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Attributes of Yellowstone Cutthroat Trout Redds in a Tributary of the Snake River, Idaho

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Abstract.—We characterized spawning sites of Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri*, described the microhabitat of completed redds, and tested the influence of habitat conditions on the morphology of completed redds in Pine Creek, Idaho. Cutthroat trout spawned in June as flows subsided after peak stream discharge. During spawning, minimum and maximum water temperatures ranged 4–9°C and 16–20°C, respectively. Trout spawned where water depths averaged 20 cm beside redds and 22 cm upstream of redds. Water velocities averaged 42 cm/s beside redds and 46 cm/s upstream of redds. More than 80% of the redds were constructed in water 10–30 cm deep with velocities of 25–60 cm/s. Trout spawned in gravel with particles up to 100 mm in diameter. Most of the substrate was smaller than 32 mm; an average of 20% was less than 6.35 mm and 5% was less than 0.85 mm. The geometric mean particle size of the spawning gravel averaged 16.6 mm and the fredle index averaged 8. Microhabitat conditions differed within completed redds. Water depth decreased and velocity increased from the redd pit downstream to the leading edge of the tailspill and to the tailspill crest. The redd shape may facilitate movement of water through the egg pocket. Redds averaged 1.58 m long by 0.60 m wide, and the pit covered an average of 46% of the redd area. Water depths and velocities in redds were correlated with water depths and velocities adjacent to redds. Redd dimensions were typically not correlated with water depths, velocities, or particle size distributions, suggesting that other factors such as the size of spawning fish may influence redd dimensions.

Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* are the most abundant and widely dispersed subspecies of inland cutthroat trout (Varley and Gresswell 1988). The historical range of the subspecies included the Yellowstone River drainage in Montana and Wyoming downstream to the Tongue River; the Snake River drainage above Shoshone Falls in Idaho, Nevada, Utah, and Wyoming; and two isolated (now extinct) populations in Waha Lake, Idaho and Crab Creek, Washington (Behnke 1992). A combination of factors including habitat degradation, genetic introgression, and exploitation have contributed to the decline of indigenous cutthroat trout populations (Thurow et al. 1988). Remaining populations are largely confined to the waters of Yellowstone Park and to headwater drainages within the subspecies' historical range in Idaho and Montana. In recognition of the decline in numbers and distribution, state management agencies in Idaho and Montana currently list Yellowstone cutthroat trout as a species of special concern (Johnson 1987). Understanding critical habitat requirements of Yellowstone cutthroat trout could assist efforts to maintain existing populations and programs to restore this subspecies to portions of its former range. Detailed descriptions of spawning habitats may be applied to develop criteria for instream flow recommendations for streams during the spawning period, restoration of spawning conditions in altered streams, and design of spawning channels where sufficient habitat no longer exists (Smith 1973).

This paper characterizes spawning sites used by a fluvial population of Yellowstone cutthroat trout and describes the microhabitat of completed redds. Although the spawning habits of cutthroat trout, including timing, homing, and behavior, are well documented (Smith 1941; Ball 1955; LaBar 1971), few studies provide detailed descriptions of spawning sites or redds. Cope (1957), Kiefling (1978), and Varley and Gresswell (1988) provided general descriptions of spawning habitats, including gravel sizes and water temperatures preferred by spawning cutthroat trout. Detailed studies of other cutthroat trout subspecies include the work of Hunter (1973), who sampled water depths and velocities at redds of resident and sea-run coastal cutthroat trout *O. c. clarki*. Although Hooper (1973) listed velocity and substrate criteria for spawning cutthroat trout, he did not describe how he derived the criteria or the subspecies to which they apply. Bovee (1978) applied Hunter's (1973) depth and velocity criteria and substrate data for Gerrard rainbow trout *Oncorhynchus mykiss* to build spawning probability-of-use curves repre-

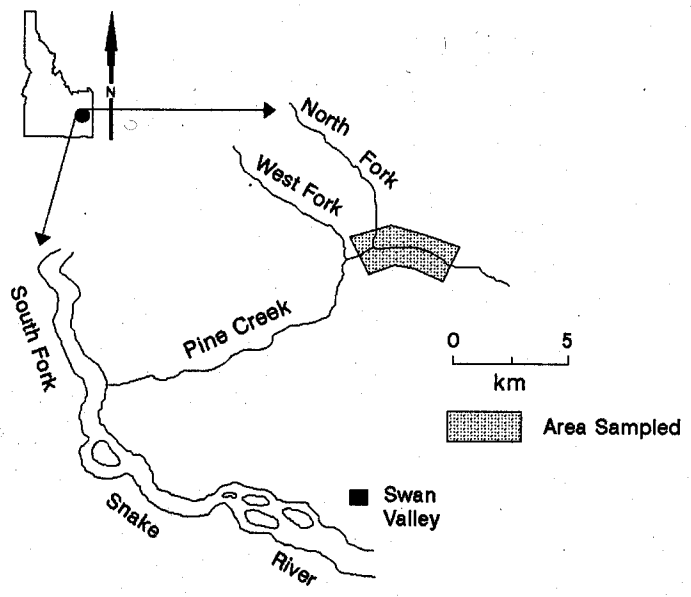

FIGURE 1.—Spawning areas of Yellowstone cutthroat trout sampled in Pine Creek, Idaho, 1991.

senting a "composite" cutthroat trout. Hickman and Raleigh (1982) similarly applied data from Thompson (1972), Hooper (1973), and Hunter (1973) and data for rainbow trout to construct a composite habitat suitability index curve for cutthroat trout. We found no detailed studies of the spawning sites or redds of Yellowstone cutthroat trout in the literature. The spawning criteria for any subspecies may deviate from the composite species criteria (Bovee 1978). We report data specific to Yellowstone cutthroat trout and describe depths, velocities, and substrates in spawning reaches and microhabitat conditions in completed redds.

In this paper, we also test whether habitat conditions influenced the morphology of completed redds. Other researchers have suggested that characteristics of the spawning habitat, including water velocities and substrate particle sizes, are correlated with the dimensions of completed redds (Burner 1951; Ottaway et al. 1981).

