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Substrate Alteration by Spawning Brook Trout in a Southeastern Wyoming Stream

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Abstract.—To measure the changes in substrate composition produced by spawning brook trout *Salvelinus fontinalis,* we collected 187 freeze-core samples, both before and after spawning, from egg pockets, inside redds but excluding egg pockets, and outside redds. In the upper strata of redd-associated samples, we found that the proportions of particles 0.85–1.70, 0.425–0.85, 0.212–0.425, and less than 0.212 mm in diameter were significantly lower in egg pockets than outside redds, and the proportions of particles 0.425–0.85, 0.212–0.425, and less than 0.212 mm in diameter were also lower in egg pockets than in other areas inside redds. Samples collected outside redds were similar to samples collected before spawning. We observed no significant correlations between the proportion of fine sediment in samples from outside redds (and presumably the proportion present before spawning) and the proportion of fine sediment in egg pockets. In vertically stratified samples, the lower strata contained a greater proportion of the smaller substrate particles than the upper strata. Spawning brook trout removed fine sediment from the substrate during redd construction, and this removal was most apparent in the egg pocket. Thus, egg pockets, rather than entire redds, should be the focus of studies of survival to emergence.

Fine sediment often affects the survival of embryonic trout and salmon (Cordone and Kelly 1961; Iwamoto et al. 1978; Everest et al. 1987). Survival to emergence of salmonid embryos decreases as the quantity of fine sediment in the incubation substrate increases (Phillips et al. 1975; Witzel and MacCrimmon 1983a). To determine the consequences of human-induced sediment introduction into spawning streams, researchers have linked models that predict sediment delivery (Cline et al. 1981) with sediment-related predictions of survival to emergence (Tappel and Bjornn 1983). Stowell et al. (1983), who used this approach, suggested that predictions of survival to emergence might be based on substrate samples collected before the spawning season. This implies that increases in fine sediment deposition before spawning will be reflected in the substrate composition of redds, that is, that there is a direct relationship between prespawning and postspawning substrates.

Everest et al. (1987) stated that salmonids are not passive users of substrates, but that they distinctively modify substrate composition during redd construction. For example, McNeil and Ahnell (1964) suggested that pink salmon *Oncorhynchus gorbuscha* removed 3,600 kg of sediment particles less than 0.1 mm in diameter from a single spawning riffle. Helle (1970) reported a 3.6% decrease in sediment particles less than 0.8 mm in diameter after the spawning of pink salmon. Compared to 1-year-old redds, new redds of coho salmon *Oncorhynchus kisutch* contained 25% fewer sediment particles less than 3.33 mm in diameter (Ringler and Hall 1988). Thus, predicting the survival to emergence of embryos based on the sediment content of undisturbed prespawning substrates may be unrealistic.

Most research on substrate modification has focused on large, anadromous salmonids in the Pacific Northwest (Everest et al. 1987). To determine if relatively small resident salmonids could measurably alter substrate composition during spawning in small, high-elevation streams and if a correlation existed between undisturbed prespawning substrates and disturbed postspawning substrates, we examined substrate modification by brook trout *Salvelinus fontinalis* in a second-order mountain stream.

Besides identifying substrate changes caused by spawning brook trout, we hoped to collect information on the substrate composition of redds and

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egg pockets of this species. Salmonid redds usually have a depression in the anterior (upstream) portion (the pit or pot) and a mound of substrate (the tailspill) that has been excavated from within and upstream of the egg pocket(s) (Ottaway et al. 1981). Though much research has focused on measuring the responses of incubating salmonid embryos to various intragravel environments (Irving and Bjornn 1984), less work has concentrated on defining the natural environment of embryos (Tagart 1976). Frequently, survival has been evaluated in laboratory studies of simulated redds with artificial structure or substrate composition (Hamor and Garside 1976; MacCrimmon and Gots 1986); yet Chapman (1988) noted that conditions in the egg pocket, rather than in the entire redd, probably determine embryo survival.

We also studied the depth and location of egg pockets. Some researchers (Hausle and Coble 1976) appeared to arbitrarily assign a variety of depths to egg pockets of brook trout. From unstratified redd samples, Witzel and MacCrimmon (1983b) estimated that the maximum depth of brook trout egg pockets was 14 cm. Also, Chapman et al. (1986) suggested that the tailspill of a redd may not cover the majority of egg pockets in a redd, but others have found most egg pockets under the anterior portion of the tailspill (Ottaway et al. 1981).

