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Description of Brown Trout Redds in a Mountain Stream

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Abstract.—We sampled redds of brown trout *Salmo trutta* in a mountain stream to describe egg location and substrate composition after spawning and during egg incubation. A single-probe freeze-coring device was used to sample egg depth and substrate composition. We found eggs throughout redds but most often in the front half of the tailspill (the substrate mound that accumulates as the redd is excavated progressively upstream). Eggs were buried between 2 and 23 cm below the substrate surface but were most frequently 9–12 cm deep. Spawning fish cleaned substrate particles less than 6.3 mm in diameter from egg pockets, yet the percentage of particles smaller than 1.7 mm in egg pockets was correlated with that outside redds. Egg pockets contained particles larger than 50 mm more often than did any other location, indicating that particles of this size were used as egg pocket centrums. The percentage of 1.7-mm and smaller particles in egg pockets was higher in winter than in fall. We conclude that (1) spawning brown trout 20–40 cm in total length substantially alter the substrate in egg pockets; (2) the amount of fine sediment in egg pockets is positively correlated with that in the adjacent streambed; and (3) fines accumulate in egg pockets during the incubation period.

Stream-spawning salmonids bury their eggs in the streambed to incubate. Before depositing eggs, the female cuts into the streambed by turning sideways to it and violently flexing her body. This forms a depression (pit) into which eggs are deposited. Subsequent cutting upstream from the pit loosens additional substrate, which accumulates in a mound (tailspill) over the eggs. Thus, cutting appears to alter substrate composition at points (egg pockets) where eggs are buried (Jones and Ball 1954; Chapman 1988; Young et al. 1989).

The substrate composition of egg pockets may be critical to embryo survival, yet the substrate alteration caused by spawners is not well described (Chapman 1988). Further, substrate composition may change while eggs are incubating: Hobbs (1948) and Witzel and MacCrimmon (1983) suggested that fine sediment settles over the eggs as a redd ages. In most laboratory investigations, the survival of incubating embryos has been inversely related to the amount of fine sediment (Chapman 1988). Before these laboratory-derived relations are used to evaluate salmonid survival in the field, however, they must be considered with respect to the characteristics and dynamics of natural redds and egg pockets.

Existing literature does not adequately describe the physical structure of individual redds and egg pockets for resident stream salmonids. Most investigations of egg location and depth in redds have involved large anadromous salmonids (Orcutt et al. 1968; Vronskiy 1972; Chapman et al. 1986). Information on redds of brown trout *Salmo trutta* is largely based on observation rather than measurement (Hobbs 1948; Stuart 1953; Jones and Ball 1954). In some investigations, study objectives precluded sampling egg pockets during incubation (Avery 1980; Witzel and MacCrimmon 1983).

Brown trout redds have been investigated in Great Britain, but few egg pockets were sampled. Ottaway et al. (1981) collected 61 substrate samples but found only seven egg pockets; eggs were noted at depths between 0 and 25 cm. Crisp and Carling (1989) found eggs in seven brown trout redds but did not report egg depth. Neither investigation characterized substrate composition specific to egg pockets or changes in composition as incubation progressed. Using large substrate samples, Crisp and Carling (1989) found no dif-

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ference in substrate composition inside and outside redds. However, Young et al. (1989), using smaller samples, reported such differences for redds of small (15–30 cm total length) brook trout *Salvelinus fontinalis*.

Our goal was to describe the redds and egg pockets created by moderate-size (20–40 cm total length) brown trout in a high-elevation stream in the Rocky Mountains. Our objectives were (1) to describe the location and depth of eggs in redds; (2) to determine if brown trout modify the substrate composition in egg pockets during redd construction; and (3) to compare substrate composition in egg pockets soon after spawning with that found later in the incubation period.

Study Area

We studied redds in a 20-km reach of Douglas Creek between 2,700 and 3,100 m above mean sea level in the Medicine Bow National Forest, southeastern Wyoming. During fall sampling, stream width ranged from 3 to 10 m and discharge was stable, averaging 0.16 m^3/s in the upstream end of the reach and 0.31 m^3/s in the lower end. In the winter, most of Douglas Creek was covered by ice up to 40 cm thick and snow up to 3 m deep.

Methods

Brown trout redds were identified by their clean appearance and characteristic pit-and-tailspill configuration during the October spawning season. We sampled during fall 1987, winter 1988, and fall 1988. All fall sampling occurred from mid-October, when brown trout had completed spawning, to mid-November. Winter sampling extended from January to April, when eggs were eyed but not yet hatching.

