

Sediment Transport and Resulting Deposition in Spawning Gravels, North Coastal California

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Incubating salmonid eggs in streambeds are often threatened by deposition of fine sediment within the gravel. To relate sedimentation of spawning gravel beds to sediment transport, infiltration of fine sediment (<2 mm in diameter) into clean gravel beds, bed material size distributions, scour-fill depths, and sediment transport during 10 storm flow events were measured in three streams of north coastal California. Although suspended sediment comprised most (75-94%) of the clastic load during storm flows, bed load material (0.25-2 mm) accounted for most (70-78%) of the fine sediment accumulated in experimental gravel implanted in the streambeds. Sand trapped in the interstices of the top several centimeters formed a seal that impeded deeper deposition of very fine sand and finer material. The seal was responsible at least in part for a decrease in the rate of fine-sediment accumulation with increasing cumulative bed load transport. Areas of the streambeds commonly scoured or filled 0.1 m or more during storm flows, and thus scour and fill commonly created a sandy layer at least as thick as the seal formed by sediment infiltration. Scour could erode eggs laid in the bed and expose deeper levels of the bed to infiltration by fine sediment, but at the same time could allow fine sediment to be winnowed away. Great temporal and spatial variation in sedimentation in these streams suggests that individual storms of moderate size pose a threat to eggs in many but not all areas selected by fish for spawning.

INTRODUCTION

The interchange of fine sediment (sand and finer sizes) in transport with that stored in a natural gravel channel is an important link between the sediment transport regime and the suitability of benthic habitat for stream organisms. Although particle sizes of bed material and the sediment load are ultimately related, they are not always in phase. Logging and road construction, for example, can introduce sediment with abundant fine material to streams with relatively clean gravel beds [Platts and Megahan, 1975]. Even in channels without new sediment inputs, the size of sediment in transport can change with discharge because of size-dependent entrainment thresholds [Jackson and Beschta, 1982]. Changes in bed topography can alter transport vectors and local shear stress and thereby cause sediment that is coarser or finer than was present before in a local area to deposit. As a consequence, the spatial distribution of bed material size in natural gravel channels in undisturbed watersheds can vary considerably over time [Adams and Beschta, 1980; Scrivener and Brownlee, 1981].

Salmon and trout lay their eggs in a pit (redd) excavated most commonly just upstream of riffle crests and then bury them under 10-40 cm of bed material. The choice of location of redds and the initial winnowing of fine sediment by the female during redd construction enhances gravel permeability and intergravel flow to oxygenate the eggs and allow fry to emerge through the bed surface. Until the fry emerge (commonly 2-6 months), the redd is vulnerable to deposition of fine sediment within or over the bed, which reduces permeability, and to scour, which can remove the eggs. For many species and races, the incubation period coincides with seasons of high flow and sediment transport.

The depth to which fine sediment can infiltrate a stable gravel bed depends on the size of the fine sediment relative to the size of the bed material [Einstein, 1970; Diplas and

Parker, 1985; Carling, 1984]. (Fine sediment infiltrating a streambed is the "matrix" material; bed material forming the pores through which fine sediment passes is the "framework" material.) Particles larger than gaps in the gravel framework are excluded from the bed unless they are incorporated in the surface material or deposited as the bed fills. Particles that are smaller than some interstices but larger than others or that are able to bridge gaps through interference with other ingressing particles become lodged in a layer just beneath the bed surface. Particles much smaller than interstices can readily pass into the bed and deposit deeply within. Ratios of framework particle diameter to matrix particle diameter that determine these three ranges of penetration of matrix particles depend on the sorting of matrix and framework material and the shape and packing of framework material.

Most commonly, sand is deposited near the surface of heterogeneous gravel beds and silt and clay pass through to deeper layers. Winnowing by turbulent bursts over the bed surface aids this segregation by removing suspendible fractions from the surface layer.

Laboratory experiments where fine sediment is fed into flow over a stable gravel bed have provided important insights into the infiltration of fine sediment into gravel beds [Einstein, 1968; Beschta and Jackson, 1979; Carling and Reader, 1982; Diplas and Parker, 1985], but they have been unable to simulate some important aspects of bed dynamics of natural channels. First, fine sediment fed into flumes has been smaller than the bed material, and in some cases, there has been little or no overlap in grain size distributions of material composing the bed and that fed into the channel. In natural channels, all sizes of transported sediment are already present in bed material. Thus grain size distributions of bed material and sediment in transport usually overlap to some degree during all transport stages. Second, natural gravel beds commonly scour and fill during high flows, altering the interface where fine sediment enters the bed.

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TABLE 1. Characteristics of Study Reaches

	Jacoby	Prairie	North Caspar
Drainage area, km ²	36.3	34.4	5.0
Gradient, m m ⁻¹	0.0063	0.0032	0.0132
Bank-full discharge m ³ s ⁻¹	19.6	9.9 19.4	5.4
width, m	17.2	12.9	7.7
depth, m	1.0	0.77	0.55
Bed surface material			
D_{50} , mm	22.0	25.5	21.5
σ_v	5.0	3.1	6.1
Bed material*			
D_{50} , mm	8.0	9.0	8.8
σ_v	5.0	6.9	4.8
percent fines†	24.8	25.0	22.8
Bed load‡			
D_{50} , mm	2.6	3.3	3.5
σ_v	4.8	5.3	5.4
percent fines§	44.2	41.0	39.5

* $D < 32$ mm.† $D < 2$ mm.‡ $0.25 < D < 32$ mm.§ $0.25 < D < 2$ mm.

Moreover, fine sediment in bed load can be deposited during the fill phase, a process quite distinct from infiltration.

The purpose of the study reported here was to relate infiltration of fine sediment and scour and fill to sediment transport in natural streambeds during individual hydrograph events. Experiments in three natural channels were designed to replicate what occurs in gravel streambeds after being cleaned by spawning fish and later subjected to storm flows.

STUDY SITES

Three gravel bed streams that drain 5-36 km² in the redwood forests of the Coast Range of northern California were studied: Jacoby, Prairie, and North Caspar Creeks (Table 1, Figure 1). Peak streamflow results primarily from moderately intense rain that falls mostly from late fall to early spring and averages 1000-2000 mm/annum. All three streams support runs of steelhead trout (*Salmo gairdnerii*) and coho salmon (*Oncorhynchus kisutch*); Prairie Creek also contains chinook salmon (*Oncorhynchus tshawytscha*). Jacoby Creek was described by Lisle [1986], Prairie Creek by Briggs [1953], and North Caspar Creek by Rice *et al.* [1979] and Ziemer [1981]. Variations in bed material size in North Caspar Creek were previously studied by Burns [1970].

The three streams provide contrasts in bed material and basin area, which may affect fine sediment deposition. Bed material of Prairie Creek, which lies mostly in Pliocene gravel and sands of the Gold Bluffs unit [Moore and Silver, 1968], is better sorted than that of Jacoby and North Caspar Creeks, which lie within interbedded sandstone and shale units of the Franciscan Assemblage [Bailey *et al.*, 1964]. Basin areas of Jacoby and Prairie Creeks are nearly equal, and each is approximately 7 times that of North Caspar Creek.

Study reaches (Figure 2) were 230-1600 m long and were selected to include at least four spawning areas upstream of a bridge to be used for measuring discharge and sediment transport. The channels appeared to be in equilibrium with their sediment loads and are formed predominantly in alluvium.

METHODS

Bed Material Size

Bed material was sampled at 1.3-m intervals across spawning areas using the frozen core technique [Everest *et al.*, 1980; Walkotten, 1976]. Three probes were driven 40 cm into the streambed and injected with liquid CO₂, which froze interstitial water around the probe. When the probes were withdrawn, a 20 to 30-cm-thick frozen core was removed with them. The cores were vertically stratified by having them melt over a series of 4-cm-wide rectangular containers. Pounding the probes into the bed may have shaken fine material deeper into the bed, thus vertical distributions of fine material reported here should be regarded with caution. At a few sites, copper tubes ("freeze tubes") were inserted flush with the bed surface into 0.4-m deep volumes of streambed from which fine sediment (<2 mm) had been removed. After a storm, frozen cores around these tubes were taken to obtain an undisturbed stratigraphic record of fine sediment deposition.

All samples were dried, sieved into 2 phi intervals from 0.062 to 32 mm, and weighed. Sizes were truncated at 32 mm because of the smallness of core diameters and sample size (about 10 kg). On the basis of bed surface size distributions, I estimated that no more than about 20% of bed material at riffle crests was larger than 32 mm.

Pebble counts across the bed of each stream were taken at 10 locations selected by stratified random sampling [Cochran, 1963]. At least 100 particles were measured in each count. Channels were stratified longitudinally into reaches having three visually estimated grain size classes, and pebble count locations in each stratum were selected randomly in numbers proportional to the total channel length in that stratum. Stratified random sampling tends to reduce the standard error of the estimated mean, in this case, of the percent of bed material in each grain size class. Mean bed surface size distributions from pebble counts were computed by summing the weighted means of all strata.

Sediment Transport

Suspended and bed load transport rates were measured during six storms in Jacoby Creek, two in North Caspar Creek, and two in Prairie Creek and integrated over time to compute total transport for each storm. Gaging stations were installed at the downstream ends of the study reaches of each stream and operated continuously over the high runoff seasons from 1979 to 1986. North Fork Caspar Creek station has operated since 1962 [Ziemer, 1981].

Crews on rotating shifts measured suspended and bed load sediment transport rates throughout the storm flow periods, which ranged from 10 to 40 hours. Recurrence intervals of peak discharges (partial duration series) during measured storms was 0.6 years for Jacoby and Prairie Creeks and 2.2 years for North Caspar Creek. Suspended sediment was collected and analyzed using standard procedures [Guy, 1969; Guy and Norman, 1970].

Bed load was measured with a Helley-Smith sampler with a 3-inch-square orifice using the procedure of Emmett [1980]. Samples were taken at 7-16 points at constant intervals across the bed; each measurement included two transects. Individual sample time was 15-120 s. Because of the large spatial and temporal variations of bed load transport rates noted elsewhere [Reid *et al.*, 1985; Campbell and Sidle,

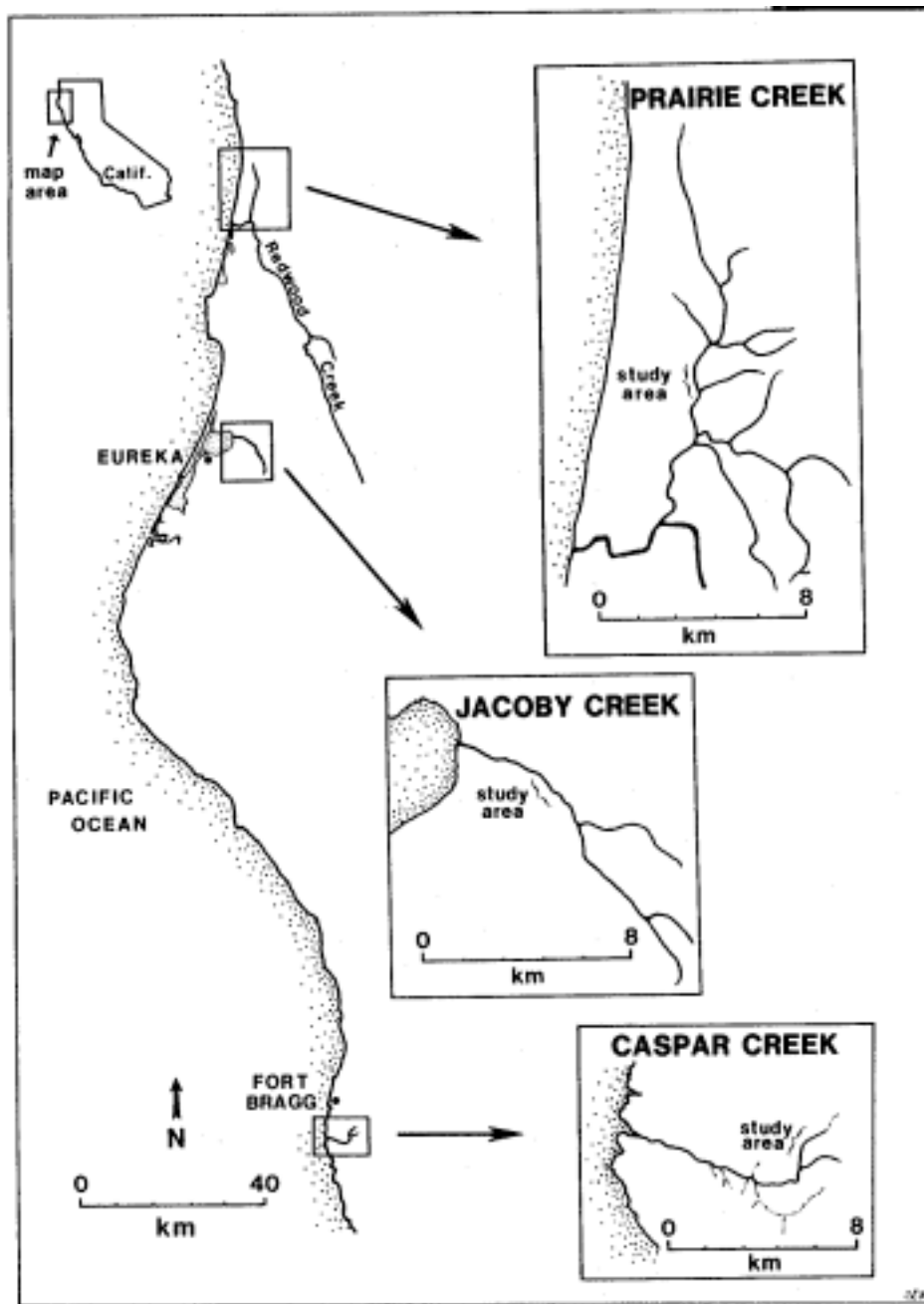


Fig. 1. Location of study reaches.

1985] and uncertainties in the efficiency of Helley-Smith samplers [Hubbell, 1987], transport rates reported here should be regarded as crude measurements with accuracy errors as large as 50-100%. We also measured bed load transport at a single point on the bed of Prairie Creek every 15 min for 36 hours to assess temporal variation. Bed load samples were processed in the same manner as bed material samples, but size-class intervals ranged between 0.25 and 32 mm.

Infiltration of Fine Sediment

Fine sediment infiltrating streambeds was collected in cans buried at 1.3-m intervals along transects across riffle crests in spawning areas (Figure 2). All spawning areas within the study reaches were instrumented. These areas

were identified by signs of previous spawning activity or as likely spawning sites by a fishery biologist (William Brock, personal communication, 1978). Cans 17 cm in diameter by 22 cm deep were filled with well-sorted, subangular gravel ($D_{50} = 15.2$ mm; $\sigma_g = 1.8$) and buried flush with the streambed during low flow. To install the cans, we first removed the armor layer, excavated a hole inside a metal cylinder, inserted the cans, and then replaced the armor layer over the cans. After a storm flow during which we measured sediment transport, we replaced the cans with ones filled with clean gravel. Thicknesses of strata inside the infiltrated cans were measured as they were emptied. The contents were dried, sieved into 2 phi size-class intervals between 0.062 and 8 mm, and weighed.

Solid-walled containers have been used in several exper-

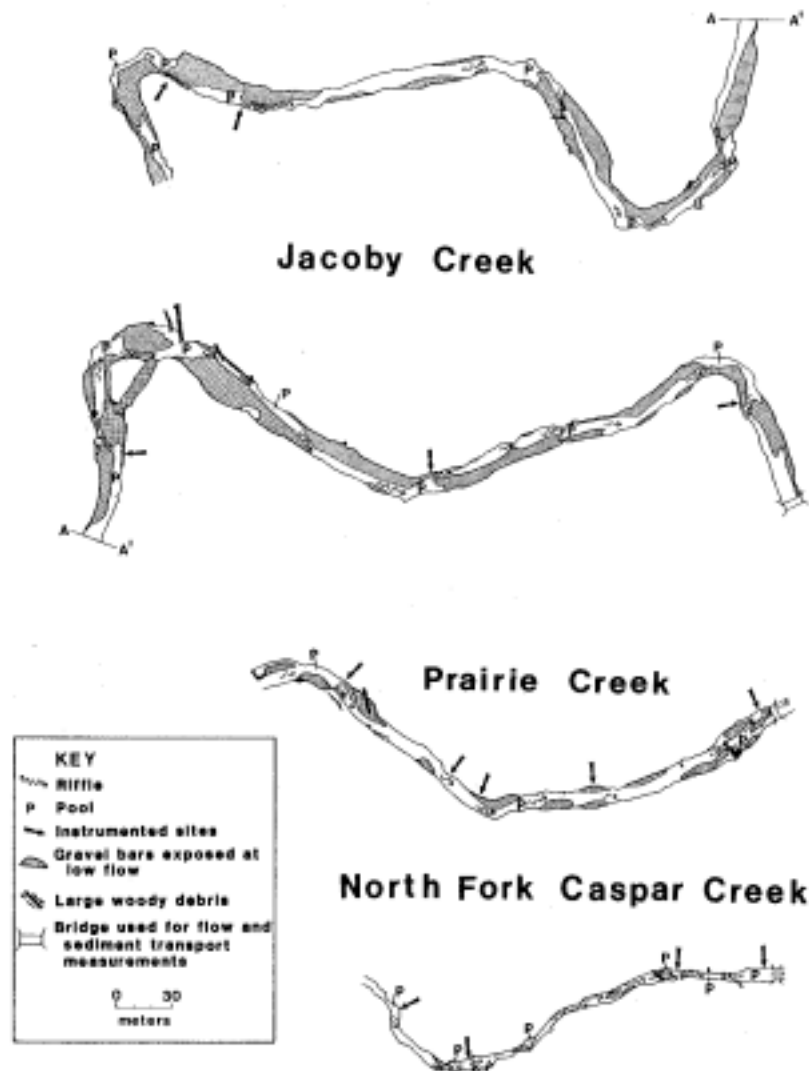


Fig. 2. Study reaches and instrumented spawning areas.

iments to measure sediment infiltration (Slaney *et al.* [1977], Beshta and Jackson [1979], Carting [1984], and Frostick *et al.* [1984] among others). Such containers collect only the sediment that enters a volume of bed material through the surface interstices and excludes sediment that is introduced laterally by intergravel flow, which can have high instantaneous accelerations due to turbulence near the bed. Gravity fall has been found to be the dominant mode of ingress of fine sediment into gravel beds [Einstein, 1968; Slaney *et al.*, 1977; Beshta and Jackson, 1979]. However, Curling [1984] found that impermeable container walls reduced trapping efficiency to 62% due to elimination of intergravel flow that could distribute sediment throughout a sample. Sand used in 22 of 25 runs of his experiment was apparently fine enough (smaller than 0.2 mm) to be significantly affected by the low instantaneous velocities of intergravel flow. The degree to which the walls of the cans used in my study affected trapping efficiency of fine sediment is not known. The finest sediment was probably affected most. In a single comparison of trapping rates of a can and an unbounded cylindrical section of experimental gravel in Prairie Creek, rates were found to be 3% greater in the can. Rates of sediment infiltration reported here should be regarded as minimum measures of true values.

The effect of the experimental gravel on infiltration of sediment as it would occur in natural streambed material cleaned by fish was tested in one section of Jacoby Creek. Accumulation in cans that were filled with experimental gravel was compared with that in cans filled with natural gravel ($4 < D < 45$ mm) from which fine and coarse fractions were eliminated. We placed three cans of each gravel mixture alternately in two lines running parallel to the channel centerline and separated by 1 m. We retrieved the cans after a storm and sieved their contents to measure the accumulation of material finer than 2 mm. Accumulation averaged 18.3 kg m^{-2} (SE = 1.0) in the cans with natural gravel and 18.8 kg m^{-2} (SE = 0.85) in cans with experimental gravel. Although the validity of standard error values is questionable because cans were not placed randomly, these results indicate no difference in accumulation rates between the two mixtures of gravel.

After storms, many cans were found to be either buried by several centimeters of fresh deposits or exposed by scour. However, analysis of covariance indicated that fine sediment accumulation rates in buried, unaffected, and exposed cans did not differ significantly (significance level = 5%). One fourth of the cans were lost altogether, most during the largest storms.

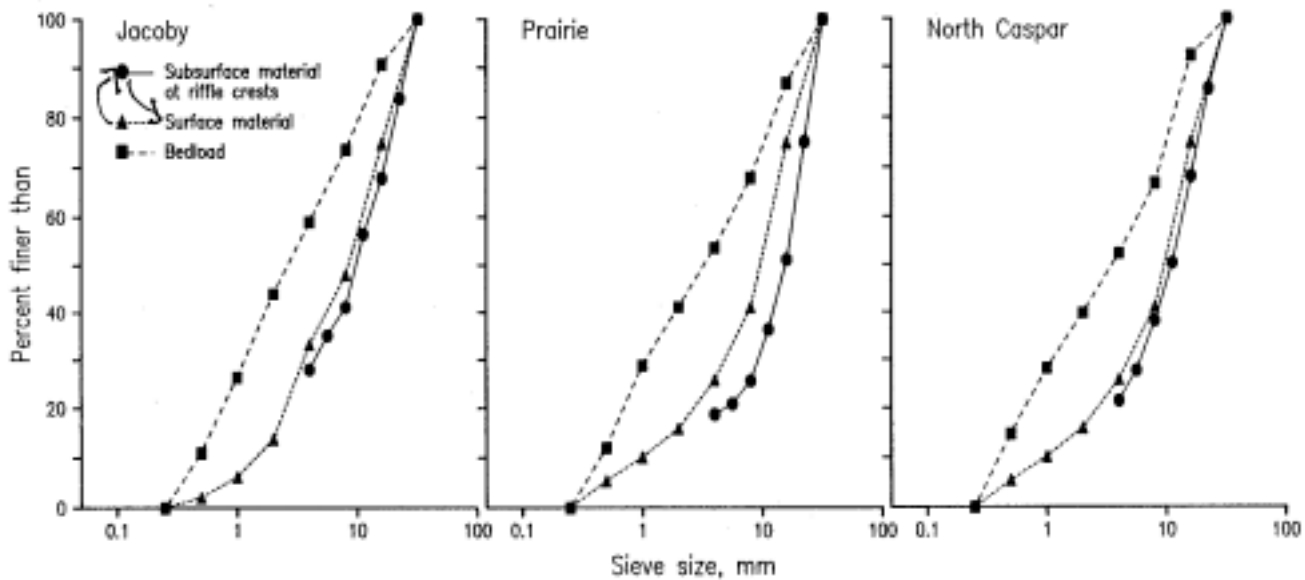


Fig. 3. Average size distributions of bed surface material in study reaches ($D < 32$ mm), bed load compounded over storm flows ($0.25 < D < 32$ mm), and subsurface material at instrumented sections ($0.25 < D < 32$ mm).

Scour and Fill

Cross sections were installed over each line of gravel cans in each stream and resurveyed after each storm for a 2- to 4-year period. Scour chains [Leopold *et al.*, 1964] were implanted during the fall before high runoff and excavated and resurveyed the following spring. Depths of scour or fill were measured by superimposing consecutive surveys of each cross section.

RESULTS

Bed Material

Surface material. Median particle sizes (D_{50}) in the surface of the three streambeds were similar (21.5-25.5 mm), but sorting of bed material in Prairie Creek was superior (Table 1). Considering the entire streambed, Prairie Creek offered more favorable spawning habitat than the other creeks because a greater majority of its surface material fell within the preferred range of sizes (80% between 10 and 100 mm). Prairie Creek's bed also felt the loosest underfoot. These differences in sorting may reflect the primary breakdown and sorting of Franciscan bedrock in Jacoby and North Caspar drainages and the secondary sorting of Tertiary gravels in Prairie Creek.

Subsurface material. Frozen core samples across riffle crests showed similar size distributions for all three streams (Table 1). Within the size interval of < 32 mm, D_{50} ranged from 8.0 (Jacoby) to 9.0 mm (Prairie); percent of bed material finer than 2 mm ranged from 22.8 (North Caspar) to 25.0% (Prairie). Grain size distributions were unimodal (Figure 3). Similarities in subsurface size distributions probably resulted in part from sampling in similar sedimentological environments and truncation of the upper end of the size distribution.

The proportion of material finer than 2 mm in streambeds showed little consistent variation with depth, although fines may have increased below the surface layer in Prairie Creek (Figure 4). This trend is questionable because of large standard errors for deep layers. Increases in fines with depth in Prairie Creek may have resulted from large pore spaces in

its relatively well sorted bed surface, which would allow greater winnowing of fines from near-surface layers and deeper penetration of fines below surface layers than in the other streambeds. Fines could also have been displaced downward by insertion of the sampling probes. Adams and Beschta [1980] found no variation in concentration of fines with depth under the armor layer in coastal streams in Oregon, but Scrivener and Brownlee [1981] detected a small but significant increase in fines with depth in some sections of Carnation Creek, Vancouver Island, British Columbia.

Size compositions varied widely across the sampled riffle crests. The coefficient of variation in the percentage finer than 2 mm for sampled transects was 0.29 for Jacoby Creek and 0.20 for Prairie Creek. In riffles downstream of bends or large bedrock obstructions (Figure 5a), bed material commonly contained more fine material at greater distances from the outside bank (Figure 5b). Transverse components of

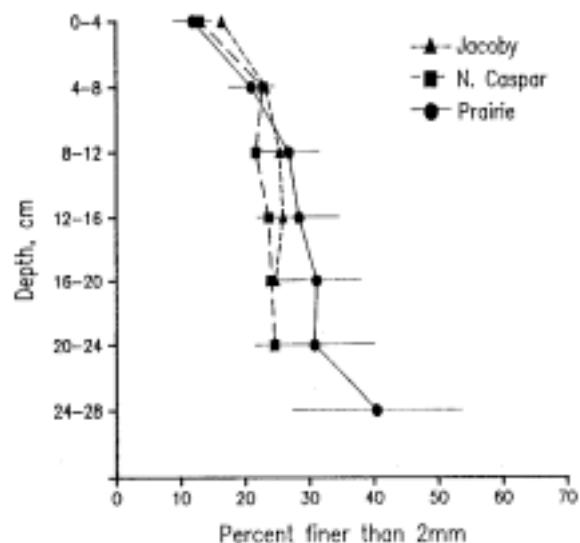


Fig. 4. Variation of fine sediment ($D < 2$ mm) with depth in bed material at instrumented sections in Jacoby, Prairie, and North Caspar Creeks.

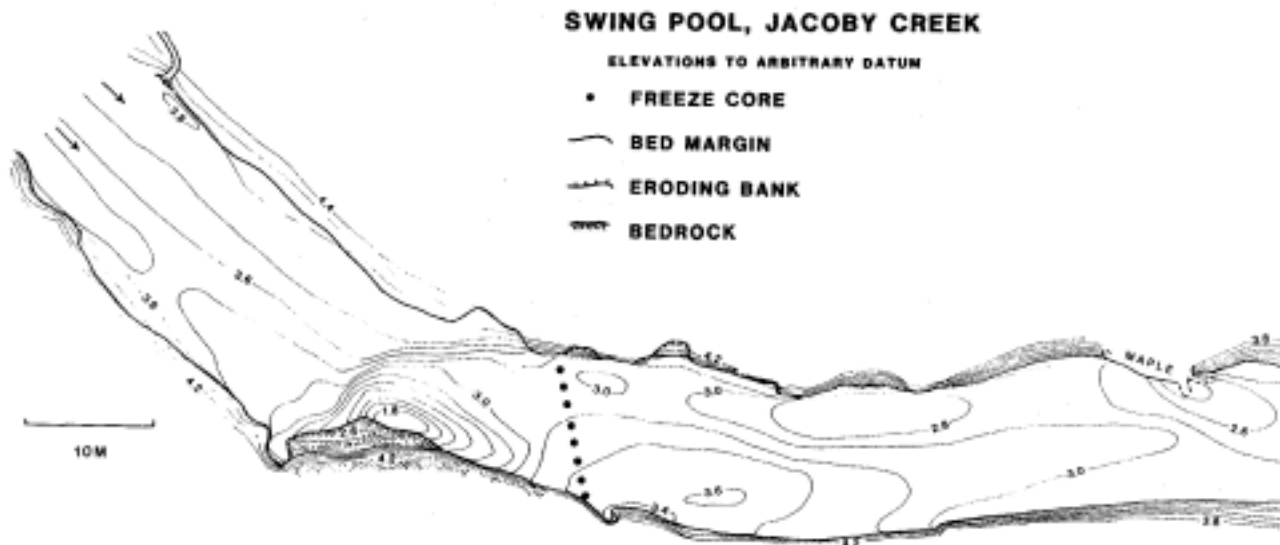


Fig. 5a. Frozen core locations downstream of a bend in Jacoby Creek.

near-bed velocities directed away from the outside bank may have swept fine sediment toward the inside bank [Dietrich and Smith, 1984].

Size distributions of bed load and bed material. Within the same size range ($0.25 < D < 32$ mm), bed material in transport was consistently finer than in the surface of the entire streambed and the subsurface material at riffle crests (Figure 3, Table 1). Bed load size compositions were averaged by integrating transport rates of each size fraction over all storms. Subsurface and surface grain size distributions do not have a lower bound, but can be compared with those of bed load because bed material finer than 0.25 mm comprised only a few percent.

Ratios of median sizes of surface material to bed load were 3.2 (North Caspar), 3.7 (Jacoby), and 4.7 (Prairie). These ratios are larger than 2.5, the ratio of D_{50} of surface to subsurface material for streams in Colorado [Andrews, 1983]. This difference could arise from greater armoring in the California streams, or possible reduced trapping efficiency of the bed load sampler for large particles.

Although size distributions of bed load and subsurface material can be expected to be equal [Parker, 1982; Andrews, 1983], bed load was substantially finer than subsurface material sampled at riffle crests. The proportion of sand in bed load, for example, was 2-3 times greater (Table 1). This is probably due in part to the relative coarseness of riffle crests, where subsurface material was sampled. Apparently, riffle crests already contain lower proportions of fines than other areas before spawning fish clean the bed during redd construction.

Sediment Transport

Suspended sediment. Suspended sediment concentrations in the three streams were moderate, ranging over one to two orders of magnitude, with the lowest concentrations in Prairie Creek. Suspended sediment concentrations were usually low (50-200 ppm) during initial and final stages of storm hydrographs and moderately high (500-2000 ppm) during peak stages. Suspended sediment constituted 75-94% of the total clastic load transported during sampled storm flows. The proportion of sand ($D > 0.062$ mm) in suspended

sediment samples averaged 24-38% in each creek and ranged from a few percent at low discharges in Jacoby and Prairie Creeks to 55% at high discharges in all three creeks. Maximum particle size of sediment suspended during bank-full stages was 0.3 mm, as calculated from Bagnold's [1973] suspension criterion.

Suspended sediment transport relations (transport rate (kilograms per second per kilometer) versus runoff rate (cubic meters per second per square kilometer) (Figure 6) did not differ significantly for Jacoby and North Caspar Creeks, but Prairie Creek had a different relation from that for Jacoby Creek (Chow's test, significance level = 0.05). At low storm runoff rates, Jacoby and North Caspar Creeks carried higher concentrations of suspended sediment than Prairie Creek, but this difference disappeared at high runoff rates. Differences in suspended sediment curves may not be significant because of the nonrandomness of selecting times to sample sediment [Thomas, 1985] and the small sample size for Prairie Creek.

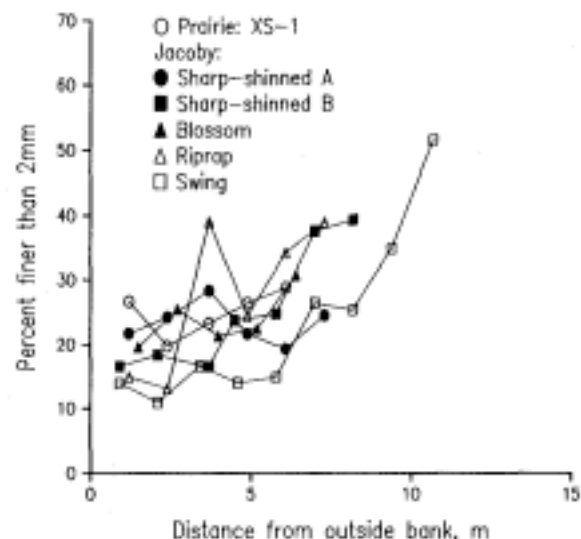


Fig. 5b. Variation of the proportion of fine sediment ($D < 2$ mm) in frozen cores with distance from the outside bank of bends in Jacoby and Prairie Creeks. Locations are shown in Figure 2.

