to mimic egg pocket depths observed in cutthroat trout redds (B. May, Gallatin National Forest, personal communication). We labeled cores as egg pocket samples if we observed eggs or alevins in the core.

Oven-dried core samples were weighed after being mechanically shaken through sieves of 50.8, 25.4, 12.4, 9.5, 6.35, 2.36, 0.85, and 0.074 mm (see Magee 1993 for further detail). We collected an average of 3.6 kg of substrate per core. As recommended by Chapman (1988) and Young et al. (1991), we expressed substrate composition by two methods: the percentage of fine substrate smaller than a given size (6.35, 2.36, and 0.85 mm) and by a measure of central tendency, the fredle index F_i ($F_i = D_g/S_o$; D_g is the geometric mean particle diameter and S_o is a sorting coefficient; see Young et al. 1991). As in previous studies (Grost et al. 1991; Thurow and King 1994), we calculated F_i by excluding particle sizes greater than 50.8 mm to minimize bias. (Particles greater than 50.8 mm ranged from 0% by weight in 17 redds to 3.3–37.5% in 19 redds.) This procedure also allowed us to compare our results with other studies that used truncated data.

We compared substrate composition among spawning reaches with a Kruskal–Wallis nonparametric analysis of variance and Tukey's multiple comparison test (Zar 1984). We used rank correlation to examine associations between redd density and measures of substrate composition (F_i; proportion of particle sizes less than 6.35, 2.36, 0.85 mm). Stepwise multiple regression was used to assess how the proportion of different-sized fine particles influenced variation in F_i. A Mann–Whitney U-test was used to compare redd substrate composition among egg pocket and non-egg pocket cores and to compare redd substrate composition among subbasins having low (Wapiti Creek) and high (Cache Creek) land disturbance.

Fry production.—We predicted fry emergence success for each cored redd using the equation developed by Weaver and Fraley (1993) for westslope cutthroat trout:

$$\% \text{ emergence} = -0.7512 \text{ (arcsine } \% \text{ SP}_{6.35}) + 39.67;$$

$$\% \text{ SP}_{6.35} = \text{percentage of substrate particles smaller than 6.35 mm.}$$

Total fry production per reach was estimated by combining data on total redd number, estimated egg deposition, and average substrate composition of cored redds. To account for effects of female size on egg deposition, we divided the length-frequency distribution of females captured in the Cache Creek spawning trap into 25-mm intervals and calculated egg deposition (E) for each size-class using a length–fecundity relation for westslope cutthroat trout: $E = 82.63e^{0.0007958L}$, where L is fork length in millimeters (C. Downs and B. Shepard, Montana State University, personal communication). We assumed all mature females had an equal likelihood of spawning and apportioned egg deposition to redds by the percentage of females within each size-class (25%, 150–174 mm; 50%, 175–199 mm; 16%, 200–224 mm; 6%, 225–249 mm; and 3%, >250 mm). Fry production in a reach was estimated by multiplying total estimated egg deposition by estimated emergence success.

Results

Spawner and Redd Distribution

The majority (271, 94%) of trout trapped during upstream spawning migration were captured in the Cache Creek weir; only 10 trout were captured in Deadhorse Creek and 6 in Little Wapiti Creek weirs. Cutthroat trout accounted for 99.6% of fish caught in the upper basin weir at Cache Creek; rainbow trout constituted a larger proportion of the catch at the two lower-elevation weirs (10% in

TABLE 2.—Number and density (redds/100 m^2) of trout redds by stream order in Wapiti (W), Little Wapiti (LW), Deadhorse (D), and Cache (C) creeks.

Reach	Length (m)	Number of redds	Redd density
	First order		
W1	2,262	57	1.7
C8	500	1	0.1
C9	900	25	3.3
C10	843	34	3.4
C11	859	14	1.4
C13	585	13	2.0
C14	656	9	1.1
C15	464	3	0.6
C16	493	3	0.6
C17	1,025	39	3.8
Total or mean	8,587	198	1.8
	Second order		
W2	472	17	2.4
W3	1,258	32	0.8
LW4	575	1	0.1
D5	324	3	0.7
C7	833	39	3.3
C12	477	24	2.8
Total or mean	3,939	116	1.7
	Third order		
C6	3,020	48	0.5
Grand total or mean	15,585	362	1.7

Deadhorse Creek and 70% in Little Wapiti Creek). Mature male cutthroat trout averaged 189 mm (N = 282) and females 191 mm (N = 156) in fork length.