Study Area

All measurements were taken in Pine Creek, a tributary to the South Fork Snake River in southeastern Idaho (Figure 1). Pine Creek is the largest tributary accessible to spawning cutthroat trout downstream from Palisades Dam (Moore and Schill 1984). The drainage encompasses 163.7 km^2 near the Idaho–Wyoming border. Pine Creek meanders through an alluvial valley and flows southsouthwest toward its confluence with the South Fork of the Snake River near Swan Valley, Idaho. Major tributaries include the North and West forks of Pine Creek and Tie Creek. The terrestrial canopy is predominantly willow *Salix* sp. and lodgepole pine *Pinus contorta.* Snowmelt causes peak stream discharge during a 4–6-week period beginning in April or May. Elevation, snowpack, and climate influence the onset and duration of runoff. Few historical flow records are available for Pine Creek; years with more than 1 month of records include 1934–1936. Streamflows ranged from an October 1935 mean flow of less than 0.5 m^3/s to a May 1936 mean flow exceeding 25 m^3/s. During 1935 and 1936, flows peaked in May, and declined through June (Figure 2). Discharges in Pine Creek have not been measured since 1936. However, flows have been measured in Flat Creek near Jackson, Wyoming (about 40 km east), from 1933 to 1941 and since 1989 (Harenberg et al. 1992). We compared timing of peak flows measured in Pine Creek with peak flows measured in Flat Creek from 1934 to 1936. Pine and Flat creeks have similar drainage areas (164 km^2 and 104 km^2, respectively), gauges are at similar elevations (1,700 m and 2,000 m, respectively), and there are no diversions upstream from either station. We estimated the timing of 1991 peak flows in Pine Creek by evaluating 1991 flow records for Flat Creek.

Besides Yellowstone cutthroat trout, the native fish fauna in Pine Creek includes mountain white-

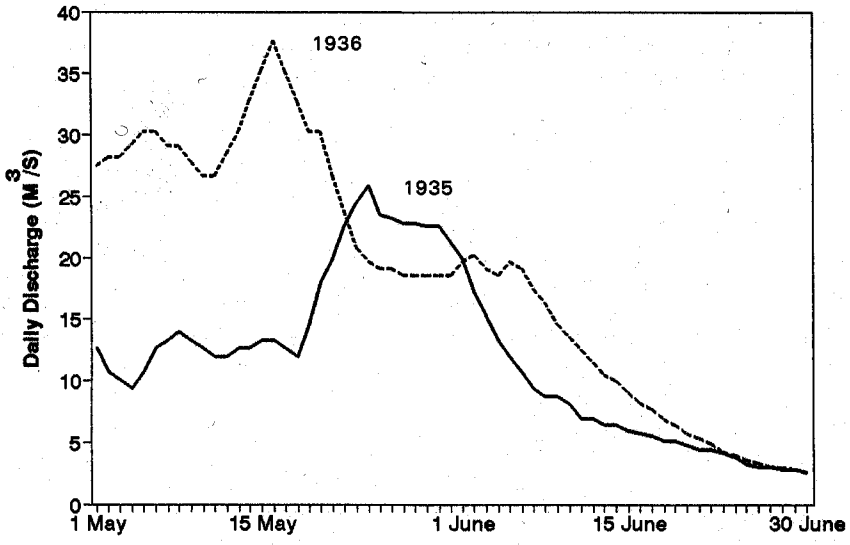

FIGURE 2.—Daily stream discharge in Pine Creek, May and June 1935–1936 (Harenberg et al. 1992). Stream discharge data were not available for the years of our study.

fish *Prosopium williamsoni,* bluehead sucker *Catostomus discobolus,* longnose dace *Rhinichthys cataractae,* speckled dace *Rhinichthys osculus,* mottled sculpin *Cottus bairdi,* and Paiute sculpin *Cottus beldingi* (Moore and Schill 1984). Although nonnative rainbow trout and brook trout *Salvelinus fontinalis* were formerly introduced, no exotics have been released in Pine Creek since 1981 and few persist (V. K. Moore, Idaho Department of Fish and Game, personal communication).

We selected a study reach within the upper portion of the drainage (Figure 1). The reach encompassed a 3-km section of stream beginning 0.5 km downstream from the confluence of Pine Creek and the North Fork Pine Creek and ending 2.5 km upstream from the confluence. The study reach lies within the Targhee National Forest and is typical of much of the current range of Yellowstone cutthroat trout outside of Yellowstone Park in that it lies within an area grazed by livestock (Varley and Gresswell 1988). As elsewhere (Varley and Gresswell 1988), improvements in grazing management in areas of Pine Creek, including the study reach, are deemed necessary to restore habitat and improve conditions for Yellowstone cutthroat trout (IDFG 1991).

Methods

Yellowstone cutthroat trout typically spawn in Pine Creek during June. We made a preliminary reconnaissance of spawning activity in the reach in early June. Beginning on June 10, 1991, we spent 9 d surveying the study reach, marking the location of spawning fish and redds. We also installed a continuously recording thermograph (probe on the substrate) in the center of the reach and recorded hourly temperatures during June 10–21. We completed multiple surveys daily. Observers walked the stream bank, taking care to avoid detection by fish, and looked for fish and redds. Redd locations were marked by inserting a numbered stake in the adjacent bank. We marked 66 redds and defined redds as completed if they met two criteria: fish abandoned them after spawning activity was observed but were not driven from redds; and the redd exhibited the characteristic pit (upstream depression) and tailspill (downstream mound of disturbed substrate) described by Burner (1951). Redds were not included if no spawning activity was observed or if redds did not exhibit a pit and tailspill.

Within 48 h after fish abandoned redds, we characterized sites immediately adjacent to redds believed typical of initial conditions (pre-redd construction) and described microhabitat conditions in completed redds. We assumed that conditions in undisturbed substrate immediately adjacent to redds reflected the initial conditions selected by spawning fish. Reiser and Wesche (1977) reported that depth and velocity measured immediately upstream from redd pits most closely represented those present prior to redd construc-

tion. Hunter (1973) measured depths and velocities immediately upstream from redd pits and compared them with measurements about 0.91 m downstream and beside redds. At water depths of about 20 cm, downstream sites averaged 6 cm shallower and velocities 5 cm/s faster than at upstream sites. Grost (1989) averaged depth measurements taken immediately upstream from redd pits and at tailspill edges. He concluded that because this mean value closely approximated depths taken immediately upstream from the redd pit, the upstream depth measurement accurately approximated the depth prior to redd construction.