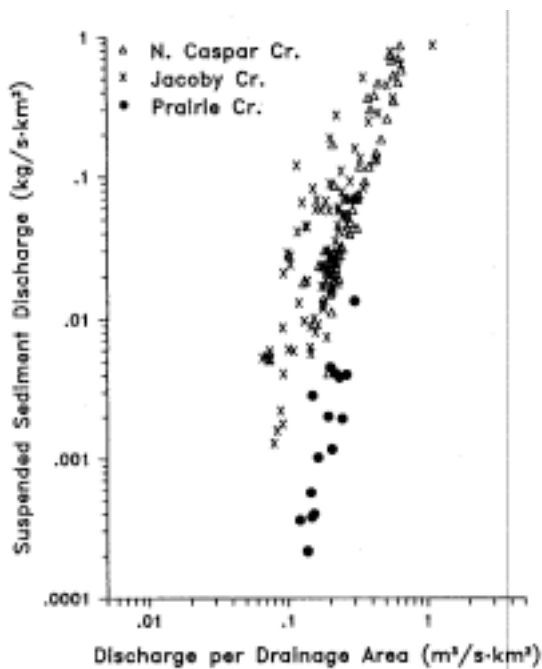


Fig. 6. Variation of suspended sediment discharge with runoff rate.

Bed load transport. Bed load transport rate increased rapidly with increasing shear stress in each creek and varied widely for a given shear stress (Figure 7). Such rapid increases are common for shear stresses less than twice the entrainment threshold [Carson and Griffiths, 1987]. Mean bank-full shear stress, calculated from mean hydraulic radius and water surface slope, exceeded threshold shear stress, estimated from bed load transport data, by factors of 1.7 (Jacoby), 1.6 (Prairie), and 2.1 (North Caspar). These factors exceed a theoretical factor (1.2) for stable gravel channels [Parker, 1978]. Mean shear stress calculated in this manner, however, includes that exerted on banks, bars, beds, and large roughness elements such as woody debris and outcrops, and thus it is greater than that exerted solely on bed particles.

Prairie Creek showed significantly higher rates of bed load transport for a given shear stress than the other streams. This difference is associated with low hydraulic friction in Prairie Creek, which had a poorly developed pool-riffle sequence and low sinuosity. A common but inverse measure of friction is the ratio of mean velocity to shear velocity, which is proportional to the square root of shear stress. This value at bank-full stage was nearly twice as much in Prairie Creek (8.0) as in Jacoby (4.6) and North Caspar (4.8) Creeks.

Appreciable transport of sand over a stable gravel bed during moderately high discharges [Jackson and Beschta, 1982] did not occur in these streams. Sand would be selectively transported between a discharge (Q_0) corresponding to incipient bed load transport (defined as $0.0001 \text{ kg m}^{-1} \text{ s}^{-1}$) and a discharge (Q_c) corresponding to entrainment of the median size of the bed surface (defined here as that below which the median size is not present in bed load samples). During discharges between Q_0 and Q_c , however, maximum size classes of bed load were most commonly coarser than sand (Figure 8). The median size of the armor layer (21-26 mm) was represented in bed load sampled at discharges as low as those approximately equal to Q_0 and was represented in all samples at discharges greater than 1.6-3.0 times Q_0 .

Because of the smallness of bed load samples taken at low transport rates, gravel particles would be rarely captured even if they were entrained [Wilcock, 1988]. Thus true values of Q_c were probably closer to those of Q_0 .

The most likely cause for the absence of selective transport of sand was a lack of supply of sand in these streambeds, manifested in part by the unimodality of size distributions of surface and subsurface material. In addition, deposits of unarmored sand in pools, for example, were small. In North Fork Caspar Creek, however, maximum bed load particle size was less (commonly finer than 2 mm) during rising stages than falling stages. This difference suggests that more sand was available for transport at rising stages or that gravel, once entrained during high stages, continued to be transported at low falling stages before finding a stable position on the streambed. This pattern was not evident in the other streams.

Bed load was entrained at rising stages, and transport rates remained high and fluctuated after peak discharge passed (Figures 9a and 9b). Bed load transport measured at a single point every 15 min for 36 hours in Prairie Creek (Figure 9c) showed that gravel continued to be transported at waning discharges which were lower than those for incipient gravel transport at rising stages, as Reid *et al.* [1985] observed. Transport of gravel ($2 < D < 32 \text{ mm}$) varied more than that of sand ($0.25 < D < 2 \text{ mm}$) and, as in Jacoby and North Caspar Creek, gravel transport rates at a given discharge covered a greater range than those for sand. Discontinuities in transport rates may have been caused by the passage of low bed forms or bed load sheets [Whiting *et al.*, 1988; Kuhnle and Southard, 1988]. Autocorrelation of bed load transport rates for the Prairie Creek point samples failed to show any significant periodicity, however, suggesting that pulses of bed load were irregular or had periods shorter than 15 min.

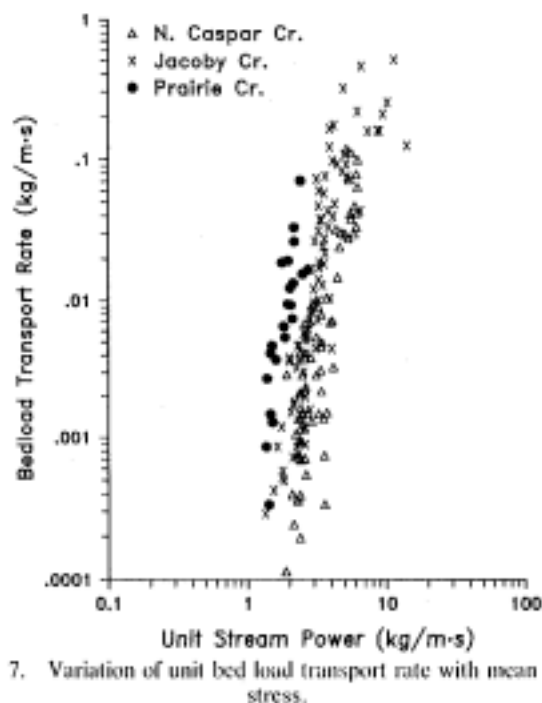


Fig. 7. Variation of unit bed load (transport rate) with mean shear stress.

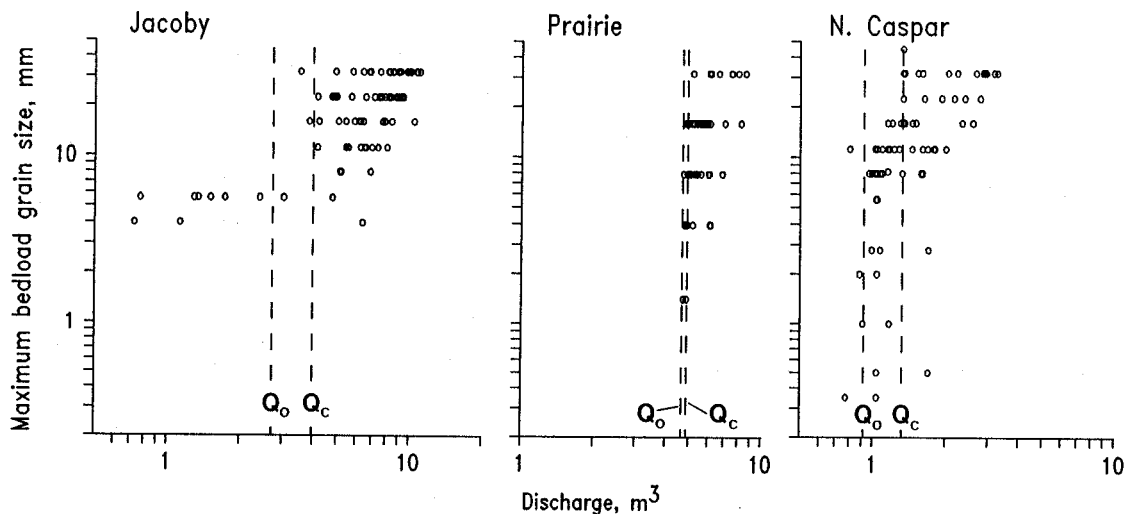


Fig. 8. Variation of maximum bed load particle size with discharge. Samples were truncated at 32 mm. Maximum bed load size is the sieve size larger than that retaining the coarsest fraction of a bed load sample.

Deposition of Fine Sediment in Gravel Beds

Gravel cans. Fine sediment that infiltrated into gravel cans was found predominately at the tops and bottoms of the cans (Figure 10). A similar pattern was observed in a core obtained from a freeze tube inserted into the bed of Prairie Creek and frozen after a storm (Figure 11). Sand and fine gravel completely filled interstices from the top layer of gravel as far down as several centimeters. The seal thus formed would seem to hinder deposition into underlying layers. Natural bed load particles as large or larger than the experimental gravel were sometimes found in these deposits, indicating that some of the experimental gravel had been scoured from the cans and replaced by gravel bed load. Fine sand, silt, and fine organic matter were deposited mostly on the bottoms of cans; small amounts were found also in the middle depths of the experimental gravel. Formation of a surface seal appeared most pronounced following stormflows which were large enough to entrain the armor layer. Deposition during smaller storms was concentrated at the bottoms of cans.

Accumulation in cans varied widely across the channel and from reach to reach. Rates of accumulation of sediment finer than 2 mm ranged mostly between 10 and 70 kg m⁻². The coefficient of variation (CV) across channel for all lines with three or more cans remaining after a storm averaged 0.30. (This is not a true measure of variation, however, since cans were located nonrandomly.) In Jacoby Creek, the variation across channel (CV = 0.23-0.47) approximately equalled the longitudinal variation of mean values of each line (CV = 0.24-0.49) for five storms. The downstream-most line of cans consistently accumulated relatively small amounts of sediment, perhaps because this line was wider than the others and thus unit bed load transport rates were less. Similarly, the range in cross-channel variation for one storm in Prairie Creek (CV = 0.31-0.49) encompassed the longitudinal variation (CV = 0.38). Zones of high accumulation of fine sediment did not necessarily correspond to zones of high concentration of fines in natural bed material, perhaps because unit bed load transport in some of these areas was low.

Relation to sediment transport. Although suspended sediment comprised 75-94% of the elastic load during storm

flows, sizes most likely carried in suspension (<0.25 mm) accounted for only 22-30% of the sediment accumulated in gravel cans (Table 2). The cans were a barrier to lateral intrusion of suspended sediment carried by intergravel flow, but low concentrations measured in the frozen cores (averaging 6-8%) indicated that rates of lateral intrusion would be low naturally. Relatively little suspended sediment was deposited in the streambeds because most was carried in the flow above the bed surface. Also, suspended sediment could most easily enter a clean gravel bed at low discharges before bed load particles could plug surface interstices, but suspended sediment concentrations at discharges less than Q_0 rarely exceeded a few hundred ppm.

The most abundant particle size fraction deposited in the gravel cans was medium sand (0.25 < D < 0.5 mm). In all three streams, sediment accumulation increased with grain size and peaked at the medium sand size range. Medium sand, which was the finest bed load fraction, was also the most abundant bed load fraction in North Fork Caspar and Prairie Creeks, but it was the least abundant in Jacoby Creek. Accumulation efficiency (the ratio between accumulation and total transport) was greatest for medium sand in Jacoby and North Caspar Creeks. Intermittent suspension and traction of very fine to medium sand would cause accumulation efficiency for finer-than-medium sand (here classified as part of the suspended load) to be calculated too low and that for medium sand (classified here as bed load) to be too high. Large amounts of medium sand were deposited, most likely, for these reasons: it was abundant in the sediment loads of the three streams and large enough to be in intermittent contact with the bed yet small enough to pass through small interstices.

Despite the large proportion of coarse sand (1 < D < 2 mm) in bed load in Jacoby Creek, relatively little was deposited in the cans because large interstices near the surface that would allow ingress of coarse sand would tend to quickly plug. Accumulation efficiency was greatest for coarse sand in Prairie Creek, however, perhaps because superior sorting and rounding of its armor layer created larger interstices than in the other two creeks.

Log-transformed values of accumulation of fine sediment (0.25 < D < 2 mm) averaged for all gravel can lines and

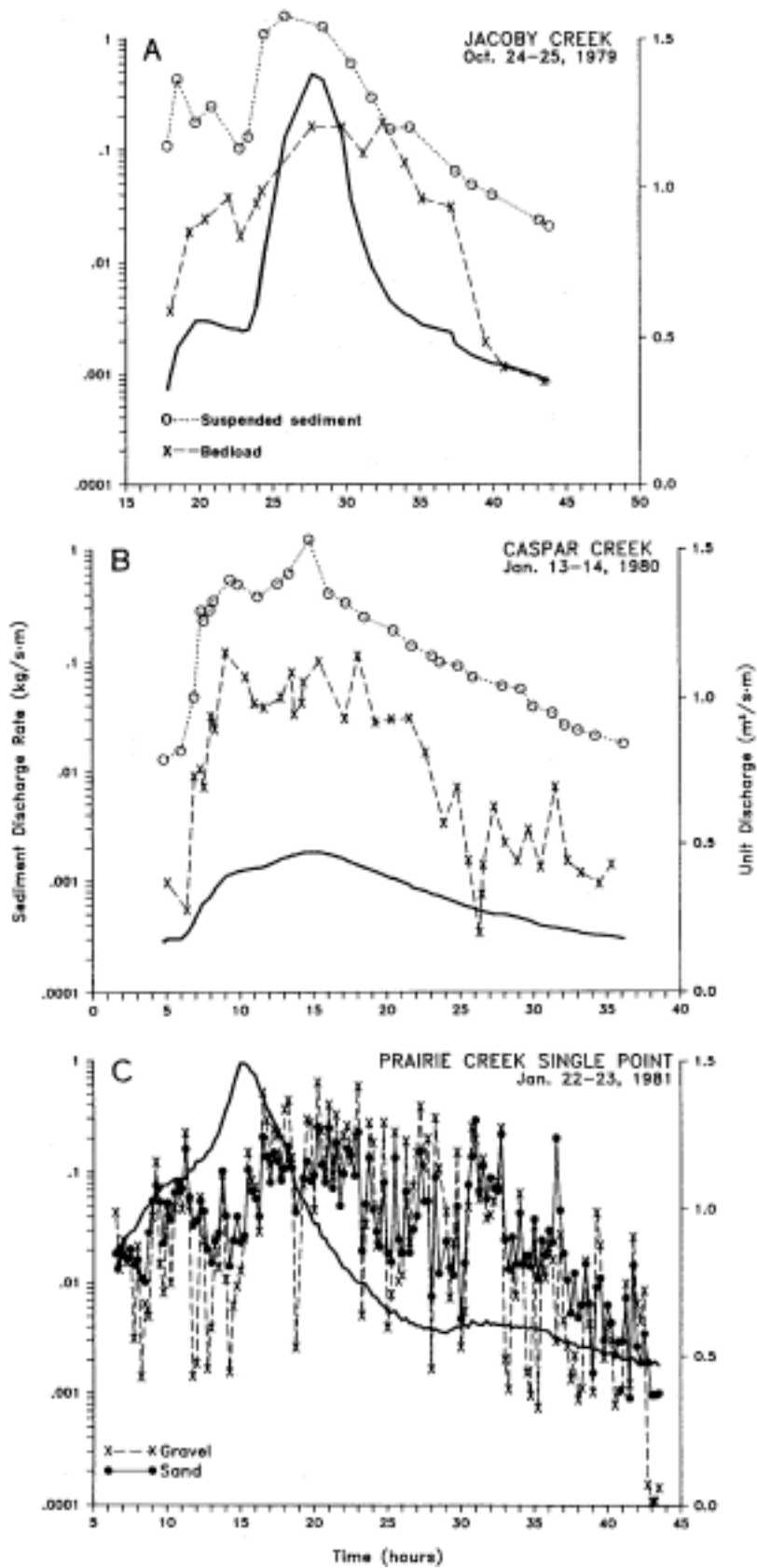


Fig. 9. Sample of storm flow hydrographs and bed load and suspended sediment discharge rates in (a) Jacoby and (b) North Caspar Creeks. (c) Storm hydrograph and sand and gravel transport rates taken at a single point in Prairie Creek.

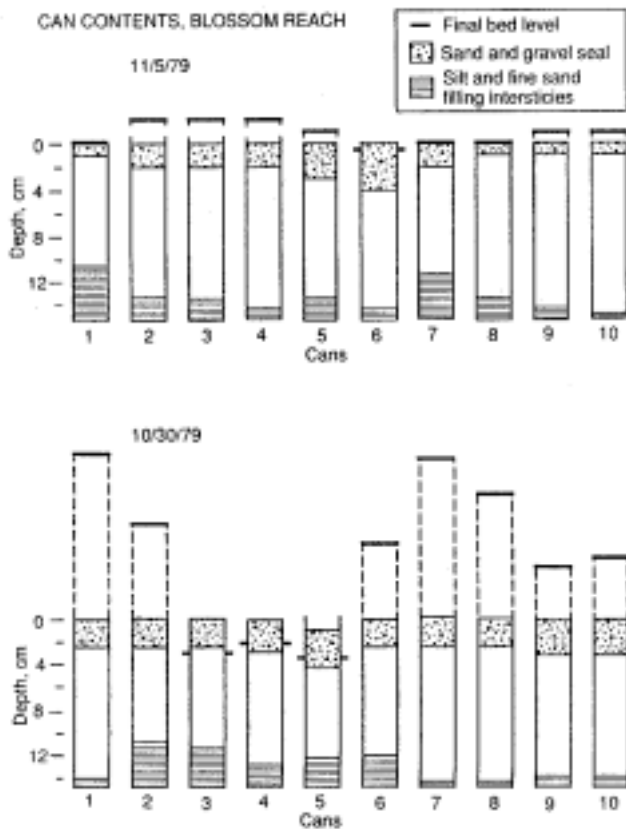


Fig. 10. Stratification of fine sediment infiltrated into experimental gravel in cans.

cumulative unit bed load transport during storms (same size range) correlated well ($r^2 = 0.93$) when data from all three creeks were combined (Figure 12):

$$A = 1.88(q_B)_T^{0.365}$$

where A is the accumulation of dry sediment per unit bed area (kilograms per square meter) and $(q_B)_T$ is the cumulative unit bed load transport (kilograms per meter). The line

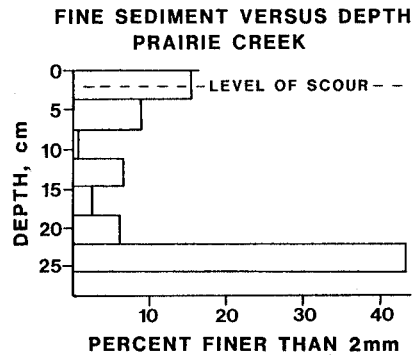


Fig. 11. Variation in fine sediment ($D < 2$ mm) with depth deposited around a freeze tube inserted into a clean gravel bed in Prairie Creek.

describing this relation passes through points selected from *Beschta and Jackson's* [1979] experiment to best represent conditions in the three stream channels (Froude number less than 1 and introduced sediment 0.5 mm in diameter).

The percentage of fine sediment that accumulated in cans decreased as the cumulative volume of bed load passing over the bed increased. In fact, the data suggest that sediment accumulation reached a maximum of about 40 kg m^{-2} and remained constant after cumulative unit bed load transport surpassed about 3000 kg m^{-1} (Figure 12). This accumulation corresponds to a concentration of fines (< 2 mm) of 20.5% in a 10-cm-deep bed or 11.4% in a 20-cm-deep bed, which roughly corresponds to the level that begins to seriously reduce the survival of incubating fish eggs [*Raiser and Bjornn*, 1979].

Slaney et al. [1977] report a similar relationship between accumulation of fines ($D < 1.19$ mm) and cumulative suspended sediment concentration (milligrams per liter per days) in Carnation Creek, British Columbia. A large y-intercept value ($\sim 10 \text{ kg m}^{-2}$) for a linear relationship among three data pairs indicated that accumulation increased at lower rates as cumulative sediment transport increased. Maximum accumulation equalled 25 kg m^{-2} .

Thickness of a seal formed by completely filling the voids

TABLE 2. Accumulation Efficiency by Grain Size of Sediment Collected in Gravel Cans

	Grain Size, mm				
	<0.062	0.062-0.25	0.25-0.5	0.5-1	1-2
<i>Jacoby</i>					
Accumulation kg m^{-1}	145	568	658	632	446
Transport, kg	1.47×10^6	4.62×10^6 *	31,500	47,800	61,600
Efficiency, m^{-1}	1.00×10^{-4}	4.18×10^{-4}	0.0209	0.0132	0.0069
<i>North Fork Caspar</i>					
Accumulation, kg m^{-1}	12.6	66.0	72.1	59.4	54.4
Transport, kg	1.67×10^5	58,700	3100	2840	2460
Efficiency, m^{-1}	7.55×10^{-5}	0.00112	0.0232	0.209	0.0222
<i>Prairie</i>					
Accumulation, kg m^{-1}	13.6	48.6	90.4	79.3	47.8
Transport, kg	1.16×10^5	72,400	3870	3380	1860
Efficiency, m^{-1}	1.18×10^{-4}	6.71×10^{-4}	0.0233	0.0235	0.0257

Accumulation efficiency is the ratio of accumulation (in kilograms per meter length of channel) to transport (in kilograms). Data is from all measured storms. Bed load sediment ranges from 0.25-2 mm in diameter; suspended sediment finer than sand is < 0.062 mm, and suspended sand is assumed to range from 0.062 to 0.25 mm.

*Suspended sand sizes were not segregated between 0.062-0.12 and 0.12-0.25 mm.

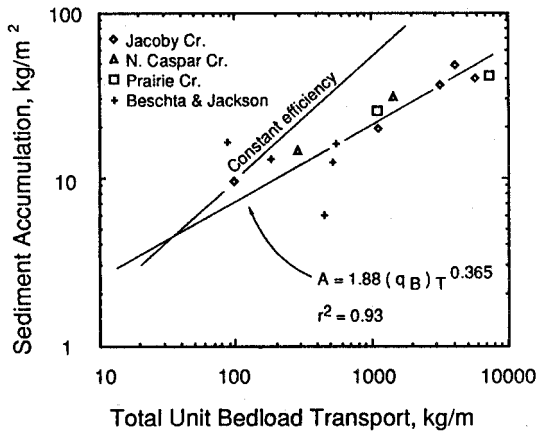


Fig. 12. Variation in accumulation of fine sediment in gravel cans with cumulated bed load transport for $0.25 < D < 2$ mm. The line labeled "constant efficiency" shows constant values of the ratio of accumulation to transport.

of a layer of gravel can be estimated from values of sediment accumulation in mass per area by using the equation

$$T = 0.1A[\rho_s P_g (1 - P_s)]^{-1}$$

where T is seal thickness (in centimeters), ρ_s is density of sediment, P_g is porosity of gravel, and P_s is porosity of sand. Using average values for the three creeks ($\rho_s = 2.3$, $P_g = 0.42$, and $P_s = 0.35$), maximum seal thickness equals 6.4 cm. Relative seal thickness expressed as a ratio to the 90th percentile fraction of the framework material, T/D_{90} , equals 2.6 for natural bed material finer than 32 mm or 3.6 for the experimental gravel. These values agree well with those measured in experimental channels, 2.4-3.0 [Diplas and Parker, 1985] and 2.5-5.0 [Beschta and Jackson, 1979].

In the study period (1979-1986), storm flows that had magnitudes estimated to be capable of causing the maximum

deposition of fine sediment cited above (40 kg m^{-2}) were relatively frequent in Jacoby and Prairie Creeks, but relatively infrequent in North Caspar Creek. Such flows occurred 2.3 times/year, on average, in Jacoby and Prairie Creeks, and ranged in frequency between 0 and 5/year. The frequency for such flows in North Caspar Creek averaged 0.25/year and ranged from 0 to 2/year. Their recurrence intervals (partial duration series) were 0.5 years for Jacoby and Prairie Creeks and 2.25 years for North Caspar Creek. Thus sedimentation by fines clearly posed a threat to incubating ova, especially in Jacoby and Prairie Creeks.

Scour and Fill

Scour and fill of the streambeds was sufficiently deep and frequent to affect particle size composition of spawning gravels as much or more so than infiltration of fine sediment. Cross sections surveyed between storms showed that local bed elevations commonly changed several centimeters or more during storms (Figure 13), presumably as a result of imbalances between transport and deposition of bed load moving as individual particles or in bed forms a few grain diameters thick. Despite frequent scour and fill, cross sections maintained their same general shape, reflecting an overall channel stability borne out by inspecting the study reaches after storms with reference to detailed maps. Occasional movement of large woody debris caused the deepest scour or fill, as when a woody debris jam formed and collected as much as 0.3 m of new gravel and sand at a spawning section (6A) in North Caspar Creek (see also Figure 9 in the work by Lisle [1986]).

Depths of scour and fill varied widely both at individual cross sections and between sections. The mean elevations of cross sections remained roughly constant from storm to storm (Figure 14). However, segments of these sections commonly scoured or filled to depths of 0.1 m or more during

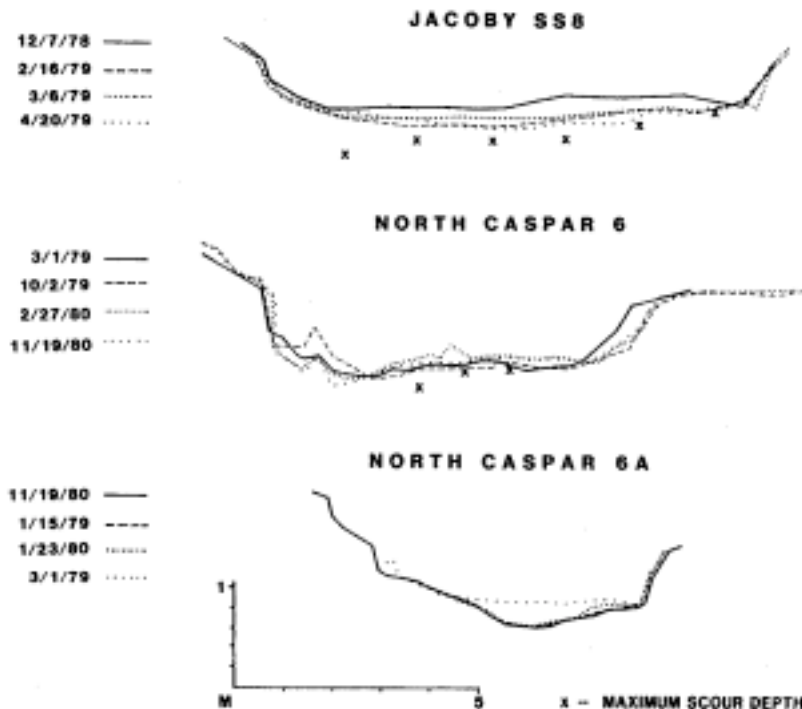


Fig. 13. Examples of scour and fill at cross sections surveyed between storm flow events. Jacoby cross section SS8 is in sharp-shinned B reach; North Caspar cross section 6A is 5 m upstream of cross section 6 (Figure 2).

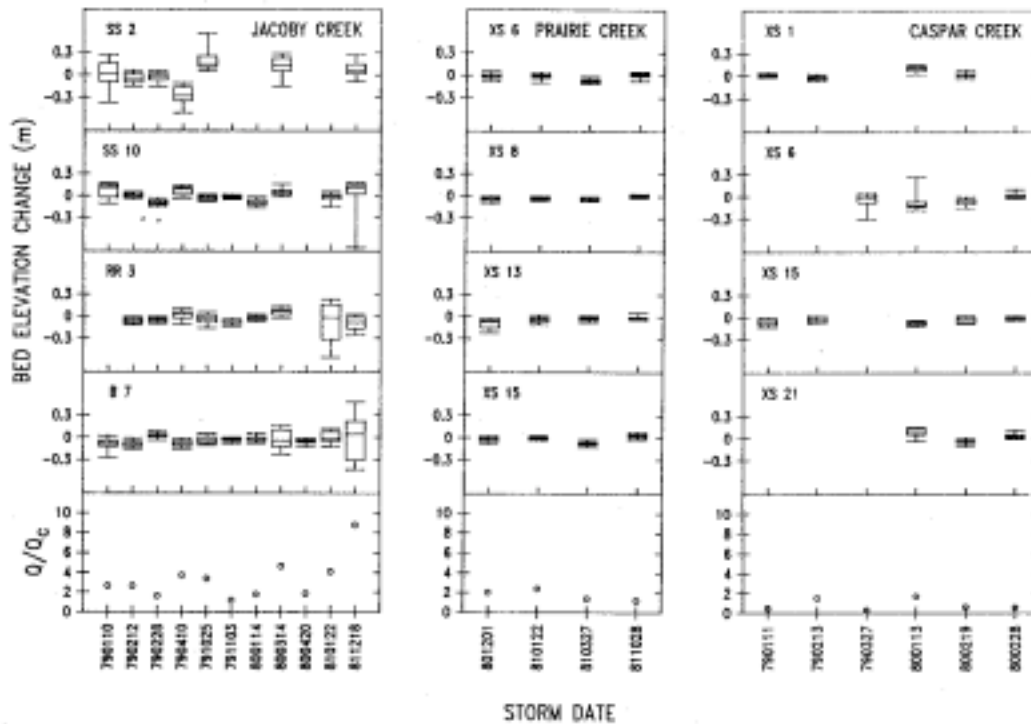


Fig. 14. Bed elevation changes resulting from storm flows and peak discharges expressed as ratios to discharge at the entrainment threshold of bed material at cross sections at spawning sites. Horizontal lines through boxes express median bed elevation change, upper and lower limits of boxes express 75th and 25th percentiles, and brackets express 95th and 5th percentiles. Positive values express fill; negative values express scour. Locations are shown in Figure 2. Jacoby cross section SS2 is in Sharp-shinned A Reach, SS10 in Sharp-shinned B, RR3 in Riprap, and B7 in Blossom.

individual storms. Jacoby Creek sections showed the greatest scour-fill range, but sampled storm size (measured as the ratio between peak storm discharge and threshold discharge for bed load transport) was also greatest in this stream. The range of mean scour-fill depths increased with storm size, but even the largest storms caused less than 0.1 m of net scour or fill at some sections.

During high flow periods, channel beds can scour below the level surveyed beforehand or afterwards. This "excess" scour accounted for more than one half of the active bed thickness in as many as 10 of 17 cross sections and showed the same magnitude of variation as scour-fill depths measured from between-storm surveys (Figure 13, Table 3). Active bed thickness, defined as the difference between the highest bed elevation surveyed between storms and the lowest level of scour measured by scour chains, was more than twice as great in Jacoby (mean value 0.32) and Prairie Creeks (0.39) than in North Caspar Creek (0.11 m). The maximum values of active bed thickness were approximately equal to one half of the mean depth of the highest flow recorded during the period when scour chains were in place. This maximum value equals those measured by *Palmquist* [1975].

DISCUSSION

Infiltration of Fine Sediment

The ratio of pore size to matrix material size determines whether a particle is excluded, becomes trapped near the surface, or passes through to the base of the bed. This ratio varies widely in natural streambeds because of the wide range of framework and matrix particle sizes, particle shape, and structure of the framework. Matrix particles too large to

fit through some interstices become trapped near the surface of the bed and form successively smaller interstices that trap successively smaller matrix particles. As a result, the subsurface layer of the framework soon becomes plugged, preventing deeper penetration of matrix particles. On the other hand, matrix particles much finer than the framework particles pass through the framework interstices and settle at the base of the permeable gravel layer and on top of individual framework particles. If unhindered by a surface seal, these finer matrix particles can fill framework interstices from the base to the surface of the bed. Since deposition of coarser, seal-forming material (usually sand) can hinder deeper deposition of finer material, the mixture of matrix material sizes affects not only the level but also the total amount of deposition.

In the streams studied, most fine sediment entering the bed was deposited in a subsurface layer up to several centimeters thick. Size distributions of bed material were unimodal. Therefore distinctions between populations of matrix and framework particles were not clearcut. (The upper level of matrix particles was drawn arbitrarily in this study at 2 mm, the boundary between sand and gravel.) Even at low transport stages, enough coarse sand, granules, and small pebbles were entrained to plug the largest interstices near the bed surface. At the same time, few large interstices were available because of the heterogeneity of bed particles. As a result, infiltration of fines into the beds of these streams was mostly restricted to the surface layers, although minor amounts of silt and clay were deposited at the base of experimental gravel beds and were concentrated in Prairie Creek beneath the level of scour and fill of the bed.