Ninety percent of upstream migrants entered Cache Creek from 19 May to 4 June at mean daily water temperatures of 7–9°C. Fish were observed on redds in Cache Creek from 25 May to 19 June and in Wapiti Creek from 8 to 22 June when mean daily temperatures were near 8°C. Peak spawning in Cache Creek occurred from 3 to 5 June, when 77 redds (40% of total) were observed. Peak spawning in Wapiti Creek occurred about 1 week later. Water temperatures in the main-stem Taylor Fork were similar to those in Cache Creek. Mean daily temperatures in Lightning Creek did not reach 8°C until mid-July. Females remained in spawning tributaries an average of 11 d; males remained for an average of 9 d.

Most of the 362 redds counted in the Taylor Fork basin in 1992 were clustered in two areas (Table 2). Nearly all redds were observed in the upper reaches of Cache Creek (252, 70%) and Wapiti Creek (106, 29%). Despite large numbers of redds in these areas, no redd superimposition was observed. In 1991, no redds or fry were observed in the main stem of Taylor Fork or in Eldridge Creek, Meadow Creek, Left Fork Creek, lower Cache Creek, middle Wapiti Creek, or Alp Creek. Small numbers of newly emerged fry were observed in lower Wapiti Creek, Little Wapiti Creek, and Lightning Creek.

Most redds were found in first- and second-order tributaries, but redd density varied widely, even among adjacent reaches (Table 2). Cache Creek reaches 15 and 16 contained three redds each (0.6/100 m^2), whereas adjacent reach 17 contained 39 redds (3.8/100 m^2). Similarly, reach 8 contained 1 redd (0.01/100 m^2), whereas adjoining reaches 7 and 9 contained 39 and 25 redds (3.3/100 m^2), respectively.

Spawning Habitat

Cutthroat trout spawned in reaches of small (1–3-m-wide) tributaries with low to moderate gradients (0.5–3.8%) and suitable spawning gravels (Table 3). Redds were typically not observed at gradients greater than 4%. Streambank stability of spawning reaches averaged less than 50% stable, and no reaches had streambanks classified as greater than 75% stable. Substrate embeddedness was high, averaging about 50%.

Measured habitat features generally varied little among reaches that supported redds. Features, including gradient, width, depth, embeddedness, bank stability, percent riffle, and substrate composition, were not significantly correlated with redd density (Table 3). Only the proportion of potential spawning gravel was highly correlated with redd density (Figure 2; Table 3). Proportion of potential spawning gravel varied widely, ranging from 3 to 25%, even among nearby reaches. We found no association (P = 0.1–0.6) between abundance of spawning gravel and reach gradient, proportion of pea gravel, or proportion of gravel substrate.

Redd Characteristics

We found eggs in 11 of the 36 redds cored. We found no significant differences (U-test, $P > 0.47$) in percentages of substrate smaller than 6.35, 2.36, and 0.85 mm or in F_i values between cores with and without eggs. We therefore used all 36 core samples to characterize substrate composition of redds.

Cutthroat trout redds consisted primarily of small gravels (75% less than 25.4 mm in diameter) and contained a high proportion of particles less than 6.35 mm (Figure 3). Forty percent of the substrate was smaller than 6.35 mm and 18% was

TABLE 3.—Means of habitat features in spawning reaches of Wapiti (W), Deadhorse (D), and Cache (C) creeks. Spearman's rank correlation with redd density (Table 1) shown as r_s. Asterisk denotes significance at $P < 0.01$.