We sampled each redd only once because sampling disturbed the substrate and eggs. To describe substrate alteration by spawning trout, we used redds sampled in both fall periods and assumed that the substrate collected outside each redd represented prespawning conditions (Young et al. 1989). To describe changes in substrate composition during incubation, we compared redds sampled in winter 1988 with those sampled in fall 1987. Adjacent redds were sampled during this interval to strengthen temporal comparisons.

Redd morphology.—We defined redd morphology as follows: the tailspill end was the point where the clean tailspill gravel ended; the tailspill crest was the point of shallowest water over the tailspill; the tailspill front was the inflection point of the cross-sectional contour between the tailspill and pit; the pit bottom was the point of deepest water in the pit; and the pit front was the upstream end of the pit, where undisturbed streambed began. The location of eggs and substrate samples were identified with respect to these points in each redd.

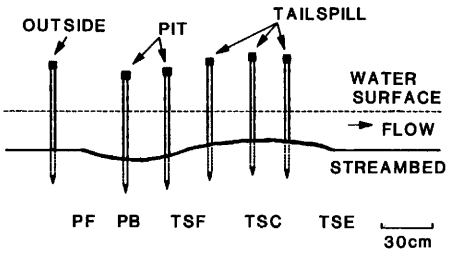

FIGURE 1.—Side view of redd with freeze-coring probes driven into substrate and ready for freezing. Redd is defined by the pit front (PF), pit bottom (PB), tailspill front (TSF), tailspill crest (TSC), and tailspill end (TSE).

Egg location and depth.—We sampled redd substrate and eggs with a single-probe freeze-coring apparatus (Walkotten 1976; Everest et al. 1980) that retained the vertical stratification of the sample. Hollow probes (2.2-cm diameter) with solid steel points were driven into the substrate and injected with gaseous carbon dioxide to freeze a sample of substrate to the outside perimeter of the probe. Carbon dioxide was delivered to the probe through a hose-and-manifold assembly similar to that used by Walkotten (1976).

Freeze-coring probes were driven into several points along the long axis of each redd, where most eggs were assumed to occur (Hawke 1978; Crisp and Carling 1989). Typically, we placed two to four probes in the tailspill, one or two in the pit, and one to three outside but near the redd (Figure 1). Probes were driven 20–26 cm deep when possible and were spaced at least 20 cm apart. Probes were individually frozen in a downstream-to-upstream sequence. Carbon dioxide was injected into each probe for 2 min, and the frozen substrate sample was extracted from the streambed by gently lifting the probe.

Immediately after extraction, we recorded the depth range of eggs visible on the outside perimeter of the sample. To reduce any potential bias from eggs that may have been pushed deeper when the probe was driven into the streambed, we used only those eggs visible on the outside of the sample for the description of egg depth. When freeze coring was completed, we excavated the regions between samples with a shovel to locate additional egg pockets.

Egg location was described in terms of the per-

centage of core and shovel samples from each part of the redd that contained eggs. Student's t-test was used to test the hypothesis that there was no difference in egg-depth means between fall and winter (Sokal and Rohlf 1981). The Kolmogorov–Smirnov procedure was applied to test the hypothesis that there was no difference in the overall distributions between fall and winter (Zar 1984).

Substrate composition.—Following egg-depth measurements, we thawed each substrate sample in the field with a propane torch and divided it below the level of eggs or into roughly equal upper and lower halves if no eggs were present. Both halves of the substrate sample were stored in polyethylene bags and transported to the laboratory. Because we were not concerned with substrate composition below the level of incubating eggs, we used only the upper halves of frozen substrate samples for statistical comparisons of substrate composition.

Freeze-core samples were oven-dried for 3 d at 50°C and shaken on a soil shaker for 1 min through a set of 10 Tyler USA standard testing sieves (mesh openings: 50, 25, 12.5, 9.5, 6.3, 3.4, 1.7, 0.85, 0.42, and 0.21 mm). The fraction of each sample that passed through all sieves was classified as less than 0.21 mm. Because they did not occur consistently, particles retained on the 50-mm sieve were excluded from overall composition analyses. Each fraction was weighed to the nearest 0.1 g and described as a percentage of the total sample weight.

Substrate samples were divided into four categories. Egg pocket samples were samples with one or more eggs. Pit samples were from redd pits but had no eggs. Tailspill samples were from redd tailspills but had no eggs. Outside samples were from outside but adjacent to redds. For individual redds, multiple samples within a category were averaged to create a set of paired samples.