Because of the wide spread in particle sizes in most

TABLE 3. Scour-Fill Depths Measured With Scour Chains

Cross Section	Chains Lost/Implant	Excess Scour Depth* (m) and Mean (s.d.)	Active bed Thickness† (m) Mean (s.d.)	Bed Thickness Mean Depth‡
<i>Jacoby Creek</i>				
Winter 1978-1979				
B6	1/7	0.055 (0.12)	0.27 (0.27)	0.35
B7	0/6	0.0027 (0.0065)	0.15 (0.053)	0.19
SS2	3/5	0.21 (0.20)	0.42 (0.23)	0.52
SS3	0/6	0.091 (0.047)	0.35 (0.11)	0.43
SS8	2/6	0.16 (0.14)	0.36 (0.13)	0.44
SS9	1/6	0.12 (0.074)	0.29 (0.12)	0.35
Winter 1979-1980				
B6	0/8	0.054 (0.044)	0.22 (0.43)	0.25
B7	0/7	0.011 (0.017)	0.19 (0.060)	0.21
SS2	2/5	0.19 (0.18)	0.28 (0.27)	0.32
SS3	1/6	0.11 (0.10)	0.19 (0.10)	0.22
SS8	5/6	0.33 (0.15)	0.45 (0.095)	0.48
RR2	7/7	0.30 (0.088)	0.48 (0.10)	0.55
RR3	7/7	0.37 (0.083)	0.50 (0.062)	0.57
<i>North Fork Caspar Creek</i>				
Winter 1979-1980				
1	0/3	0.006 (0.010)	0.14 (0.037)	0.37
6A	0/3	0.057 (0.069)	0.16 (0.058)	0.59§
15	0/2	0.076 (0.065)	0.15 (0.027)	0.28
21	0/3	0.0 (0.0)	0.15 (0.023)	0.43
January-November 1980				
6A	0/3	0.067 (0.043)	0.085 (0.061)	0.35
15	0/2	0.053 (0.033)	0.084 (0.011)	0.18
21	0/3	0.0 (0.0)	0.066 (0.0087)	0.19
<i>Prairie Creek</i>				
October 1980 to May 1983				
6	1/3	0.12 (0.060)	0.26	0.24
8	5/5	0.22 (0.10)	0.43 (0.07)	0.29
13	6/6	0.40 (0.03)	0.49 (0.08)	0.33

*Depth of maximum scour measured by scour chains below the lowest bed elevation surveyed between storms.

†Difference between the highest surveyed bed elevation and the level of maximum scour.

‡Mean depth over sections at peak flow during measurement period.

§Fill behind newly formed log jam.

natural gravel beds, the formation of a surface seal after a bed has been cleaned of fine sediment appears to be inevitable once bed load transport begins. Critical ratios governing the depth of ingress are most easily determined for uniform spheres [Sakhivadivel and Einstein, 1970]. In a tightly packed framework of equal-diameter spheres, the ratio of sphere diameter to pore diameter is 6.5. When the ratio of framework particle diameter to matrix particle diameter (D_f/D_m) is between 6.5 and 13, two matrix particles can bridge gaps in the framework, and thus matrix particles tend to lodge near the bed surface. For D_f/D_m greater than 14, matrix particles pass to the base of the bed or come to rest in dead zones.

Zones of deposition observed in experiments that have used natural framework gravels appear consistent with theory and experiments using uniform spheres. In the case of natural materials, the ratio of minimum framework particle diameter to maximum matrix particle diameter (min D_f /max D_m) is used to express the least potential for matrix particles to penetrate into the bed, and the ratio of mean diameters (D_f/D_m) is used to express the average potential (Table 4). In laboratory experiments, matrix material has been deposited predominantly in the uppermost layers of the framework when min D_f /max D_m is less than 17. For values of min D_f /max D_m small enough to suggest that the largest matrix

material cannot enter the framework, values of D_f/D_m are much larger than the critical ratio for particle entry. Thus the range of particle ratios conducive to the deposition of matrix particles within surface layers of the framework are well represented. In such cases a layer of mostly sand has been deposited in framework interstices just below the surface of the bed. Moreover, a coarse surface layer enhances deposition of fines in surface layers [Frostick et al., 1984], and yet an armor layer has been formed as a condition in only one of these experiments [Diplas and Parker, 1985].

The difference between framework and matrix grain sizes must be quite large ($D_f/D_m > 60$) to allow infiltration of fines below the surface layer of framework particles. This could be achieved in channels that have bimodal distributions of bed material, but the ratio of diameters of the modes would have to exceed 60, and there could be little overlap between the coarse tail of the distribution of the fine mode and the fine tail of the distribution of the coarse mode. Silt is perhaps fine enough to penetrate most interstices in many gravel streambeds, and silt and clay entering streams as pollutants have found their way into gravels [Turnpenney and Williams, 1980]. Suspended sediment (very fine sand, silt, and clay) accounted for 80-95% of the total load of 10 storms in the study streams. Silt and clay constituted only about 10% of the material deposited in gravel cans, however, and less than

TABLE 4. Ratio of Median Diameters of Framework and Matrix Material (D_M/D_F) and Depth of Penetration of Fines Into Bed

Source	Framework Material	D_F/D_M	min D_F /max D_M	Depth of Deposition
Einstein [1968]	poorly sorted gravel		85 21	base of bed base of bed
Sakthivadivel and Einstein [1970]	uniform spheres	<7 7-14 >14		no entry surface layers base of bed
Beschta and Jackson [1977]	well-sorted gravel	30 75	6.5 22	surface layers base of bed
Dhamotharan et al. [1980]	poorly sorted gravel	19	~1	surface layers
Carling [1984]	well-sorted gravel	104 82 11	28 17 2.5	base of bed base of bed surface layers
Diplas and Parker [1985]	poorly sorted gravel	30 22	3 1.8	surface layers surface layers

5% of bed material at riffle crests. Accumulation of silt in streambeds is also inhibited by winnowing from the surface layers of a stable gravel bed and infrequent contact with the bed during transport.

Winnowing of fines probably has limited effectiveness in removing fines from deep within a stable bed. Fines can be winnowed no deeper than a few median armor particle diameters [Beschta and Jackson, 1979; Carling and Reader, 1982; Diplas and Parker, 1985; O'Brien, 1987], and only suspendible fractions can be removed [Caning, 1984]. Differential levels of deposition and susceptibility to winnowing both tend to concentrate sand near the bed surface and silt, clay, and suspendible sand deeper within the bed.

Origin of bimodal bed material. Natural gravel streambeds commonly have a bimodal size distribution with a gravel framework and a sandy matrix [Pettijohn, 1975]. Pettijohn [1975] argued that framework and matrix material must be deposited as separate populations at different times and under different conditions in beds in which the framework gravels are in grain-to-grain contact; framework and matrix could be deposited contemporaneously in beds that have matrix-supported frameworks. However, a gravelly framework and a sandy matrix are close enough in size, in most cases, to cause entrapment of most matrix material in the surface layers of the framework. Deep infiltration of matrix material appears therefore to be an unlikely mechanism for introducing matrix material into a bed in which there is grain-to-grain contact of framework particles. More likely, matrix particles are deposited nearly contemporaneously with framework particles near the bed surface as the bed fills.

Filling of open frameworks by matrix material could result from the segregation of sand and gravel fractions into thin sheets during transport [Iseya and Ikeda, 1987]. Gravel at the front of a gravel sheet is in grain-to-grain contact and relatively free of sand. When the front advances, gravel left behind is infiltrated by the advancing sand sheet. Thicker lenses of gravel could remain relatively free of sand if a surface seal prevented deeper penetration by successive sheets of sand. As sand exceeds a certain proportion of bed material (50%, in Iseya and Ikeda's [1987] experiment), sand and gravel are no longer segregated during transport and thus are likely to be deposited together. Beds with matrix-supported frameworks commonly contain more than about 30% matrix material, while beds with framework-supported frameworks contain less [Church et al., 1987]. The distinc-

tion in origins of matrix- and framework-supported beds in fluvial deposits therefore does not depend necessarily on a widely separated sequence of events but on the concentration of matrix material.

Scour and Fill

Scour and subsequent filling of streambeds can deposit fines abundantly in the bed depending on local concentrations of fines in bed load and near-bed velocities affecting winnowing of surface layers. Scour-fill depth from individual storms is frequently greater than the thickness of the seal formed by infiltrating fines trapped in the interstices of the bed surface. Scour exposes lower levels of the bed to infiltration by fines, and as the bed subsequently fills, successively higher layers can be infiltrated. Scour and fill of a bed may reduce the concentration of suspendible fines in the bed, however, provided that the bed fills rapidly and winnowing of the surface removes fines faster than they infiltrate the bed. Scour and fill therefore appear to be critical to changes in the concentration of fine sediments in gravel beds.

Scour and fill of streambeds posed a serious threat to salmonid ova in all three study streams, depending on storm flow magnitude and frequency, and on shifts in channel structure. The pit and tailspill of redds were obliterated by the first high flow event to exceed the entrainment threshold of the armor layer, which usually occurred several times per year. In contrast, the topography of redds can be preserved over the incubation period in channels with less active armor layers and in those in which eggs incubate in seasons of low or moderate flow (William Platts, personal communication, 1986). Active bed thicknesses measured annually and Scour-fill depths measured between storms were frequently equal to the depth at which salmonids buried eggs (20-40 cm). Therefore eggs were in danger of being scoured from the bed or buried by thick layers of sandy gravel.

The potential survivability of ova appears to be greatest in North Caspar Creek, the smallest stream of the three. Scour-fill depths were least. Flows capable of transporting enough bedload to cause deleterious amounts of deposition of fines in cleaned gravel beds had a recurrence interval of over 2 years, compared with less than 1 year for the other two streams. Because geology, sedimentology, and suspended sediment transport curves were similar to those for Jacoby Creek, the more favorable spawning habitat in North Caspar Creek is most likely due to its being higher in a

drainage. Thus there appears to be an advantage for fish to migrate as far upstream as possible before spawning.

Variation in Processes of Sedimentation

The preceding discussion has generalized some of the processes of fine sediment deposition in gravel beds. However, the distribution of bed material sizes, depths of scour and fill, and rates and grain sizes of sediment transported over a streambed are characterized better by their variability than by their average condition.

For example, fine sediment can infiltrate deeply into gravel streambeds if size distributions of transported sediment and framework particles do not overlap, at least temporarily in local areas of a stable bed. Fine sediment can become segregated from coarser bed load during waning transport stages and become concentrated in pools and other areas of low shear stress [Lisle, 1979; Jackson and Beschta, 1982]. At subsequent rising stages, fine material can be transported over the bed before the armor layer is entrained [Jackson and Beschta, 1982]. Spawning beds cleaned by fish in the tails of pools between the falling stage of one storm flow and the rising stage of another may thus be vulnerable to deep infiltration by fines before a seal is formed during entrainment of the armor layer. The potential for this problem could become serious during long intervals between high flows when fines tend to accumulate over streambeds [Adams and Beschta, 1980; Scrivener and Brownlee, 1982; Frostick et al., 1984]. Significant volumes of sand transported before entrainment of the armor layer were not measured in the study streams because there was an insufficient supply of fines, and also, perhaps, because bed load was not measured immediately downstream of pools. During these same stages, suspended sediment concentrations did not exceed a few hundred ppm.

Bed material is sorted locally as a result of complexities in channel morphology, which cause differences in magnitude of shear stress and divergences in bottom velocity and local bed slope. Bed material commonly contains less fine material, for example, at the heads of bars where fish commonly spawn than at the tails. Strong secondary currents set up by large obstructions and bends can sweep finer material away from one side of the channel. Unstable obstructions such as large woody debris that maintain a clean area of bed may shift locations and allow fine sediment to infiltrate a matrix-free area of bed. These complexities incur both opportunities and hazards for spawning fish and incubating ova.

The great variability of scour-fill depths indicates that on one hand, even small storm flows can destroy salmonid ova and embryos, and on the other, some areas of the streambed remain stable during the highest flows of several years. Shifts in channel structure such as woody debris can cause deep scour or fill during flows even less than the entrainment threshold of the bed. Because of this high degree of variability and the multiplicity of factors causing scour and fill (migrating bed forms, shifting structure, flow magnitude and duration, channel migration, anomalies in sediment routing) accurately predicting scour-fill depths without highly detailed measurements of flow and sediment transport does not appear feasible.

CONCLUSIONS

Fine sediment can enter a stable bed by infiltrating through the framework interstices, or by depositing along with bed

load in an active armor layer as the bed scours and fills. The distinction between these two processes is important in determining the amount and vertical distribution of fine sediment that accumulates in streambeds and the channel conditions under which fine sediment is a problem for salmonid egg survival.

Gravels cleaned by spawning fish in the three California streams appeared to change during the first storm flow according to the following sequence of processes, which should apply elsewhere to similar channels with mobile beds of unimodal material.

1. Fish excavate a pit, deposit eggs, and cover them with a mound of bed material that has reduced amounts of fine sediment.

2. During rising stages of a subsequent storm flow, increasing amounts of suspended sediment and fine bed load are transported over the bed. Some enters the bed, and because of its small size, deposits at all depths down to the level that eggs were laid.

3. As the entrainment threshold of the bed surface is exceeded, the topography of the redd is obliterated, and a surface seal of sand forms. The seal inhibits further infiltration of fine sediment, despite the increase of suspended sediment concentration in the surface flow.

4. As bed load transport fluctuates during peak flow, the bed scours, eroding and forming seals at successively lower levels. Scour may be deep enough to excavate and wash away the eggs.

5. Alternatively, bed load is deposited over the bed and forms a thick seal in combination with ingressing sand deposited below the original bed surface. Bed load deposited at riffle crests may be coarser than that in transport because of local sorting. Other scenarios are possible with different sequences of scour and fill.

6. Little change in bed material occurs after scour and fill cease during waning stages of the hydrograph.

In these channels with unimodal bed material of sand and gravel, bed load coarse enough to become entrapped in surface framework interstices was transported at all transport stages. The main component of sediment infiltrating the bed was fine bed load, not suspended sediment, because of its frequent contact with the bed and ability to fit into framework interstices. Deposition was necessarily most concentrated near the bed surface and sealed off underlying depths to more infiltrating sediment. The seal decreased the rate of infiltration as bed load transport progressed, but not before enough fine sediment was deposited to endanger egg survival.

Scour and subsequent fill deposited as much or more fine sediment in cleaned gravel matrices as infiltration. In some instances, scour extended below common depths of egg burial and thus posed a direct threat to egg survival.

Scour and fill depths and rates of fine sediment infiltration were best characterized by their variability in time and space. This variability poses the greatest challenge to predictions of spawning success as a function of flow and sediment transport. Small streams, however, apparently offer the least risk to spawning because of low rates of unit bed load transport. Given an adequate number of spawning fish, it appears that during any year some eggs will survive the effects of sediment transport and ultimately contribute to sustaining the presence of fish in the stream.

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Modelling the probability of salmonid egg pocket scour due to floods¹

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Abstract: Flood disturbance plays a key but complex role in structuring lotic ecosystems. Empirical models proposed here allow salmonid resource managers to quantify the probability of egg pocket scour during floods and to predict how the expected losses vary with flood strength and reach characteristics. The models are based on comparisons between published salmonid egg pocket depth criteria and statistics on the intensity and spatial distribution of scour and fill produced by three flood events of widely different magnitudes in three separate reaches of a gravel-cobble Atlantic salmon (*Salmo salar*) river in the Saguenay region, Quebec. A simple substrate mobility index, based on reach-scale geomorphic characteristics and flood hydraulics, was shown to provide useful predictions (R^2 up to 74%) of the fraction of the area of potential spawning zones undergoing flood scour greater than 30 cm. Any Atlantic salmon egg pockets present in these deeply scoured areas would be destroyed. The models also predict the distribution of fill (net rise in bed) potentially causing fry entombment at redds. The flood disturbance data suggest that average probability of scour of an Atlantic salmon egg pocket in the study reaches ranges from under 5% for frequent-recurrence spring floods to approximately 20% for an extreme, multicentenary-recurrence flood.

Résumé : Les perturbations causées par les crues jouent un rôle clé mais complexe dans la structuration des écosystèmes lotiques. Les modèles empiriques proposés ici permettent aux gestionnaires des ressources de salmonidés de quantifier la probabilité d'affouillement des poches d'œufs pendant les crues et de prédire comment les pertes prévues vont varier en fonction de la force de la crue et des caractéristiques du tronçon. Les modèles se fondent sur des comparaisons entre des critères publiés sur la profondeur des poches d'œufs de salmonidés et sur des statistiques concernant l'intensité et la distribution spatiale de l'affouillement et du colmatage produits par trois épisodes de crue d'ampleur très différente, survenus dans trois tronçons séparés d'un cours d'eau à saumon à fond de gravier et de cailloux de la région du Saguenay, au Québec. Un indice simple de la mobilité du substrat, fondé sur des caractéristiques géomorphologiques à l'échelle du tronçon et sur l'hydraulique de la crue, a fourni des prévisions utiles (R^2 jusqu'à 74%) de la fraction de la superficie des frayères potentielles qui subissait un affouillement sur plus de 30 cm. Toutes les poches d'œufs de saumon atlantique présentes dans ces zones profondément affouillées seraient détruites. Les modèles prédisent aussi la distribution du colmatage (hausse nette du lit), qui risque de causer l'étouffement des alevins prisonniers des nids. Les données sur les perturbations causées par les crues permettent de penser que la probabilité moyenne d'affouillement d'une poche d'œufs de saumon dans les tronçons d'étude va de moins de 5% pour les crues printanières fréquentes à environ 20% pour une crue extrême à récurrence pluricentenaire.

[Traduit par la Rédaction]

Introduction

The physical and spatial complexity of stream microhabitat poses real challenges to the study of running-water ecosystems. However, the paradoxical role of flood disturbance in structuring running-water communities arguably poses even greater challenges to understanding lotic ecosystems. The problem of defining optimum physical disturbance regimes for various lotic communities, raised by several authors (e.g., Resh et al. 1988; Allen 1995; Sparks and Spink 1998), applies in particular to stream salmonid communities.

On the one hand, substrate entrainment by flood flows is necessary to maintain the long-term productivity of gravel stream habitat for salmonids. Indeed, the curtailment of regular high-flow events and associated gravel transport (e.g., following reservoir construction) can lead to excess sand encroachment into substrate, resulting in degradation of spawning habitat (e.g., Kondolf and Wilcock 1996; Wilcock et al. 1996; Milhous 1998) and in the displacement of the lithophilous benthic insect populations, a major food source during juvenile salmonid growth (Waters 1995). Conversely, intense and frequent disturbances to gravel substrate may limit salmonid production by destroying fish eggs during incubation (Seegrist and Gard 1972; Holtby and Healy 1986; Lisle 1989), by temporarily decimating benthic insect populations (Elwood and Waters 1969; Milner et al. 1981) or by directly inhibiting foraging by juvenile salmonids.

In particular, flood scour of salmonid eggs in spawning beds can directly affect cohort and population dynamics. Numerous studies have indicated the importance of spawning bed grain size distribution in controlling intergravel flow, egg maturation, and fry emergence (Scrivener and Brownlee

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1989; Kondolf and Wolman 1993). However, the impact on salmonid reproductive success of flood disturbances to spawning beds has been poorly studied. Payne and Lapointe (1997) showed that, in an unstable gravel-cobble river, high rates of erosion of sand-rich cutbanks during floods did not necessarily lead to enhanced sand encroachment into the spawning substrate in the reach. Their study did not, however, address the possible effects of intense spawning bed disturbance during floods on embryos incubating in such unstable channels.

A variety of flood-related geomorphic processes can directly hinder salmonid incubation and emergence from redds. Sediment fill (i.e., accreting sediment producing a net rise in bed level) over egg pockets during floods may be harmful to fry emergence, particularly if the accreting sediments have a high content of fine sediments. Conversely, substrate mobilization (i.e., scour) down to egg pocket depths can entrain and destroy embryos (DeVries 1997). Allen (1951) and Elwood and Waters (1969) highlighted the transient effects on salmonid communities of the destruction of incubating eggs by strong flood flows. Montgomery et al. (1999) hypothesized that interreach geomorphic contrasts in flood scour patterns constrain salmonid distributions through the requirement that egg burial depth must exceed typical scour depths in spawning beds. In particular, egg loss due to flood scour has also been thought to affect the relative distribution of spring- versus fall-spawning species, depending on the seasonal timing of high flows (Kondolf et al. 1991; Pearsons et al. 1992). Finally, the simple infiltration of fine sediments into egg pockets in fresh redds during high-flow events can also smother incubating embryos (Gibbons and Salo 1973). Lisle and Lewis (1992) presented a model predicting embryo losses due to this latter process. Their model is particularly useful in regions such as northern California where repeated, moderate-winter high flows, capable of mobilizing sands on the river bed, can occur during the period of incubation. The model did not, however, quantify the losses directly due to egg pocket scour during stronger floods, the focus of this paper. For Atlantic salmon (*Salmo salar*) populations in northeastern North America, which spawn mainly in fall and whose fry emerge in late spring, very low winter flows are typical of much of the egg incubation period. In such settings, disturbance to egg pockets during the dominant, gravel-mobilizing, late-winter or spring flood associated with snowmelt is a notable but poorly quantified cause of juvenile loss.

To begin understanding the complex role that floods play in structuring salmonid stream communities, ecologists need analytical methods developed by geomorphologists to model how severely physical disturbances affect stream habitats and organisms at various life stages using those habitats. This study proposes tools to quantify the flood damage to salmonid egg pockets. Based on observations on the Sainte-Marguerite River, Quebec, empirical models are presented that predict the intensity of scour and fill affecting spawning redds as a function of local stream characteristics and flood strength. An unusually broad range of flood intensities during the study period provided a unique opportunity to characterize a response curve for disturbance to spawning beds. Observed scour patterns were then compared with typical salmonid egg pocket depths (DeVries 1997) to estimate

probabilities of egg pocket losses due to various flood events.

Materials and methods

Study sites and flood events

The Sainte-Marguerite River drains a catchment of 2135 km² into the Saguenay Fjord, Quebec, Canada (Fig. 1). The river supports an Atlantic salmon sport fishery, which plays a prominent role in the local economy. Research was carried out along the upper section of the main branch of the Sainte-Marguerite River, an area draining a 285-km² subbasin. In several locations along this section of valley (Fig. 2), meanders were rectified over 35 years ago to facilitate highway construction. This reach displays a general downstream decrease in channel gradient and concomitant substrate sizes, a common pattern along gravel rivers. Atlantic salmon have been observed to spawn on riffles with gravel to cobble substrate at various points along the upper 8 km of the reach shown in Fig. 2.

Three flood events, covering a particularly wide range of magnitudes, occurred during the 1995–1997 study period. The May 1996 and May 1997 events, both generated by spring snowmelt, were moderate (recurrence period 8–10 years) and small (2–3 years) in magnitude, respectively. In contrast, the July 1996 event was a flood event of very large magnitude, the largest on record in the study basin, with a recurrence period measured in centuries. This high-intensity flooding occurred when an extreme frontal precipitation system stalled for 48 h over the entire Saguenay region (Lapointe et al. 1998). Although this July flood did not coincide with a period of salmonid egg incubation, it provided a unique opportunity to assess the level of physical disturbance to spawning habitat corresponding to a very large flood.

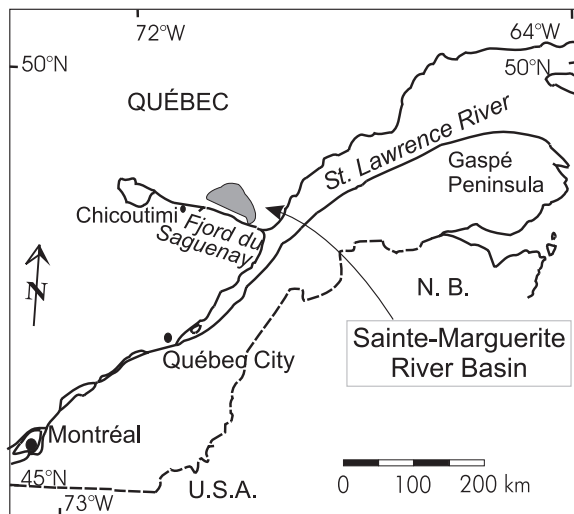
For each event, detailed patterns of flood disturbance to the spawning zones were studied in three reaches (Fig. 2). There are no significant tributaries in this section of valley, and the three study reaches share a common discharge regime. These study reaches were selected to represent a range of sedimentological, morphological, and channel slope characteristics (Table 1) typical of the spawning habitat in this section of valley. Within these three reaches, a total of seven separate riffle spawning zones were monitored in detail for flood disturbance. Two potential spawning zones were directly flanked by artificially stabilized banks.

Delimitation of potential spawning zones

Potential spawning zones were carefully identified before each flood event to focus on scour and fill patterns that could affect incubating embryos. The limits of these zones were defined based on generally accepted sedimentological, morphological, and hydraulic criteria for Atlantic salmon spawning habitat (Beland et al. 1982; Gibson 1993). Due to year-to-year variations in spawning pressure, the seven spawning zones monitored in this study were not used by spawners every year. Zone locations are consistent, however, with historical redd location patterns in this reach. Potential spawning zones were operationally defined here as the segments of the low-flow (summer-stage) channel extending one bankfull width upstream of each riffle crest (the latter defined as the local peak in bed elevation between pools) (Fig. 3). In the study reaches, mean flow depths at the lateral edges of these zones would generally be 15–25 cm in October, the usual spawning season. The upstream limit of each zone corresponds to sectors where depths increase rapidly upstream towards the preceding pool. Analysis showed that the statistics on bed disturbance probabilities presented below are not very sensitive to the precise lateral and upstream limits used to delimit potential spawning zones.

During high flows, stronger velocities tend to be concentrated towards the outside of a bend, due to the effects of channel sinuosity (Chang 1992), producing lateral gradients in flood shear

Fig. 1. Location map of the Sainte-Marguerite River study basin.



stresses and substrate size distributions at riffle cross sections (Payne and Lapointe 1997). To account for this spatial variation in geomorphic conditions, spawning zones were laterally broken down into three subzones (Fig. 3). The thalweg subzone was defined as a 3-m-wide swath centred on the thalweg within each spawning zone. High-velocity subzones (on the cutbank side with respect to the previous bend) and low-velocity subzones (on the point bar side of the previous bend) were identified on each side of the thalweg subzone.

Observations of scour and fill in potential spawning zones

A key parameter for modelling egg scour is the depth of egg pocket emplacement at redds. In a review of data on egg burial depths for various salmonids, DeVries (1997) proposed scour depth criteria corresponding to the typical levels of the top and the bottom of egg pockets. At Atlantic salmon redds, scour to a depth of 15 cm below the original bed level begins to affect the top of egg pockets, while 30 cm of scour would generally reach the base of egg pockets, causing total egg loss (DeVries 1997). For most other salmonid species, thresholds for the start of egg scour varied from 10 to 15 cm (top of egg pockets below the original bed level), while egg pocket bottom depths varied from 20 to 50 cm. Unfortunately, no study is available yielding precise criteria on thickness of fresh flood fill (i.e., net rise of bed level) over egg pockets leading to inhibition of fry emergence and entombment.

Initially, scour chains were emplaced at riffle sites during the 1995–1996 period. However, floods during the study period were powerful enough to produce easily surveyed net scour or fill with clear implications for egg pocket integrity. Scour chains were not employed after 1996. Between each flood, repeated high-resolution topographic surveys of the bed in the three study reaches were carried out under low-flow conditions. Topographic soundings were collected approximately every 3–4 m (i.e., 500–600 survey points in a 400 × 25 m wetted zone) using 5-mm-precision total station surveys. Analysis of replicate surveys showed that this technique yields digital elevation models with a mean vertical uncertainty of approximately 5 cm (due mainly to interpolation errors between sounding points). All surveys were precisely referenced to permanent benchmarks on the floodplain, allowing for an accurate assessment of net topographic changes caused by intervening flood events. Maps of the topographic changes (net scour and net fill) associated with each flood event were derived by subtracting the preevent topographic model from the postevent model. To the extent that observed net lowering (or raising) of the bed at spawning sites can destroy (or entomb) eggs, these net change maps yield

conservative or minimal estimates of embryo loss probabilities. The potential of additional egg losses due to deep scour followed by fill during a single event is addressed in the Discussion.

Predictors of substrate scour and fill depths

Bed scour depths have been empirically correlated with peak flood discharges and associated bed load transport rates in a number of studies (Carling 1987; Ziemer et al. 1991). However, scour depth (and egg pocket integrity) during floods cannot be accurately predicted solely from peak discharge values. The substrate scouring potential of a discharge level in a particular stream reach depends on a number of local geomorphic variables, such as channel cross-sectional geometry and slope, as well as sediment calibre (size) on spawning beds. Erman et al. (1988) argued, for example, that variations in the height of banks along Sagehen Creek (due to differential snow buildup in winter) produced, at the same flood discharges, downstream variations in the bed shear forces, bed scour, and salmonid egg loss. Fluvial geomorphologists model substrate transport intensity using measures such as bed mobility ratios or “Shield’s stresses” (Chang 1992; Montgomery et al. 1996). These parameters express the ratio of the hydraulic mobilizing forces of the flood at its peak (shear stresses, τ_o) to the mechanical forces resisting substrate entrainment (critical entrainment stresses, τ_c), which depend on substrate grain sizes.

The spatial distribution of peak shear stresses during a flood, locally over the various zones of the spawning riffle, is extremely difficult to measure or reconstruct. However, the average shear stress over a whole reach can be estimated from hydraulic principles (Chang 1992) using simple measures of the flood flow geometry, particularly the flow hydraulic radius (approximately mean flow depth) and energy slope (approximately water surface slope). Precise peak water surface levels for all three flood events were reconstructed using observations from maximum stage recorders installed at the upstream and downstream limits of each study reach. Flood flow geometry (cross-sectional depths, etc.) was derived by comparing the channel topographic model (excluding floodplain zones) with the elevation of the flood water surface. The average shear stress on the bed at flood peak ($\bar{\tau}_o$) is given by

$$(1) \quad \bar{\tau}_o = \rho g R S$$

where ρ is water density and g is acceleration due to gravity. The flood hydraulic radius (R) in each reach was averaged over several cross sections. The energy slope (S) was assumed equal to the water surface slope to a good approximation, since peak flow cross sections (and thus mean velocities) were very similar at the entrance and exit sections of each reach.

The nominal critical shear stress (τ_c) required to entrain the surface layer of substrate at riffles was estimated from riffle surface median diameter (D_{50}) using Shield’s law (Dingman 1984):

$$(2) \quad \tau_c / (\rho_S - \rho) g D_{50} = 0.06$$

which corresponds to the rough equivalence τ_c (pascals) = D_{50} (millimetres) for particles with the density of quartz ($\rho_S = 2.65$ times the density of water). The average riffle zone median grain size (D_{50}) in each reach was estimated from standard Wolman, or grid-by-number, samples (Church et al. 1987) measured on the high-velocity side of each riffle or at the adjacent point bar head (Fig. 3). Where riffle substrate could not be sampled accurately underwater, samples were taken at the head of the adjacent point bar, as close as possible to water’s edge and to the submerged riffle (a common practice in fluvial geomorphology). Such bar head samples taken at low stages generally reflect the coarsest mobile alluvium within a pool–riffle reach and have a median size comparable with that found on the adjacent high-velocity side of the submerged riffle. Finally, the reach-average mobility ratio was defined as

Fig. 2. Map and long profile of study reaches A, B, and C located in the upper section of the main branch of the Sainte-Marguerite River approximately 50 km from the mouth of the river in the Saguenay Fjord.

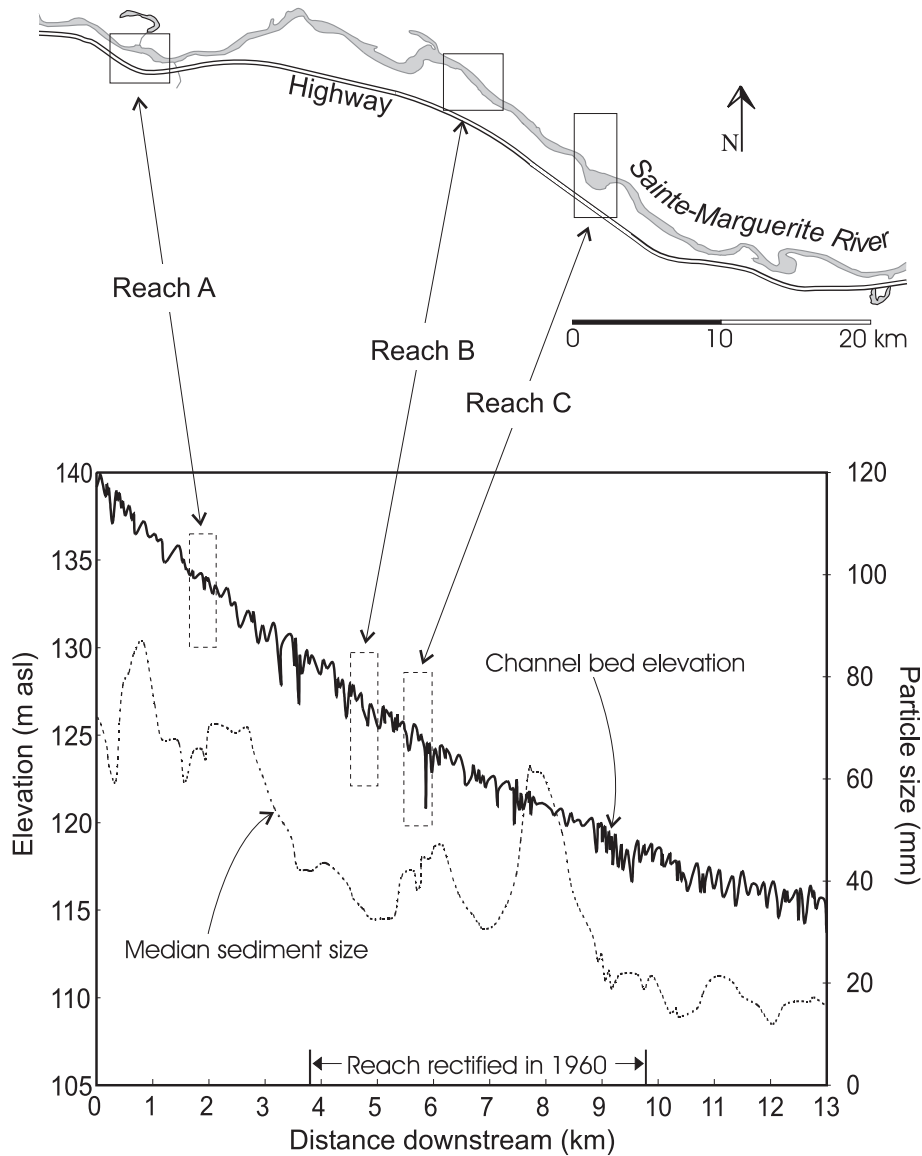


Table 1. Main geomorphological characteristics of the study reaches.