Two sites adjacent to each redd were selected, one beside the center of the redd pit and the other immediately upstream from the center of the pit. These sites were within 5 cm of the edge of the pit in undisturbed substrate with a surface particle size distribution visually similar to that surrounding the redd and at a depth similar to that surrounding the redd. We did not attempt to sample sites before fish began spawning because we could not predict specific locations where fish would construct redds. We also did not rely on measurements within completed redds to describe conditions fish selected because fish alter the substrate during redd construction (Chapman 1988).

To characterize the undisturbed sites selected by spawning fish, we measured depths and velocities at the two sites adjacent to each completed redd with a wading rod and Marsh-McBirney current meter, accurate to about 1.5 cm/s. Velocity was measured at a depth 0.6 times the water column depth, the depth where velocity approximates a mean vertical water column velocity (Orth 1983). We measured mean velocity because at the depths at which we encountered most redds (about 20 cm), average water velocity would approximate the facing velocity of a fish within 8 cm of the substrate and because the published literature describing spawning habitats listed average water velocities (Bovee 1978; Hickman and Raleigh 1982).

We collected substrate samples from the sites adjacent to redds to describe the particle size distribution in spawning gravels believed typical of gravels selected by fish. Six samples were collected immediately after spawning was completed on June 19, and 10 samples were collected near the end of the incubation period on July 23. On both dates, we randomly selected either the upstream or alongside site and cored a substrate sample. We used a tri-tube freeze-coring apparatus with liquid CO_2 (Everest et al. 1980) to extract vertical substrate samples approximately 20 cm long and 15 cm in diameter. Each core sample was separated vertically by 5-cm depths. For the segment of the study reported here, we analyzed the surface strata (0–5-cm depth) only. We air-dried the samples and sieved them for 5 min on a mechanical shaker through mesh sizes of 100, 64, 32, 16, 9.5, 8, 6.35, 4, 2, 1, 0.85, 0.5, 0.25, 0.125, and 0.063 mm. Core samples were analyzed in two ways. Initially we weighed the material retained on each sieve and calculated the percent of the sample passing through (less than) each sieve size. Secondly, because we observed larger particles being lost as we extracted our cores, we avoided bias by truncating our data to exclude particles 64 mm and larger from our analysis. Because large particles are often lost as cores are extracted, many workers have excluded larger size categories from analysis (Adams and Beschta 1980; Tappel and Bjornn 1983).

For each core sample, we calculated two measures of central tendency: the geometric mean and the fredle index. The formulas we used for the geometric mean (D_g) and fredle index (F_i) were described by Lotspeich and Everest (1981) and were identical to those listed by Young et al. (1991). The geometric mean is calculated by raising the midpoint size of particles retained by a sieve to a power equal to the decimal fraction of the entire sample weight retained on that sieve. The resulting values for each sieve are multiplied to calculate the geometric mean. For example, the midpoint size of material retained on the 2-mm sieve would be (2 mm + 4 mm)/2 = 3 mm. If 4.4% of the sample weight were retained on the 2-mm sieve, the midpoint particle size (3 mm) would be raised to the power of 0.044. This value would be multiplied by analogous values for all other particle size-classes. Lotspeich and Everest (1981) proposed the F_i because they concluded that the D_g did not give sufficient weight to the finer particle sizes in gravel samples. The F_i is the D_g divided by the Trask sorting coefficient (the square root of the quotient of the particle diameter at the 75th percentile divided by the particle diameter at the 25th percentile) (Kondolf 1988). The Trask sorting coefficient provides a measure of the spread of the central 50% of the distribution, so the F_i is similar to an inverse coefficient of variation (standard deviation/mean) (Kondolf 1988). We calculated measures of central tendency because use of the percentage of fines to characterize gravel quality has been criticized (Platts et al. 1979). Although attempts to derive a single variable to index gravel quality may be flawed, size of spawning

gravels can be described by a measure of central tendency (Kondolf 1988).

To describe microhabitat conditions in redds, we measured depths, water velocities (0.6 × depth), and dimensions of 66 completed redds. We measured depths and water velocities at three locations in each redd: the bottom of the pit, the leading edge (upstream one-third) of the tailspill, and the tailspill crest. Salmonid egg pockets are typically found under the leading edge of the tailspill (Chapman 1988; Grost 1989; Young et al. 1989). We estimated the area of substrate required for redd construction by measuring pit and tailspill dimensions. Pit length was measured parallel with the streamflow between the upstream edge of the pit and the upstream edge of the tailspill. We measured the tailspill length from its upstream edge to the downstream, tapered edge of disturbed gravel. Pit and tailspill widths were measured perpendicular to the streamflow at the center of the pit and crest of the tailspill. We calculated the surface areas of the pit and tailspill and summed them to estimate the total redd area. Our redd area estimates represent a maximum rectangular-shaped area used by spawning fish. Because redds are roughly elliptical (Ottaway et al. 1981), and the actual area may be smaller than our estimates, the equation for an ellipse may more closely approximate the actual area covered by a redd.

Yellowstone cutthroat trout were observed on each of the 66 sampled redds. We estimated the size range of all fish observed and did not attempt to capture individual fish or relate estimates of fish size to redd size. In 1992, we resurveyed the study reach and described redd locations but we did not measure microhabitat conditions.

We described the distributions of water depths, velocities, and substrate used by spawning Yellowstone cutthroat trout and statistically tested differences between redd sites. Paired *t*-tests were used to compare depths and velocities measured upstream from and beside redds and to compare the particle size distributions of the June and July substrate samples. Measures of central tendency (the fredle index and geometric mean) were regressed against each other and against the percentage of substrate less than 6.4 mm. We used *t*-tests to determine if the slopes of regression lines were significantly different from zero. We used frequency analysis to describe and compare the ranges of depth, velocity, and dimensions of completed redds. An analysis of variance was used to test for differences in depth and velocity across redd pits, tailspill edges, and tailspill crests. We used a Tukey test to determine where significant differences in depths and velocities occurred. A correlation matrix was used to determine if depths, velocities, and particle sizes adjacent to redds influenced the physical characteristics and dimensions of completed redds. Statistical analyses were performed with PC SAS (SAS Institute 1989).