Reach or corre-lation	Gra-dient (%)	Width (m)	Depth (cm)	Embed-dedness[a]	Bank stability[b]	Percent by area					
						Spawning gravel	Riffle	Silt	Pea gravel	Gravel	Rubble
W3	1.2	3.1	25	2.8	1.9	14.1	39	17	24	52	8
D5	0.5	1.3	15	2.6	2.5	9.9	42	20	9	59	7
C5	0.5	3.2	27	2.9	3.4	8.5	34	18	14	46	16
C7	0.5	1.4	19	3.1	2.7	17.3	38	16	22	58	3
C8	4.0	1.1	6	3.2	2.2	3.2	50	23	11	44	15
C9	2.5	1.1	6	3.7	2.7	16.2	42	20	14	46	11
C10	3.0	1.2	7	4.4	3.4	13.9	46	19	18	40	15
C12	0.5	1.8	9	2.8	2.1	18.0	44	22	16	50	10
C13	1.0	1.1	12	2.6	2.9	13.3	43	24	24	42	4
C14	3.8	1.2	27	2.9	3.4	8.5	34	16	8	37	28
C17	1.5	1.0	7	3.2	2.5	25.4	45	25	18	54	4
r_s	0.05	−0.38	−0.36	0.47	0.15	0.80*	0.25	0.14	0.48	0.06	−0.39

[a] Rated on a scale from 1 to 5 for percent of substrate embedded: 1 = >75%; 2 = 50–75%; 3 = 25–49%; 4 = 5–24%; 5 = <5% (Platts et al. 1983).

[b] Rated on a scale from 1 to 4 for percent stable banks: 1 = <25%; 2 = 25–49%; 3 = 50–75%; 4 = >75% (Platts et al. 1983).

smaller than 0.85 mm. When substrate samples were truncated to remove particles larger than 50.5 mm, the percentage of substrate smaller than 6.35 mm ranged from 26 to 73%, the percentage smaller than 0.85 mm ranged from 8 to 40%, and F_i values ranged from 0.48 to 5.14. The F_i was negatively correlated with percentage of substrate smaller than 6.35, 2.36, and 0.85 mm (r_s = −0.86 to −0.97, $P < 0.001$). However, when all three measures of fines were regressed against F_i by multiple regression, only percentage of substrate smaller than 0.85 mm accounted for a significant proportion of the variation in F_i ($R^2 = 0.75$, $P = 0.001$).

The proportion of substrate smaller than 0.85 mm was the only substrate measure that differed significantly (Kruskal–Wallis: $H = 14.8$, $P = 0.04$) among the eight spawning reaches. Other redd substrate measures (F_i, proportions smaller than 6.35 and 2.63 mm) were not significantly different. Coefficients of variation (SD/mean) in redd substrate variables differed widely both among and within reaches, being low (less than 15%) in some reaches (e.g., C6 and C8–11) and high (up to 106%) in others (e.g., W3 and C7). We found no significant associations ($P > 0.16$) between redd density and various measures of redd substrate composition.

Both the low-disturbance subbasin (Wapiti Creek) and the high-disturbance subbasin (Cache Creek) had high percentages of fines smaller than 6.35 mm (means, 42.6 and 44.6%). However, the percentage of substrate smaller than 0.85 mm was

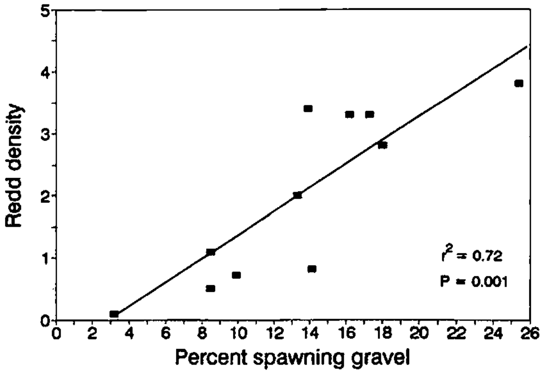

FIGURE 2.—Relationship between redd density (number/100 m^2) and percentage of the substrate consisting of potential spawning gravel in 11 reaches of Taylor Fork, 1992.