Study reach	Total length (m)	Bankfull width (m)	Bankfull water surface slope	Average D_{50} on bar heads (mm)
A	385	44	0.0033	42.5
B	335	38	0.0028	29
C	392	58	0.0026	45.5

Note: D_{50} refers to the median diameter of surface pavement particles.

(3) Mobility ratio = $\bar{\tau}_o / \bar{\tau}_c$

where $\bar{\tau}_o$ is the estimate of reach-average shear stresses and $\bar{\tau}_c$ applies to the reach-average riffle zone substrate (i.e., applying eq. 2 to the average D_{50} for all riffle zones in the reach).

For ease of estimation and application to other systems, the simple form of mobility index used here is based on reach-average

shear stresses (rather than difficult to estimate local stresses) and riffle zone mean substrate size (rather than the much harder to estimate reach-average substrate size). Because of variations in bed pavement structure, there is some uncertainty in the literature concerning the precise value of Shield's constant (0.06 in eq. 2 is the conventional value) that best describes the onset of sediment motion (Dingman 1984). The value selected under any given conditions will affect the computed τ_c and predicted local bed transport rates. However, given the uncertainty in the precise distribution of local shear stresses, and given the variation in substrate size among individual riffles in a reach, the computed reach-average mobility ratio (eq. 3) is not intended, nor is it designed, to produce meaningful estimates of local gravel transport rates. The mobility ratio is used here only as an empirical predictor, useful for explaining observed variations in levels of spawning bed disturbances across a range of reach characteristics and flood levels.

Results

The main hydraulic variables reconstructed for each flood

Fig. 3. Definition diagram illustrating the distinction between high- and low-velocity sides of the thalweg at riffles and potential spawning zones. See text for further explanation.

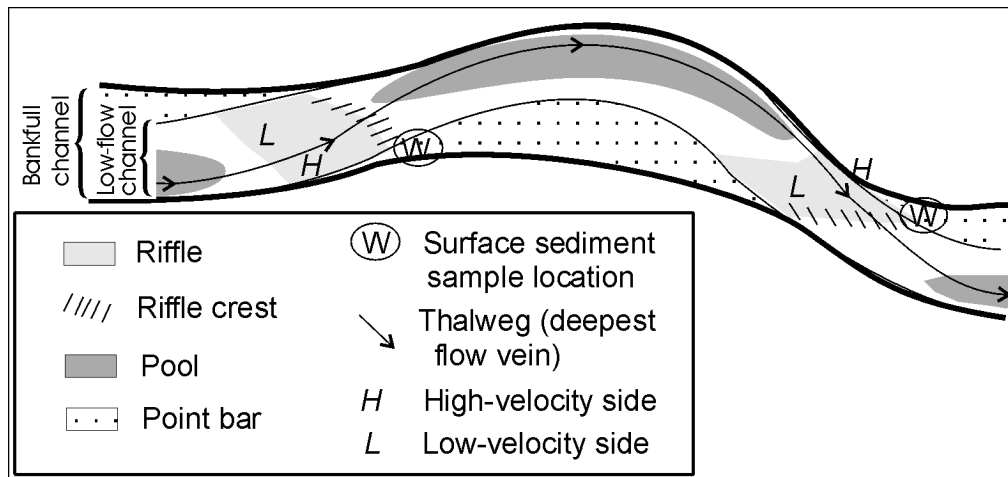


Table 2. Hydraulic and sediment transport characteristics of the study floods in each reach.

Flood event	Reach	Peak discharge ($\text{m}^3 \cdot \text{s}^{-1}$)	R (m)	$\bar{\omega}$ ($\text{W} \cdot \text{m}^{-2}$)	$\bar{\tau}_o$ (Pa)	$\bar{\tau}_c$ (Pa)	Mobility ratio
May 16, 1996	B	140	1.5	104	41	29.0	1.4
	C		1.5	61	38	45.5	0.8
July 20, 1996	B	250	2.0	178	54	29.0	1.9
	C		2.1	105	53	45.5	1.2
May 25, 1997	A	90	1.2	71	39	42.5	0.9
	B		1.4	54	38	29.0	1.3
	C		1.3	37	33	45.5	0.7

Note: $\bar{\omega}$ is the reach-average unit flow power (Dingman 1984). Other symbols are as described in Materials and methods.

in the three study reaches are presented for a total seven reach–flood combinations (Table 2). Reach A measurements were made only for the May 1997 flood. Mobility ratios vary by a factor of 2.7, from a minimum of 0.7 (May 1997 flood in reach C) to a maximum of 1.9 (July 1996 flood in reach B). Potential spawning zones and corresponding high-velocity, thalweg, and low-velocity subzones were delimited for each reach and flood event (e.g., Fig. 4). Reach A includes three distinct riffle zones, while reaches B and C each include two.

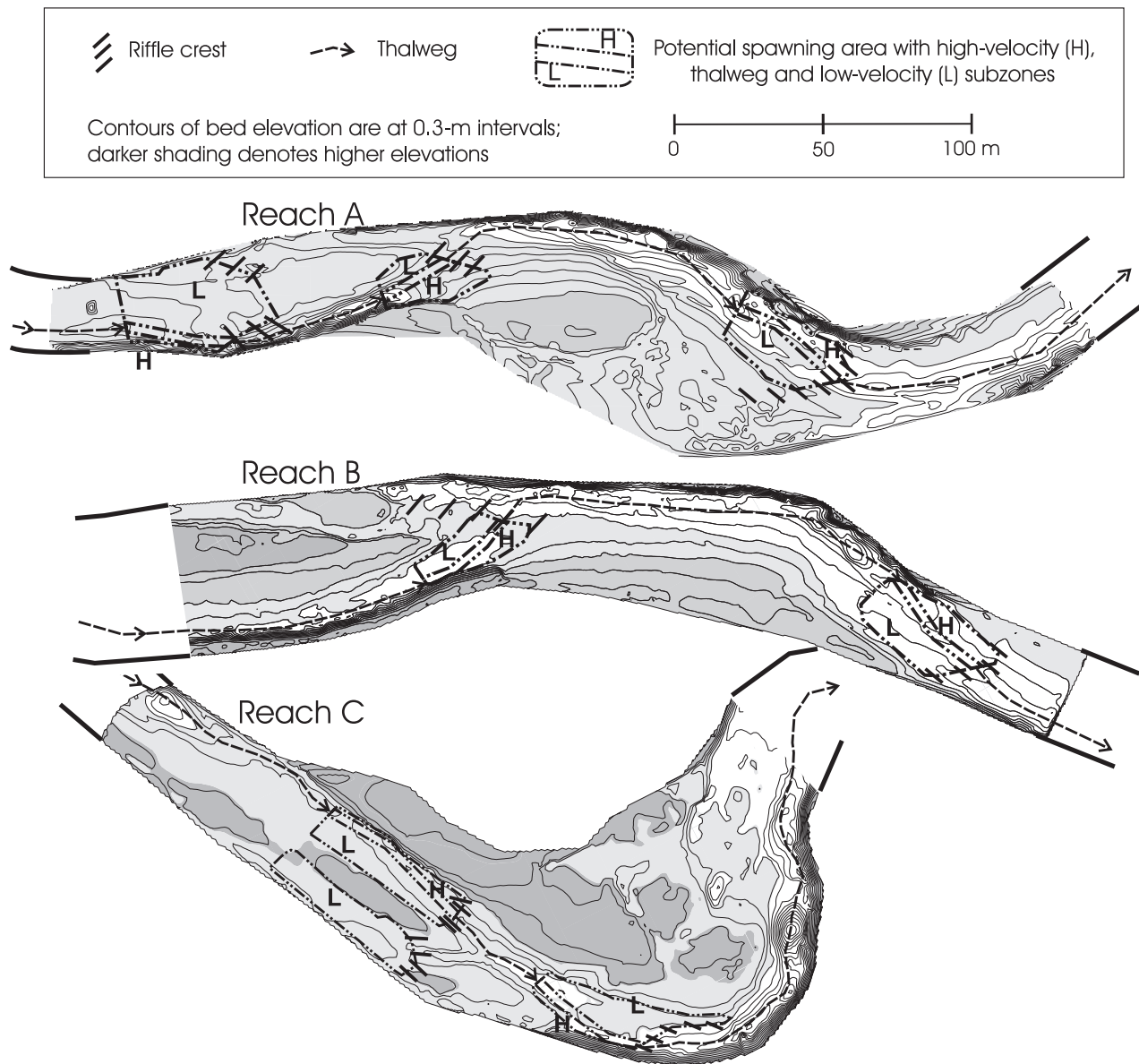
Important scour and fill disturbances were triggered in the study reaches and the corresponding spawning zones by each of the three study flood events (Fig. 5). Over large areas, vertical changes exceeded 0.4 m in amplitude. In the downstream half of reach B, the extreme July 1996 flood produced over 0.8 m of scour near the eroding left bank, extending to the head of the following point bar. Over 0.8 m of fill accompanied the advance of the right bank point bar in that zone.

The statistics on the distribution of scour and fill in the spawning zones and subzones are summarized for the three reaches and flood events (Table 3). During the extreme flood of July 1996, 43% of the entire potential spawning area of reach B underwent over 20 cm of net scour, with 78% of the high-velocity subzones similarly affected. Net fill greater than 20 cm, for the same event, affected 19% of the total spawning area in reach B and 36% of the low-velocity subzones. The 20- and 30-cm scour thresholds were chosen

conservatively, in light of the published egg scour criteria for Atlantic salmon (15 cm depth to top and 30 cm to bottom of egg pockets; DeVries 1997). These two thresholds thus correspond to different intensities of damage to existing egg pockets. Scour exceeding 20 cm would most likely lead to some egg loss at any Atlantic salmon redd site, while essentially complete egg loss would be expected where scour exceeds 30 cm. A symmetrical tabulation to that for scour was also done for fill using the same 20- and 30-cm thresholds (Table 3). However, until studies establish clear criteria for thickness of freshly accreted sediments (i.e., net fill) causing entombment, these results are merely descriptive and cannot be firmly tied to fry mortality. The probable implications of net accretion of more than 30 cm over redd sites will be considered further in the Discussion.

Given the interreach variability in slope, channel geometry, and substrate size, the estimated reach-scale mobility ratios, integrating information on these three types of factors, can be used as empirical predictors of the intensity of scour and fill disturbance for various flood events and reaches (Fig. 6). Regressions are given for the percentages of reach-aggregate spawning areas having undergone more than 20 and 30 cm of scour and fill plotted against mean event mobility ratio in each reach ($N = 7$, corresponding to each reach–event combination listed in Table 2). The plots display clearly that the higher the mobility ratio achieved by the peak flow, the more spatially extensive are the spawning areas deeply disturbed by either scour or fill (all regression

Fig. 4. Bed topography prior to the first study flood in the three study reaches. Potential spawning zones and corresponding hydraulic subzones for that period are shown.



slopes are significantly greater than zero at the $p = 0.05$ level). In the study reaches, the nominal mobility ratio explains between 31 and 58% of the variations in the relative extent of disturbed areas within the potential spawning habitat (i.e., combining all subzones).

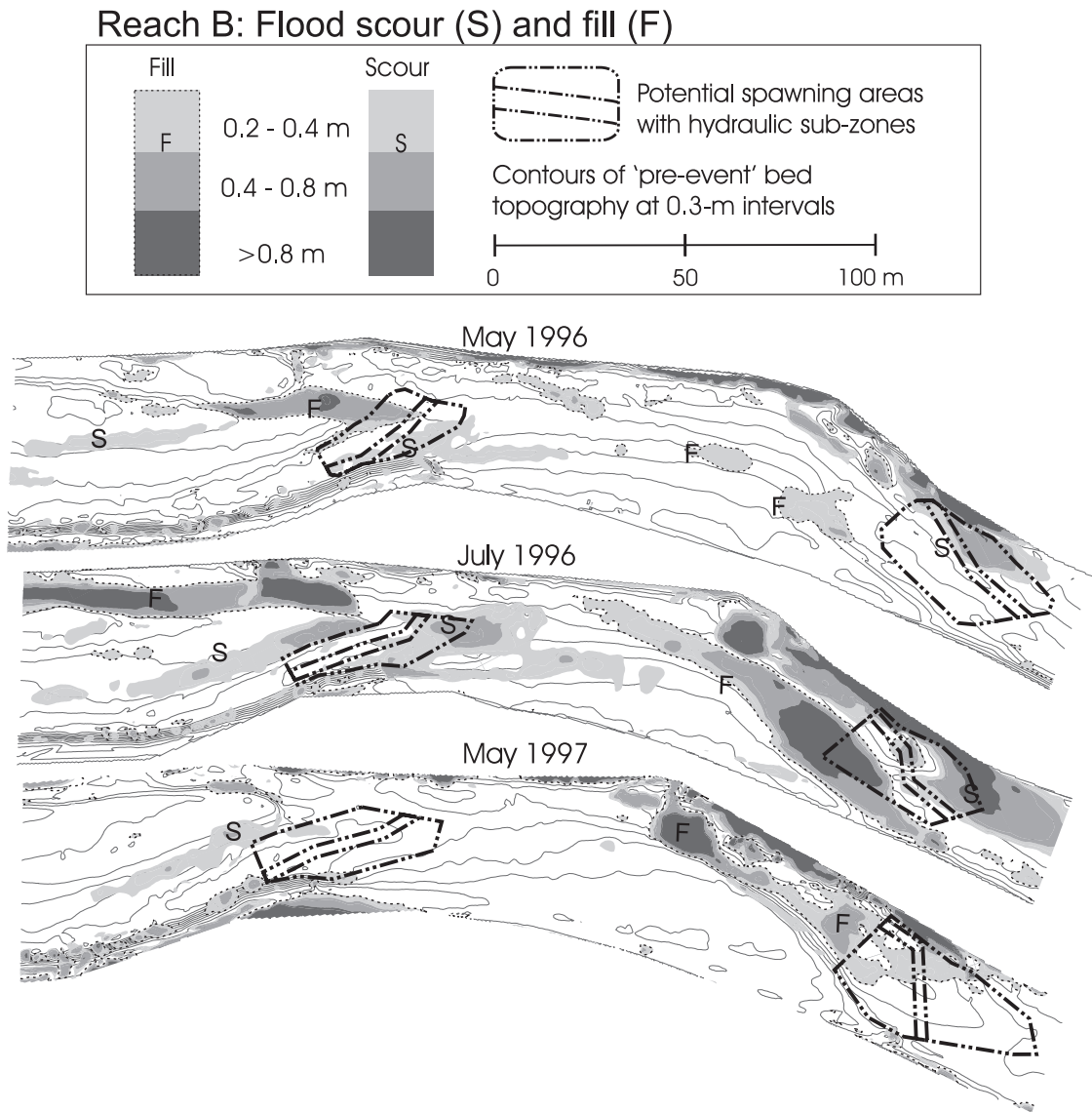
Analysis of the disturbance patterns for each hydraulic subzone separately (Fig. 7) discloses spatial differences among subzones (i.e., high velocity, thalweg, and low velocity) in the susceptibility to scour or fill, particularly for stronger flood events. The relationships for scour exceeding 20- and 30-cm thresholds (Fig. 7) reveal that the percentage of spawning areas undergoing significant scour increases with event mobility ratio in the high-velocity and thalweg subzones (although less rapidly in the latter). In the low-velocity subzones, however, the percent scoured areas (approximately 10%) is essentially invariant with flood mobility

ratio (Fig. 7c). The patterns for the spatial distribution of net fill (Fig. 7) are qualitatively the opposite of those just described for scour. The proportions of areas within the low-velocity subzones undergoing significant fill increase with mobility ratio (Fig. 7c), while in the thalweg and high-velocity zones, they are variable and relatively unresponsive to flood strength. The mobility ratio explains around 75% of the variation in areal extent of scour within high-velocity subzones (Fig. 7a) and 75–79% of the areal extent of fill within low-velocity subzones (Fig. 7c).

Discussion

The residual scatter observed about the regression models is to be expected, given the simplified nature of the reach-average mobility ratio as a predictor of riffle surface distur-

Fig. 5. Maps of net changes to the channel bed (scour or fill) in reach B caused by each of the three flood events. Note that because of the ongoing bed change, the limits of the potential spawning zones were redefined prior to each flood using the criteria described in the text (see Materials and methods).



bance. This scatter mostly reflects the considerable variability of local geomorphic conditions over riffles of various shapes within a natural reach. The overall trends are relatively clear, however, linking mobility ratio to average percentage of spawning area undergoing significant scour or fill.

It is important to recall that the mobility ratio calculated here does not represent a ratio of shear stress at one riffle to the threshold for the entrainment of the bed material at the same location. Instead, a much more easily estimated ratio was employed, relating reach-average shear stress to the nominal stress level necessary to mobilize the average material located on riffles (or point bar heads) within the reach. Therefore, scour that was observed in riffle zones at mobility ratios as low as 0.7–0.8 in our data set reflected that, during floods, shear stresses systematically greater than reach-averaged values tend to affect high-velocity sides of riffles and nearby point bar heads (Yen 1970).

Andrews (1984), Ferguson and Ashworth (1991), and

Milhous (1998) use reach-averaged mobility indices (or related Shield's stress ratios), conceptually similar to the one used here, to compare average sediment mobilization conditions among river reaches. Such reach-scale mobility ratios, although crude, provide a simple method of scaling flow strength by bed material calibre for interreach and interevent comparison. Development of more precise riffle-specific mobilization ratios based on two- or three-dimensional numerical resolutions of local stress distributions may eventually improve predictions of spawning bed evolution, but at a substantial cost in analytical complexity.

Interpreting scour and fill patterns in terms of egg loss probabilities

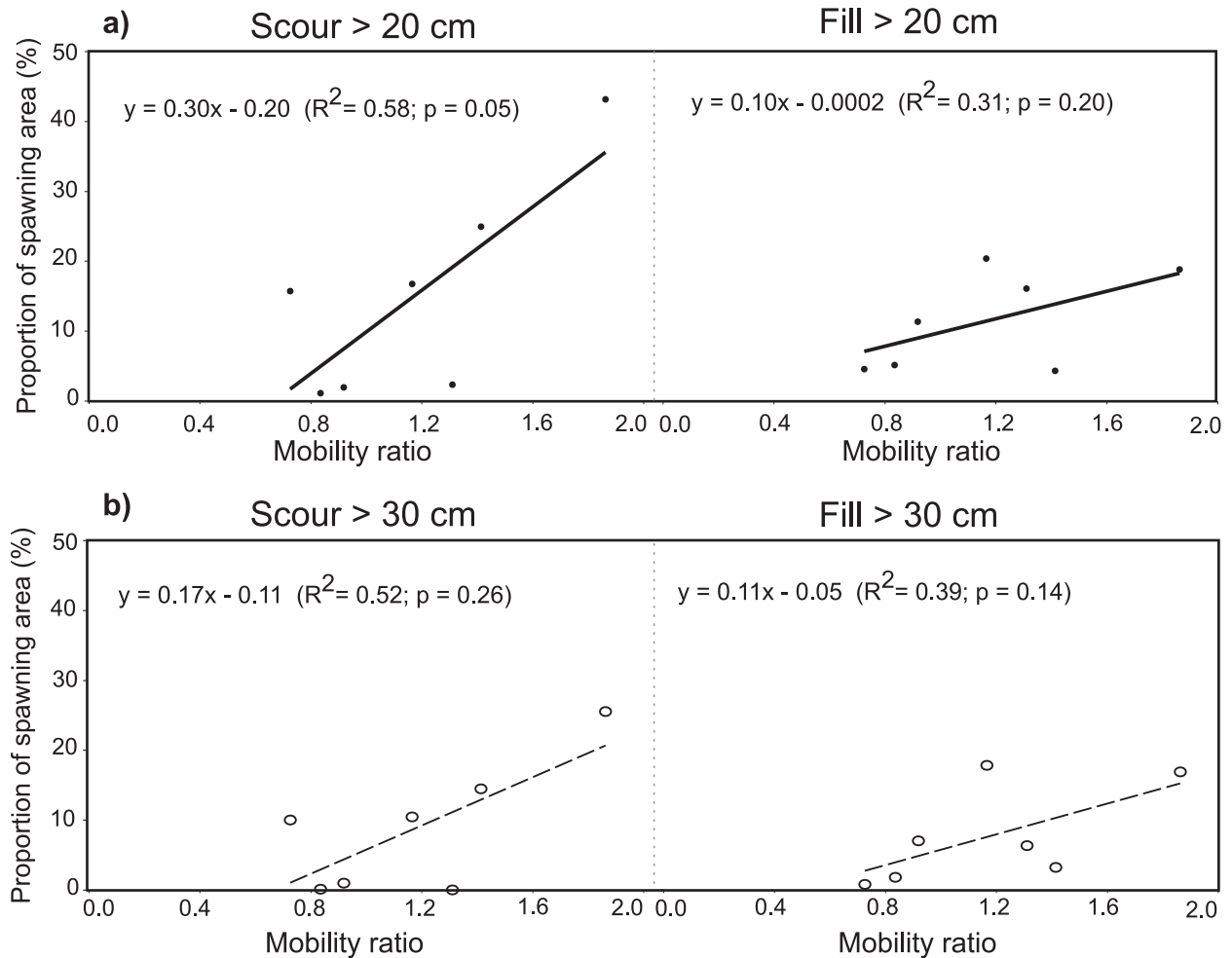
Observed scour patterns can further be interpreted in terms of probabilities of erosion of egg pockets for a flood of a given magnitude occurring during the egg incubation period. In light of the egg pocket scour criteria of DeVries

Table 3. Spawning zone disturbance statistics.

Reach	Event	Percentage of high-velocity subzone		Percentage of thalweg subzone		Percentage of low-velocity subzone		Percentage of total spawning area	
		S	F	S	F	S	F	S	F
A	May 1997	7 (5)	16 (14)	2 (0)	25 (12)	0 (0)	7 (4)	2 (1)	11 (7)
B	May 1996	57 (37)	0 (0)	32 (20)	0 (0)	6 (1)	8 (6)	25 (14)	4 (3)
	July 1996	78 (56)	6 (4)	37 (10)	10 (8)	12 (2)	36 (33)	43 (26)	19 (17)
C	May 1997	0 (0)	13 (5)	0 (0)	11 (6)	6 (0)	21 (8)	2 (0)	16 (6)
	May 1996	8 (1)	2 (0)	1 (0)	9 (5)	0 (0)	5 (2)	1 (0)	5 (2)
	July 1996	29 (26)	53 (48)	13 (8)	53 (47)	16 (9)	11 (9)	17 (10)	20 (18)
	May 1997	1 (0)	5 (3)	0 (0)	3 (1)	24 (15)	5 (0)	16 (10)	5 (1)

Note: Given are the percentages of the total area of spawning zones within each reach that underwent scour (S) or fill (F) exceeding significant thresholds during each flood event. Values are for scour or fill beyond the 20-cm threshold followed by values corresponding to the 30-cm threshold in parentheses.

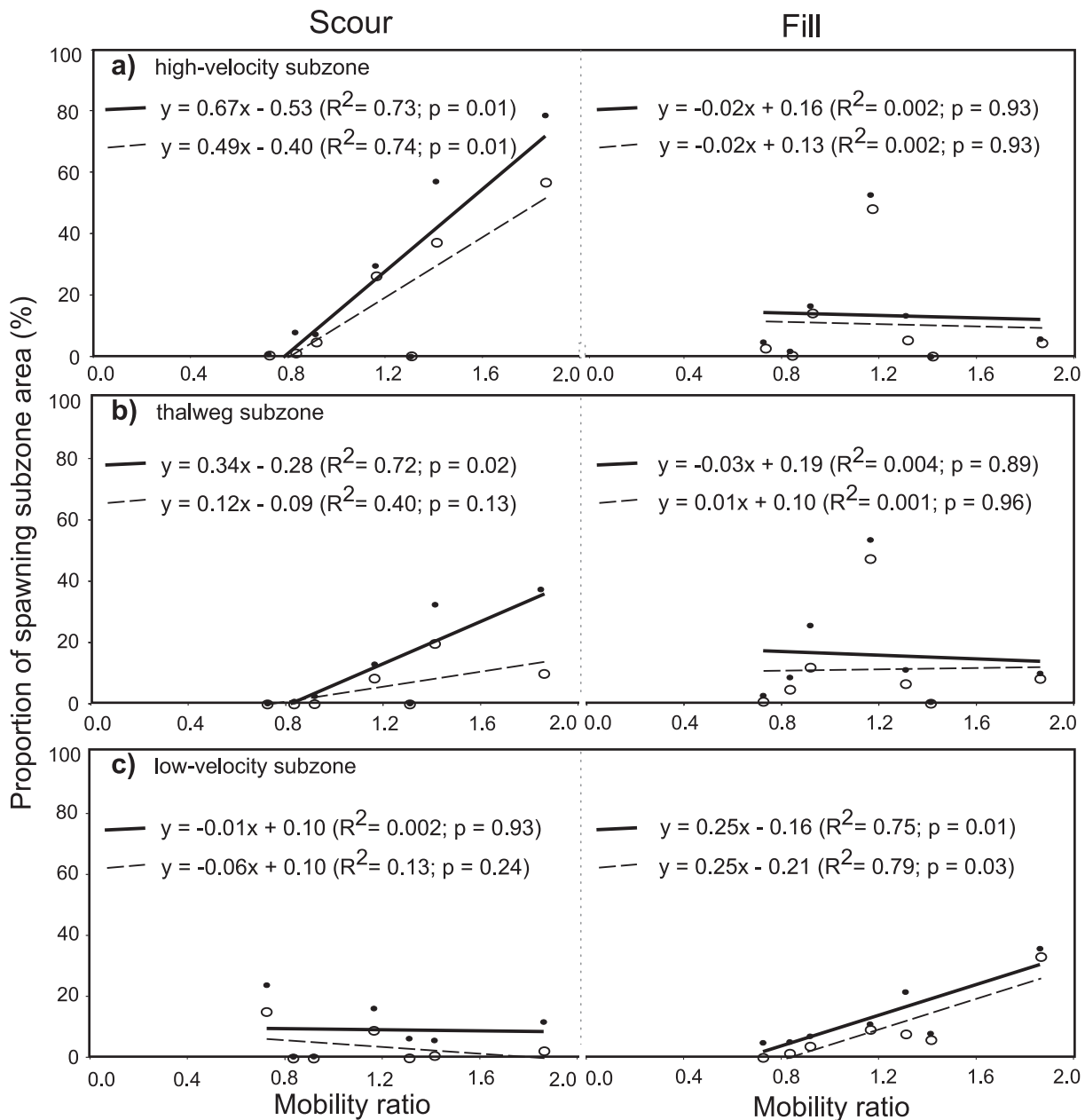
Fig. 6. Regressions of the proportion of the total spawning areas within each reach that was affected (a) by over 20 cm or (b) by over 30 cm of net scour or net fill against the mobility ratio achieved by the flood in the reach; *p* values for the slope terms are given.



(1997), the areal percentages of spawning zones with scour greater than the two thresholds can be interpreted as the probability of partial (scour >20 cm) or total destruction (scour >30 cm) of Atlantic salmon egg pockets, assuming that the pockets are uniformly distributed in the spawning zones of the reach. The trends for scour exceeding 30 cm imply that, during the weakest flood events recorded (mobility ratio = 0.7–0.8), egg pockets randomly distributed in the

spawning zones had approximately a 2–3% probability of being totally eroded. For an extreme flood (e.g., mobility ratio = 1.8) occurring while eggs are incubating, the probability of total egg pocket destruction rises to around 20%, although pockets situated in high-velocity subzones would have a better than even (i.e., >50%) chance of being eroded in such strong events. The effects on Atlantic salmon reproduction of flood fill deposits exceeding 20 or 30 cm over

Fig. 7. Regressions of the proportions of (a) high-velocity, (b) thalweg, and (c) low-velocity spawning area subzones that were affected by net scour or net fill over the 20- and 30-cm thresholds against the mobility ratio achieved by the flood in the reach. The solid circles and solid regression lines are for the 20-cm threshold, and the open circles and broken lines are for the 30-cm threshold; p values for the slope terms are given.



redds are less clear. Precise criteria based on thickness and sediment texture of flood accumulations will need to be developed and tested before our predictions of the extent of spawning zones with over 20 and 30 cm of fill can be interpreted explicitly in terms of probabilities of embryo mortality. However, the common occurrence of a high sand matrix content in flood fills over 30 cm thick, within low-velocity subzones in the study reaches, suggests a real potential for entombment of incubating embryos.

Potential egg scour in the absence of net bed lowering

In certain situations, egg scour might occur during floods in the absence of net bed lowering. During a single flood

event, scour greater than 20–30 cm over a given redd could potentially be followed immediately by comparable fill. As well, egg pocket scour could theoretically ensue simply from deep gravel mobilization over a redd site in association with very intense transport, the bed level remaining essentially constant throughout. In theory, both of these processes could lead to the scouring of egg pockets that would not be detected by our field surveys of net change.

Hydraulic principles and published scour chain surveys suggest, however, that alternating sequences of scour and fill during a single flood wave occur mostly at pool cross sections or at constricted cross sections that are narrower than the reach average and are less common at riffle sites. Fur-

thermore, the detailed analysis of all flood change maps in this study (e.g., Fig. 5) indicated that the nature of bed change (either net scour or net fill) at any point on the riffle was generally predictable from the lateral position of the point, the antecedent channel shape, and the volume of gravel produced upstream by an eroding bank. These patterns suggest that, at least in moderate-energy and -sinuosity streams such as the one in this study, flood-induced disturbance over individual egg pockets will consist predominantly of either scour or fill, depending on lateral position. In very high intensity transport systems (e.g., braided rivers) or during protracted flood events, the occurrence of alternating scour/fill at a given point on a riffle during a single flood may, however, be more common.

Diverse lines of evidence also suggest that the thickness of the layer of gravel in motion at any instant during high flow is less than the depth at which egg pockets of many salmonid species are buried. A range of gravel transport studies (Carling 1987; Wilcock et al. 1996) indicate that the mean thickness of the mobilized gravel layer is in the order of the diameter of the coarsest particles common in the surface substrate (approximated by the D_{84} or D_{90} diameters in the mix), with a maximum thickness of mobilized gravels at any given time that may approach twice the local D_{90} . Many large salmonids appear to excavate redds below this one- to two-particle-deep surface layer. After comparing scour chain and egg pocket depth data at chum salmon (*Onchorhynchus keta*) spawning sites in Washington and Alaska, Montgomery et al. (1996) concluded that the top of egg pockets systematically lay below the surface traction layer of flood-entrained gravel. At Atlantic salmon redds, median sub-armour particle diameter is often in the range of 1.5–3.0 cm, and the D_{90} at the redd surface rarely exceeds 7–8 cm (Peterson 1978; Kondolf and Wolman 1993). Thus, the maximum thickness of entrained bedload layers at high flow may in general be less than 15 cm, the typical depth corresponding to the top of egg pockets (DeVries 1997), implying that egg pocket scour is unlikely in the absence of bed lowering. This evidence suggests that our surveys of net change captured the dominant mode of egg pocket scour in the study reaches. We believe that the egg scour probability estimates presented above, although they may be conservative, are generally realistic for moderate-energy and -sinuosity streams comparable with the study system.