Results

Although some cutthroat trout began spawning before peak discharge, most fish spawned as flows subsided after peak discharge. From 1934 to 1936, peak flows in Pine Creek occurred an average of 18 d before peak flows in Flat Creek (Harenberg et al. 1992). Following peak discharge, flows in both drainages typically receded until the base flow period in September. If we assume this relationship has not changed, flows peaked in Pine Creek approximately May 26, 1991, about 2 weeks prior to our initial redd measurements.

Yellowstone cutthroat trout spawned after minimum Pine Creek water temperatures exceeded 4°C and mean daily temperatures exceeded 10°C. Temperatures fluctuated as much as 12°C within a day during the spawning period. Maximum daily water temperatures ranged from 16 to 20°C, mean temperatures from 10 to 14°C, and minimum temperatures from 4 to 9°C. Daily water temperatures were highest during 1700–1800 hours and lowest during 0600–0700 hours.

The estimated lengths of cutthroat trout observed on redds ranged from 300 to 500 mm. We did not attempt to relate fish size to redd size. Moore and Schill (1984) trapped 457 spawning cutthroat trout ranging from 250 to 530 mm in Pine Creek in 1981. Females averaged 363 mm and males 378 mm total length. Most trout remained on redds for about 3 d.

Attributes of Sites Adjacent to Redds

Yellowstone cutthroat trout spawned in water 9–55 cm deep. Depths averaged about 20 cm beside redds and 22 cm upstream from redds when spawning was completed (Table 1). Water depths measured beside the redd pit did not differ significantly from depths measured immediately upstream ($P > 0.29$). Yellowstone cutthroat trout constructed more than 80% of the redds at depths between 10 and 30 cm (Figure 3). The distribution of depths was skewed toward greater depths so that median depths were less than mean depths at both sites.

Mean water column velocities within 5 cm of completed redds were 16–73 cm/s, averaging 42

TABLE 1.—Characteristics of sites adjacent to those selected by Yellowstone cutthroat trout for spawning in Pine Creek, 1991. Sites immediately adjacent to (within 5 cm of) redds were assumed to be typical of the site before redd construction.

Characteristic	*N*	Mean	SD	Minimum	Maximum
Water depth (cm)					
Beside pit	66	20.3	7.5	10.7	47.3
Upstream from pit	66	21.8	9.5	9.2	54.9
Water column velocity (cm/s)					
Beside pit	66	42	12.8	16	72
Upstream from pit	66	46	12.5	18	73
Substrate (0–5 cm depth) particle size distribution[a]					
Percent less than:					
64.00 mm	10	100.0	0.0	100.0	100.0
32.00 mm	10	60.6	11.1	48.5	78.6
16.00 mm	10	36.6	8.4	25.8	51.8
9.50 mm	10	25.7	8.2	12.1	39.1
8.00 mm	10	22.7	8.0	9.5	35.2
6.35 mm	10	19.6	7.5	6.8	31.0
4.00 mm	10	14.8	6.5	4.3	24.5
2.00 mm	10	9.6	4.9	2.3	17.7
1.00 mm	10	5.7	3.1	0.9	11.9
0.85 mm	10	5.0	2.7	0.7	10.6
0.50 mm	10	3.3	1.8	0.4	6.8
0.25 mm	10	2.0	1.0	0.3	3.8
0.12 mm	10	1.2	0.6	0.2	2.2
0.06 mm	10	0.7	0.4	0.1	1.2
Geometric mean D_g (mm)	10	16.61	4.08	9.80	23.36
Fredle index F_i	10	8.00	3.10	3.46	13.42

[a] Truncated data; particle sizes 64 mm and larger were omitted from this analysis.

cm/s beside redds and 46 cm/s upstream from redds (Table 1). Water velocities beside redd pits did not differ significantly from velocities measured immediately upstream from the pit ($P >$ 0.10). Water velocities were between 25 and 60 cm/s at more than 80% of the sites adjacent to redds (Figure 4). Unlike depths, there was little skew in the distribution of velocities and the me-

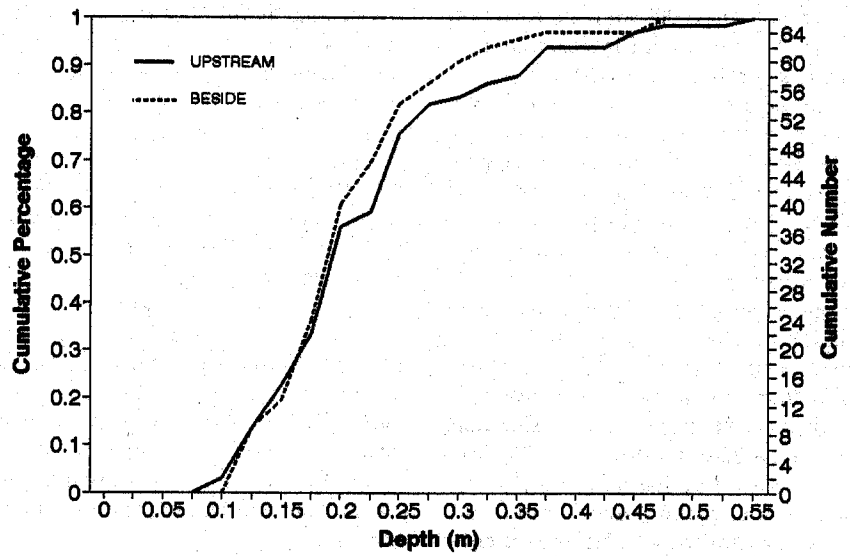

FIGURE 3.—Cumulative frequency distribution of water depths upstream from and beside Yellowstone cutthroat trout redds, Pine Creek, 1991.