Methods

We obtained samples from a low-gradient ($<1.5\%$) reach of Telephone Creek, a high-elevation (about 2,900 m above mean sea level), second-order stream in the Snowy Range of southeastern Wyoming. Chisholm (1985) reported that this stream's standing stock of brook trout averaged 318 kg/hectare, and that most of these fish were less than 25 cm long. Mean daily flow in Telephone Creek in September is 0.02 m^3/s (Wyoming Water Research Center, unpublished data). We sampled this stream because many brook trout redds had been found there by Reiser and Wesche (1977).

To determine substrate composition before brook trout spawned, we established 27 transects on 28 August 1987 in riffles known to be used for spawning, and we used a freeze-coring technique (Walkotten 1976) to collect three substrate samples per transect from 2 September to 11 September 1987. After spawning began, we stopped sampling transects and began sampling redds. We identified redds by the presence of cleaned gravel and characteristic redd morphology. Typically, we removed samples from the pit, the leading third of the tailspill, and from one to four sites outside but within 10 cm of the redd. Occasionally, we took only a single sample from small redds because one sample disturbed the entire redd in such cases.

A variety of substrate sampling techniques has been used to collect samples from redds (Sheridan et al. 1984), and several researchers have noted that fine sediment tends to increase with depth (Adams and Beschta 1980; Everest et al. 1982). Because the freeze-core technique can be used to stratify substrate samples vertically (Everest et al. 1982), it can be used to determine whether only the upper portion of a redd sample or the entire sample yields more information about substrate modification. Freeze-core sampling also provides an indirect evaluation of the efficiency of sampling techniques that do not allow vertical stratification of samples.

We measured water depths at each site, then obtained freeze-core samples with a single-probe apparatus, similar to that described by Walkotten (1976), along transects and in or near redds. Freeze-core probes were driven 20 cm deep, injected with liquid CO_2 for at least 2 min, and extracted. We first collected samples at the downstream end of each redd and progressed upstream.

We collected 81 freeze cores from transects between 2 and 11 September 1987. We first observed redds on 12 September and discontinued transect sampling on that date. By 4 October 1987, we had obtained 106 cores from or near 31 redds. The surface area of redds averaged 1,900 cm^2, and weight of the substrate samples averaged 1,100 g.

We described three kinds of redd-associated samples. When we found eggs in a core or in the depression created by removal of the core, we defined that core as an egg-pocket sample. We defined other cores from disturbed sites without eggs as inside-redd samples, and cores from immediately outside the disturbed area were referred to as outside-redd samples. Multiple samples from inside or outside of a single redd were pooled to determine an average for each location near that redd. Of the 106 cores, we had 12 pairs of inside-redd and outside-redd samples, 13 pairs of egg-pocket and inside-redd samples and 28 pairs of egg-pocket and outside-redd samples.

The three kinds of samples were divided into upper and lower strata. The lower boundary of the upper stratum was defined by the bottom of the egg pocket, the bottom of the area that appeared to have been disturbed by fish, or at the core midpoint if no difference could be detected visually between the lower and upper portions. Transect samples were not stratified. We thawed samples with a propane torch and placed them in plastic bags for transport to the laboratory.

After drying a sample for 72 h at 60°C, we weighed it, sieved it for 8 min on a mechanical shaker, and weighed separately the material retained on sieves with meshes of 50, 25, 12.5, 9.5, 6.3, 3.35, 1.70, 0.85, 0.425, 0.212, and less than 0.212 mm. Adams and Beschta (1980) excluded large particle sizes from their analysis; they stated that freeze-core samplers may be biased in favor of large particles. Alternatively, Chapman et al. (1986) noted that large particles tended to be lost from frozen cores during extraction of the sample. To avoid bias in either direction, we excluded particles retained on the 50- and 25-mm-mesh sieves. However, these large particles appeared more frequently in egg-pocket samples (39 and 100%, respectively) than in inside-redd samples (9 and 82%) or outside-redd samples (26 and 84%).