Redd location and spawner fitness: implications

The evidence presented, showing a systematic contrast in susceptibility to scour between high- and low-velocity sides of spawning zones, raises interesting questions concerning evolutionary pressures towards selection by salmonids of precise redd location at riffle sites. During the strongest floods, probabilities of significant scour are much greater in high-velocity subzones (over 50%), where flood shear stresses are particularly strong, compared with spawning sites on the low-velocity side of the riffles (probabilities under 10%). Our data thus indicate that there is a greater risk of loss of progeny if adults spawn on the high-velocity side of the thalweg, should a strong flood occur during the incubation period. Conversely, spawning on the low-velocity side may lead to higher probabilities of entombment due to fill during large floods. Moreover, gravel substrate on the low-

velocity side of riffles often has significantly higher sand content (Payne and Lapointe 1997) due to somewhat weaker flood shear stresses and a helical circulation pattern that accumulates a finer sediment mix on this side of the riffle, closer to the downstream end of the previous point bar. Thus, irrespective of the heightened risk of postflood entombment, sedimentary cues might induce females to avoid spawning in these low-velocity subzones. One can hypothesize that, at least for the kind of simple riffle geometries illustrated in Fig. 3, observed gradients in flood disturbance probabilities across spawning zones and their implications for fitness may entail a selection for spawning behaviour in the deeper thalweg subzone at riffle sites.

In conclusion, fisheries biologists are aware of the possible adverse effects of strong floods on incubating salmonid embryos. The challenge for resource managers, however, is to quantify, even approximately, the effect on subsequent fry emergence of a strong flood in a given spawning reach or to identify stream reaches that are, due to their geomorphic characteristics, more susceptible to geomorphic disturbance and salmonid egg scour. The models presented provide a simple tool for predicting the average degree of riffle substrate disturbance and potential egg loss associated with a flood event in a given reach. The validity of the empirical relationships fitted to the Sainte-Marguerite River should, however, be further tested in gravel bed rivers of very different size and sedimentology. In particular, these empirical models are unlikely to apply to very small boulder-rich streams, where flood shear stresses are largely dissipated on well-anchored boulder structures that shelter pocket-sized gravel-cobble spawning beds from the full force of the flood.

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Assessing Physical Quality of Spawning Habitat

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Introduction

Human activity often degrades natural spawning habitat, so there is a frequent need to assess the quality of spawning gravels and determine whether gravel quality limits spawning success. Degradation of spawning gravels is recognized as a primary contributing factor in the widespread decline of salmon and trout populations throughout North America and Europe. The bed material may be too coarse for spawning fish to move, a problem common where dams eliminate the supply of smaller, mobile gravels (e.g., Parfitt and Buer 1980; Buer et al. 1981). Excessive levels of interstitial fine sediment may clog spawning gravels, an effect that has been documented downstream of several types of land use that increase sediment yields, such as timber harvest, road construction, and agriculture (Cederholm and Salo 1979; Everest et al. 1987; Meehan 1991; Theurer et al. 1998; Sear et al. 2008, this volume).

If salmonids spawn successfully in a gravel (i.e., if they dig a pit, deposit, and bury eggs; the eggs incubate and hatch; and the alevins develop and emerge), then we might assume that the hyporheic habitat in the gravel is suit-

able for spawning. However, a deeper analysis of the problem should also consider the quality of the subsurface or hyporheic habitat and the fitness and viability of emerging alevins or fry and include biological factors in the evaluation of spawning habitat.

Habitat assessment is difficult because we must often judge whether gravels in a given reach of river are suitable for spawning without the presence of salmon to provide a direct demonstration of the gravel's qualities. For example, the San Joaquin River in California once supported about a half million spring-run Chinook salmon *Oncorhynchus tshawytscha*. Since construction of Friant Dam and agricultural diversions in the 1940s, the river now dries up in the downstream reaches, and the once abundant run is extinct. The operators of the reservoir were sued under Section 5937 of the California Fish and Game Code, which holds that operators of dams and diversions must release flows sufficient to maintain fish downstream in good condition. As part of the legal proceeding in this case, expert witnesses for the defendants (the dam operators) insisted that historical gravel mining and other activities had so degraded gravel quality and abundance that the available

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gravels would no longer support a viable population of salmon (Hanson 2005), while other experts stated that the gravels were of sufficient quality and extent to support spawning (Kondolf 2005; Moyle 2005). In a situation such as this, the suitability of the riverine gravel resources to support spawning can only be assessed in terms of the gravel properties; similar assessments are common in other situations as well. In this chapter, we summarize the habitat requirements of salmonids during the life stages that depend on the intragravel or hyporheic habitat: redd construction and spawning, incubation, and emergence. We then consider how to assess fry viability, hyporheic conditions, and sediment size distributions.

incubation, and emergence (Figure 1). The spawning female must be able to move gravels to excavate a depression in the bed to create the redd. Fish need not move all rocks present (some larger particles can remain unmoved as a lag deposit), but most of the particles present must be movable or the redd cannot be excavated. Larger fish are capable of moving larger rocks, so the upper size limit for suitable gravel varies with fish size (Figure 2; Kondolf and Wolman 1993). Incubating eggs and alevins must obtain oxygen from hyporheic water and dispose of metabolic wastes in the gravel, which requires that hyporheic water in the redd be renewed by subsurface flow (see Malcolm et al. 2008 and Gibbins et al. 2008, both this volume). Alevins must also be able to squirm through the gravel to reach the surface stream. Fine sediments that block pores between gravel clasts may block hyporheic flow or emerging alevins, rendering gravel unsuitable for salmonid reproduction.

Physical Conditions that Affect Spawning, Incubation, and Emergence

The spawning gravel requirements of salmonids differ during redd construction,

Dye studies in the field and laboratory

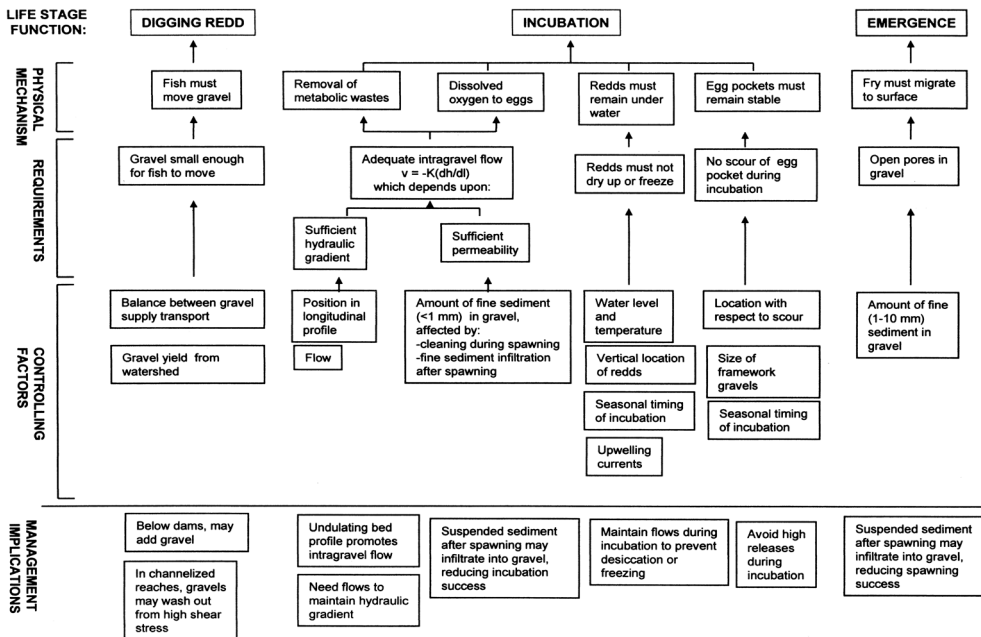


Figure 1. Flow chart showing gravel requirements of salmonids during redd construction, incubation, and emergence. The intergravel flow equation is defined in Figure 3.

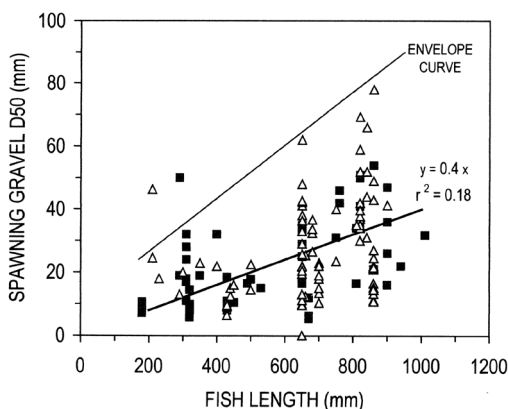


Figure 2. Median diameter (D_{50}) of spawning gravel plotted against body length of a spawning salmonid. Solid squares denote samples from redds; open triangles are unspawned gravels, which are potential spawning gravels sampled from the undisturbed bed near redds. (Modified from Kondolf and Wolman 1993.)

have confirmed that irregularities in the bed profile tend to promote exchanges of water between the stream and the interstices of the gravel bed (Cooper 1965; Vaux 1968). These patterns can be explained by a fundamental equation of groundwater flow, Darcy's Law, which states that the rate of groundwater flow (or Darcy velocity, V) is the product of the permeability (or hydraulic conductivity, K) and the hydraulic gradient dh/dl (Figure 3; Freeze and Cherry 1979). The lower elevation of the water surface in the riffle creates a hydraulic gradient that induces downwelling at the tail of the pool. The redd mound (or tailspill) produces a similar effect at a smaller scale, inducing inflow of stream water into the mound.

Fry as Assessment Tools

Concern about gravel quality is usually based on concern about the well-being of salmonid embryos and alevins, and there is a long tradition of assessing gravel by planting eggs in artificial redds (e.g., Gustafson-Marjanen and Moring 1984; Meyer et al. 2005) or incubators (e.g., Vibert 1949; Scrivener 1988; Rubin 1995; Bernier-Bourgault et al. 2005) or by putting caps over natural redds to capture emerging fry (e.g., Phillips

and Koski 1969). Incubators are permeable containers containing fertilized eggs and perhaps gravel or artificial substrate that are buried in the gravel. The number of reported designs for incubators suggests that none are optimal in all circumstances, so a design should be selected based on the site and purpose of the experiment. Considerations include the expected hydraulic conditions at the site, potential intrusion of fine sediments, whether samples will be recovered repeatedly or only once, and the purpose of the study; a project that is designed to assess hyporheic conditions will have different requirements for study design than a comparison of the performance of eggs from different strains of fish in seminatural conditions. Incubators offer greater experimental control than artificial redds but probably do not represent conditions in natural redds as well as artificial redds do. Redd caps can be used on natural or artificial redds but may collect sediment (e.g., Meyer et al. 2005) or otherwise alter conditions in the redd, and the caps may not capture all emerging fry (Rubin 1995). Excavating natural redds is also an option (e.g., Briggs 1953), but the number of eggs deposited will not be known.

Studies of eggs in gravel typically estimate percent survival to emergence, which

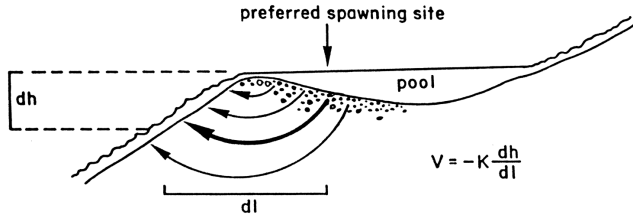


Figure 3. Diagram of groundwater flow through the tail of a pool. The lower elevation of the water surface in the riffle creates a hydraulic gradient that induces downwelling at the tail of the pool; V is Darcy velocity, and K is hydraulic conductivity. Vertical scale is greatly exaggerated. (From Kondolf 2000.)

has several drawbacks as a metric. First, marginal hyporheic conditions may allow for survival to emergence, but with reduced probability of survival to maturity due to poor circulation (Silver et al. 1963; Chapman 1988). Second, measuring percent survival to emergence requires that the initial number eggs be known and that all emerging fry be captured, which imposes methodological constraints that may compromise the objective of the assessment (Rubin 1995). Third, the viability of eggs is variable among females (Young et al. 1990), although this can be accounted for by growing eggs under controlled conditions. These problems might be reduced if measures of growth and condition were used as indices instead, or in addition to, survival to emergence. Such individual-based metrics have proven more informative than attributes of populations or physical habitat in monitoring programs in other situations (Osenberg et al. 1994). In this section, we offer suggestions for using the growth and condition of alevins or fry as indices of gravel quality. These are ideas for development, rather than established methods for immediate implementation.

Alevins and Fry as Indices of Gravel Condition

As alternatives to percent survival to emergence, it should be possible to develop useful indices of gravel quality from measures of the growth and condition of alevins, if these are compared to reference standards. The standards could come either from em-

bryos or alevins incubated in controlled conditions, or from models, and the indices could be simple or complex.

Length and weight or relative weight (Sutton et al. 2000) are simple indices of condition. More informative indices could be developed from analyses of variable body constituents of alevins. For example, the nonpolar lipid content varied from ~0% to 15% for newly emerged Chinook salmon (<37 mm standard length) in the American River, California (Castleberry et al. 1993). It seems likely that fry with higher levels of energy stored as lipids are more likely to survive. Other measures of energy stores such as triacylglycerol normalized to cholesterol have been used on juvenile Chinook salmon (e.g., MacFarlane and Norton 2002) and could be used on alevins as well. Simple performance measures, such as testing whether alevins can orient themselves in a slight current (Merz et al. 2004), are also indices of condition. At a more esoteric level, poor hyporheic conditions produce various adaptive responses in embryonic or larval salmonids (Bams 1969), and if genes that are activated by environmental stress in embryos or alevins can be identified, then hyporheic conditions might be assayed by using tissue samples and gene microarrays. Gene microarray technology is already in use with salmonids in GRASP, the Genomic Research with Atlantic Salmon Project, and has been applied to genes involved with the maturation of eggs in rainbow trout *O. mykiss* (von Schalburg et al. 2004).

The results of growth models for brown

trout *Salmo trutta* at full ration (Elliott 1975; Elliott et al. 1995) that account for temperature have been used as reference standards for evaluating observed rates of growth in streams (Nicola and Almodóvar 2004). In a similar way, the results of growth models for embryos and alevins in good hyporheic conditions might be used as reference standards for embryos or alevins sampled from natural or artificial redds, or for emerging fry. A model by Beer and Anderson (1997), available online at www.cbr.washington.edu/egg_growth, seems suitable for the purpose, although various factors such as temperature would need to be measured or estimated to apply the model to a particular site. Because of the strong effects of egg size on the growth of embryos and alevins (Rombough 1988; Beacham and Murray 1993), this would also need to be estimated. The mean temperature of hyporheic water generally will not vary too much from the temperature of the surface stream, but it is also possible to measure temperature in the redd or incubator directly. Measurements of dissolved oxygen and other aspects of water quality would be desirable but not necessary (micropiezometers, discussed below, are suitable for obtaining samples of water from redds or incubators). Fortunately, the eggs of individual female salmonids normally vary little in size (Rombough 1985), so that egg size can be estimated from a sample. This is easy to do if eggs are placed in incubators or artificial redds. Even if natural redds are studied, it may be possible to capture the breeding pairs on the redds as they are being constructed, using gear such as drop nets, so that samples of eggs can be obtained and fertilized for measurement and rearing in controlled conditions.

Finally, the emergence of alevins before they are buttoned up apparently represents a response to poor hyporheic conditions (Bams 1969). If so, then the frequency of sac fry in samples collected in seines or rotary screw traps in the surface stream could also be useful as an index of the condition of hyporheic habitat.

Assessing Intragravel Dissolved Oxygen, Permeability, and Intergravel Flow

Measurements of physical and geochemical conditions in stream gravel are rapid and inexpensive and may quickly identify limiting factors that prevent successful spawning or have detrimental effects on early life stage development. Measurements that are routinely used to characterize spawning gravel quality include hyporheic dissolved oxygen content, gravel permeability, and intergravel flow. These variables should be included in spawning gravel studies, but it is important to understand the constraints and limitations of each physical or geochemical measurement and minimize error or ambiguity during field studies.

Dissolved Oxygen

Dissolved oxygen measurements are an important part of many gravel assessment studies, and previous work has documented the harmful effects of low dissolved oxygen concentrations in spawning gravels (Sowden and Power 1985; Einum et al. 2002; Malcolm et al. 2003b; Greig et al. 2007). Dissolved oxygen is one of the more difficult parameters to measure in the field. Pore water samples should be collected from a depth in the gravel that is similar to the depth of the egg pockets or from the actual egg pockets, and there are several opportunities for contamination or equipment problems during this process.

Field meters need regular maintenance that can affect the accuracy of dissolved oxygen measurements. Dissolved oxygen is related to temperature, pressure, and salinity, so each of these values must be included in the daily calibration process. Most dissolved oxygen meters also need new fluid and probe tip membranes on a daily or weekly schedule to obtain accurate measurements. Newer optical methods are just emerging on the consumer market as this article is written (Malcolm et al. 2006), and they may someday replace the current style of field meters that use electrodes. Until that time, field meters

should be serviced frequently and calibrated carefully to obtain accurate readings.

Electrode-based dissolved oxygen meters also need a minimum flow past the probe tip; without this minimum flow, the instrument will underreport dissolved oxygen values (Weight and Sonderegger 2001). Because of this issue, the most common field meters do not give accurate readings if they are lowered into a standpipe or piezometer because the water in the standpipe does not have sufficient flow velocity past the probe tip. The solution to this problem is to induce a flow past the probe tip. Stirring in the piezometer adds oxygen from the surface, so the only viable option is to pump the sample to the surface. Contamination becomes a serious issue during this process.

Contamination usually increases the dissolved oxygen reading of subsurface samples, and this equilibration happens relatively quickly. Subsurface samples should not be exposed to surface conditions or atmospheric oxygen before dissolved oxygen is measured. Because of these problems, samples should not be placed in an open container, poured between containers, or allowed to stand for extended periods of time.

Several sampling strategies can minimize contamination by atmospheric oxygen. Dissolved oxygen should be measured in situ or immediately after samples are collected in the field whenever possible. Samples that are transported to the laboratory for analysis should be analyzed the same day. If a portable field meter is used, exposure to the atmosphere can be eliminated using a closed flow-through sampling chamber and portable pump or hand pump (Koterba et al. 1995; Radtke et al. 1998). This approach avoids the issues of atmospheric contamination and maintains the appropriate flow past the probe tip. The Winkler titration method and various photometric methods of analysis use chemicals that fix the dissolved oxygen content and minimize some of the problems mentioned with field meters, but there is still a chance of contamination when sample vials are open to the atmosphere or analysis is delayed during transport to a laboratory.

The U.S. Geological Survey Water Resources Division does not recommend iodometric (Winkler) titrations because of the variability introduced by individual operators (Radtke et al. 1998).

Gravel Permeability

Laboratory and field studies have established that higher permeability results in increased embryo survival and fitness in the early life stages, while low permeability is harmful. Much of this focus on permeability is related to the secondary effect of oxygen delivery to the redd environment, which is most critical just before the eggs hatch (Rombough 1988; Greig et al. 2008, this volume). When permeability is high, natural hydrodynamic processes force oxygenated surface water into the hyporheic zone because of a pressure differential, as shown in Figure 3.

Several approaches have been used to characterize the permeability of spawning gravels. Early work by Pollard (1955) and Terhune (1958) used dye dilution methods to measure intergravel flow in a specially constructed standpipe. Barnard and McBain (1994) used an identical standpipe but introduced a portable backpack pump and constant drawdown method to measure flow into the standpipe. Slug tests are another method of measuring sediment permeability in a well, standpipe, or piezometer. Slug tests are commonly used by hydrologists and use a physical object (the slug) to displace a volume of water in a well or standpipe. Permeability of the sediment is related to the response curve as water returns to its static level (Bouwer and Rice 1976; Springer et al. 1999).

These methods of measuring gravel permeability have several limitations when used for spawning site assessment. A fundamental problem is leakage along the sides of the standpipe (Figure 4). Standpipes used for spawning gravel assessment are usually pounded into the gravel without any surface seal, and water penetrates down the sides of the standpipe during the tests. Hydrogeologists call this phenomena "piping," and

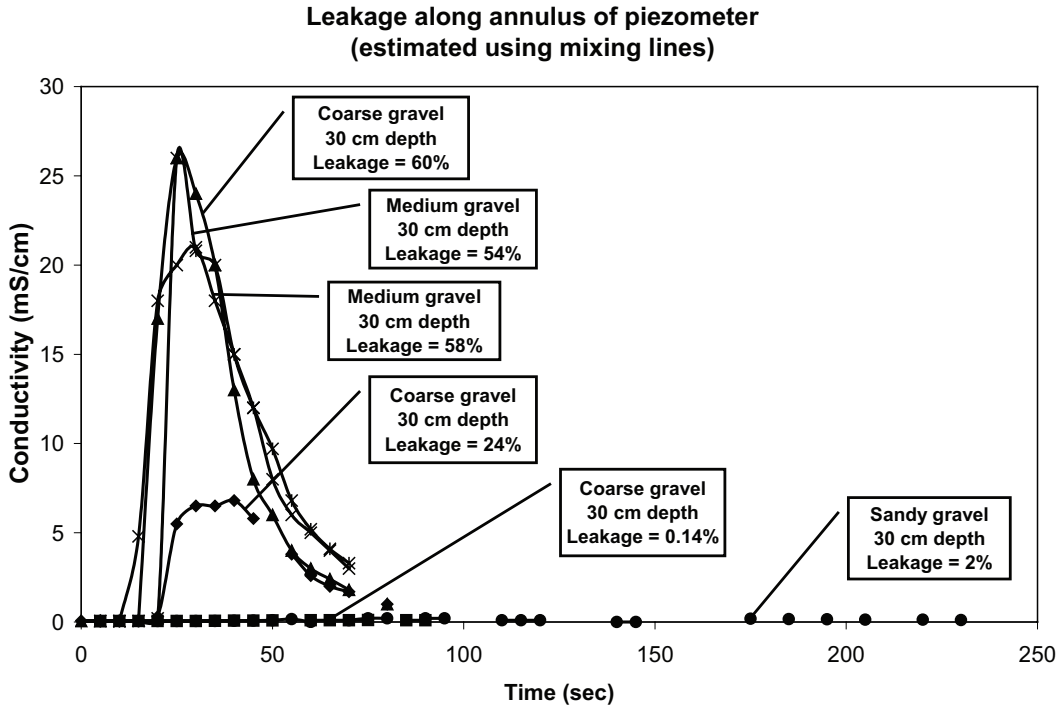


Figure 4. Curves show leakage along a standpipe when salt water tracer enters the screened interval from the surface during a constant drawdown test in sand and gravel using a Terhune (1958) type standpipe. This piping along the edge of the standpipe is common in coarse gravel installations.

it introduces surface water to the perforated interval of the standpipe during the test. Under some field conditions, this problem can be overcome by creating a clay seal between the outside of the pipe and the bed surface.

Leakage along the annulus of the of the standpipe was quantified by conducting permeability tests in standpipes fitted with an external sleeve that held colored dyes and saltwater tracers. Results presented here show that up to 68% of the water that enters the standpipe through the perforated interval may actually be flowing down the side of the pipe from the surface (Figure 4). Coarse, well-sorted gravels show the highest leakage from the surface, and in general, there is progressively less leakage in finer sediments or in tests run deeper in the gravel. Spawning gravel tends to be coarse, and permeability tests are most often conducted at shallow depths where this leakage is greatest. Constant drawdown tests (Terhune 1958; Barnard and McBain 1994)

and slug tests should not be conducted in shallow gravels where the piezometer is installed without a surface seal. Some long-term installations may avoid this issue by allowing a standpipe or piezometer to "silt in" over a period of weeks or months. This can create a natural surface seal that minimizes this problem. Tests in sand or silt may experience less leakage from the surface, and subsurface dye dilution tests or tracer tests will avoid this issue if the dye is injected slowly.

It is not possible to judge the amount of leakage along the standpipe solely on the basis of surface grain size or to generate a leakage correction factor based on surface grain size. There is generally more leakage with coarser surface gravels, but heterogeneity in the subsurface is probably responsible for the observed difference in leakage between similar-sized gravels (Figure 4).

Another fundamental problem with permeability tests in gravel is the small zone of

influence characterized by each test. Standpipes milled to exact specifications of the original Terhune study (Terhune 1958) were used to evaluate this zone of influence. Constant drawdown tests (Barnard and McBain, 1994) and slug tests were performed in this standpipe, and an array of similar standpipes was installed at distances of 20, 50, and 100 cm from the test pipe. Tests were conducted in well-sorted spawning gravel with a median grain size of 5–8 cm. All standpipes were purged before the tests to remove any silt or clay that might have clogged the perforated interval. Electronic pressure transducers that measure water level twice per second were installed in all standpipes, and water level fluctuations were recorded during each test. Results show that the zone of influence for each test has a radius less than 20 cm (Figure 5A, 5B). This is the limit of resolution with this particular array of standpipes, and the actual zone of influence may be smaller.

The small zone of influence encompassed by each test creates similar problems during assessment of a heterogeneous stream environment. A small number of permeability tests may not accurately characterize a habitat zone such as a riffle, and the number of these tests required to accurately characterize the permeability of a habitat zone could be prohibitive. Field workers who have used these methods commonly report one or two orders of magnitude variability in permeability estimates within a habitat zone or over small intervals of the stream (Bush 2006). This variability may be a combination of leakage along the annulus of the standpipe, small zone of influence for individual tests, and a highly heterogeneous natural environment. A potential solution to these problems is to evaluate gravel permeability (intergravel flow) over a larger area using pressure differentials, natural tracers, or artificial tracers. These approaches are outlined below.

Intergravel Flow

Intergravel flow describes water movement through the spawning gravel, and it depends on permeability (a property of the sediment)

and hydraulic gradient. Common field measurements used to measure intergravel flow during spawning gravel assessment include hydraulic gradient, seepage, and tracer tests.

Vertical hydraulic gradient drives upwelling and downwelling through the hyporheic zone, and this vertical flux has been identified as a factor for site selection by spawning salmonids (Lorenz and Eiler 1989; Geist and Dauble 1998; Geist et al. 2002). Vertical gradient is the most common gradient measurement and is easily obtained by recording the difference in water level between the stream and a measured depth in the gravel. From a more technical standpoint, water level represents the total energy of the fluid or total hydraulic head. The hydraulic head in a stream is a function of the water depth in the stream and the elevation of the streambed above sea level. The hydraulic head in the gravel is related to the elevation of the monitoring point above sea level and the length of the water column in a standpipe or well that is screened at the specified depth (see Malcolm et al. 2008, this volume). Standpipes or wells are used to measure water level (hydraulic head) in the gravel using an electronic water level meter or steel tape. The difference in water level from the inside to the outside of the standpipe is divided by the depth of the piezometer installation and produces a dimensionless gradient. Gradients are often reported as positive numbers if there is net upwelling (subsurface pressure is higher than surface pressure) or negative numbers if there is downwelling (subsurface pressure is lower than surface pressure).

Vertical gradient can also be obtained from mini-piezometer tips by drawing stream water and subsurface water into a bubble manometer board (Horner et al. 2004; Horner 2005; Bush 2006; Zamora 2006). The shift of the bubble shows pressure differences between surface and subsurface conditions and is comparable to measurements made in wells, standpipes, or piezometers. These techniques only address changes in hydraulic head (pressure differences) between the surface and subsurface and show potential for upwelling or downwelling conditions. From

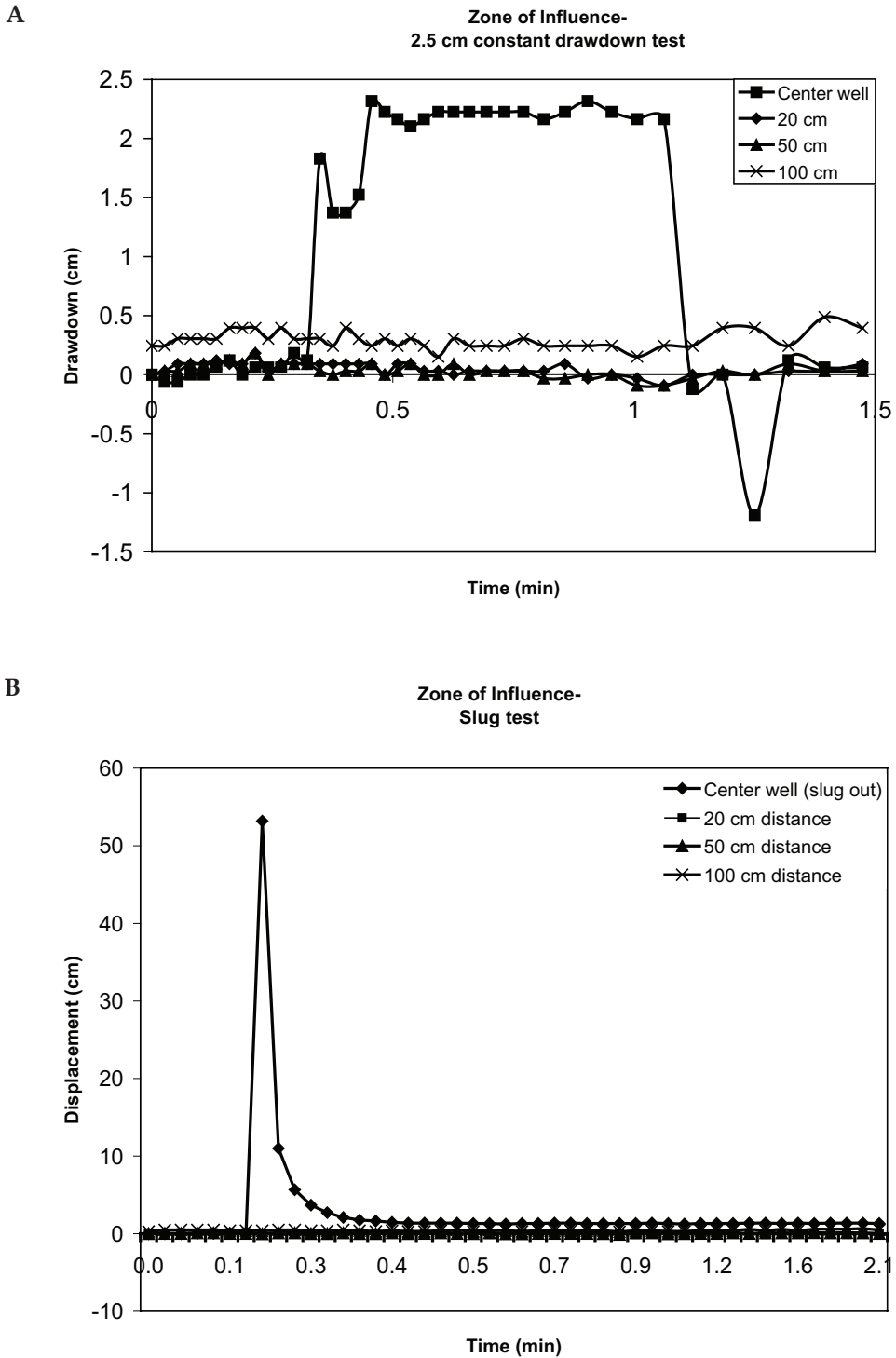


Figure 5. (A) Zone of influence for Terhune-style 2.5-cm constant-drawdown test is less than 20 cm laterally. Test was conducted for 45 s. (B) Zone of influence for slug test with 20 cm vertical displacement in the wellbore is less than 20 cm laterally.

a habitat standpoint, upwelling and downwelling are important because upwelling water is often depleted in dissolved oxygen, while downwelling water is usually saturated with dissolved oxygen. Direct knowledge of upwelling or downwelling conditions is an important component of habitat assessment (Malcolm et al. 2003a)

Lateral hydraulic gradient drives lateral flow and is measured using two wells or standpipes. Lateral gradient is measured by recording the hydraulic head (water level) difference between adjacent piezometers and dividing the head difference by the distance between the piezometers. Head differences are often very small, and this requires precise elevation control between sites. Delivery of oxygenated surface water to redds is a combination of vertical and lateral flow, and it is important to understand both flow vectors when predicting subsurface flow paths.

Gradient measurements give the pressure difference or potential for vertical or horizontal flow, but the actual flow is also determined by the hydraulic conductivity. Impermeable layers in the subsurface can prevent subsurface flow in either direction, regardless of the gradient. Seasonal changes in organic matter input and infiltration of fine clastic sediment can also cause temporal change in subsurface flow by clogging the pore spaces of coarser gravels (Lisle and Eads 1991; Sear et al. 2008).

Seepage meters are another common method of estimating vertical flow through stream sediment. Seepage meters provide an actual rate of flux and have been used to distinguish between upwelling and downwelling areas. When combined with piezometer measurements, Darcy's law is solved to provide an estimate of hydraulic conductivity of the sediment. Seepage meters were originally intended for use in drainage canals, swamps, estuaries, or slow-moving streams (Lee and Cherry 1978). Since that time, seepage meters have been used in faster moving streams, often with less useful results (Shaw and Prepas 1989; Libelo and MacIntyre 1994; Zamora 2006). It is common to have a nearby piezometer or standpipe indicate one direc-

tion of vertical flow, while the seepage meter shows the opposite (Zamora 2006). This can occur due to a pressure effect as moving water impacts the upstream side of the seepage meter, inducing lateral flow under the meter (Shinn et al. 2002). Conductiometric probes can be used in seepage meters to record the progressive dilution of a saline solution from which intragravel flow rates can be calculated. Laboratory tests indicate that recent refinements to this technique to account for different grain-size distributions can improve performance (Greig et al. 2005a).