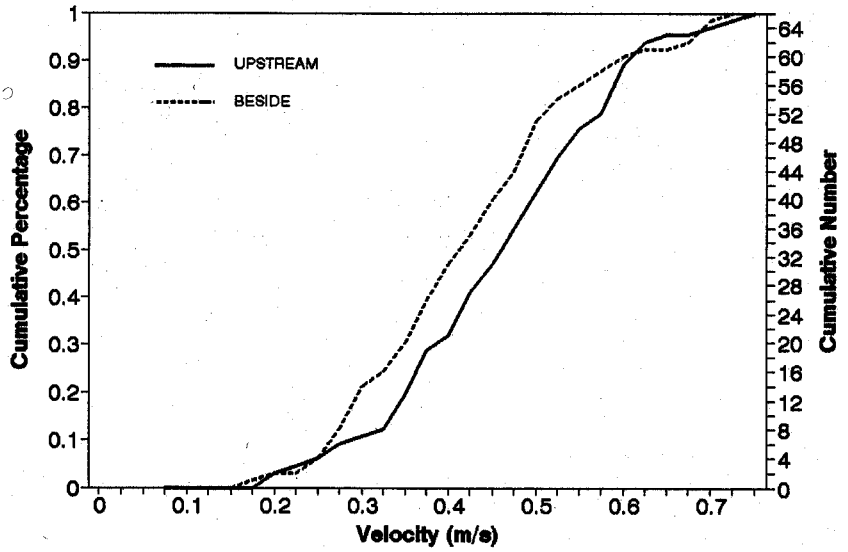

FIGURE 4.—Cumulative frequency distribution of water velocities upstream from and beside Yellowstone cutthroat trout redds, Pine Creek, 1991.

dian velocities were only slightly less than the mean velocities at both sites.

Cutthroat trout spawned in substrate less than 100 mm in diameter. A mean of 6% of the substrate ranged from 64 to 100 mm and 36% ranged from 32 to 64 mm; most (58%) of the substrate was less than 32 mm (Figure 5). When data are truncated to disregard particles 64 mm and larger to eliminate bias, most redds were constructed in substrate in which an average 20% of particles were less than 6.35 mm and 5% were less than 0.85 mm in diameter (Table 1; Figure 5).

Samples of undisturbed substrate beside redds at the start of incubation did not differ significantly from samples in undisturbed substrate beside redds at the end of incubation ($P > 0.1$ to $P > 0.8$ for individual particle sizes and cumulative particle size distributions).

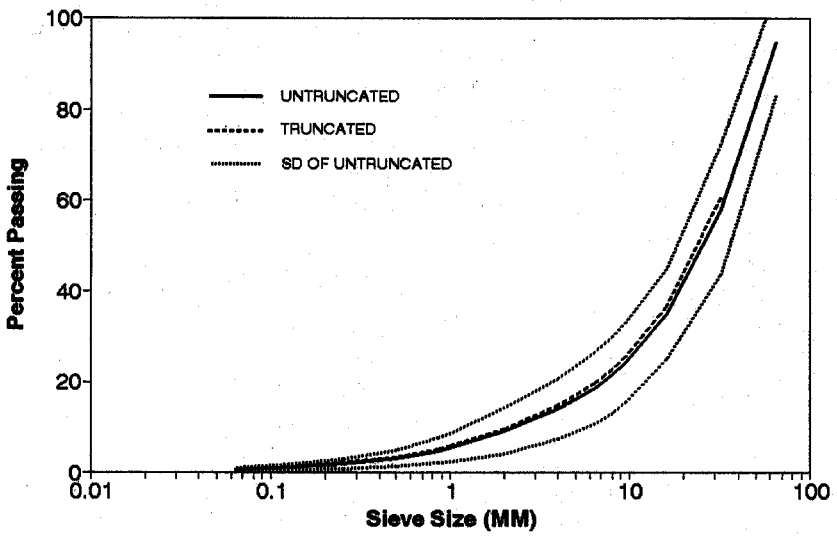

FIGURE 5.—Particle size distribution of Yellowstone cutthroat trout spawning gravels in Pine Creek, 1991. Untruncated samples were analyzed for particles less than 100 mm in diameter and truncated samples were analyzed for particles less than 64 mm in diameter.

TABLE 2.—Attributes of 66 redds constructed by Yellowstone cutthroat trout in Pine Creek, 1991.

Attribute	Location in redd	Mean	SD	Minimum	Maximum
Depth (cm)	Pit	24.4	7.2	13.7	51.9
	Tailspill edge	18.1	5.7	10.7	42.7
	Tailspill crest	13.6	5.0	6.1	39.6
Velocity (cm/s)	Pit	39	10.6	17	61
	Tailspill edge	46	11.9	22	74
	Tailspill crest	56	12.9	30	93
Length (m)	Pit	0.73	0.24	0.47	1.36
	Tailspill	0.85	0.21	0.35	1.47
	Total redd	1.58	0.37	0.95	2.60
Width (m)	Pit	0.60	0.11	0.44	0.91
	Tailspill	0.59	0.09	0.42	0.85
	Total redd	0.60			
Surface area (m^2)	Pit	0.45	0.20	0.22	1.16
	Tailspill	0.51	0.18	0.17	0.96
	Total redd	0.96	0.33	0.43	2.11

Both measures of the central tendency of particle sizes in undisturbed spawning gravels followed similar trends. The geometric mean particle size increased as the fredle index increased and the slope of the regression line was significantly larger than zero ($P < 0.001$, $r^2 = 0.92$). Both D_g and the F_i were inversely correlated with the percentage of particles less than 6.4 mm. The D_g decreased as the percent of the substrate less than 6.4 mm increased and the slope of the regression line was significantly less than zero ($P < 0.001$, $r^2 = 0.91$). Similarly, F_i decreased as the percent of the substrate less than 6.4 mm increased and the slope of the regression line was significantly less than zero ($P < 0.001$, $r^2 = 0.97$). The average D_g of all substrate samples was 16.6 mm (Table 1); 70% of the D_g values fell between 15 and 20 mm. The average F_i for all samples was 8; 70% of the calculated F_i fell between 5 and 10.

In 1992, spawning cutthroat trout selected new spawning locations that had not been used in 1991. Many areas of suitable gravel that had been used in 1991 were not used in 1992. Severe drought reduced Pine Creek flows in 1992 and many of the spawning locations used in 1991 were nearly dewatered.

Attributes of Completed Redds

Water depths and velocities in completed redds differed from depths and velocities measured at undisturbed sites adjacent to redds. If we assume that adjacent sites represented pre-redd construction conditions, we must conclude that cutthroat trout altered water depths and velocities by constructing redds. Pits averaged 4.2 cm deeper (SD, 3.5), leading tailspill edges averaged 2.2 cm shallower (SD, 4.1), and tailspill crests averaged 6.7 cm shallower (SD, 5.5) than the undisturbed sites beside redds (Tables 1, 2). Compared with water velocities beside redds, velocities in pits averaged 3 cm/s slower (SD, 11), velocities at tailspill edges averaged 4 cm/s faster (SD, 10), and velocities at tailspill crests averaged 14 cm/s faster (SD, 11).