To determine if the substrate composition of the three kinds of samples differed, we compared the proportions of each substrate particle size from the upper stratum of cores from these locations. After combining upper and lower strata, we again compared redd-associated samples and also compared these to a set of 27 unstratified transect samples that had been collected from the reach that contained the majority of sampled redds. We also examined the differences in substrate composition between upper and lower strata at all three locations by use of a sign test (Sokal and Rohlf 1981). To test for differences among redd-associated samples we used the Wilcoxon signed-rank test, and to compare redd-associated samples with transect samples we used the Mann–Whitney *U*-test (Sokal and Rohlf 1981).

To evaluate the relationship between prespawning and postspawning substrates, we used rank correlation (Mosteller and Rourke 1973) on data from upper stratum samples to compare the proportion of each substrate particle size in the three kinds of samples. We assumed that unstratified outside-redd samples were equivalent to samples collected before spawning and combined the upper and lower strata of the three kinds of redd-associated cores to assess their relationship to samples from nearby transects.

We expected spawning brook trout to reduce the proportion of substrate particles less than 1.7 mm in diameter and correspondingly increase the proportion of substrate particles greater than 3.35 mm in diameter inside redds and in egg pockets; thus, we used one-tailed tests of significance for those particle sizes. For substrate particles from 1.70 to 3.35 mm in diameter (the central size in our set of sieves), we used a two-tailed test. We used the Bonferroni procedure to produce an experimentwise $P_\alpha = 0.09$ (for individual comparisons, $P_\alpha = 0.01$) that was accepted as the level of significance for all nonparametric tests (Neter et al. 1985).

We calculated both water depth over egg pockets and egg-pocket depth in the substrate and determined whether the pit or the tailspill was more likely to contain an egg pocket according to binomial probabilities (Sokal and Rohlf 1981). For these tests, $P_\alpha = 0.05$ was accepted as the level of significance.

Results

Brook trout altered substrate during spawning; comparisons of substrate particle sizes 0.85–1.70, 0.425–0.85, 0.212–0.425, and less than 0.212 mm in diameter from upper strata revealed significant differences among egg-pocket, inside-redd, and outside-redd samples (Table 1). The number of significant differences in substrate composition among these three kinds of samples decreased when we performed the same tests on samples in which the upper and lower strata were combined (unstratified samples). In these comparisons, we found no significant differences between inside-redd samples and either outside-redd or egg-pocket samples (Table 1).

The correlation of substrate composition among the redd-associated locations was inconsistent. For upper strata, we found no significant correlations of substrate composition among the three kinds of samples. In unstratified samples, we found significant correlations between certain pairs of the three locations for the proportion of substrate particles 0.425–0.85, 0.212–0.425, and less than 0.212 mm in diameter (Table 2).

Samples collected before redds were built appeared to be similar to unstratified outside-redd samples. The proportion of sediment retained on the 3.35-mm sieve provided the only significant difference between transect samples and both unstratified outside-redd and inside-redd samples. Unstratified egg-pocket samples differed significantly from transect samples for the 3.35-mm sieve size and for five other substrate sizes (Table 1).

There were significant differences between upper and lower strata within egg-pocket, inside-redd, and outside-redd samples for seven, five, and five, respectively, of the nine substrate sizes. Lower strata consistently contained a greater proportion

TABLE 1.—Mean proportions (ranges in parentheses) of substrate retained on sieves from both upper strata samples and unstratified samples collected outside redds, inside redds, and in egg pockets and from unstratified samples along transects. Significant differences between redd-associated samples for a given substrate size are based on a Wilcoxon signed-rank test; those between transects and other locations are based on Mann-Whitney *U*-tests (P_α for individual comparisons = 0.01). Within each row for upper strata samples and for unstratified samples (separately), values with a letter in common are not significantly different.