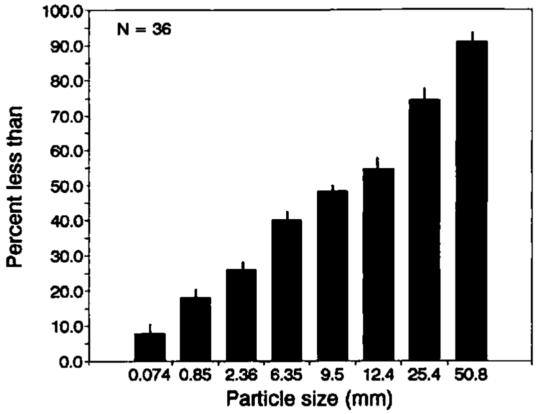

FIGURE 3.—Mean (+2 SE) particle size distribution of cutthroat trout redds sampled in Cache and Wapiti creeks, 1992.

TABLE 4.—Number of redds observed and cored, mean fredle index (F_i) of substrate composition of cores (range in parentheses), estimated egg deposition, predicted mean emergence success, and estimated fry production per spawning reach in Cache (C) and Wapiti (W) creeks.

	Number of redds					
Reach or subbasin	Observed	Cored	F_i	Egg deposition	Emergence success	Number of fry
Reach						
W1	57	7	2.8 (1.4–4.8)	20,606	11.6	2,392
W2	17	3	1.3 (0.7–1.8)	6,679	6.8	455
W3	32	5	2.3 (0.5–5.1)	11,565	7.9	916
C6	39	4	1.0 (0.5–1.6)	13,927	6.8	940
C7	39	3	1.6 (0.8–2.7)	13,927	8.3	1,149
C8–11	74	6	1.0 (0.7–1.4)	26,536	7.8	2,080
C12	33	4	2.0 (1.3–2.5)	11,907	10.5	1,254
C13–17	67	4	1.0 (0.5–1.6)	24,174	7.9	1,931
Subbasin						
Wapiti	106	15	2.3 (0.7–5.1)	38,850	8.2	3,763
Cache	252	21	1.3 (0.5–2.7)	90,471	9.4	7,354
Totals	358	36	1.4	129,321	8.5	11,117

significantly higher in Cache Creek (21.6%, versus 17.1% in Wapiti Creek; $U = 2.57$, $P = 0.01$) and the F_i was significantly lower in Cache Creek (Table 4; $U = 2.32$, $P = 0.02$).

Fry Production

Predicted emergence success was low, averaging 8.5% for all redds (Table 4). Estimated egg deposition ranged from 292 to 699 eggs/redd. Of the total estimated deposition of 129,321 eggs, it was estimated that 11,117 fry were produced, averaging 24–42 fry/redd. Estimated numbers of fry produced per redd were similar in Cache and Wapiti creeks, but because more fish spawned in Cache Creek, total estimated fry production there was about twice that of Wapiti Creek.

Discussion

Spawner and Redd Distribution

Previous studies have documented low-order tributaries as important spawning habitat for cutthroat trout (Rieman and Apperson 1989). We also found most redds (88%) in first- and second-order tributaries. However, we found high variation in use of these sites. Nearly all redds (99%) were observed in the upper reaches of the high-elevation subbasins of Cache and Wapiti creeks even though these areas represent a relatively small proportion (15%) of the basin. Substantially fewer redds were observed in lower-elevation tributaries in the basin, although these areas contained some spawning gravels and had suitable water temperatures (for example, Deadhorse and Little Wapiti creeks).

Trout species composition and density varied with elevation and appeared to contribute to differences observed in number of redds and spawners within the basin. Segregation by elevation between native cutthroat trout and nonnative rainbow trout and brown trout is common where the species co-occur (Bozek and Hubert 1992). Spawning cutthroat trout used high-elevation tributaries almost exclusively. At lower elevations, cutthroat trout numbers declined and the proportion of rainbow trout increased. Ireland (1993) found that juvenile and adult cutthroat trout were abundant (20 fish/100 m^2) in reaches immediately downstream of Cache Creek and Wapiti Creek spawning tributaries but were rare in the rest of the basin. The close association between redd distribution and density of juvenile and adults has been reported by other investigators (Beard and Carline 1991). Conversely, rainbow and brown trout were found only in the main-stem Taylor Fork and lower-elevation tributaries at low densities (2 fish/100 m^2). Ireland (1993) attributed the low densities of rainbow trout and brown trout in the main-stem Taylor Fork to poor habitat conditions.