Seepage meters are also subject to leakage along the edges, similar to the piping described for standpipes. This effect is most pronounced in coarser gravels, and in general, seepage meters are not effective in fast-moving, gravel-bed streams. Previous studies that use seepage meters in faster-flowing streams may have excessive scatter in the data or may not correctly identify upwelling and downwelling regions. The volumetric bags used to measure flux in seepage meters can also induce error, especially if they have a high elastic property (Shincariol and McNeill 2002; Zamora 2006). Volumetric bags should be isolated from the buffeting effects of the current (Murdoch and Kelly 2003). All of these issues raise questions about the effectiveness of seepage meters, and in general, people who do stream assessment in faster water or coarser gravel use other methods of estimating flow through the gravel.

Tracer tests are a relatively new method of assessing intergravel flow. Use of conservative tracers (including lithium, chloride, or bromide) and heat flow measurements are two different approaches to tracer tests in streams. It may not be appropriate to inject a large amount of a foreign tracer into a spawning reach while eggs are incubating, although high seepage velocities found in riffles will usually remove the tracer within a matter of minutes or hours. Tracer tests can also be conducted with relatively low concentrations and low volumes of injected fluid, thus minimizing the impact on the environment. Conservative tracers that are added to the surface water provide additional information about

the interaction between groundwater and surface water at the subreach scale of streams (Harvey et al. 1996; Harvey and Wagner 2000; Zellweger 1994). These types of tracer studies may someday be used to characterize spawning gravels and help with restoration project design. Finally, heat flow studies provide estimates of seepage, flux, or hydraulic conductivity (Constantz et al. 2002; Stonestrom and Constantz 2003) and can distinguish between vertical and lateral flow in the hyporheic zone. These methods promise to open an exciting new chapter in habitat assessment.

Given the limitations of permeability measurements, gradient measurements, and seepage meters, future work should consider other methods of estimating intergravel flow. Tracer tests have significant advantages, although tracer tests have not been applied extensively to habitat assessment. Tracer tests average subsurface flow over a scale of meters (rather than centimeters), integrating flow velocity through all material encountered along a flow path. These meter-scale averages provide broad understanding of habitat zones but, in turn may not address the specific conditions surrounding an egg pocket or individual redd. Tracer tests are designed to minimize problems associated with heterogeneity and limited zone of influence. Tracer tests also provide realistic seepage values and are not limited to analysis of highly permeable areas.

Gravel Size Assessment

Techniques used to sample spawning gravels range widely in effort and cost, and the more expensive and seemingly sophisticated techniques are not necessarily better. Selection of sampling technique should be driven by the purpose of the study, adequacy of sample size, and comparability of results. Table 1 lists some of the techniques commonly used to samples surface and subsurface sediments and highlights their positive and negative attributes.

To assess gravel suitability for spawning requires that we compare gravel size on site with information from laboratory studies or

field observations (Kondolf 2000), and this requires the choice of some measures for the comparison. Here, we briefly review some common reporting and sampling methods and refer the reader to Kondolf et al. (2003) for methodological details.

Particle Size Attributes of Spawning Gravels

Laboratory and field researchers have attempted to relate fine sediment content to incubation and emergence success, producing a wide range of results (Table 2). Fine sediment has three distinct effects on embryo survival: it reduces hydraulic conductivity of the gravel so that less-oxygenated water can pass through it to the embryos; organic matter in the fine sediment has an oxygen demand, which reduces the dissolved oxygen concentration available to the embryos; and fine sediment particles can inhibit exchange of oxygen across egg membrane (Greig et al. 2005b). Because embryo survival responds more directly to effects of fine sediment on oxygen supply, rather than fine sediment content per se, fine sediment metrics can only be imperfect predictors of survival. In any event, relations between fine sediment content and embryo survival are useful for assessment only to the extent that the data can be applied to gravels elsewhere, which requires standardized descriptions of the size distributions.

Natural streambed gravels can contain particles ranging in size over five orders of magnitude. Size distributions are typically presented in cumulative frequency curves, from which the cumulative percentage finer than a given size can be read directly from the curve (Figure 6A). For example, the D_{84} is the grain size at which 84% of the sample is finer (and 16% coarser). Gravel size distributions tend to resemble lognormal, gamma, or Weibull distributions rather than normal distributions (Kondolf and Adhikari 2000).

Statistics can be drawn from the cumulative frequency distribution curves for comparisons. The median particle diameter, D_{50} , is widely used as a measure of central tendency

Table 1.

Sampling method	Details	Advantages	Disadvantages	Papers considering error and sample size
Visual sampling Bovee (1982)	<ul style="list-style-type: none"> Visual/subjective estimate used to assess relative percentages of different size fractions required. 	<ul style="list-style-type: none"> Rapid assessment of grain size. No data processing. Data are not comparable to grain-size distributions normally presented in geomorphic and engineering literature. 	<ul style="list-style-type: none"> May not be reproducible among different investigators. Limited to bed surface. 	
Photography and image analysis Adams (1979); Rice (1995); Lane (2001); Carbonneau et al. (2005)	<ul style="list-style-type: none"> Gravel surface photographed, size determined from scale-bar. Image analysis involves automated derivation of DEMs from image, or grey-level histogram segmentation. 	<ul style="list-style-type: none"> Possible to recover complete grain-size distribution. Provide data on percentage of fines present on surface. Bed surface is not disturbed. 	<ul style="list-style-type: none"> Clasts may be partially hidden and imbricated, therefore clast axis measurement problematic. Limited to bed surface 	Church et al. (1987)
Pebble count Wolman (1954); Kondolf and Li (1992); Kondolf (1997)	<ul style="list-style-type: none"> Random selection and measurement of 100 clasts from specific geomorphic features on the bed surface. Variants include the zigzag count (Beverger and King 1995) and the transect method (Rosgen 1996). 	<ul style="list-style-type: none"> Data are normally presented as cumulative grain-size curves, able to compare data presented in engineering and geomorphic literature 	<ul style="list-style-type: none"> Variants should be avoided as they mix points from different channel features. 	Hey and Thorne (1983); Fripp and Diplas (1993); Rice and Church (1996)
Bulk sampling	<ul style="list-style-type: none"> Collection of surface and/or subsurface sediments. Variants include shovel; bulk-core; FRI/McNeil (McNeil and Ahnell 1964), sampling cylinders (Orcutt et al. 1968; Horton and Rogers 1969; Kondolf et al. 1989; Wilcock et al. 1996). 	<ul style="list-style-type: none"> Better approximation of true substrate than shovel and freeze-core sampling 	<ul style="list-style-type: none"> Very large samples (>200 kg) required in order to represent all grain size present. Largest particle should constitute no more than 1% of the total sample mass. 	Church et al. (1987); Bunte and Abt (2001); Horner (2005)

Table 1. Continued

Sampling method	Details	Advantages	Disadvantages	Papers considering error and sample size
Freeze-sampling Everest et al. (1980); Petts (1987); Milan et al. (2001)	<ul style="list-style-type: none"> Steel or copper probe driven into bed substrate. Liquid CO₂ or N₂ is injected to the base of the probe. Sediment and water freezes to the outside of the probe. 	<ul style="list-style-type: none"> Freezing avoids loss of fines fines under flowing water. Vertical sediment fabric and fine-sediment content may be observed. May be used to study the structure of redds. 	<ul style="list-style-type: none"> Labor, equipment, and supply intensive. Difficult to obtain sample sizes large enough to satisfy Church et al. criterion. Surface sediments tend not to freeze well. Insertion of probe may disrupt bed structure. Core may have irregular boundary, dominated by large clasts. Packing character of clean gravel placed on top of bag may not reflect natural packing. 	Thoms (1992); Milan et al. (1999)
Infiltration bags/pots Carling and McCahon (1987); Thoms (1987); Lisle and Eads (1991); Sear (1993); Milan (2000); Soulsby et al. (2001); Levasseur et al. (2006)	<ul style="list-style-type: none"> Armor layer and subsurface sediments excavated to the predicted depth of the egg pocket. A collapsed bag with a metal rim is then placed at the bottom of the hole, and cables attached to the metal rim are stretched to the bed surface. Clean gravel is then placed on top of bag. Fines that infiltrate voids can be sampled by pulling bag up via cables. Variants include permeable pots and wire baskets. 	<ul style="list-style-type: none"> Main advantage over freeze-sampling is the increased sampling frequency and reduced sampling effort. Has been used in conjunction with egg survival studies (Levasseur et al. 2006) 		

Table 2. Gravel quality criteria for salmonids, developed from experimental studies showing the maximum levels of fine sediment that allow 50% emergence.

Source	Maximum percent finer than grain size (mm)			
	0.83	2.00	3.35	6.35
Bjornn (1969)				15.0
Bjornn (1969)				26.0
Cederholm and Salo (1979)	7.5			
Cederholm and Salo (1979)	17.0			
Hausle (1973)		10.0		
Hausle and Coble (1976)		20.0		
Irving and Bjornn (1984)				20.0–33.0
Iwamoto et al. (1978)		15.0		
Koski (1966)	21.0		30.0	
Koski (1975)			27.0	
McCuddin (1977)				27.0–35.0
NCASI (1984)	12.0			40.0
Phillips et al. (1975)			25.0–36.0	
Reiser and White (1990)	13.0			
Shepard et al. (1984)				34.0
Taggart (1976, 1984)	11.0			
Tappel and Bjornn (1983)				40.0
Mean	13.6	15.0	29.5	30.3
SD	4.8	5.0	4.8	7.7

Modified from Kondolf (1988, 2000).

because it is easily read, unambiguously interpreted, and relatively unaffected by extremes of the distribution (Inman 1952; Vanoni 1975). The geometric mean (of the D_{16} and D_{84}) (Table 3), is another measure of central tendency complementary to the median diameter, more influenced by extremes of the distribution.

Other commonly reported attributes of size distributions are sorting and skewness. Sorting refers to the degree of concentration (or dispersion) among the particle size fractions, reflecting the degree to which fluvial processes have concentrated particles of a given size together. In large rivers, currents may deposit bars composed entirely of gravel, other bars entirely of sand, thus producing well-sorted deposits having low dispersion. Skewness refers to the degree to which the distribution is skewed from a normal or lognormal distribution. Gravel size distributions tend to be positively skewed (i.e., the coarse tails extend farther than the fine, or put another way, the mode is shifted toward the coarse end of the size distribution), while

the log-transformed distributions tend to be negatively skewed (the geometric mean diameters tend to be less than median diameters; Kondolf and Wolman 1993).

Modified box-and-whisker plots (Tukey 1977; Kondolf and Wolman 1993) can also be used to compare gravel-size distributions. This method permits multiple distributions to be presented on the same graph without overlap (Figure 6B). In the box-and-whisker plots, the rectangle (box) encompasses the middle 50% of the sample, from the D_{25} to D_{75} values, with lines (whiskers) extending above and below the box to the D_{90} and D_{10} values. The D_{50} is represented by a horizontal line through the box.

To assess whether gravels are small enough to be moved by a given salmonid to construct a redd, the size of the framework gravels (the larger gravels that make up the structure of the deposit) is of interest, and the D_{50} or D_{84} of the study gravel should be compared with the spawning gravel sizes observed for the species elsewhere.

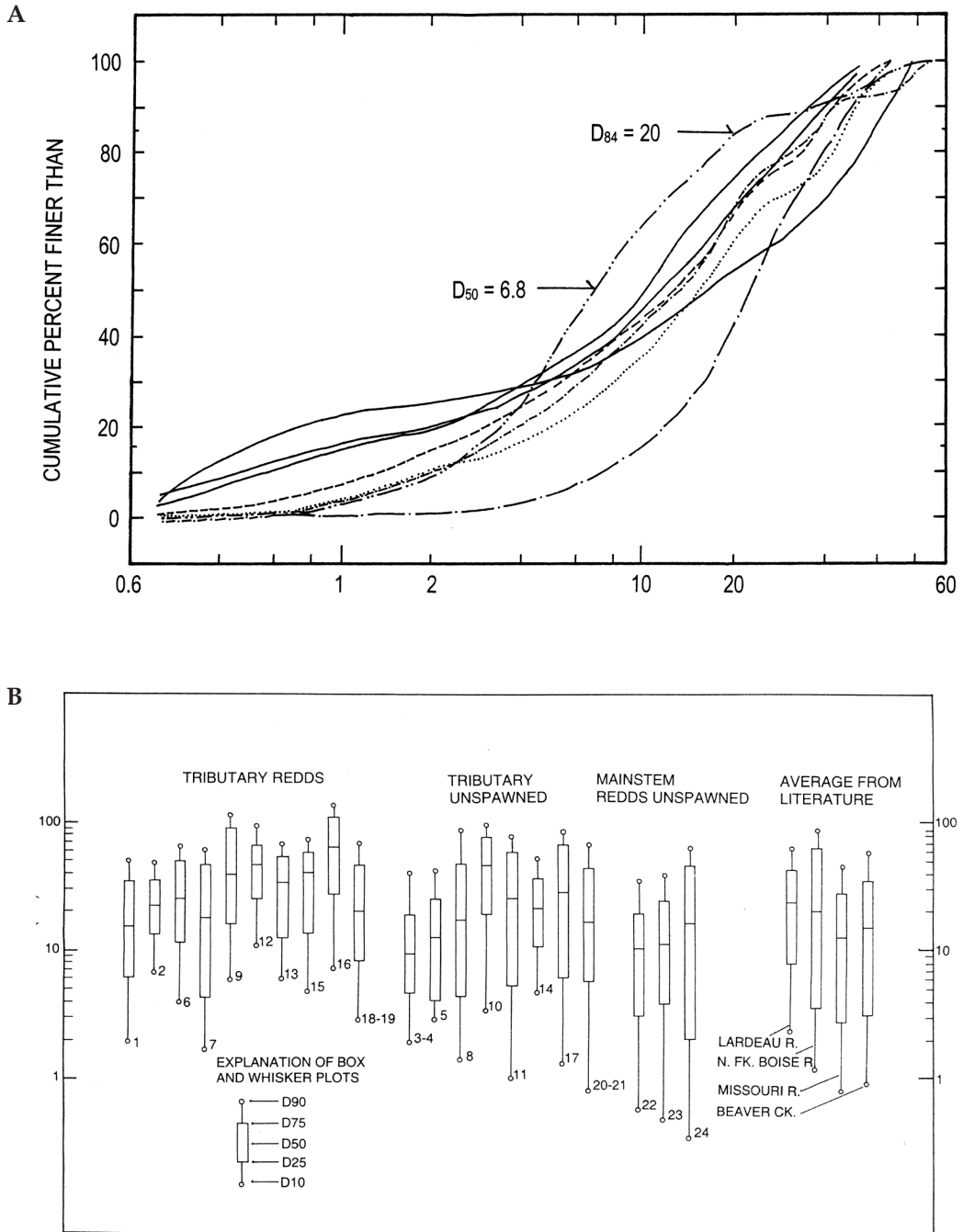


Figure 6. Multiple gravel-size distributions, presented as cumulative frequency curves (A) and (B) box-and-whisker plots (for rainbow trout spawning gravels in the Colorado River and tributaries downstream of Glen Canyon Dam, along with averages for other rainbow trout spawning gravels). For each sample, the rectangle (box) encompasses the middle 50% of the sample, from the D_{25} and D_{75} (quartile grain diameters), termed "the hinges." The median diameter, D_{50} , is represented by a horizontal line through the box. Above and below the box are lines (whiskers) extending to the D_{90} and D_{10} values, a modification of the standard box-and-whisker plot of Tukey (1977).

Table 3. Size descriptors comomonly drawn from sediment-size distributions (Kondolf et al. 2003).

Measure of	Quartile-based descriptors	Descriptors based on D_{16} , D_{50} and D_{84}
Central tendency	Median, D_{50}	Median, i.e., D_{50} Geometric mean $D_g = [(D_{84})(D_{16})]^{0.5}$
Dispersion	Trask sorting coefficient $si = (D_{75}/D_{25})^{0.05}$	Geometric sorting coefficient $sg = [(D_{84})(D_{16})]^{0.5}$
Skewness	Quartile coefficient of skewness $SK = [(D_{75}D_{25})/(D_{50})^2]^{0.05}$	Geometric skewness coefficient $sk = \log(D_g/D_{50})/\log(sg)$

Assessing fine sediment content is more complicated. As female salmonids construct redds, they winnow fine sediment from the gravel, so that the gravel within the redd typically has less fine sediment than it did before redd construction (Figures 7A, 7B). Laboratory emergence studies attempt to represent conditions in redds, so the probable cleaning effect of spawning should be allowed for in applying the results of these studies to field assessments. The reduction in fine sediment during spawning depends largely on the amount of fine sediment initially present, and the reduction can, in some cases, transform unsuitable gravels into suitable gravels. However, assessments should also consider that fine sediments may infiltrate into the gravel during incubation, so the typical transport of fine sediment by the stream should be taken into account. Finally, note that the coarse lag gravels encountered in many redds may not be reflected in the homogenized sediment mixtures typically used in laboratory studies (Chapman 1988).

Pebble Counts and Visual Sampling Methods

Pebble counts and visual estimates provide a measure of the surficial grain size but cannot measure fine sediment in the subsurface. Visual estimates (ocular assessments), typically used as input to the PHABSIM fish habitat model (Bovee 1982), are subjective estimates of percentages of various size-classes in the bed and may not be reproducible among different investigators. Moreover, the results are usually reported in the form of dominant

and subdominant size-classes or as percentages of classes such as 80% cobble, 10% sand, and 10% silt. Even if accurate, these estimates are not reported in a form that can be readily compared with sediment sizes reported in the engineering and geomorphic literature, in which statistics are drawn from standard size distributions.

The pebble count method (Wolman 1954; Kondolf 1997) involves measurement of the diameters of 100 or more stones randomly selected from the surface of a single facies, or patch, of gravel, which occur in specific geomorphic features on the bed surface. Pebble counts provide reproducible surface grain-size distributions and can be readily adapted for use in fish habitat studies (Kondolf and Li 1992). Sources of error in pebble counts have been addressed by Fripp and Diplas (1993). Rice and Church (1996) discuss the rate at which standard errors of estimates of parameters such as D_{50} (the median particle size) or D_{84} (the particle size at which 84% of the sample is finer) from pebble counts decrease as sample size increases. Two recent modifications have become popular among nongeomorphologists: the zigzag count (Bevenger and King 1995), and the transect method of Rosgen (1996). Both should be avoided because they mix sample points from many different channel features (i.e., spawning riffles, intervening pools, and banks), thereby yielding a mix with unclear geomorphic meaning. Because they mix data points from different geomorphic features and typically do not adequately sample any individual deposit, they do not yield reproducible size distributions (Kondolf 1997).

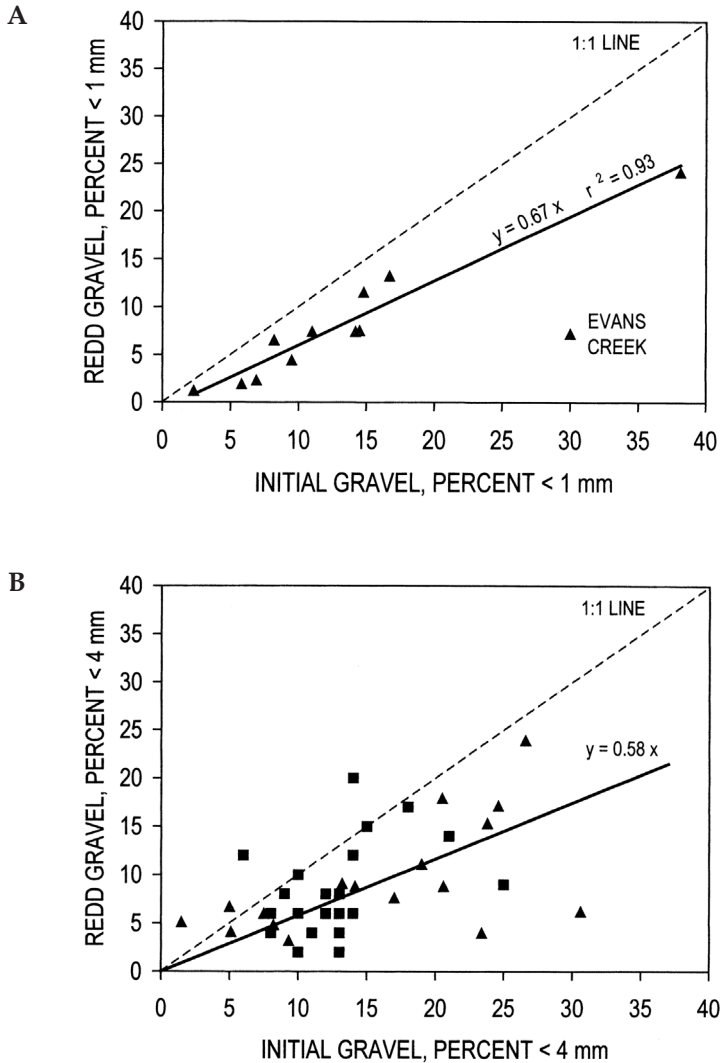


Figure 7. (A) Percentage of sediment finer than 1 mm in redds and potential (comparable, unspawned) gravels. The data point for Evans Creek is excluded from the regression. (See Kondolf et al. 1993 for sources of data.) (B) Percentage of sediment finer than 4 mm from pairs of redd and potential spawning gravel sampled by Chambers et al. (1954) (squares) and by Kondolf et al. (1993) (triangles).

Bulk Sampling

Bulk sampling involves collecting a volume of sediment (usually from surface and sub-surface), which is passed through sieves. Very large samples are often needed for statistically accurate sampling and analysis of typical river gravels (Bunte and Abt 2001). In general, coarser-grained substrates require larger samples. An oft-used standard is

that the largest particle should not constitute more than 1% of the total sample (Church et al. 1987; Petts 1987; Milan et al. 1999), and samples of 200 kg or more are commonly required in spawning gravels. In cobble- and boulder-bed streams, this guideline can produce representative samples in excess of 2,000 kg (Horner 2005). At some point, practical considerations and ecological sensitivity enter into this discussion, and many spawn-

ing gravel studies use less rigorous criteria to determine sample size. Studies that use smaller sample sizes should be aware that streambed heterogeneity and accurate statistical representation of the grain population are serious concerns.

More fundamentally, when sampling redds themselves, the redds of many salmonids simply do not contain enough gravel to meet conventional sample size standards. For example, trout redds, especially in small streams where the redds may be excavated in pocket gravels (Kondolf et al. 1991), are often too small to contain enough gravel for the sample-size standards. To obtain enough gravel, the sample would extend beyond the edge of the redd into the adjacent, unspawned gravel. However, the redd and adjacent unspawned gravel represent different populations because of the removal of fine sediment by spawning females (Kondolf and Wolman 1993). For most study objectives, the two gravel populations should not be mixed.

Bulk core sampling involves driving a cylindrical core sampler into the bed and removing (by hand) the material within it down to a predetermined depth. In a comparison of shovel, bulk core (McNeil), and freeze-core sampling, Young et al. (1991) found that the bulk core samples most frequently approximately the true substrate composition. Geomorphologists have used bottomless oil drums in various forms to obtain sufficiently large bulk core samples, such as the 140–240-kg samples collected by Wilcock et al. (1996). Common sampling cylinders are 50-cm-diameter drums, with the top and bottom removed (and usually shortened to permit the operator's arms to reach the bottom of the sampler) (e.g., Orcutt et al. 1968); 46-cm-diameter well casing (Horton and Rogers 1969), 25-cm-diameter polyvinyl chloride (Kondolf et al. 1989), and other variants, such as the FRI or McNeil sampler. The McNeil sampler is a 50-cm drum with a 15- to 30-cm-diameter pipe welded on the bottom. The smaller pipe is worked into the bed, the gravel is removed by hand, and the muddy water within the sampler is retained to sample suspended fine sediments (McNeil and Ahnell 1964).

Church et al.'s (1987) bulk sampling recommendations are generally accepted in fluvial studies. Church et al. recommend that the largest particle in the sample should constitute no more than 0.1% of the total sample mass up to 32 mm, and 1% of the sample mass if the largest particle is between 32 and 128 mm, typically resulting in samples sizes of 150–350 kg. Church et al. sampled dry bar sediments in their analysis using bulk/grab sampling methods, with the retrieval of all size fractions. In contrast, the sampling of salmonid redds or spawning grounds usually takes place in submerged areas of the bed. Retrieval of the important finer size fractions is problematic, due to the preferential loss of finer fractions under flowing water. One method that has been widely used to obtain representative samples of both the gravel and finer fractions in flowing water is freeze-core sampling, discussed below.

Freeze-core sampling involves driving steel or copper probes into the bed, discharging a cooling agent (such as liquid CO₂ or nitrogen) into the probes to freeze the interstitial water adjacent to the probe and withdrawing the probes (with gravel samples frozen to them) from the bed with a tripod-mounted winch (Everest et al. 1980). Freeze core samples provide information about sediment fabric and fine-sediment content that is not available with other bulk sampling methods. Freeze core techniques allow intact vertical sections of the channel bed to be removed, bound by frozen interstitial water, thus avoiding the loss of the fine-grained sediments through elutriation. Freeze cores can also be used to study the structure of redds (Peterson and Quinn 1996).

Freeze-core sampling is labor-, equipment-, and supply-intensive, requiring the use of CO₂ cylinders, N₂ dewars, and winching apparatus; consequently, a balance usually has to be struck between the required level of accuracy and sampling effort. Individual freeze core samples are typically less than 10 kg and will be too small to accurately represent gravels that include particles 64 mm and greater, unless multiple cores from a given deposit are combined into a composite

sample. It is difficult to obtain enough freeze-cores from a single site to satisfy Church et al.'s (1987) 1% criterion, especially in remote or inaccessible settings.

Thoms (1992) undertook a controlled laboratory study to identify the effectiveness of freeze-coring in comparison to grab sampling under flowing water. He filled a flume with a known mixture of grain sizes and took 20 freeze-cores and 20 grab samples. He then compared the grain size of the bulk 20-core sample and the grab samples with the known grain-size distribution. He found a significant difference for the grab samples, which he attributed to loss of fines when sampling; however, no significant differences for the freeze-cores. Thoms (1992) also looked at the number of samples required to represent the grain size from a single riffle. For this, he took 32 freeze cores from a single site on the gravel-bed Blackbrook in Leicestershire, UK. The number of samples (N) required was calculated using

$$N = \left(\frac{s \cdot t_{n-1}}{L} \right)^2,$$

where s is the standard deviation of the samples and t the value of the Student's t ($p = 0.05$) for a sample size of N . From this analysis, he concluded that five freeze-cores randomly collected from this site would be required to provide accurate grain-size data allowing for a 5% sampling error at the 95% confidence level. These sampling criteria have been employed for sampling salmonid spawning riffles at a number of locations within the United Kingdom (Milan et al. 2001).

Two other significant problems can arise with freeze core techniques. First, the insertion of the pipes into the bed may disrupt stratification of fine sediments. Second, bias may be created by an irregular sample boundary (ragged edge), which is dominated by large particles. Many workers overcome this by truncating the sample population—often excluding large particles from their freeze core investigations (Church et al. 1987; Milan et al. 1999). Fracturing of fragile clasts upon retrieval of the core from the riverbed may also introduce error to grain-size estimates.

Infiltration bags or pots have been used to assess temporal variations in fine sediment deposition. Lisle and Eads (1991) employed fabric bags with a metal rim sewn into the opening. Using this method, the armor layer and subsurface sediments are excavated from inside an open cylinder to the desired depth, usually the predicted depth of the egg pocket. The collapsed bag is then placed at the bottom of the hole, and cables attached to the metal rim are stretched to the bed surface. Cleaned experimental gravel consisting of framework material with the fines sieved out is poured back into the hole, burying the bag. After a specified period of time (or after a high flow), the cylinder is removed by pulling up the cables using a chain hoist. As the bag is pulled upward, the fines and gravel are retained within the bag, with minimal loss to the flowing water (Kondolf et al. 2003).

Variations on this technique have been used elsewhere. Carling and McMahon (1987) used permeable pots filled with gravel. Sear (1993) and Milan (2000) used baskets made from chicken wire (15 cm deep, 30 cm diameter), with compressed infiltration bags at the base. These traps were then filled with framework gravel, reflecting the local grain-size distribution.

The main advantage with infiltration bags or pots is the increased sampling frequency and reduced sampling effort in comparison to techniques such as freeze-coring. After sample retrieval, fine sediments may be rinsed from the experimental framework gravel in the field. The framework grains are then replaced in the trap on top of the compressed bag in preparation for the next sampling event, and the fine sediment sample is taken back to the laboratory for grain-size analysis. More recently, Levasseur et al. (2006) included fertilized embryos in the clean gravels inserted into the bed, allowing egg survival to be directly measured along with fine-sediment accumulation rates. Zimmerman and Lapointe (2006) measured interstitial velocities using a hotwire approach and documented reductions in intragravel velocity resulting from threshold amounts of fine sediment deposition.

A Checklist to Assess Spawning Gravel Quality

We have focused on gravel quality, inter-gravel conditions, and fry condition as tools to assess the condition of spawning habitat. We have not emphasized flow depth and velocity requirements, bed complexity as a factor in inducing intragravel flow, water temperature, and influences of changes in flow on all of the above (frequently an issue downstream of dams). Taking all these into account, we propose the checklist in Table 4 as a guide to assessing physical habitat quality. Frequently, there is a need to assess the quality of potential spawning gravels (i.e. gravel deposits that have not already been used for spawning). In such cases, we cannot use fry conditions or directly measure the redd environment to assess incubation habitat. Instead, we can conduct a systematic life stage-specific assessment of the gravel itself (Figure 8), using the steps described below:

Sample the gravel and develop a size distribution (steps 1–2).—The sampling method depends upon the purpose of the assessment. If the concerns are limited to whether the fish can move the gravels, pebble counts may be adequate, although such values (ob-

tained from the surface layer) may be larger than those from bulk samples because the latter would be influenced by interstitial fine sediment in the subsurface. If fine sediment content is also a concern, subsurface samples must be obtained. The large sample sizes necessary for statistical reproducibility make bulk core samples (of adequate size) preferable, or composites of multiple freeze cores from one site. Pebble counts directly yield size distributions, but bulk subsurface samples must be passed through sieves and weighed to obtain size distributions (Vanoni 1975). In either case, the size distribution should be plotted as a cumulative frequency curve; to compare multiple distributions, box-and-whisker plots can be plotted from percentile values drawn from the cumulative distributions.

Determine whether gravel is small enough to be moved by spawning fish (step 3).—The D_{50} or D_{84} values reported for the species can be used to determine whether the framework gravels are too large for the fish to move. These values are compared to values reported for the species in other spawning locations and can also be compared to the maximum movable size predicted by Figure 2, which suggests that spawning fish can move gravels with a median diameter up to about 10% of their body

Table 4. Checklist for assessing physical salmonid spawning habitat.

Gravel size and condition

- ✓ Framework grains small enough to be movable by target species?
- ✓ Percentage fine sediments (<1 mm) below harmvul level (or likely to be after spawning effect)?
- ✓ Percentage fine sediments (<10 mm) low enough to prevent entombment of alevins?
- ✓ Gravel texture loose enough to be movable? (i.e., not cemented or compacted)
- ✓ Channel bed sufficiently complex to induce downwelling and upwelling?

Flow depth, velocity, and temperature

- ✓ Water, depth, velocity, and temperature suitable for spawning adults during spawning season?
- ✓ Water depth and velocity sufficed to drive intragravel flow during incubation season?
- ✓ Water temperatures suitable during incubation?

Intragravel conditions

- ✓ Intragravel flow sufficient to remove metabolic waste?
- ✓ Fry able to orient in slight current?

Fry conditions

- ✓ Fry able to orient in slight current?
 - ✓ Emergence of prebuttoned-up alevins? (i.e., frequency of sac-fry caught in screw traps)
 - ✓ Alevin and/or fry length, weight, relative weight?
 - ✓ Nonpolar lipid content?
-

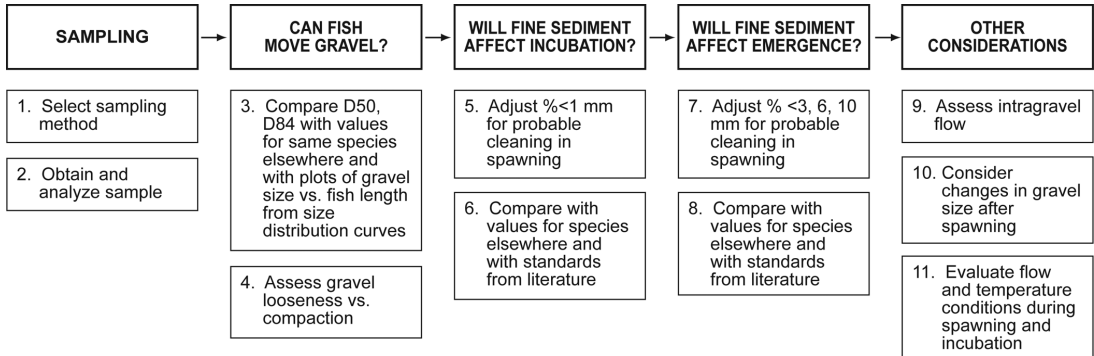


Figure 8. Flow chart illustrating nine discrete steps in evaluating quality of potential salmonid spawning gravel.

length, regardless of species (Kondolf 2000).