We described substrate composition in terms of particle size to evaluate the type and degree of streambed modification caused by spawning fish. To allow for the simultaneous testing of particle sizes that were mutually dependent within samples, we applied the Bonferroni procedure (Neter et al. 1985) to test hypotheses at an ultimate protection level of 0.10. We evaluated 10 particle sizes simultaneously, so the null hypotheses were rejected for individual particle sizes only at $P < 0.01$.

Using the Wilcoxon signed-rank procedure, we tested the null hypothesis that substrate composition in egg pocket, tailspill, pit, and outside samples was not different. Spearman's rank correlation was evaluated to test the null hypothesis that substrate composition in different sample categories was unrelated. Regression analysis was applied to determine if substrate composition in egg pockets was related to that in other areas. To compare substrate composition between fall and winter within each sample category, we used the Mann–Whitney U-test with unpaired fall and winter samples.

Results

We used 80 redds in our analyses, all of which contained eggs. Most spawning brown trout were 20–40 cm total length (TL); the largest individual observed was about 50 cm TL. Redds averaged 150 cm in length (range, 70–259 cm).

Egg Location and Depth

Ninety-nine freeze-core samples and 167 shovel samples from the 80 redds contained at least one egg and were used in analyses of egg location. The location of eggs within redds was independent of sampling period; consequently, we pooled fall and winter samples for the overall description of egg location. Eggs were found throughout redds but were most frequent in the front half of the tailspill (Figure 2).

Of the 99 core samples with eggs, 75 had eggs visible on the outside perimeter of the core and were used in our description of egg depth. These represented 48 redds. Fall and winter egg depths were not different; consequently, we pooled fall and winter samples to describe egg depth. For all 75 samples, mean egg depth averaged 11 cm (range, 2–20 cm); minimum egg depth averaged 9 cm (range, 2–16 cm); and maximum egg depth averaged 12 cm (range, 2–23 cm). For samples containing 20 or more eggs, the average mean egg depth increased to 12 cm. Relative to location in the redd, egg depth increased from the pit to the tailspill end (Figure 3).

Substrate Composition

We used 408 frozen substrate samples to evaluate substrate composition. Most (96%) of the samples had lengths in the 18–30-cm range. Particles greater than 50 mm in diameter occurred in only 54% of the frozen substrate samples, but in these they constituted an average of 52% (and as much as 97%) of the total sample weight. To reduce variance caused by the inconsistent presence and substantial weight of particles larger than 50 mm, we omitted them from samples before cal-

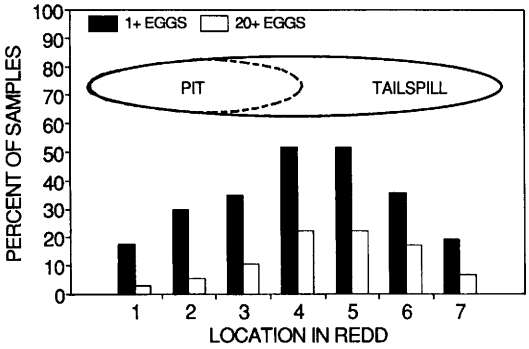

FIGURE 2.—Relative location of eggs within brown trout redds in Douglas Creek, Wyoming. For each portion of the redd, the percentage of freeze-core and shovel samples containing 1 or more and 20 or more eggs is shown. Redds were divided into seven portions; location 2 was the pit bottom, 4 the tailspill front, and 6 the tailspill crest. The ellipses form a dimensionless plan view of a brown trout redd corresponding to locations on the abscissa.

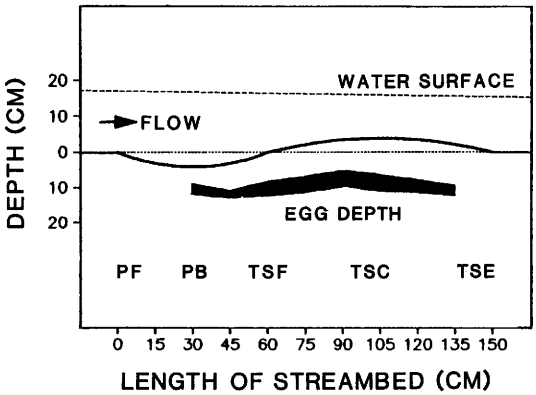

FIGURE 3.—A hypothetical brown trout redd in Douglas Creek, Wyoming, based on mean values of redd length, water depth, and egg depth measured within redds. Locations of the pit front (PF), pit bottom (PB), tailspill front (TSF), tailspill crest (TSC), and tailspill end (TSE) are shown.

culating particle percentages. The 25–50-mm particle size occurred in 100% of egg pocket samples and in 95–97% of samples in all other categories.