Some higher-elevation subbasins, such as Lightning Creek, may have been too cold for extensive spawning and fry recruitment. Peak spawning temperature of 8°C occurred there 1 month later than in Cache and Wapiti creeks. We observed newly emerged fry in Lightning Creek in early September as compared with late July to early August in Cache and Wapiti creeks. Such late-emerging fry may have poor overwinter survival (Smith and Griffith 1994).

Cutthroat trout in the Taylor Fork basin appear to conform to a resident form of life history (Liknes and Graham 1988; Rieman and Apperson 1989), because we captured very few (3%) large spawners (>250 mm) characteristic of fluvial populations (Shepard et al. 1984b; Rieman and Apperson 1989). Ireland (1993) found that after spawning, most cutthroat trout in Cache Creek and Wapiti Creek moved relatively short distances (<2,000 m) to summer and winter habitats in second- and third-order tributaries. Historically, spawners following a fluvial life history were probably common in the basin, but negative interactions with nonnative trouts, habitat disruption, and angler exploitation in lower portions of the basin probably selected against this life history form (Liknes and Graham 1988).

Spawning Habitat

Abundance of potential spawning gravels was a key factor influencing redd density at the reach

TABLE 5.—Mean proportion of fines smaller than 6.35 mm and 0.85 mm and the mean fredle index (F_i) of egg pockets in salmonid redds from the Rocky Mountain region, USA.

Trout species	Location	Time of sampling	Percent fines smaller than: 6.35 mm	0.85 mm	F_i	N	Reference
Cutthroat	Montana	Near emergence	41.6	17.9	2.0	11	This study
Cutthroat	Montana		27.4	5.9		13	Weaver and Fraley (1993)
Cutthroat	Idaho	Near emergence	24.4	6.5	7.6	13	R. Thurow and J. King, unpublished data
Steelhead	Idaho	Near emergence	15.4	3.7	10.5	9	R. Thurow and J. King, unpublished data
Brook	Wyoming	Near spawning	12.1	6.4		31	Young et al. (1989)
Brown	Wyoming	Near spawning	15.0	3.0		69	Grost et al. (1991)

scale (Figure 3). Similar relations between redd density and availability of spawning gravel were noted by Cope (1957) for Yellowstone cutthroat trout and by Beard and Carline (1991) for brown trout. The lack of strong association between spawning gravel abundance and several reach characteristics (gradient, proportion of gravel and pea gravel) suggests that local hydrologic features influenced spawning gravel availability. Although the distribution of spawning substrate was patchy within the Taylor Fork drainage, there appeared to be adequate habitat to support resident spawners because redd superimposition was minimal. The distribution of redds apparently was not strongly influenced by the levels of fine sediment in spawning gravel, because we found no negative relations between redd density and various measures of redd substrate composition.

Studies of spawning habitat selection by salmonids have focused on the microhabitat features of redds (e.g., Thurow and King 1994). The high variation we observed in redd density across the basin and even among nearby study reaches suggests that biotic and abiotic factors operating at larger scales are also important in describing spawning habitat suitability (Beard and Carline 1991; Bozek and Rahel 1991). Our data suggest that temperature, fish density, and availability of spawning gravels interacted to influence redd density across the entire basin.

Redd Characteristics

Taylor Fork redds contained some of the highest proportions of fine sediments observed in egg pockets of salmonid redds in the Rocky Mountain region (Table 5). Several factors may account for differences among sites, including sampling method, geology, and sediment transport. Other investigators, using freeze core samplers, have documented the unique qualities of egg pockets and their significantly lower concentrations of fines (Chapman 1988; Young et al. 1989). The lack of differences in our egg pocket and non-egg-pocket samples may have been influenced by the inability of hollow core samplers to preserve the vertical stratification of redd samples (Everest et al. 1980) or by rapid infiltration of fines into redds soon after construction, as Grost et al. (1991) observed. Time of sampling also may result in redd particle size differences (Grost et al. 1991). We sampled redds at the time of emergence, whereas some other authors sampled egg pockets near the time of spawning (Table 5). Everest et al. (1987) and Lisle and Lewis (1992) recommended sampling redds near the time of emergence to document actual incubation conditions.