Microhabitat conditions (physical attributes at specific locations) differed among locations in completed redds. Depth decreased significantly ($P < 0.0001$) as measurements progressed downstream from the redd pit to the leading edge of the tailspill to the tailspill crest (Table 2; Figure 6). Conversely, velocity increased significantly ($P < 0.0001$) downstream from the redd pit (Table 2; Figure 7).

The 66 redds we measured averaged 1.58 m long by 0.60 m wide, encompassing nearly 1 m^2 (Table 2). On average, the pit occupied about 46% of the redd area and the tailspill occupied the remainder. We observed some redds clustered less than 0.5 m apart in pockets of suitable gravel, particularly along gravel bars or at the downstream end of pools. Other redds were spaced more than 400 m apart. We observed cutthroat trout superimposing new redds over portions of existing ones. In most cases, superimposed redds were constructed lateral to or immediately downstream from existing redds.

Factors Influencing Redd Morphology and Dimensions

Water depths adjacent to and inside completed redds were significantly correlated ($P < 0.05$, $r =$

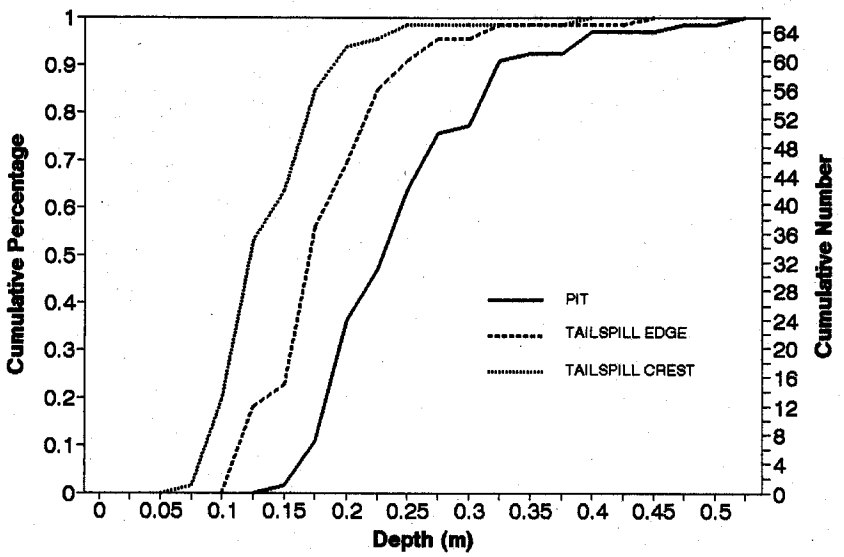

FIGURE 6.—Distribution of water depths at three locations within Yellowstone cutthroat trout redds, Pine Creek, 1991.

0.61–0.92: Table 3). Up to 85% of the variation in depth at a given location in the redd (e.g., pit depth) was explained by depth at a location outside the redd (e.g., depth upstream from the pit). Similarly, depths at the three locations within the redds were significantly correlated ($P < 0.05$, $r =$ 0.69–0.90). Depth at one location could be used to predict depths at other locations.

Water velocities adjacent to and inside completed redds were also significantly correlated ($P < 0.05$, $r = 0.57$–0.69: Table 3). Water velocities at the three locations within redds were similarly significantly correlated ($P < 0.05$, $r = 0.73$–0.87). Velocity at one location could be used to predict velocities at other locations.

We did not detect any significant correlations between depths (either adjacent to redds or within redds) and velocities within redds (Table 3). With

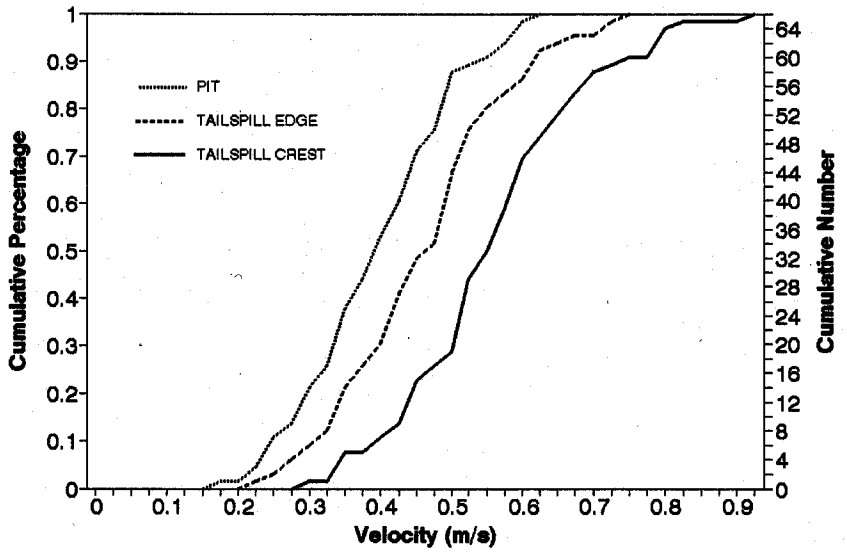

FIGURE 7.—Distribution of water velocities at three locations within Yellowstone cutthroat trout redds, Pine Creek, 1991.

TABLE 3.—Correlation coefficients (r) for depths and velocities measured outside and within 66 completed redds in Pine Creek, 1991. Asterisks denote significant correlations at $P < 0.05$*.