Sieve mesh size (mm)	Upper strata samples (*N*)			Unstratified samples (*N*)			
	Outside redds (28)	Inside redds (13)	Egg pockets (31)	Outside redds (28)	Inside redds (13)	Egg pockets (31)	Transects (27)
12.5	35.4 z (11.9–63.5)	38.7 z (14.1–80.6)	40.8 z (24.8–61.5)	29.8 zy (6.4–58.6)	28.8 zy (5.5–50.0)	34.1 z (21.1–61.4)	28.0 y (18.3–37.6)
9.5	11.2 z (4.0–17.5)	10.7 z (4.0–20.3)	14.1 z (5.3–40.0)	9.9 z (3.8–14.4)	8.8 z (2.6–14.6)	11.3 z (6.1–25.6)	9.7 z (6.8–13.8)
6.3	11.7 z (5.8–20.8)	11.2 z (3.6–15.8)	12.1 z (4.9–17.5)	10.5 z (5.0–14.8)	10.0 z (4.1–14.0)	11.1 z (6.1–14.8)	11.5 z (8.0–15.3)
3.35	12.0 z (5.1–18.2)	12.7 z (3.6–19.7)	12.2 z (8.8–16.9)	12.2 z (5.9–15.6)	11.6 z (6.0–14.7)	12.5 z (9.9–15.5)	13.5 y (9.6–15.9)
1.70	10.3 z (1.1–18.2)	10.3 z (2.5–17.7)	9.0 z (5.4–15.7)	11.1 z (3.4–15.6)	11.1 z (7.1–14.0)	10.8 z (6.5–15.1)	11.9 z (8.2–13.6)
0.85	8.6 z (0.7–17.5)	8.1 zy (2.0–13.1)	6.4 y (2.4–13.7)	10.1 zy (3.1–15.0)	10.7 zy (7.0–15.7)	9.1 z (3.7–12.8)	10.6 y (7.8–13.4)
0.425	5.9 z (0.8–11.4)	5.1 y (1.4–8.7)	3.6 x (0.8–7.6)	7.5 z (2.5–15.7)	8.7 zy (4.9–20.2)	5.9 y (2.0–8.9)	7.5 z (5.2–10.4)
0.212	2.6 z (0.5–7.6)	1.9 y (0.4–3.0)	1.0 x (0.2–2.0)	4.3 z (1.1–13.8)	5.2 zy (1.4–19.8)	2.4 y (0.8–5.4)	3.4 z (2.0–4.9)
<0.212	2.3 z (0.6–9.2)	1.5 y (0.2–2.8)	0.7 x (0.2–1.3)	4.6 z (1.4–22.4)	5.1 zy (1.3–15.0)	2.7 y (0.8–6.9)	4.0 z (2.5–7.9)

of substrate particles 0.85–1.70, 0.425–0.85, 0.212–0.425, and less than 0.212 mm in diameter and a lesser proportion of substrate 12.5–25.0 mm in diameter than upper strata.

Egg pockets tended to be in shallow water and buried close to the substrate surface in the tailspill of the redd. Mean depth of the water over egg pockets was 8.1 cm (*N* = 31; SE = 3.7 cm; range, 3.0–15.0 cm). The base of egg pockets was 8.4 cm (*N* = 31; SE = 1.7 cm; range, 5.5–12.0 cm) below the streambed surface. Egg pockets were more likely to be found in the leading third of the tailspill than in the pit (28 of 31 egg pockets; $P < 0.002$).

TABLE 2.—Spearman's rank correlation coefficients (probability in parentheses) for unstratified substrate particles retained on sieves with mesh sizes of 0.425, 0.212, and less than 0.212 mm. For each comparison, P_α = 0.01 was the accepted level of significance. All comparisons of larger particle sizes were nonsignificant.

Sieve mesh size (mm)	Comparison of samples (*N*) from		
	Inside and outside redds (12)	Egg pockets and inside redds (13)	Egg pockets and outside redds (28)
0.425	0.37 (0.12)	0.03 (0.46)	0.66 (<0.01)
0.212	0.54 (0.03)	0.67 (<0.01)	0.43 (0.01)
<0.212	0.87 (<0.01)	0.74 (<0.01)	0.55 (<0.01)

Discussion

Despite the small size of brook trout in Telephone Creek, their excavation of the substrate during spawning removed sediment less than 1.70 mm in diameter. These reductions in fine sediment parallel those observed for much larger steelhead *Oncorhynchus mykiss* (formerly *Salmo gairdneri*) and Pacific salmon *Oncorhynchus* spp. in the Pacific Northwest, though these species also removed larger particles (Everest et al. 1987).

Chapman (1988) contended that egg pockets should be the focus of sampling in evaluations of the intragravel environment of embryonic salmonids. In our study, the differences in substrate composition between upper strata samples from the egg pocket and from inside the redd were significant for small particles, and confirmed the unique substrate composition of the egg pocket. Our results suggested that researchers should sample the upstream third of the tailspill to locate egg pockets in brook trout redds, but we recognize the difficulty in locating egg-pockets consistently. Ideally, researchers would like to characterize intragravel water velocity, dissolved oxygen concentration, and substrate composition to predict survival to emergence of embryonic salmonids, but most techniques for determining intragravel conditions (Terhune 1958) alter the structure of egg pockets and preclude collection of accurate data on all three of these variables.