We believe that the erosive geology and associated sediment loading in Taylor Fork contributed to the high percentages of fines in redds compared with other sites in the region. The proportion of small fines (<0.85 mm) in our study redds (17.9%) averaged two to six times higher than in redds elsewhere. These small fines are readily removed during redd excavation (Young et al. 1989; Grost et al. 1991), yet apparently reaccumulate to high levels before emergence, attesting to the high fine-sediment load in spawning reaches. High proportions of fines within the undisturbed Wapiti Creek subbasin further illustrate the highly erosive nature of the siltstone geology of the basin.

Proportions of small fines in redds were highly variable, accounting for a significant proportion of variation ($R^2 = 0.75$, $P = 0.001$) in the F_i. Small-scale differences in sediment transport and infiltration, particularly in streams with high loads of fine sediment, commonly cause high variation in smaller particle sizes among redds (Lisle and Lewis 1992). Everest et al. (1987) and Chapman (1988) emphasized that predicting the effects of fine sediments on salmonid embryo survival requires accurate sampling of egg pockets and greater attention to measuring temporal changes in substrate conditions during incubation. Our findings suggest that accurate predictions of effects of fines also require knowledge of spatial variability of redd substrate conditions and knowledge of the influence of basin geology on substrate size composition (Everest et al. 1987; Lisle and Lewis 1992).

Our data further suggest that land disturbance exacerbated the high levels of fine sediments in Taylor Fork redds. Previous reports have noted that small fines (<0.85 mm) are the most sensitive indicator of the level of disturbance in watersheds (McNeil and Ahnell 1964; Cederholm and Reid 1987; Young et al. 1991; see also Scrivener and Brownlee 1989). The high-disturbance Cache Creek subbasin had significantly greater proportions of small fines in redds than the relatively undisturbed Wapiti Creek subbasin. Cederholm and Reid (1987) found that road surface erosion was the major contributor to higher proportions of small fines in redds in disturbed subbasins of the Clearwater River, Washington. We did not quantify the source of small fines in our study; however, road surface erosion was not responsible for increased sedimentation of Cache Creek because most surveyed spawning areas were located upstream from roads. Streambanks in Cache Creek were degraded (Snyder et al. 1978) and we speculate that increased erosion resulting from livestock disturbance may be a primary source of elevated small fines; cattle are common on streambanks and within the stream channel during incubation (Magee 1993).

Is Fine Sediment Limiting Recruitment?

High levels of fine sediment in Taylor Fork redds led to very low predictions of overall embryo survival (mean, 8.5%) and numbers of fry produced per redd (mean, 30). Our estimates of emergence success were made by using proportions of fine sediment less than 6.35 mm in diameter, based on the experiments of Weaver and Fraley (1993) with artificial egg pockets planted in stream substrate. Actual emergence success may have been even lower than predicted due to high proportions of small fines (<0.85 mm). Small fines are more detrimental to survival of incubating eggs (Reiser and White 1988) and intrude deeper into spawning gravels (Beschta and Jackson 1979) than coarser fines. The proportions of both small (<0.85 mm; mean, 17.9%) and coarse (<6.36 mm; mean, 44.3%) fines in Taylor Fork are considerably above the levels for these particle sizes (10 and 30%, respectively) shown to adversely affect salmonid emergence success (McNeil and Ahnell 1964; Shepard et al. 1984a; Cederholm and Reid 1987; Reiser and White 1988).

Previous studies have demonstrated that reduced emergence success from high sedimentation can result in low juvenile densities and low adult recruitment (Cederholm and Reid 1987; Scrivener and Brownlee 1989). Despite high fine-sediment levels and low predicted emergence success of fry from Taylor Fork redds, there was little supporting evidence for low recruitment. Juvenile and adult densities in pools of Cache Creek (43.5 fish/100 m^2) and Wapiti Creek (32.5/100 m^2) are notably higher than both the average (9.2/100 m^2) and maximum (26.1/100 m^2) density in pools reported for seven other westslope cutthroat trout populations in Idaho and Montana (Shepard et al. 1984b; Ireland 1993). Beard and Carline (1991) found evidence for recruitment limitation of a resident brown trout population as reflected by low redd density, high ratios of mature females to redds, high rates of redd superimposition, low embryo survival, and low juvenile and adult density. We predicted low embryo survival in our study; however we observed high numbers of redds, low redd superimposition, low ratio of females to redds, and high juvenile and adult density.