Brown trout substantially altered the substrate composition in egg pockets relative to substrate outside of redds and in the surrounding tailspill. In the fall, the percentage of particles larger than 25 mm was higher and the percentages of all size-classes less than 6.3 mm were lower in egg pockets than in samples outside of redds (Table 1). Similarly, the percentage of particles larger than 25 mm was higher and the percentages of all size-classes less than 3.4 mm were lower in tailspills than in samples outside of redds. Egg pocket samples differed from tailspill samples for two particle sizes (0.42 mm and 0.21 mm) and from pit samples for one particle size (<0.21 mm). Pit samples had a high variance and were not statistically different from outside or tailspill samples, however, and they were not considered further.

Although different, the fall substrate composition in egg pockets and outside of redds was correlated for particle sizes less than 1.7 mm. Egg pocket and tailspill samples were correlated for all particle sizes except 12.5 mm. No other comparisons yielded correlations for more than three particle sizes.

In winter, egg pocket and tailspill samples still differed from those outside redds but only for particle sizes less than 0.85 mm (Table 1). Egg pocket samples, however, were no longer different from tailspill samples. Also in contrast to fall samples, winter egg pocket samples and those outside redds were correlated for only one particle size (<0.21 mm). There were no correlations between egg pocket and tailspill samples.

The composition of egg pockets seemed to change during incubation. Egg pocket samples had significantly ($P < 0.10$) higher percentages of two particle sizes (0.85 mm and 0.42 mm) in winter than in fall. Samples from all other locations did not differ between fall and winter or between the two fall periods.

Discussion

Egg Location and Depth

Eggs were most frequently found under the front half of the tailspill and the tailspill crest, generally confirming the existing reports (Chapman 1988; Ottaway et al. 1981). However, we found eggs in all parts of redds, and most redds (76%) had multiple egg pockets, which supports the conclusions of Chapman (1988) and Young et al. (1989) that it is difficult to predict the precise location of egg pockets within a given redd.

The average egg depth range (9–12 cm) derived from our samples was identical to that reported by Reiser and Wesche (1977) for brown trout in the same study reach. Furthermore, the total range of egg depths (2–23 cm) in Douglas Creek was similar to that reported by Ottaway et al. (1981) for fish of similar size in Great Britain. In contrast, larger brown trout buried eggs 20–30 cm deep (Hobbs 1948; Stuart 1953). Crisp and Carling (1989) found that egg burial depth was related to salmonid body length in two of three study sites.

TABLE 1.—Comparison of substrate compositions in and around brown trout redds in Douglas Creek, Wyoming, fall and winter. Three sample categories were compared: egg pockets, tailspills (without eggs), and outside redds. Inequality signs indicate the direction of the relationship for individual particle sizes at an ultimate $P < 0.10$.

Particle size (mm)	Egg pocket versus outside		Egg pocket versus tailspill		Tailspill versus outside	
	Fall	Winter	Fall	Winter	Fall	Winter
25.0	>				>	
12.5						
9.5						
6.3						
3.4	<					
1.7	<				<	
0.85	<				<	
0.42	<	<	<		<	<
0.21	<	<	<		<	<
<0.21	<	<			<	<

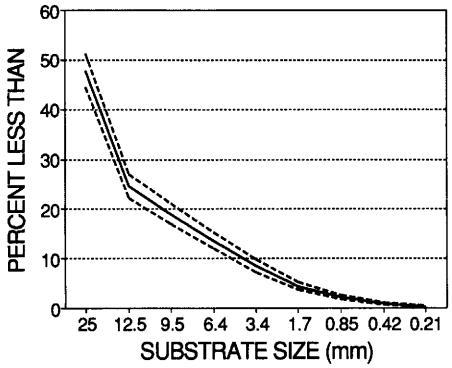

FIGURE 4.—Mean cumulative particle-size distribution and 95% confidence limits (dashed lines) for frozen substrate samples from fall egg pockets ($N = 69$) collected from brown trout redds in Douglas Creek, Wyoming.

Hence, the relationship between egg depth and fish size appears limited by streambed characteristics.