Because we were unable to detect differences between inside-redd and egg-pocket locations based on unstratified samples, we concluded that sampling techniques incapable of preserving the vertical stratification of substrates (e.g., sampling with a shovel or McNeil device) may be less informative than the freeze-core technique. This may be partially due to the increase in fine sediment with depth. Everest et al. (1982) also noted that McNeil samples cannot reveal differences between the upper modified substrate and the undisturbed deeper layers. However, we inferred from our data that one might still differentiate between egg pockets and undisturbed locations by use of unstratified samples. Sampling with either a shovel or McNeil device is much faster than freeze-coring, requires less equipment, and is less costly.

Fisheries biologists often assume that increases in fine sediment delivery to a stream will be reflected in the substrate composition of egg pockets, but our failure to find strong correlations between the proportions of fine sediment in upper strata samples from egg pockets and outside redds implies otherwise. Such correlations could develop later during incubation because fine sediment can rapidly infiltrate egg pockets if streams are transporting such material (Beschta and Jackson 1979). This may happen during the winter incubation of eggs and alevins of fall-spawning salmonids in the Pacific Northwest. Yet, due to high flows in winter that apparently disturbed the upper layer of substrate, gravel quality increased throughout the incubation period in one stream in British Columbia (Scrivener 1988). In the central Rocky Mountains, streams may carry little sediment during incubation of embryos of either fall-spawning or spring-spawning species because flows (and hence sediment transport) are low or declining during fall and spring. Consequently, substrates collected before spawning may not reflect the actual substrate conditions that affect survival to emergence.

Perhaps the lack of a relationship between outside-redd (and presumably undisturbed substrates before spawning) and egg-pocket substrates is due to brook trout reducing the amount of fine sediment to a given "standard," regardless of the prespawning conditions. This interpretation centers on the narrow range in the proportions of substrate 0.212–0.425 and less than 0.212 mm in diameter in the upper strata from egg pocket samples and the broader range of those two sizes in upper strata from outside-redd samples. However, Telephone Creek is relatively undisturbed, and we do not know how brook trout would modify substrates that contain a greater proportion of fine sediment.

We suggest that substrate samples used to predict survival to emergence should be collected after spawning but before the complete emergence of alevins. Additionally, samples from egg pockets should yield the most information about the immediate environment of eggs and alevins of salmonids. Our data on egg-pocket depth, structure, and location should be useful for designing laboratory tests of survival to emergence of embryonic brook trout; for example, researchers can construct more realistic substrates than those devised in previous studies (Hausle and Coble 1976; Witzel and MacCrimmon 1983a). Our data also can be compared to other field samples of brook trout spawning sites before redd construction (Witzel and MacCrimmon 1983b) and after spawning (Reiser and Wesche 1977) to help describe the natural variation in substrate composition produced by spawning.

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References

Adams, J. M., and R. L. Beschta. 1980. Gravel bed composition in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 37:1514–1521.

Beschta, R. L., and W. L. Jackson. 1979. The intrusion of fine sediments into a stable gravel bed. Journal of the Fisheries Research Board of Canada 36:204–210.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1–21.

Chapman, D. W., D. E. Weitkamp, T. L. Welsh, M. B. Dell, and T. H. Schadt. 1986. Effects of river flow on the distribution of chinook salmon redds. Transactions of the American Fisheries Society 115:537–547.

Chisholm, I. M. 1985. Winter stream conditions and brook trout habitat use on the Snowy Range, Wyoming. Master's thesis. University of Wyoming, Laramie.

Cline, R., G. Cole, W. Megahan, R. Patten, and J. Potyondy. 1981. Guide for predicting sediment yields from forested watersheds. U.S. Forest Service, Northern and Intermountain Regions, Ogden, Utah.

Cordone, A. J., and O. W. Kelly. 1961. The influences of inorganic sediment on the aquatic life of streams. California Fish and Game 47:189–228.

Everest, F. H., R. L. Beschta, J. C. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. Pages 98–142 *in* E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. University of Washington, College of Forest Resources. Contribution 57, Seattle.