Several factors may buffer the effects of high sedimentation of redds. High fry mortality is common in resident salmonids, but low fry densities may result in decreased competition, increased growth, and compensatory survival (McFadden 1969). High fry survival is suggested for Taylor Fork cutthroat trout. A population estimate of juvenile and adult cutthroat trout in Cache Creek in fall 1994 (our unpublished data; N = 3,726, 95% confidence interval = 2,894–4,588) was 50% of the predicted numbers of fry produced in Cache Creek in 1992 (Table 3; N = 7,354). Typical annual mortality rates for cutthroat trout are estimated at 95% for fry and 30–50% for older age-classes (Rieman and Apperson 1989).

Variation in substrate quality among redds (F_i = 0.48–5.14) also could lead to underestimates of fry recruitment. With a large number of redds, the small proportion with high substrate quality may produce enough fry to compensate for low emergence success in remaining redds (Lisle and Lewis 1992). Reductions of fines during redd building may counteract the effects of high sediment loads (Everest et al. 1987; Chapman 1988), but this is probably not an important factor for Taylor Fork cutthroat trout because of the small size of spawners and the very high proportion of fines. It is possible that the population has evolved other reproductive adaptations to compensate for the naturally high sediment load in the basin (e.g., differences in egg size, fecundity, egg depth; Holtby and Healey 1986). For example, van den Berghe and Gross (1989) reported that small salmonid eggs survive better than large eggs in highly sedimented substrates. Small, resident cutthroat trout in Taylor Fork therefore may have adapted to the inherently high fines and have better emergence success than the values we applied from Weaver and Fraley (1993). Additional measurements of egg deposition, fecundity, and emergence success are needed to evaluate compensatory mechanisms.

Our results support the theory that resident salmonid populations are typically not limited by reduced spawning success and that recruitment is probably limited by available rearing habitat, except when seeding is very low (Everest et al. 1987). However, the high levels of fine sediments in Taylor Fork redds, among the highest reported in the literature for salmonids (Table 5; Chapman 1988; Scrivener and Brownlee 1989; Beard and Carline 1991), suggest that fine sediments may be approaching the level that would limit recruitment. The loss of larger, more fecund fluvial cutthroat trout together with degradation of remaining habitats may threaten the persistence of cutthroat trout in the basin. Populations with reduced genetic diversity and those in degraded habitats will be less resilient and at increased risk of local extinction from both stochastic and deterministic processes (Rieman and McIntyre 1993).

A potential confounding factor in our study was the genetic introgression of Taylor Fork cutthroat trout. Little is known about how phenotypic traits are influenced by the level of introgression (Leary et al. 1995). Comparative studies of habitat use and survival of cutthroat trout having varying levels of introgression are needed, given that pure populations represent only a small proportion of remaining populations (Liknes and Graham 1988; Leary et al. 1995).

Spatial Variation

Our results concur with studies illustrating that different spatial scales are important in characterizing fish habitat requirements and assessing land use effects (Frissell et al. 1986; Bozek and Rahel 1991). Bozek and Rahel (1991) noted that many fish habitat studies are conducted at the microhabitat or reach spatial scales. In our study, reach measurements helped explain why certain spawning reaches had higher redd densities than others. However, knowledge of basin scale variables (e.g., temperature, fish species composition and density) was also important. For example, extrapolation of data on redd density obtained from a subset of Taylor Fork reaches without more general knowledge of redd distribution across the entire basin would result in a high degree of error. High variation in fish population and habitat characteristics across watersheds illustrates the importance of using multiple scales to define suitable habitat and to design appropriate monitoring programs (Frissell et al. 1986; Hankin and Reeves 1988; Bozek and Rahel 1991).

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