Assess gravel looseness versus compaction (step 4).—Some gravel deposits, especially downstream of dams, develop a compacted or cemented texture and become virtually immobile, rendering otherwise suitably sized gravels unsuitable. For successful spawning, however, the gravel must be loose enough that it can be moved by the spawning female. Sear (1995) and Milan et al. (2001) used a penetrometer, commonly used in soil studies, to assess influence of compaction upon sediment transport. This approach has the potential to be applied to assessment of spawning habitat.

Determine whether fine sediment content is excessive for incubation (steps 5–6).—The question is whether the amount of sediment finer than 1 mm is so great that gravel permeability, and thus intragravel flow, is negatively affected. The percentage finer than 1 mm should be read from the grain-size distribution curves and adjusted downward using Figure 7A to reflect the probable cleaning effect of redd construction.

The resulting values can be compared with values reported from other studies. A summary of laboratory and field studies of incubation and emergence (Table 2) shows values for 50% survival. Conclusions drawn from field observations by McNeil and Ahnell (1964) and Cederholm and Salo (1979) show that 12–14% of gravels should be finer than 0.83 mm for successful incubation. However, as useful and reassuring as such threshold

standards may be, they may apply poorly to many spawning habitats (Greig et al. 2005b).

Assess whether fine sediment content is excessive for emergence (steps 7–8).—While the fine-sediment (<1 mm) threshold for incubation effects can be estimated at 12–14%, the upper limits of the (larger) fine sediments affecting emergence (percents less than 3–10 mm) are more difficult to select (Table 2). Alevins and emerging fry have well-developed behaviors for moving through sediment (Bams 1969) and can emerge successfully through as much as 8 cm of sand (Crisp 1993). However, fry that are compromised by poor hyporheic conditions may be too weak to execute these behaviors successfully, and reports in the literature of fry that were unable to emerge because of larger fine sediments may have been confounded by this effect. The percentages less than 3, 6, or 10 mm should be adjusted downward to reflect the probable cleaning effect of redd construction (Figure 7B), with the realization that the effects of redd building on these sizes are more variable than the effects on the percentage finer than 1 mm (Kondolf et al. 1993).

Assess whether intragravel flow is adequate for incubation (step 9).—For eggs to successfully incubate, there must be a flow of stream water through the gravels, and salmonids are often observed to select gravels into which surface water is downwelling or intragravel water upwells. An undulating bed topography or increase in gradient (such as created

by natural riffles, bars, and other channel complexity) promotes this surface water-groundwater exchange (Savant et al. 1987; Thibodeaux and Boyle 1987), so the bed surface should be evaluated for such complexity. Intergravel flow depends both on gravel permeability and hydraulic gradient, the former being affected by fine-sediment content. The hydraulic gradient is more complex to evaluate, as it depends on flow level, channel bed geometry, and possibly on large-scale groundwater circulation patterns. In addition to assessing permeability and hydraulic gradient, intergravel flow, permeability, and dissolved oxygen can be directly measured using the techniques described earlier in this chapter to evaluate the suitability of gravels for spawning and incubation.

Consider changes in gravel size after sampling (step 10).—Potential changes in sediment yield and local sediment transport capacity should be evaluated at the watershed scale to identify potential sources of fine sediment during the incubation period and to evaluate the potential for bed scour or coarsening. Field studies to monitor changes in fine sediment percentages over the course of the incubation season (Adams and Beschta 1980; Lisle and Eads 1991) may be appropriate. Long-term changes in bed material size may compromise the future applicability of gravel-size data, so monitoring of bed material sizes in future years may also be appropriate.

Evaluate flow and temperature conditions during spawning and incubation (step 11).—If possible, potential spawning gravels should be assessed during the season when spawning would occur, so that water depths, velocities, and temperatures observed are comparable to those expected during spawning for the species of concern. If the potential spawning gravels are assessed during different conditions (such as higher flows), the observed values should be adjusted for the conditions expected during spawning and then evaluated for suitability for spawning and incubation based on published requirements (e.g., Reiser and Bjornn 1979; Flosi et al. 1998). In the absence of site-specific rating curves, conditions at a different (usually lower) flow

than observed can be estimated from a step-backwater model like HEC-RAS or simply application of the Manning equation (Chow 1959).

Summary and Conclusions

Spawning success is often limited by the quality of physical habitat, and a variety of techniques exist with which to assess grain size (whether large gravels are movable by spawning fish and whether interstitial fine sediment will affect incubation or emergence), permeability and interstitial flow, and dissolved oxygen content. To assess a gravel that is actually being used for spawning, the best indication of its suitability may be measures of the condition of fry emerging from the gravel. Often, however, the gravel must be assessed for its potential use by salmonids but without fish present to observe. We often judge potential spawning gravels using data drawn from actual redds. In such cases, percentages of fine sediment should be adjusted for the probable cleansing effect of the spawning fish. The appropriate sampling technique depends on the question posed: to determine if the gravel can be moved by the fish, pebble counts may suffice, but to assess fine sediment content, bulk sampling of subsurface deposits are needed. Better yet would be observations of fish use and direct measures of intragravel conditions and fry condition. All physical habitat assessment methods have limitations. The results obtained from these traditionally employed measures can be enhanced if used in conjunction with measures of fry conditions. Integrating these two types of approaches holds promise of more meaningful assessments and greater capacity to explain observed trends.

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Impact of Fine Sediment on Egg-To-Fry Survival of Pacific Salmon: A Meta-Analysis of Published Studies

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*Egg-to-fry survival of salmonids is tempered by habitat degradation, including increased sediment in streams. To best manage multiple salmon species and prioritize scarce habitat restoration funds for the benefit of fish recovery, many studies have described and predicted the relationship between fine sediment deposited in spawning gravels and salmonid egg-to-fry survival. In this article, we used published studies, agency reports, and university theses (N = 14) to create predictive relationships between percent fine sediment and egg-to-fry survival of Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*) and chum (*O. keta*) salmon, and steelhead trout (*O. mykiss*). In our analysis, coho survival tended to decline more rapidly per unit sediment increase and chum survival least rapidly. Threshold effects were observed, with survival dropping rapidly when percent fines less than 0.85 mm was greater than 10%. For other size classes of fines, a threshold was primarily observed only for eyed egg survival when fines exceeded 25–30%. Our predictive models combine both field and laboratory data and take into account a variety of conditions; they include estimates of uncertainty in the impact of sediment on egg-to-fry survival. These models can be used to forecast effects of watershed management practices on salmonids and to make comparisons between predicted salmonid survival rates under alternative management strategies for conditions where fine sediment is the limiting factor for survival.*

Keywords salmon incubation, salmon spawning, sediment deposition

INTRODUCTION

Since six species of Pacific salmonids were listed by the U.S. Endangered Species Act (ESA) as threatened or endangered (Knudsen et al., 2000), research and modeling has focused on factors that threaten the continued existence of these species. Habitat degradation is key among these factors (Nehlsen et al., 1991), including instream sedimentation resulting from human activities such as timber harvest, agriculture, urban and rural residential development, and road construction (e.g., Bjornn and Reiser, 1991; Waters, 1995). Increasing amounts of fine sediment (~2 mm or smaller) in spawning gravels has been shown to decrease survival of salmonid eggs to emergence (Bjornn and Reiser, 1991; Everest et al., 1987; Greig et al., 2005a, 2007).

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Because of the importance of fine sediment deposition to early salmonid survival, a great deal of research effort has gone into modeling the processes by which fine sediment enters and moves through stream systems. Our ability to model mechanisms by which land use increases sediment delivery to streams (e.g., the WEPP model: Elliot et al., 1995; Elliot and Hall, 1997; the PSYCHIC model: Davison et al., 2008) as well as our ability to model the mechanisms of transport and storage through stream networks (e.g., NetStream, Miller, 2003; the EUROSEM-GRIDSEM model, Botterweg et al., 1998; LISEM, DeRoo and Wessling, 1996) has become more sophisticated. Additional research has focused on the empirical evaluation of these processes (e.g., Collins and Walling, 2004; Heywood and Walling, 2003; Walling et al., 2008; Cai et al., 2005). As a result, we are increasingly confident in our predictions of how land use affects sediment deposition in stream reaches (Nilsson et al., 2003; Opperman et al., 2005).

However, sediment modeling exercises are often conducted at coarse resolutions across large extents, whereas our

understanding of how sediment impacts salmonid egg-to-fry survival comes from laboratory experiments or observations at the scale of a habitat unit or redd. Extrapolating results of individual survival studies to the larger scales at which we can restore sediment processes may be inappropriate because of differences in experimental conditions (i.e., season, geomorphology of stream, water chemistry), methods (i.e., laboratory vs. *in situ* studies, genetic origin of fish), and response variables (i.e., life stage, sediment metric) considered. As well, there are many factors other than sediment, such as dissolved oxygen, incubation temperatures, and biological controls, that contribute to the complexity of the spawning environment at the redd scale, and therefore to salmon survival (Malcolm et al., 2003; Greig et al., 2005b). Yet, for successful management of watersheds and salmon populations, managers need a reliable way to link disparate types of survival analyses.

Managers often rely on complex models to select restoration projects that will have positive benefits for fish (e.g., EDT, Moberland Biometrics Inc., 2004). If such models are used, then they must accurately predict not only which projects are likely to result in a decrease in fine sediment deposition but, ultimately, how survival of salmonids will respond to that reduced sediment deposition under a variety of conditions. While there are more detailed models that include several of the suite of factors present in the natural spawning environment (e.g., Alonso et al., 1996; Wu, 2000), calibration of these models is a large task and must be repeated for each new basin. Accurate prediction of fish response over large spatial extents requires models developed from studies conducted over a range of conditions. Since landscape scale studies are generally lacking, one way to address this gap is to pool results from multiple studies, thus incorporating the variability observed between individual studies into the modeled relationship. Incorporating known sources of variability is important whether the model has a narrow focus, e.g., the response of egg-to-fry survival to changes in sediment composition, or is an input to a more complex model of fish response to changes in multiple environmental factors.

Development of quantitative relationships linking sediment and survival that are robust to these differences in experimental conditions, methods, and response variables will improve our ability to link small-scale observations on fish survival to large-scale sediment input, routing, and storage models. We have compiled data from individual published studies relating egg survival to fine sediment composition, reanalyzed these data together, and developed models to predict species-specific mean survival as a function of sediment composition. In this modeling effort, we assume that it is the sediment quantity and to some extent the grain size that is primarily controlling survival. We do not account for the host of non-sediment factors, e.g., the potential impact of poor quality groundwater upwelling (Malcolm et al., 2003), on salmon survival.

We present a review of existing published data relating sediment to salmon egg-to-fry survival for steelhead trout (*Oncorhynchus mykiss*) and Chinook (*O. tshawytscha*) and chum

(*O. keta*) and coho (*O. kisutch*) salmon. We explore multiple early life stages and sediment size classes in freshwater systems of the Pacific Northwest United States to provide a meta-analysis of these existing data. Our meta-analysis is unique in that it yields models that are robust to the details of particular experiments as well as provides improved quantitative estimates of model and parameter uncertainty. We compare these robust models to identify species-specific differences and gain insight into the structure of the mechanistic relationships involved. For example, we ask whether the relationships between sediment and survival are linear, or whether they include a threshold above which survival is improbable? These robust models not only increase our understanding of watershed and salmonid ecology, but also provide powerful management tools by enabling combinations of models and estimates of uncertainty.

METHODS

Existing Data on Salmonid Egg-to-Fry Survival

We surveyed the primary literature for studies on salmonids in the Pacific Northwest that investigated the effects of fine sediment deposition on egg-to-fry survival. Of the 96 papers identified, most discussed observed or implied effects, but did not provide data or experimental analysis. Fourteen of these studies provided data that we could reanalyze, including seven experiments with Chinook salmon, four with steelhead, six with coho, and three with chum (Table 1). Some of these investigated the effects of sediment on survival of wild fish eggs in streams (e.g., Cederholm and Lestelle, 1974; Hall and Lantz, 1969), while others (e.g., Reiser and White, 1988; Tappel and Bjornn, 1983) described laboratory experiments, often using hatchery fish reared at high densities. Because of a general lack of field studies (e.g., all studies on Chinook salmon were laboratory studies), and because the laboratory studies have been well cited, we reasoned that including them would strengthen our dataset. In addition, our methodology would test whether the conclusions from field studies differed from those in the lab, and hence whether combining them was justified statistically. The sieve size used to quantify the sediment composition varied between studies, but, within each of the four groups considered here, all were within 0.2 mm (0.8–0.85 mm, 3.327–3.4 mm, 4.6–4.8 mm, 6.35–6.4 mm). We reanalyzed the data using one or more of five measures of substrate composition: percent fines < 0.85 mm, percent fines < 3.4 mm, percent fines < 4.8 mm, percent fines < 6.4 mm, and geometric mean particle size. The Fredle index (Lotspeich and Everest, 1981) has been shown to produce higher correlations with survival than the geometric mean (Chapman, 1988, using Tappel and Bjornn's (1983) data); however, the calculation of the index requires additional sediment size data not available from all papers reporting geometric means. In fact, we could only add a single study to what Chapman (1988) had summarized, so we chose not to include this metric.

Table 1 Pacific salmonid studies evaluated, including whether the study was conducted in an artificial (lab) or natural (field) environment, the number of redds monitored in each experiment, the life stage at which monitoring began, the sediment metric(s) used, and the slope of the logistic regression line fit to the original data

Source	Type no. redds ^a	Species	Life stage	Sediment metric	Slope (linear, quadratic) ^b
Bennett et al., 2003	Lab 8	Chinook	Green egg-to-fry	% fines < 0.85 mm	0.0602, -0.0032
				% fines < 3.4 mm	0.0312, -0.0038
				% fines < 4.8 mm	0.0268, -0.0029
				% fines < 6.4 mm	0.0243, -0.0022
				Geometric mean	0.1527
Bjornn, 1968	Lab 32	Chinook	Green egg-to-fry	% fines < 6.4 mm	-0.1425
Bjornn, 1969	Lab 28	Chinook	Green egg-to-fry	% fines < 6.4 mm	-0.0066, -0.0018
		Steelhead	Green egg-to-fry	% fines < 6.4 mm	-0.0795
Cederholm and Lestelle, 1974	Field 11	Steelhead	Eyed egg-to-yolk absorption	% fines < 0.841 mm	—
				% fines < 3.36 mm	+
Cederholm and Salo, 1979	Lab 31	Coho	Green egg-to-fry	% fines < 0.85 mm	-0.1971
				% fines < 3.36 mm	-0.0886
Hall and Lantz, 1969	Field 20	Coho	Egg-to-fry ^c	% fines < 0.83 mm	-0.2166
Hall, 1986	Lab 6	Chinook	Eyed egg-to-fry	% fines < 0.8 mm	-0.1578, -0.0058
		Chum	Eyed egg-to-fry	% fines < 0.8 mm	-0.1458
		Coho	Eyed egg-to-fry	% fines < 0.8 mm	-0.3328, 0.0046
Koski, 1966	Field 22	Coho	Egg-to-fry ^c	% fines < 3.327 mm	-0.1203
Koski, 1975	Lab 35	Chum	Egg-to-fry ^c	% fines < 3.327 mm	0.2469, -0.0037
Reiser and White, 1988	Lab 15	Chinook	Green egg-to-fry	% fines < 0.84 mm	-0.1447
				% fines < 4.6 mm	-0.0738
		Steelhead	Eyed egg-to-fry	% fines < 0.84 mm	-0.1630
				% fines < 4.6 mm	+
		Steelhead	Green egg-to-fry	% fines < 0.84 mm	-0.1367
				% fines < 4.6 mm	-0.0550
Reiser and White, 1990	Lab 8	Chinook	Eyed egg-to-fry	% fines < 0.84 mm	—
		Chinook	Green egg-to-fry	Geometric mean	-0.4870, 0.0119
				% fines < 0.84 mm	-0.1458
Scrivener and Brownlee, 1989	Field 13–14	Chum	Egg-to-fry ^c	Geometric mean	0.0710
		Coho	Egg-to-fry ^c	Geometric mean	0.3347
		Coho	Egg-to-fry ^c	Geometric mean	0.2048
Tagart, 1984	Field 18	Coho	Egg-to-fry ^c	% fines < 0.85 mm	—
Tappel and Bjornn, 1983	Lab 15	Chinook	Eyed egg-to-fry	% fines < 0.85 mm	-0.2818
				% fines < 4.76 mm	0.0411, -0.0034
				% fines < 6.35 mm	0.0254, -0.0025
				Geometric mean	1.2135, -0.0382
				Steelhead	Eyed egg-to-fry
		% fines < 4.76 mm	-0.1165		
% fines < 6.35 mm	-0.0969				
Geometric mean	1.1284, -0.0363				

^aNumber of redds (or artificial equivalent) is the same for each experiment unless indicated otherwise.

^bAll relationships shown are statistically significant (Wald test) at the 0.05 level. A – indicates the slope is not significant, + indicates the individual relationship is not statistically significant, but when combined with other observations within the same species and egg stage, a significant relationship emerges.

^cDevelopment stage not identified.

Meta-analysis includes a variety of statistical methods for synthesizing the results of individual studies (e.g., Hedges and Olkin, 1985). One requirement for meta-analysis is that there is a common summary statistic across studies, which is often a measure of a treatment effect in a series of experiments. Under certain assumptions, the analysis of the summary statistics is equivalent to the analysis of the original data (Olkin and Sampson, 1998; Mathew and Nordström, 1999). We chose to utilize the original data in our meta-analysis since it was generally available and the published summary statistics were not consistent across studies. Furthermore, we felt that a logistic model

more accurately reflected the relationship between sediment and survival in that survival is constrained between zero and one. By using this novel approach, we hoped to improve on past analyses.

The individual datasets that were used to develop new models (based on combined datasets) are identified in Table 1. We only combined studies where either individual relationships with fine sediment substrate were significant or a significant relationship was found when combined with other data in the same species and egg stage class. We included all data that showed any evidence of a statistical relationship between fines and survival

and excluded the few datasets without a clear relationship (only 8%).

Statistical Analysis

We used logistic regression models to fit data from multiple sources. The logit of survival was regressed on the various measures of sediment composition, where

$\text{logit}(s) = \log\left(\frac{s}{1-s}\right)$, the log of the odds of survival. The relationship between the logit of survival and fines is linear, whereas the relationship between survival and fines is not. The transformation is $\text{survival} = \frac{1}{1+e^{\beta_0 + \beta_1 * \text{Sediment}}}$. With a single independent variable that has only a linear component, the odds of survival, $\left(\frac{s}{1-s}\right)$, has an intuitive interpretation, i.e., the proportional change in the mean odds of survival with a one-unit change in sediment.

The reasoning behind these models is that each egg has a specific probability of surviving to produce a fry, and that probability depends on sediment composition (at least in part; recall that we did not include other factors influencing survival in our models). Further, each observation of a group of eggs (e.g., an experimental tray or a redd in the stream) is considered a binomial experiment with N trials, where N is the number of eggs in the observational unit. We require an estimate of N , the number of eggs in the observational unit, in order to fit this model. In most of the studies, the number of observed eggs or the estimated number of eggs per female was reported. For studies without this information, we used species-specific average fecundity values. In a few of the studies, the reported data were means of two to six observational units; these data were pooled and treated as one observational unit, but weighted to compensate for the expected reduction in variability.

We first fit logistic regression models to the data from each experiment independently. This initial fitting indicated that nearly all of the data were over-dispersed, i.e., the observed variation exceeded that expected under a binomial model. Quasi-likelihood procedures (after McCullagh and Nelder, 1989) were used to fit the models to the data. We used Williams' method (Williams, 1982) to estimate the over-dispersion parameter, which was subsequently used to adjust the standard errors of the regression parameter estimates. We also checked for quadratic relationships between sediment metrics and egg-to-fry survival.

Next, we compared the slopes of the relationships between percent fines and survival among studies using Wald tests (see McCullagh and Nelder, 1989). If the slopes were significantly different, we did not try to combine the datasets. Otherwise, a parallel slopes model was fit to the combined dataset. This combined data model was used to estimate the change in the odds of egg-to-fry survival as a function of changes in the percentage of fines in the substrate. We tested whether models with a common slope shared a common intercept. If not, a weighted average of the intercepts was calculated.

To construct 95% Wald confidence intervals for the estimated mean survival when a weighted average was used for

the intercept, we used a bootstrap procedure (Efron and Gong, 1983). A bootstrap sample was drawn from each of the groups having a common slope. We fit a parallel lines model to the bootstrap sample and used the slope of the lines as an offset in a subsequent model to estimate the intercept. We repeated this 5000 times and used the output to estimate the variances of the intercept and slope, as well as the covariance between them.

RESULTS

The datasets included in this meta-analysis are from studies that represent both lab and field experiments on coho, steelhead, Chinook, and chum salmon. In 34 out of 39 regressions, when the data were reanalyzed using our approach, there was a significant linear relationship between the proportion of fines and (logit) egg-to-fry survival. In 13 of these, a significant quadratic relationship was also detected, but there was no obvious pattern across species. Two of the five non-significant relationships were statistically significant when combined with data from other studies in the same species, even though the studies were initially modeled with separate regression lines, and, in two additional data sets, there was a second sediment metric that did produce a significant relationship with survival. Thus, only one dataset was completely eliminated from the analysis (Tables 1 and 2). The inclusion of non-significant datasets would not have contributed much to the estimation of the slope of the regression line, as they all had large 95% confidence intervals; though, by eliminating them, we have probably underestimated the confidence intervals of the final models for percent fines < 0.85 mm. There were several groups (e.g., chum salmon and steelhead vs. geometric mean) with only a single source dataset. These are included in the tables that follow, even though the parameters are the same as those in Table 1. The annual survival estimates reported by Scrivener and Brownlee (1989) were based on calculated egg deposition and enumeration of emergent fry for the entire study area. Since the other studies monitored individual redds or some laboratory equivalent, the Scrivener and Brownlee data were not included in the meta-analysis.

For the smallest sediment size class (percent fines < 0.85 mm), we were able to create a new, combined model for Chinook and coho salmon together based on five and three datasets, respectively; however, only one dataset was available for chum salmon (Table 2, Figure 1). The three steelhead datasets did not share a common slope.

As mentioned above, the most intuitive way to understand the impact of sediment on survival is through changes in the odds of survival. The odds of survival can be transformed into actual survival, but this relationship is nonlinear. Table 3 describes how a 1% increase in percent fines (for each size class) translates into a change in predicted odds of survival by species. For example, a 1% increase in fines < 0.85 mm will result in a 16.9% (13.3, 20.4) reduction in the odds of survival for Chinook salmon (Table 3). There was a somewhat more dramatic reduction in

Table 2 Results of comparisons within and across studies where metric is percent fines < 0.85 mm. Groups are based on species and egg stage at which monitoring began. Bold font indicates parameters of final models developed for this analysis

Species	Life stage	Source	Comparisons within groups of studies				
			Slope ^a (SE)	<i>p</i> -value ^b	Intercept ^c (SE)	<i>p</i> -value ^b	Intercept ^d (SE)
Chinook	Green egg-to-fry	Reiser and White, 1988	-0.1853 (0.0211)	>0.07	-0.1082	<0.0001	1.3418 (0.1940)
		Reiser and White, 1990			1.7497		
		Bennett et al., 2003			0.5698		
	Eyed egg-to-fry	Hall, 1986			0.9374		
		Tappel and Bjornn, 1983			2.6680		
Steelhead	Green egg-to-fry	Reiser and White, 1988	-0.1502	>0.48	0.7547	<0.0001	NA
		Reiser and White, 1988			3.1604		
	Eyed egg-to-fry	Tappel and Bjornn, 1983	-0.2869		3.3137	NA	
		Cederholm and Lestelle, 1974	Excluded	—	—	—	—
	Coho	Green egg-to-fry	Hall and Lantz, 1969	-0.2024 (0.0345)	>0.97	2.2629	0.0002
Green egg-to-fry		Cederholm and Salo, 1979			2.1563		
Eyed egg-to-fry		Hall, 1986			0.4670		
		Tagart, 1984	Excluded	—	—	—	—
Chum	Eyed egg-to-fry	Hall, 1986	-0.1458 (0.0288)	NA	0.1436 (0.3156)	NA	NA
		All species	-0.1846 (0.0125)	>0.18	—	<0.0001	1.9890 (0.1523)

^aThe same estimate within a group signifies that studies were not significantly different from one another ($p > 0.05$), and different estimates indicate significant differences within the group ($p < 0.05$). Standard error is from logistic regression if bootstrapping was unnecessary; otherwise, it was from bootstrap. Excluded studies were those with non-significant slopes (Table 1).

^b*p*-value refers to the test of whether the parameter is the same for all group members.

^cIntercept fit using logistic regression. Standard error was included if no bootstrapping was necessary.

^dIntercept fit during bootstrap procedure with bootstrap standard error.

survival for coho salmon (18.3%), and a slightly less dramatic reduction for chum salmon (13.6%). By combining data for all species, we estimate that, on average, a 1% increase in percent fines < 0.85 mm will result in about a 17% reduction in the odds of survival over all species.

Similarly, we were able to provide combined models for percent fines < 3.3–4.8 mm for each species and for pairs of species with similar survival patterns (Table 4, Figure 2). The studies of Chinook used 4.8 mm as an upper bound on fine sediment, except for Bennett et al. (2003), who also included measurements of percent fines < 3.4 mm. We tested for a difference between the regression lines fit to each of these and found no statistical difference (slope: $p > 0.68$, intercept: $p > 0.45$); hence, only data on percent fines < 4.8 mm were used, since this size class corresponded to the other Chinook studies. Because we expect the mechanisms by which sediment affects egg-to-fry survival to be similar across species, we used these results for Chinook salmon to justify combining the two size classes in steelhead, where a direct test of differences was not possible.

The models for percent fines < 3.3–4.8 mm were based on three studies with Chinook salmon, four with steelhead, two with coho salmon, and one with chum. Changes in the odds of survival for a given increase in fine sediment are much less for this metric than when the metric is percent fines < 0.85 mm, with the exception of the eyed egg-to-fry survival in Chinook (Table 3). The pattern in the modeled odds of survival with each 1% increase in fine sediment was similar to that seen above, with a lower impact on chum (-6.0), and (with the exception of eyed Chinook eggs) the largest effect on coho (-9.2). The

impact on green Chinook eggs and steelhead was intermediate. The large change in the odds of survival with increasing fines for eyed Chinook eggs (-14.2 per 1% increase in fines) appears anomalous, but the odds of survival is actually higher for eyed eggs at any level of percent fines, even though the rate of change is greater. When evaluating actual survival, this is reflected in the fact that the impact is constrained to levels of fines above 20%, whereas, in the other groups, there is a smaller change per sediment increment over a larger range of fines (Figure 1c and 1d). In general, survival at a particular level of fines is higher when the metric includes larger size classes (Figure 1).

We provide combined models for both Chinook and steelhead salmon for the largest size class (percent fines < 6.4 mm) and for a model based on the geometric mean of the sediment grain sizes (Table 5). Comparisons within and among the studies utilizing both sediment metrics indicate that the relationship between Chinook survival and sediment is not consistent. There is a moderate to strong quadratic component in three of the four studies for the largest sediment size class, but the evidence for a quadratic relationship in Bjornn's (1968) study is weak ($p > 0.09$). Similarly, only one of the four geometric mean datasets has a significant quadratic relationship. While a single slope could be fit to the three studies with a similar relationship, no common slope model could be fit to all four studies. A common quadratic model was fit to the steelhead data from both sediment metrics. The odds of survival is not constant across sediment composition because of the quadratic relationship, but ranges from a decrease of 4.1% (-12.0, 4.6), when fines < 6.4 increase from 10% to 11%, to a decrease of 15.7% (-30.1, 1.5), when

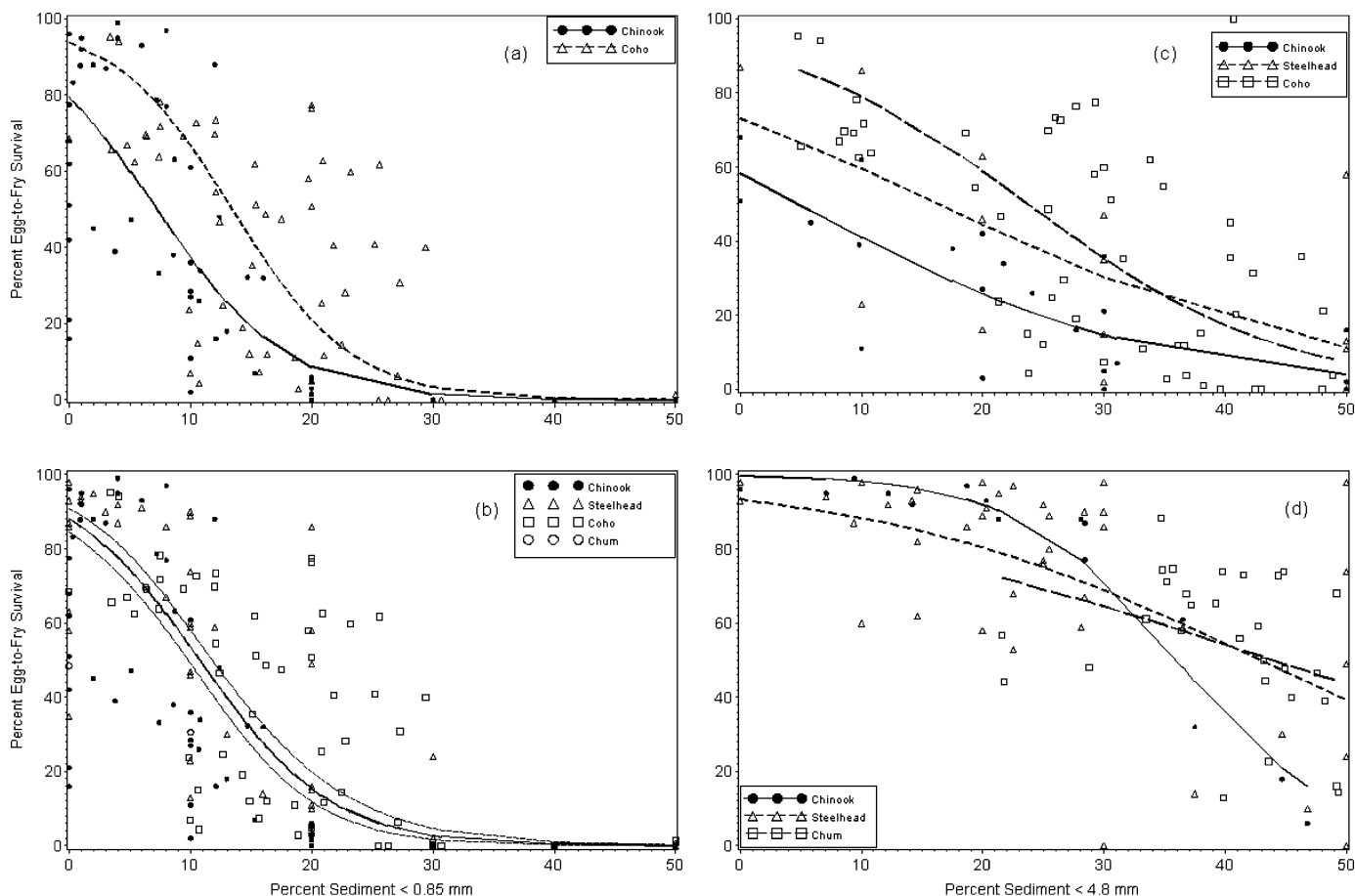


Figure 1 Relationship between egg-to-fry survival and percent sediment, showing data from the literature used in analysis. (a) Data and modeled egg-to-fry survival of Chinook and coho salmon vs. percent sediment < 0.85 mm. (b) Egg-to-fry survival for Chinook, coho, and chum salmon vs. percent sediment < 0.85 mm. Line is the modeled mean survival based on data from all species and includes the 95% confidence interval. (c) Data and modeled green egg-to-fry survival for Chinook salmon, steelhead, and coho salmon vs. percent fines < 4.8 mm. (d) Data and modeled eyed egg-to-fry survival for Chinook salmon, steelhead, and chum salmon vs. percent fines < 4.8 mm.

fines increase from 50% to 51%. The odds of survival increase by 20.8% (9.2, 33.7) when the geometric mean of sediment size increases from 5 to 5.25 mm, and by 10.3% (-3.1, 25.6) when the mean increases from 10 to 10.25 mm.