Everest, F. H., F. B. Lotspeich, and W. R. Meehan. 1982. New perspectives on sampling, analysis, and interpretation of spawning gravel quality. Pages 325–333 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

Hamor, T., and E. T. Garside. 1976. Developmental rates of embryos of Atlantic salmon, *Salmo salar* L., in response to various levels of temperature, dissolved oxygen, and water exchange. Canadian Journal of Zoology 54:1912–1917.

Hausle, D. A., and D. W. Coble. 1976. Influence of sand in redds on survival and emergence of brook trout (*Salvelinus fontinalis*). Transactions of the American Fisheries Society 105:57–63.

Helle, J. H. 1970. Biological characteristics of intertidal and fresh-water spawning pink salmon at Olsen Creek, Prince William Sound, Alaska, 1962–63. U.S. Fish and Wildlife Service Special Scientific Report—Fisheries 602.

Irving, J. S., and T. C. Bjornn. 1984. Effects of substrate size composition on survival of kokanee salmon and cutthroat and rainbow trout embryos. University of Idaho, Idaho Cooperative Fishery Research Unit, Technical Report 84-6, Moscow.

Iwamoto, R. N., E. O. Salo, M. A. Madej, and R. L. McComas. 1978. Sediment and water quality: a review of the literature, including a suggested approach for water quality criteria. U.S. Environmental Protection Agency, EPA 910/9-78-048, Seattle, Washington.

MacCrimmon, H. R., and B. L. Gots. 1986. Laboratory observations on emergent patterns of juvenile Atlantic salmon, *Salmo salar*, relative to sediment loadings of test substrate. Canadian Journal of Zoology 64:1331–1336.

McNeil, J. W., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U.S. Fish and Wildlife Service Special Scientific Report—Fisheries 469.

Mosteller, F., and R. E. K. Rourke. 1973. Sturdy statistics: nonparametrics and order statistics. Addison-Wesley, Reading, Massachusetts.

Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models, 2nd edition. Irwin, Homewood, Illinois.

Ottaway, E. M., P. A. Carling, A. Clarke, and N. A. Reader. 1981. Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. Journal of Fish Biology 19:593–607.

Phillips, R. W., R. L. Lantz, W. W. Claire, and J. R. Moring. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104: 461–466.

Reiser, D. W., and T. A. Wesche. 1977. Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations. University of Wyoming, Water Resources Research Institute, Water Resources Series 64, Laramie.

Ringler, N. H., and J. D. Hall. 1988. Vertical distribution of sediment and organic debris in coho salmon (*Oncorhynchus kisutch*) redds in three small Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 45:742–747.

Scrivener, J. C. 1988. Two devices to assess incubation survival and emergence of salmonid fry in an estuary streambed. North American Journal of Fisheries Management 8:248–258.

Sheridan, W. L., M. P. Perensovich, T. Faris, and K. V. Koski. 1984. Sediment content of streambed gravels in some pink salmon spawning streams. Pages 153–165 *in* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley, editors. Fish and wildlife relationships in old-growth forests. American Institute of Fisheries Research Biologists. (Available from J. W. Reintjes, Route 4, Box 85, Morehead City, North Carolina 28557.)

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd edition. Freeman, San Francisco.

Stowell, R., A. Espinosa, T. C. Bjornn, W. S. Platts, D. C. Burns, and J. S. Irving. 1983. Guide for predicting salmonid response to sediment yields in Idaho Batholith watersheds. U.S. Forest Service, Northern and Intermountain Regions, Ogden, Utah.

Tagart, J. V. 1976. The survival from egg deposition to emergence of coho salmon in the Clearwater River, Jefferson County, Washington. Master's thesis. University of Washington, Seattle.

Tappel, P. D., and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3:123–135.

Terhune, L. D. B. 1958. The MARK VI groundwater standpipe for measuring seepage through salmon spawning gravel. Journal of the Fisheries Research Board of Canada 15:1027–1063.

Walkotten, W. J. 1976. An improved technique for sampling streambed sediments. U.S. Forest Service Research Note PNW-281.

Witzel, L. D., and H. R. MacCrimmon. 1983a. Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. Canadian Journal of Zoology 61:1783–1792.

Witzel, L. D., and H. R. MacCrimmon. 1983b. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112:760–771.

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