Variable	Pit depth	Tailspill edge depth	Tailspill crest depth	Pit velocity	Tailspill edge velocity	Tailspill crest velocity
			Depth			
Depth beside pit	0.89*	0.84*	0.68*	−0.11	−0.12	−0.04
Depth upstream of pit	0.92*	0.82*	0.61*	−0.16	−0.19	−0.09
Pit depth	1.00	0.90*	0.69*	−0.12	−0.15	−0.02
Tailspill edge depth	0.90*	1.00	0.85*	<0.01	−0.08	−0.02
Tailspill crest depth	0.69*	0.85*	1.00	0.06	0.01	−0.07
			Velocity			
Velocity beside pit	0.08	−0.06	0.01	0.57*	0.66*	0.64*
Velocity upstream of pit	−0.34*	−0.26*	−0.18	0.61*	0.65*	0.69*
Pit velocity	−0.12	<0.01	0.06	1.00	0.85*	0.73*
Tailspill edge velocity	−0.15	−0.08	0.01	0.85*	1.00	0.87*
Tailspill crest velocity	−0.02	−0.02	−0.07	0.73*	0.87*	1.00

two exceptions, velocities adjacent to redds were also not significantly correlated with depths within redds. Velocities upstream from the redd pit were significantly ($P < 0.05$) and inversely correlated with pit depth ($r = -0.34$) and tailspill edge depth ($r = -0.26$).

The environmental conditions we measured were not highly correlated with redd dimensions, suggesting that other factors such as fish size influenced redd size. With two exceptions, water depths were not significantly correlated with redd length, width, or surface area ($P > 0.1$, $r = 0.01$–0.22). Pit width was significantly and inversely correlated with water depth beside and upstream from the redd pit ($P < 0.05$). However, depth explained less than 10% of the variation in pit width ($r^2 = 0.07, 0.09$). Similarly, water velocities were not significantly correlated with redd dimensions ($P > 0.1$, $r = 0.01$–0.31). The percentages of most individual particle sizes in undisturbed substrate beside redds were not significantly correlated with redd dimensions ($P > 0.1$, $r = 0.04$–0.58). An exception was the correlation of the percent of the substrate less than 1 mm and tailspill length. Although the correlation was negative and significant ($P < 0.02$), the percent of the substrate less than 1 mm explained less than 50% of the variance in tailspill length.

With few exceptions, the percentages of individual particle sizes in the undisturbed substrate adjacent to redds were not significantly correlated with water depths at locations within redds. Pit depth was significantly ($P < 0.025$) correlated with percent of the sample in the following particle size-classes: <9.5 mm ($r = -0.70$), <2 mm ($r = 0.75$), and <0.063 mm ($r = 0.70$). Depth of the leading tailspill edge was significantly ($P < 0.005$, $r = 0.81$) correlated with percent fines less than 2 mm. However, the trends were not consistent and we concluded that factors other than the initial substrate particle size influenced water depths in redds.

Most horizontal dimensions within redds were not significantly correlated ($P > 0.1$, $r < 0.5$). Pit length explained less than 25% of the variability in pit width, tailspill length, or tailspill width. Pit width explained nearly 50% of the variability in tailspill width, but less than 10% of the variability in tailspill length.

Discussion

Yellowstone cutthroat trout spawned over broad ranges of temperature, depth, velocity, and substrate particle size. Cutthroat trout spawned in Pine Creek at temperatures (4–20°C) similar to published ranges. Hickman and Raleigh (1982) suggested preferred spawning temperature ranges were 6–17°C, and Varley and Gresswell (1988) suggested ranges of 5.5–15.5°C.

Attributes of Sites Adjacent to Redds

Most trout in Pine Creek spawned at sites that were similar in depth and velocity to published data for cutthroat trout. Depths averaged about 20 cm beside redds and 22 cm upstream from redds, and 80% of the redds were constructed in water 10–30 cm deep. Hunter (1973) observed resident and anadromous coastal cutthroat trout spawning at depths averaging 12.8–18.9 cm and ranging from 6.1 to 45.7 cm. Bovee (1978) prepared a depth suitability curve for cutthroat trout; suitable depths (probabilities of use, 0.5–1) ranged from 16.8 to 30.4 cm.

In Pine Creek, velocities in spawning areas averaged 42 cm/s beside redds and 46 cm/s up-

stream from redds, and 80% of the redds were constructed in areas with velocities of 25–60 cm/s. Hunter (1973) reported resident and anadromous coastal cutthroat trout spawning where velocities averaged 23.5–36.3 cm/s. Bovee's (1978) velocity suitability curve indicates suitable velocities of 15.2–36 cm/s. Hickman and Raleigh (1982) assumed that the optimal spawning velocity range for cutthroat trout was 30–60 cm/s.

Yellowstone cutthroat trout in Pine Creek spawned over substrate with a broader range of particle sizes than the ranges listed in the literature. Most published accounts of cutthroat trout spawning substrate list general gravel sizes used by fish and do not include specific particle size distributions. It is likely that smaller particle sizes were also present in the spawning gravel but the authors did not report the distributions. Cope (1957) suggested cutthroat trout prefer to spawn in gravel from 19 to 76 mm in diameter. Varley and Gresswell (1988) suggested that gravel 12–85 mm in diameter was optimum. Hickman and Raleigh (1982) assumed gravel from 15 to 60 mm in diameter was optimum. We observed fish using substrate with particles ranging from less than 0.063 to 100 mm; about 60% of the untruncated substrate was in the 16–64-mm size-class, 15% was in the 6.4–16-mm size-class, and 20% was less than 6.4 mm.

The initiation of redd construction and spawning may be controlled by physical cues (Crisp and Carling 1989). Although it is likely that these physical cues include temperature, depth, velocity, and substrate particle size, the importance of each factor in spawning site selection is poorly understood. Varley and Gresswell (1988) suggested that Yellowstone cutthroat trout spawn wherever optimum gravel size and water temperatures are found. Our observations suggest Yellowstone cutthroat trout in Pine Creek did not spawn wherever suitable-size gravel was found. Severe drought reduced Pine Creek flows in 1992 and many of the spawning locations used in 1991 were nearly dewatered. In 1992, spawning cutthroat trout selected new spawning locations in areas of suitable gravel that were not used in 1991. Had fish spawned in the same locations during both years, most redds constructed in 1992 would have been dewatered prior to fry emergence. By responding to physical cues in addition to substrate and temperature, these spawners may have enhanced their reproductive success. We did not measure microhabitat conditions in Pine Creek in 1992 so we cannot test whether fish used similar depths and velocities during both years. Grost et al. (1990) similarly observed that spawning brown trout *Salmo trutta* selected new spawning locations as minimum stream flows increased 50–100% from 1975 to 1987–1988. The authors measured microhabitat conditions and found fish using consistent depths and velocities during all flow conditions. Other researchers have suggested that factors in addition to substrate size are important in spawning site selection. Shirvell and Dungey (1983) suggested that because substrate sizes are largely determined by water velocity, and because it is unclear how fish might judge substrate quality, fish may have evolved to select the "correct" water velocities as a means of selecting proper substrate. Accelerated flow and upwelling rather than just velocity may determine choice of spawning location (Tautz and Groot 1975).