Stuart (1953) suggested that gradual scouring of the tailspill could leave eggs that were originally 20–30 cm deep only half that deep after 2 months. In Douglas Creek, fall and winter egg depths were not significantly different, suggesting that tailspills were not substantially scoured during incubation.

Substrate Composition

Several investigators have described the substrate composition associated with brown trout redds (Avery 1980; Anderson 1983; Shirvell and Dungey 1983; Witzel and MacCrimmon 1983), but the different methods used in each study make comparisons difficult. Reiser and Wesche (1977) used a different sampling device (an excavated-core sampler) and sampled only in tailspills without differentiating egg pockets. However, they reported the same particle sizes we did, which allows a direct comparison. The composition of tailspill samples from the same study area was very similar in both studies. The cumulative particle-size distribution of fall egg pocket samples is presented in Figure 4 as a reference for future studies.

Although we omitted particles larger than 50 mm from size distributions, the potential importance of these large particles in egg-pocket structure should not be overlooked (Chapman 1988). The occurrence of particles larger than 50 mm in 73% of egg pocket samples but in only 47–51% of samples from other locations suggests that such particles were sought by fish for egg pocket centers (centrums). Jones and Ball (1954) observed brown trout centrums composed of stones 25–50 mm in diameter, but these were the largest stones available in their artificial stream. In Douglas Creek, eggs were often adjacent to one or several stones 50–100 mm in diameter.

Substrate Alteration by Spawning Fish

Differences between fall samples from egg pockets and outside the redds indicate that brown trout moved particles less than 6.3 mm in diameter from egg pockets and particles less than 3.4 mm from tailspills during spawning. In a similar study, Young et al. (1989) found that smaller brook trout also modified egg pockets, but moved only particles less than 1.7 mm. Thus, fish size probably influences the size of particles removed from the egg pocket. In contrast, Crisp and Carling (1989) found "no consistent and convincing evidence of changes in grain size as a consequence of redd construction"; however, they did not compare surface substrate layers inside and outside of redds as we did. Additionally, they did not distinguish among egg pocket, tailspill, and pit locations within redds, and they may have been sampling incomplete redds, because they disturbed fish by electroshocking and by sampling redds during spawning activity.

Young et al. (1989) found no correlation between the composition of brook trout egg pockets and that of the substrate outside of redds. They suggested that fish cleaned particles less than 0.21 mm from the egg pocket to a "standard" level unrelated to the composition of the original streambed. Our findings do not support this suggestion. In fall samples we found that the com-

position of egg pockets and the substrate outside of redds, though very different, was positively correlated for all particles less than 1.7 mm. Regression analysis showed that egg pocket substrate was related to the substrate outside redds in the fall for the percentage of particles less than 0.85 mm ($r^2 = 0.13$, $P < 0.05$). This indicates that the composition of the original streambed affected the composition of the egg pocket, and that brown trout did not clean the substrate to a standard level. The lack of similar correlations in winter samples may be an artifact of the smaller sample size (17 versus 43 pairs) or of sediment dynamics within the egg pocket. Egg pocket substrate was also related to the substrate of the surrounding tailspill in the fall for the percentage of particles less than 0.85 mm ($r^2 = 0.26$, $P < 0.01$).

Substrate Change During Incubation

Even though salmonids can clean the egg pocket while spawning, subsequent deposition of fine sediment during incubation could affect egg and alevin survival. Field observations have long suggested that sediments accumulate in egg pockets during incubation (Hobbs 1948; Stuart 1953; Chapman 1988). We found a higher percentage of two fine-particle size-classes (0.85 and 0.42 mm) in winter than in fall samples, which indicates that fines did accumulate in egg pockets during incubation. Reiser and White (1988) found that these were among the size-classes most detrimental to the survival of salmonid embryos and alevins. Egg pockets were the only sample type that differed significantly between fall and winter sampling periods, which implies that egg pockets are more susceptible to fine-sediment deposition than the surrounding redd or streambed.

As incubation progresses, sediment deposition may make egg pockets indistinguishable from surrounding tailspill substrate. Though unique in the fall, the substrate composition of egg pockets was not significantly different from that of tailspills during the winter (Table 1). Chapman (1988) suggested that to evaluate the survival of incubating salmonids, substrate samples must be collected from actual egg pockets. Our results suggest, however, that substrate samples collected in the tailspill may be representative of substrate in egg pockets during later stages of incubation.

Acknowledgments

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