As spring spawners, Yellowstone cutthroat trout may have access to spawning sites in intermittent streams or stream reaches that would be unsuitable as flows recede. Varley and Gresswell (1988) reported cutthroat trout spawning in intermittent streams and emergent fry migrating before the streams were dry. They suggested that the use of intermittent streams provides cutthroat trout with a reproductive advantage over introduced fall-spawning exotics.

If fish seek specific depths, velocities, and substrate for spawning, trout of similar size may select consistent spawning habitat regardless of annual fluctuations in discharge or stream size. Trout spawning in intermittent streams, perennial tributaries, and main-stem river reaches may seek similar habitats.

Redd Attributes

Our observations of completed redds support the conclusion (Chapman 1988) that the unique morphology of salmonid redds may lead to optimal physical conditions for egg incubation. The shape of the Yellowstone cutthroat trout redds we observed tended to facilitate movement of water through them, as Cooper (1965) reported. Depth decreased significantly and velocities increased significantly downstream from the redd pit to the tailspill crest. Acceleration of flow over redds may increase intragravel flow in the vicinity of the egg pocket. Water movement through the redd delivers oxygen to embryos and carries metabolic wastes away (Coble 1961).

We observed considerable spatial variability in water depths, velocities, and dimensions of redds. Variability in redd morphology may contribute to

the spatial variability in dissolved oxygen and temperature in redds reported by Ringler and Hall (1975).

Redd dimensions could be applied to estimate the number of spawners a reach could support. Individual redds averaged 1.58 m long by 0.6 m wide, covering nearly 1 m^2. Territorial behavior of spawning fish may maintain additional space between redds. Burner (1951) suggested that territorial behavior of spawning chinook salmon *Oncorhynchus tshawytscha* necessitated an area four times the size of an average redd for each pair. Although aggressive behavior of spawners maintains spacing between redds simultaneously constructed, later-arriving fish may superimpose new redds over existing ones (Van den Berghe and Gross 1984) or they may spawn in areas between existing redds. In either case, fish would use a larger proportion of the available spawning gravels in a reach than would be used if all fish built redds at the same time. In Pine Creek, we observed cutthroat trout superimposing new redds lateral to or immediately downstream from existing redds. Because egg pockets are generally located in the center of the upstream edge of the tailspill, overlap at the sides (Chapman et al. 1986) and downstream from the tailspill may not disrupt the egg pocket. Redd superimposition would only disrupt the egg pocket if subsequent redds were precisely centered over previously constructed egg pockets (Smith 1941; Van den Berghe and Gross 1984).

Influencing Factors

Cutthroat trout constructed redds of relatively uniform external physical characteristics (depths and dimensions), and we were not able to detect significant correlations of these with the environmental conditions we measured. Burner (1951) and Ottaway et al. (1981) suggested that salmonid redds constructed in fast water were longer than redds in slow water. The dimensions of cutthroat trout redds we measured were not significantly or consistently correlated with initial water depths, velocities, or substrate particle size distributions. Ottaway et al. (1981) reported that brown trout constructed larger redds over very fine gravels at one location but no relationship could be established between substrate size and redd dimensions at six other locations. Unlike Burner (1951), we did not find that the size of salmonid redds varied in inverse proportion to the size of the gravel. Pit depth appeared to be influenced by certain particle sizes, but the trend was not consistent.

The size of spawning fish, rather than environmental conditions, may be the major factor determining redd dimensions. Redd dimensions tend to be proportional to the length of spawning fish (Burner 1951; Ottaway et al. 1981; Van den Berghe and Gross 1984; Crisp and Carling 1989). Ottaway et al. (1981) developed a model to predict redd size from environmental variables and fish size. The model did not improve predictive capabilities over a regression of fish size versus redd size. Researchers also have reported a relationship between fish size and egg pocket depth (Ottaway et al. 1981; Crisp and Carling 1989).

Artificially constructed redds have been used to monitor the condition of salmonid spawning areas (Gustafson-Marjanen and Moring 1984) and as tools to restore or supplement declining fish populations (Harshbarger and Porter 1982). Artificial redds that mimic natural redds may subject eggs and alevins to more typical incubation conditions (Gustafson-Marjanen and Moring 1984). Our descriptions of the depths, velocities, and substrate characteristics of spawning sites; the relationships between depths and velocities adjacent to and within redds; and the dimensions of redds are applicable to locating and constructing suitable artificial redds.

Our analysis has some important limitations. First, we did not quantify the habitat available for spawning in Pine Creek. Consequently, we were unable to describe selection because we could not compare habitat use to habitat availability. Our observations reflect only the habitat that was used. Second, we assumed that substrate immediately beside or upstream from redds represented the conditions that fish encountered when they began spawning. The actual conditions are unknown because we were not able to sample sites before fish began spawning. Although unlikely, cutthroat trout could have selected spawning sites for criteria other than depth, velocity, and substrate. Third, spawning criteria and redd microhabitat conditions were collected during a relatively narrow period of spawning. We sampled redds constructed during 9 d in a spawning period that lasted more than 30 d. Suitable spawning sites may include a wider range of conditions than those we observed. Fourth, because we avoided disturbing spawning fish, we did not measure individual spawners. As a result, we are unable to relate fish size to redd size. Finally, we did not measure microhabitat conditions of completed redds in 1992 so we cannot test whether fish selected spawning sites with similar depths, velocities, and substrate particle sizes during 1991 and 1992.

Many cutthroat trout stocks are at risk of decline. Johnson (1987) listed 11 stocks of cutthroat trout besides the Yellowstone cutthroat trout that are legally protected or of concern. Individual spawning habitat preferences may vary among stocks. However, where site-specific data are not available, the data presented here may assist in defining microhabitat requirements for spawning site selection, characteristics of completed redds, and factors influencing reproductive success for fish of similar size.

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