Three field studies, two with coho salmon and one with steelhead, were included in the modeling and shared a common slope with the lab studies in their group. In both of the coho studies, the intercept from the field data was larger than those in the lab

Table 3 Comparison of the change in the odds of survival resulting from a 1% increase in fines

Species	Metric	Change in sediment	Egg stage	Change in odds of survival (%)	95% Confidence interval
Chinook	<0.85 mm	+1%	Green and eyed	-16.9	(-20.4, -13.3)
Coho		+1%	Green and eyed	-18.3	(-23.9, -12.3)
Chum		+1%	Eyed	-13.6	(-18.3, -8.6)
All species		+1%	Green and eyed	-16.9	(-19.1, -14.6)
Chinook	<3.4-4.6 mm	+1%	Green	-6.7	(-9.0, -4.4)
		+1%	Eyed	-14.2	(-18.3, -9.8)
Steelhead	<6.4 mm	+1%	Green and eyed	-6.0	(-8.3, -3.6)
Coho		+1%	Green and unidentified	-9.2	(-12.4, -5.9)
Chum		+1%		-4.2	(-7.3, -1.0)
All species		+1%	Green and eyed	-7.1	(-8.5, -5.7)
Steelhead	<6.4 mm	10-11%	Green and eyed	-4.1	(-12.0, 4.6)
		30-31%		-10.1	(-21.6, 3.0)
		50-51%		-15.7	(-30.1, 1.5)

Table 4 Results of comparisons within and across studies where metric is percent fines < 3.3–4.8 mm. Groups are based on species and egg stage at which monitoring began. Bold font indicates parameters of final models developed for this analysis

Species	Life stage	Source	Comparisons between groups of studies				
			Slope ^a (SE)	<i>p</i> -value ^b	Intercept ^c (SE)	<i>p</i> -value ^b	Intercept ^d (SE)
Chinook	Green egg-to-fry	Bennett et al., 2003	-0.0696 (0.0141)	>0.66	0.3336 (0.3096)	>0.89	NA
	Green egg-to-fry	Reiser & White, 1988					
	Eyed egg-to-fry	Tappel and Bjornn, 1983	-0.1528 (0.0265)		5.4962 (0.8859)	NA	NA
Steelhead	Green egg-to-fry	Reiser and White, 1988	-0.0615 (0.0126)	>0.26	1.0030 (0.4522)	NA	NA
	Eyed egg-to-yolk absorption	Cederholm and Lestelle, 1974			2.6359 (0.4184)	>0.75	NA
	Eyed egg-to-fry	Tappel and Bjornn, 1983					
Coho	Eyed egg-to-fry	Reiser and White, 1988					
	Green egg-to-fry	Cederholm and Salo, 1979	-0.0966 (0.0152)	>0.46	1.9393 2.8783	0.0303	2.2911 (0.3860)
Chum	Egg-to-fry	Koski, 1966					
Chum	Egg-to-fry	Koski, 1975	-0.0428 (0.0168)	NA	1.8774 (0.7206)	NA	NA
Chinook + Steelhead			-0.0737 (0.0115)	>0.08	—	<0.0001	2.1132 (0.3009)
Coho + Chum			-0.0760 (0.0128)	>0.25	—	<0.0001	2.3753 (0.4512)
All species			-0.0746 (0.0087)	>0.06	—	<0.0001	2.2911 (0.2646)

^aThe same estimate within a group signifies that studies were not significantly different from one another (*p* > 0.05), different estimates indicate significant differences within a group (*p* ≤ 0.05). Standard error is from logistic regression if bootstrapping was unnecessary; otherwise, it was from bootstrap.
^b*p*-value refers to the test of whether the parameter is the same for all group members.
^cIntercept fit with logistic regression. Standard error was included if no bootstrap was necessary.
^dIntercept fit during bootstrap procedure with bootstrap standard error.

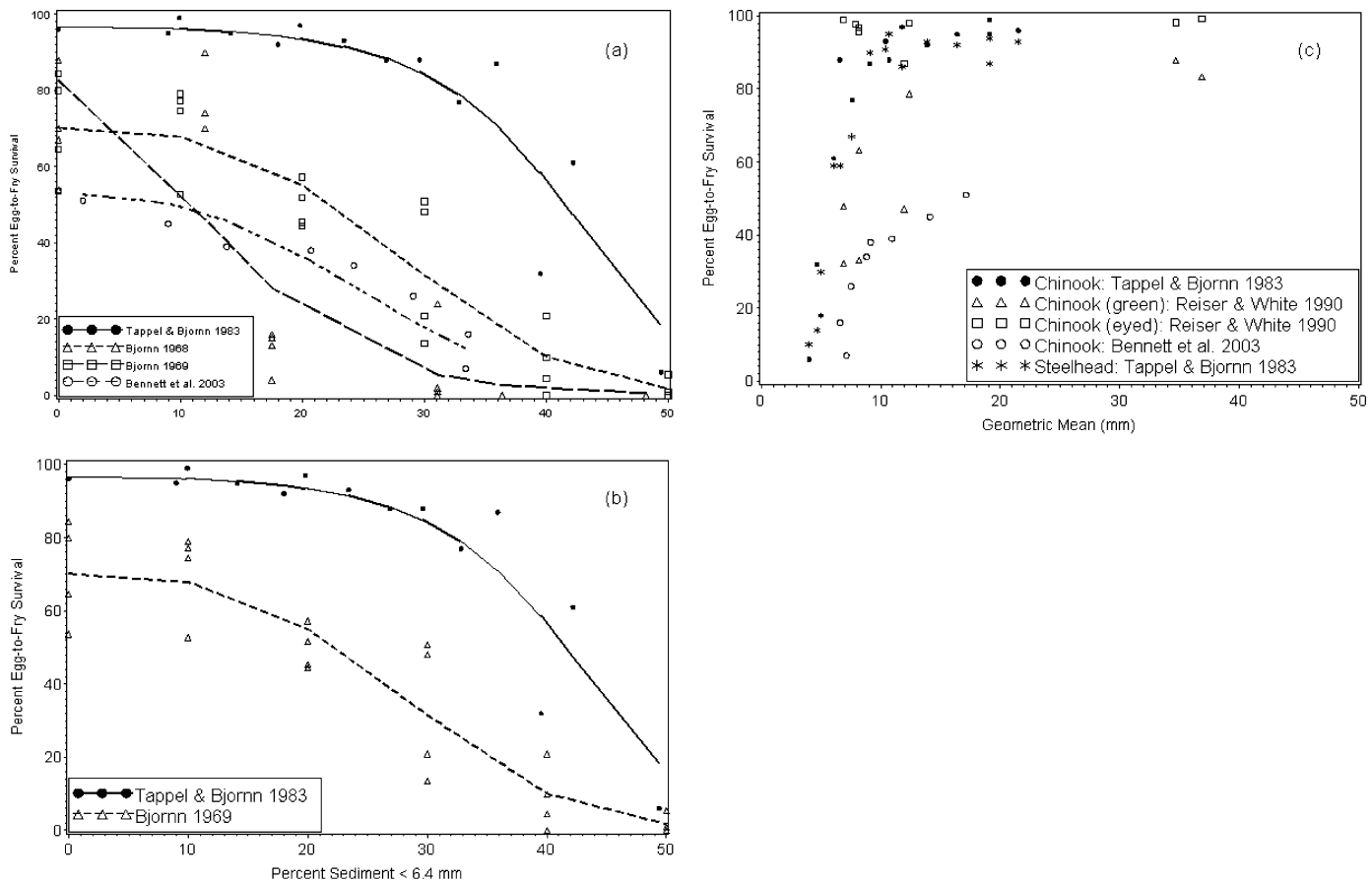


Figure 2 Relationship between egg-to-fry survival and sediment showing data from the literature used in analysis. (a) Chinook salmon data and modeled mean survival vs. percent sediment < 6.4 mm. (b) Steelhead data and modeled mean survival vs. percent sediment < 6.4 mm. (c) Chinook salmon and steelhead data vs. geometric mean of sediment size (mm).

Table 5 Results of comparisons within and across studies where sediment metric is % fines < 6.4 mm or geometric mean (mm). Groups are based on species and egg stage at which monitoring began. Bold indicates parameters of final models developed for this analysis

Species	Life stage	Source	Comparisons between groups of studies						
			Quadratic slope ^a (SE)	<i>p</i> -value ^b	Linear slope ^a (SE)	<i>p</i> -value ^b	Intercept ^c (SE)	<i>p</i> -value ^b	Intercept ^d (SE)
Sediment metric: Percent fines < 6.4 mm									
Chinook	Green egg-to-fry	Bjornn, 1968	ns	—	-0.1425 (0.0219)	NA	1.5557 (0.3755)	NA	NA
	Green egg-to-fry	Bennett et al., 2003	-0.0022 (0.0005)		-0.0110 (0.0213)	>0.68	0.0932 (0.2875)	<0.0001	NA
	Green egg-to-fry	Bjornn, 1969					0.8530 (0.2294)		
	Eyed egg-to-fry	Tappel and Bjornn, 1983					3.3068 (0.3329)		
Steelhead	Green egg-to-fry	Bjornn, 1969	-0.0016 (0.0006)	>0.75	-0.0077 (0.0308)	>0.57	0.2376 (0.3126)	<0.0001	NA
	Eyed egg-to-fry	Tappel and Bjornn, 1983					2.8925 (0.4648)		
Sediment metric: Geometric mean (mm)									
Chinook	Green egg-to-fry	Bennett et al., 2003	ns	—	0.0775 (0.0191)	>0.16	-1.6037 (0.2750)	<0.0001	NA
	Green egg-to-fry	Reiser and White, 1990					-0.7847 (0.3020)		
	Eyed egg-to-fry	Reiser and White, 1990					6.6880 (0.5132)		
	Eyed egg-to-fry	Tappel and Bjornn, 1983	-0.0382 (0.0091)	NA	1.2135 (0.2236)	NA	-5.8271 (1.0609)	NA	NA
Steelhead	Eyed egg-to-fry	Tappel and Bjornn, 1983	-0.0363 (0.0058)	NA	1.1284 (0.1471)	NA	-5.6557 (0.7317)	NA	NA

^aThe same estimate within a group signifies that studies were not significantly different from one another (*p* > 0.05), different estimates indicate significant differences within a group (*p* < 0.05). Standard error was from logistic regression if bootstrapping was unnecessary; otherwise, it was from bootstrap.

^b*p*-value refers to the test of whether the parameter is the same for all group members.

^cIntercept fit with logistic regression. Standard error was included if no bootstrapping was necessary.

^dIntercept fit during bootstrap procedure with bootstrap standard error.

studies, while there was no difference between the intercepts in the steelhead raised from eyed eggs (Tables 2 and 3).

DISCUSSION

We found evidence in the literature that increasing amounts of fine sediments in stream substrates reduces egg-to-fry survival for salmonids (see Table 1; all regression equations have a negative slope or, if quadratic, are generally concave down; the relationships with the geometric mean are reversed). Using data from published studies, we were able to construct models that predict the odds of survival for Chinook, chum, and coho salmon and steelhead for three fine sediment size classes. Fewer data were available for chum salmon than the other species analyzed, and we found no studies that investigated egg-to-fry survival of pink or sockeye salmon. When the sediment metric was percent fines < 0.85, 3.4, or 4.8 mm, the relationship with the odds of survival was generally linear, but when the metric was percent fines < 6.4 mm or the geometric mean, the relationship was often quadratic. The fact that the slopes of the modeled relationships were similar within most species and egg stage groups, despite the differences in intercept, suggests that the change in the odds of survival is constant and that differences in the environments for specific studies is reflected in the intercepts, i.e., the survival curve is simply shifted one way or the other. Adding more datasets for those groups with few sources of data would likely help establish a more robust estimate of the survival curve.

Greig et al. (2005a) identified oxygen availability as an important factor in the survival of salmon eggs, but the relationships between the sediment composition and oxygen levels were complex and varied from site to site as well as within sites.

They found low correlations between various measures of sediment composition and survival. In groundwater-fed streams, survival may not be related to substrate composition, as the oxygen content of groundwater can vary independently of substrate characteristics (Sowden and Power, 1985); yet, there is a clear relationship between survival and dissolved oxygen in these systems (Sowden and Power, 1985; Malcolm et al., 2003). In addition, the amount of organic matter in the substrate and adjacent water column influences the amount of dissolved oxygen available to developing embryos (Greig et al., 2005a). We did, however, find significant relationships between sediment composition and egg-to-fry survival in nearly all of the studies we were able to locate. Perhaps these factors explain some of the variability we saw in these data. The models incorporated into this analysis are nonlinear (on the survival scale), and thus it is possible that the low linear correlations reported by Greig et al. (2005a) reflect the nonlinearity of the relationship between sediment and survival. The inter-site variability noted by Greig et al. (2005a) may correspond to the variability in the intercept of the regression line found here. The high intra-site variation in survival found by Greig et al., as well as regional differences in stream conditions (e.g., their study rivers had higher fine silts, clays, and organic matter than are typical in Pacific Northwest streams) highlight the complexity of the spawning environment and therefore the need to exercise caution when applying models such as ours to any one particular site.

The act of spawning cleans fine sediment from the gravel in redds; thus, it is sediment deposited after eggs are laid that could decrease survival (Chapman, 1988). Multiple mechanisms have been proposed to explain the negative impacts of this fine sediment deposition on egg-to-fry survival. First, fine sediment may impede the flow of oxygenated water through gravel in the

egg pocket (Chapman, 1988; Lisle 1989), causing suffocation of eggs or reducing the removal rate of toxic metabolic wastes (Bennett et al., 2003). These reduced dissolved oxygen levels may delay embryo development, lead to early emergence (before yolk sac absorption is complete), and/or decrease emergent fry size (Chapman, 1988). Second, a layer of fine sediment may reduce interstitial spaces and physically prevent fry emergence (Beschta and Jackson, 1979).

Based on proposed mechanisms of how sediment affects survival (i.e., suffocation or entrapment), conventional wisdom suggests that relationships should be strongest when sediment size classes are smallest. Our analyses confirmed this assumption, where the odds of survival were lower and decreased faster when fines were < 0.85 mm than at larger size classes (Table 3). Note, however, that we did not have data to evaluate possible relationships with finer size classes such as silt, clay, or organic matter. Work by Greig et al. (2005b, 2007) suggests that these smaller classes are indeed important in some rivers, and therefore our models may not be applicable in all cases.

Using size classes available to us, we found four general patterns in the survival curves (Figures 1 and 2). At the smallest sediment size, percent fines < 0.85 mm, we saw evidence of a threshold in egg-to-fry survival of Chinook salmon and steelhead. There was a steep decrease in survival, leveling out at less than 10% when fines were greater than 25%. We found a similar relationship for eyed eggs when fine sediment was < 4.8 or 6.4 mm, but the threshold occurred at a much higher level of fines (above 50% for each). Mean survival for eyed eggs of Chinook or steelhead was generally greater than 90% until the percentage of fines increased beyond 20–25, at which point survival decreased rapidly. There was less of a threshold effect for green eggs of Chinook and steelhead for the same fine sediment class. For green eggs, survival was initially lower than for eyed eggs, and decreased steadily before leveling off at very low survival when fines were >30–40%. For the largest sediment size class (percent fines < 6.4 mm), the relationship with odds of survival was quadratic. When fine sediment was <10%, survival was less affected than for other sediment size classes.

While in common use, size class thresholds of, for example, <0.85 mm are relatively arbitrary. A larger or smaller threshold might just as well have been used, and the choice of threshold might impact results and, in particular, perceived differences in percent fine sediment across regions. The use of the geometric mean of particle size as the sediment metric was suggested by Platts et al. (1979) and removes reliance on arbitrary thresholds. However, in our survey, we found only four studies for which we could extract the geometric mean. Of those, the sediment size mixture was not comparable, and survival was highly variable, especially when the geometric mean was between 7 and 13 mm. This is a level at which egg survival is expected to decrease, but the sharp increase is difficult to model due to the variability in the survival data. We were able to construct some relationships using these studies; but, before we can develop any meaningful predictive relationships, more studies are needed that record geometric mean particle size, particularly in the 7- to 13-mm

range. If the geometric mean can be precisely and accurately determined, then use of this metric could decrease the variability in survival among studies because sediment sizes could more easily be classified on a similar scale.

There were several limitations of the data on our ability to construct predictive relationships. First, for many of the sediment metrics, we had too few datasets from which to build representative models. The sparse number of studies could not represent all (or even most) possible conditions encountered by fish in natural systems. Furthermore, there was a high amount of variability among studies. Much of the data we used were from laboratory studies, where experimental conditions were highly controlled, yet less realistic than field studies, where other factors (e.g., temperature, discharge) may interact to reduce egg-to-fry survival. Many of the laboratory studies used hatchery fish raised at much higher densities than found under natural conditions. Even within studies, estimates of the intercept were often not consistently precise, reflecting the inherent variability in survival. Another limitation was that to transform the predictions from odds of survival to actual survival, the intercept must be estimated even though there is little statistical justification.

Despite these limitations, our statistical approach complements existing mechanistic modeling (e.g., Alonso et al., 1996; Wu, 2000) and empirical (e.g., Lisle, 1989) approaches. Such approaches often cannot be used for conditions other than those for which they were created due to their complexity and lack of local empirical data for parameterization. A statistical meta-analysis approach, using data from a wide variety of sources, overcomes some of these limitations. In cases where researchers can appropriately match the experimental conditions of individual studies, statistical relationships can be used to estimate salmonid survival given the amount of fine sediment present in streams. Environmental conditions are variable within individual studies (e.g., Greig et al., 2005a; Sear, 1993) and our approach, which includes explicit consideration and calculation of confidence intervals can provide some estimate of the range of likely responses as well as the probability of particular responses. Across sites, conditions are even more variable. Land use management decisions and recovery planning decisions for these ESA-listed species are made over very large scales and across geographically diverse regions. Predictions from our models are averages with wide confidence intervals, and they can provide useful estimates of the changes expected in salmon survival given large-scale changes in land management or suites of proposed watershed restoration actions. For example, Steel et al. (2008) used earlier versions of these models to compare fisheries' impacts given six different watershed restoration strategies. Because they were able to model spatial variations in expected sediment deposition, they were also able to predict spatial patterns in salmon survival.

There are significant strengths of our approach. We synthesized information from available studies into simple predictive relationships that reflect underlying uncertainties in the original datasets. Due to a paucity of comparable rigorous studies,

our predictive relationships may not be robust to all conditions experienced by Pacific salmon species. However, because we combined data from various sources, the predictive relationships we have developed in this meta-analysis are more robust to the variables that often plague extrapolation of ecological relationships from small-scale studies to large-scale models. As well, they are more robust to geographical or ecological conditions than the relationships from individual studies of the relationship between fines and survival. The bootstrapped confidence intervals provide realistic ranges of predicted changes in salmon survival with changes in in-stream fine sediment. Like all models, the models presented here are best used with strong consideration, not just for the point estimate of the most likely model output, but also for the confidence intervals, the range of potential modeled outcomes. Like all models, the models presented here are also best used without extrapolating beyond the range of the data used to build the model. Our meta-analysis approach has increased the range of data used for any one relationship, but, as pointed out already, there are clearly stream types and ecological conditions for which no data are available, and extreme caution should be used if one must make estimates for stream types and conditions not represented in the original data.

Given known or modeled levels of fine sediment deposition associated with different types of land use (e.g., fines in streams can be much higher in agricultural and developed watersheds; Opperman et al., 2005), managers can use these predictive relationships to begin to identify areas where salmonid egg-to-fry survival may be limited. Moreover, our predictive relationships can be used to forecast potential effects of watershed management practices on salmonids and to make comparisons of relative predicted survivals under alternative management strategies to see what set of restoration actions is most likely to improve egg-to-fry survival (e.g., Steel et al., 2008). These predictive models should improve our ability to link large-scale models that predict how much sediment is, or will be, entering streams, to small-scale observations on fish survival and to more efficiently managing landscapes that contribute to fine sediment entering streams.

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INFLUENCES OF INCREASED SAND DELIVERY ON THE MORPHOLOGY OF SAND AND GRAVEL CHANNELS¹

William L. Jackson and Robert L. Beschta²

ABSTRACT: A flume study was conducted to examine (1) changes in the particle-size distribution of sediments in riffles due to the proportion of sand in transport and the total rate of bedload transport at the time the riffle is deposited and (2) the effect of high sand transport rates on the stability of gravel riffles. The median particle size of sediment deposited in the riffle was larger than that of the sediment in transport. Small but significant ($\alpha = 0.05$) decreases in the median particle size of riffle sediments resulted as the sand-to-gravel ratio of sediment in transport varied from 1:1 to 5:1. Gravel deposition efficiency decreased linearly as a function of the sand-to-gravel ratio. Increased concentrations of sand in transport caused previously stable gravel riffles to undergo scour. These results, in combination with information from other studies, suggest that an alluvial channel with pool-riffle sequences and with sand and gravel beds may respond to an increased delivery of sand by reducing form roughness. Form roughness can be reduced by degrading riffles and filling pools. Subsequent responses may be increases in width-to-depth ratio and slope.

(KEY TERMS: riffles; alluvial channels; streambed; bedload sediment; scour and deposition; channel morphology.)

INTRODUCTION

A strong interdependency exists between flow conditions and sediment transport, and the associated streambed composition and form (Schumm, 1971). An alluvial channel which has reached a balance among slope, channel characteristics and discharge is said to be "graded" if its resulting hydraulic characteristics are the minimum required to transport the sediment load delivered to the channel (Leopold and Maddock, 1953). If watershed conditions change and an increased supply of sand-sized sediments to a sand- and gravel-bed channel occurs, we hypothesize that a channel's initial morphologic response will be to reduce form roughness to permit increases in flow velocity and bedload transport capacity. Form roughness caused by gravel bars has been shown to account for approximately 50 to 75 percent of the total flow resistance in gravel bed streams with high width/depth ratios and low sinuities (Prestegard, 1983).

Form roughness may be reduced by filling pools and degrading riffles. Pools fill when transported sediments deposit on them at a higher rate than they are being removed. Usually

at discharges less than bankfull, most sediments will tend to deposit in pools because sediment transport capacities are generally less than over riffles (Keller, 1971; Lisle, 1979).

Riffle degradation may occur as the result of reduced riffle stability. Reductions in riffle stability may be caused by decreases in the particle-size distribution of riffle sediments resulting from less sorting of sediment sizes during riffle deposition, or by increases in the capacity of the flow-sediment mixture to transport riffle sediments. Several researchers have suggested that increased concentrations of sediment in suspension near the streambed increase the ability of the flow to transport bed sediments (Vanoni, 1941; Einstein, 1944; Leopold and Maddock, 1953; Colby, 1964a). Initial reductions in form roughness would encourage subsequent adjustments in channel width, depth, and slope.

The objective of this research was to identify responses of alluvial sand- and gravel-bed channels to increases in sand delivery. Two flume experiments tested the effects of increased sand transport on the stability, size, and particle-size composition of gravel riffles. Results of the flume experiments, in combination with evidence in the literature, provided a basis for proposing a series of responses including degradation of riffles and filling of pools (decreases in bedform roughness), and increases in width-to-depth ratio and channel slope.

The discussion is intended to relate to general response tendencies. The actual nature and degree of response for specific channels will be dependent upon initial conditions, the magnitude of increased sand deliveries, and the magnitude and frequency of flow events which transport bedload sediments.

BACKGROUND

Graded channels are dynamic during periods of high flow. Sand- and gravel-bed stream channels with sequences of pools and riffles have nonuniform cross-sections in the downstream direction. Thus, hydraulic characteristics and bedload transport capacity are also nonuniform in the downstream direction and localized episodes of streambed scour and fill are normal

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channel processes during discrete runoff events (Colby, 1964b; Dietrich and Dunne, 1978; Jackson and Beschta, 1982; Andrews, 1982). Jackson and Beschta (1982) describe a model of bed material routing in sand- and gravel-bed channels where, at discharges less than bankfull, bedload transport consists primarily of sand-sized materials being routed over stable gravel riffles. At higher discharges, riffle gravel materials are also transported downstream. However, because of nonuniform channel geometries, bedload transport rates are unsteady and one or more sequences of partial riffle scour and fill may occur during high discharges. Upon the recession of high flows, a final riffle deposition and a natural sorting of particle sizes occur. The bed material composition of riffles is considerably more coarse than that of the bedload sediment in transport at the time riffle sediments are deposited. "Left-over" sand-sized bed material must therefore deposit elsewhere in the stream channel. The sorting of sediments by particle size and the long-term maintenance of pool-riffle sequences are the result of nonuniform downstream distributions in bottom velocities and average bed shear stress, and relative differences in the rate of increase of average bed shear stress with discharge in pools and over riffles (Keller, 1971; Lisle, 1979). We did not find research results which described the effects of varying amounts of sand in transport on the relative degree of sorting of bed materials by particle size.

Scour and fill processes, operating over a range of flow regimes, provide a means by which alluvial channels can undergo morphologic adjustments to changes in sediment regime. In addition to affecting channel depth, scour and fill may influence changes in channel width (Andrews, 1982) and the particle-size composition of channel beds (Kellerhals, 1967; Beschta and Jackson, 1979). While much information is available concerning the hydraulics of streambed scour (e.g., Vanoni, 1975), there is a lack of research pertaining to the deposition process. This is particularly true with regard to the sediment size distribution of depositional features and how these distributions are affected by the flow conditions and sediment transport conditions which exist during deposition (Bagnold, 1968). There is a similar lack of information on the effects of high concentrations of sediment in flow on bed stability, although Colby (1964a), Simons, *et al.* (1963), and Yalin and Finlayson (1972) have discussed general implications of high sediment concentrations on fluid viscosity and density and, in turn, the implications for increased sediment transport.

Schumm (1971) analyzed various hydraulic geometry relationships and developed a generalized relationship to describe the response of an alluvial channel to increased sediment discharge. In that relationship, channel width, slope and meander wavelength vary directly whereas channel depth and sinuosity are inversely proportional with bed material transport. Alluvial channels may respond to increased sediment delivery by filling pools (Lisle, 1982), smothering of gravel features (Platts and Megahan, 1974; Megahan, *et al.*, 1980), and widening (Grant, 1977; Platts, 1981; Lyons and Beschta, 1983; Beschta, 1984). In addition, increases in the percentage of fine (< 0.85

mm) sediments in channel gravel beds have been attributed to increased fine sediment delivery to streams (Cedarholm and Salo, 1979).

METHODS

Two flume experiments were conducted at the Kalam Falls Springs Field Laboratory of Weyerhaeuser Company, approximately 80 km east of Longview, Washington. A sediment deposition experiment was designed to test the influence of (1) the proportion of sand-sized sediment in transport, and (2) the rate of sediment transport on the particle-size composition of the resulting depositional (riffle) feature. A second experiment tested riffle stability under increased concentrations of sand transported.

Both experiments were conducted in an outdoor rectangular flume having two distinct reaches. The upstream reach was 5.8 m long and 0.35 m wide. Slope and roughness were adjusted so that flows transported all bed sediments at the rate at which they were added at the upstream end of the flume. Downstream from a 1.8 m transition reach was an additional 5.5 m of flume with a width of 0.41 m. The bottom slope of this section was decreased and hydraulic roughness increased, resulting in the deposition of stable gravel riffles. Pretest hydraulic conditions in both the upstream and downstream flume reaches are summarized in Table 1.

Deposition Experiment

In the deposition experiment, specific volumes of sediment mixtures (consisting of sand and gravel particles) were added to the upstream reach of the flume; sediment which deposited in the downstream reach formed a riffle-like feature. After the sediment inputs were stopped, streamflow was continued until deposited sediments had armored and sediment transport out of the test reach had ceased. Average hydraulic conditions over the stabilized test riffles are shown in Table 1.

Four size gradations of bedload sediments were evaluated by pre-mixing selected proportions of gravel (median diameter = 9.0 mm) and sand (median diameter = 0.3 mm). The volume of gravel input during a given test run was held constant at 8 liters. Sand-to-gravel ratios of 1:1, 2:1, 3:1 and 5:1 were evaluated, hence the total volume of sand in transport depended upon the particular test being run. Two sediment input rates of 20,000 and 6,600 kg hr⁻¹m⁻¹ were also evaluated (all transport rates are expressed in kilograms per hour per meter width of channel); each test had two replications. After treatment, three subsamples of each riffle were extracted by inserting small metal borders and manually moving all material within the borders. One subsample was taken from each of the upstream third, middle third and downstream third of the riffle. All samples were analyzed for particle size distribution.

TABLE 1. Average Hydraulic Conditions in Regions of Uniform Flow (36 liters/sec) for Riffle Deposition Experiments.

	Flume Width (cm)	Flow		Hydraulic Radius (cm)	Average Flow Velocity (ms^{-1})	Slope (m.m^{-1})	Froude No. (v/\sqrt{gy})	Manning's n	Average Shear Stress (N.m^{-2})
		Depth (cm)	Cross-Section Area (cm^2)						
Flume, Upstream Section	35.6	10.8	384	6.7	0.94	0.025	0.92	0.009	26.5
Flume, Depositional Section (without riffles present)	40.6	12.7	516	7.8	0.70	0.0067	0.63	0.02	8.3
Flume, Depositional Section (with riffles present)	40.6	7.9	320	5.7	1.28	0.027	1.5	0.02	20.9

Stability Experiment

In the stability experiment, a riffle was created in the downstream reach with the 1:1 sand-to-gravel mixture used in the deposition experiment. One hundred and seventy six liters (280 kg) of that mixture were added at $6,600 \text{ kg m}^{-1}$ and the resultant riffle was allowed to stabilize. Sand was then added to the flow and was transported over the stabilized riffle. Gravel-sized material which was removed from the test riffle after addition of the sand was caught in a 4-mm mesh basket placed at the outfall of the flume. All exported riffle material was dried and weighed.

The volume of sand added for each test varied (i.e., 35, 70, 105 or 140 kg). Furthermore, these volumes were added to the flow at two different rates (20,000 and 6,600 kg m^{-1}) and each test condition was replicated twice. The riffle was reformed after each test.

RESULTS AND DISCUSSION

Deposition Experiment

Figure 1 illustrates the particle-size distribution of the four sediment mixtures compared to the average particle size distribution of the resultant test riffle features formed under conditions of both high and low rates of sediment input. The range of particle sizes in the test riffles was the same as the range of particle sizes of the sediment in transport. In all tests, however, the median particle size of the riffle sediments was considerably larger than that of the sediments in transport. Furthermore, as the particle size distribution of sediments in transport under the same rates became finer, the coarseness of the riffle relative to that of the sediment in transport became greater. The composition was also affected by the rate of sediment transport. Test riffles formed during the lower transport rate were more coarse, in all cases, than those formed during the higher rate of sediment transport (Figure 1).

Whereas the percentage of sand deposited within the various test riffles increases as a power function with an increase in the proportion of sand in transport (Figure 2), the increase is small over the range of sediment mixtures tested. Only

subsamples from the downstream one-third of the riffles formed during the high input rate tests showed large increases in the sand-to-gravel ratio in the riffle. These results might indicate that downstream sections of riffles may be somewhat more sensitive indicators of the relative particle size distribution of sediment in transport than upstream sections. In general, however, the ratio of sand-to-gravel in transport did not greatly affect the percentage of sand in the riffle for the range of sand-gravel mixtures tested.

When the median particle diameter (d_{50}) of the riffle material is plotted against the sand-to-gravel ratio of sediment in transport, a weak but statistically significant ($\alpha = 0.05$) decrease in the median diameter of the riffle material occurs as the sand-to-gravel ratio increases (Figure 3). No consistent changes in the longitudinal profiles of the test riffles occurred as the ratio of sand-to-gravel in transport increased. The stabilized test riffles were higher in elevation at the upstream end and sloped to the downstream end at an average of 0.027 m/m. The water surface paralleled the riffle slope. The time required for the riffles to stabilize once the sediment inputs were stopped increased from approximately 1-1/2 minutes for those formed by 1:1 sand to gravel in transport, to about 8 minutes for those formed by 5:1 sand to gravel in transport. The test riffles which developed from the five parts sand to one part gravel were smaller in height and length than the other riffles.

The deposition efficiency of the sand and gravel (i.e., the total volume of sand and gravel in the riffle divided by the corresponding total volumes of sand and gravel input into the flow) expressed as a percent, was variable but tended to decrease as the proportion of sand in transport increased (Figure 4). The difference in depositional efficiency shown for sand and gravel is a relative indicator of the amount of particle size sorting that occurs during the depositional process. There was more sorting of gravel than of sand, and the amount of sorting decreased more rapidly for gravel than for sand as the proportion of sand in transport increased. Hence a predominant effect of increased rates of sand transport in natural channels may be to decrease the amount of particle size sorting

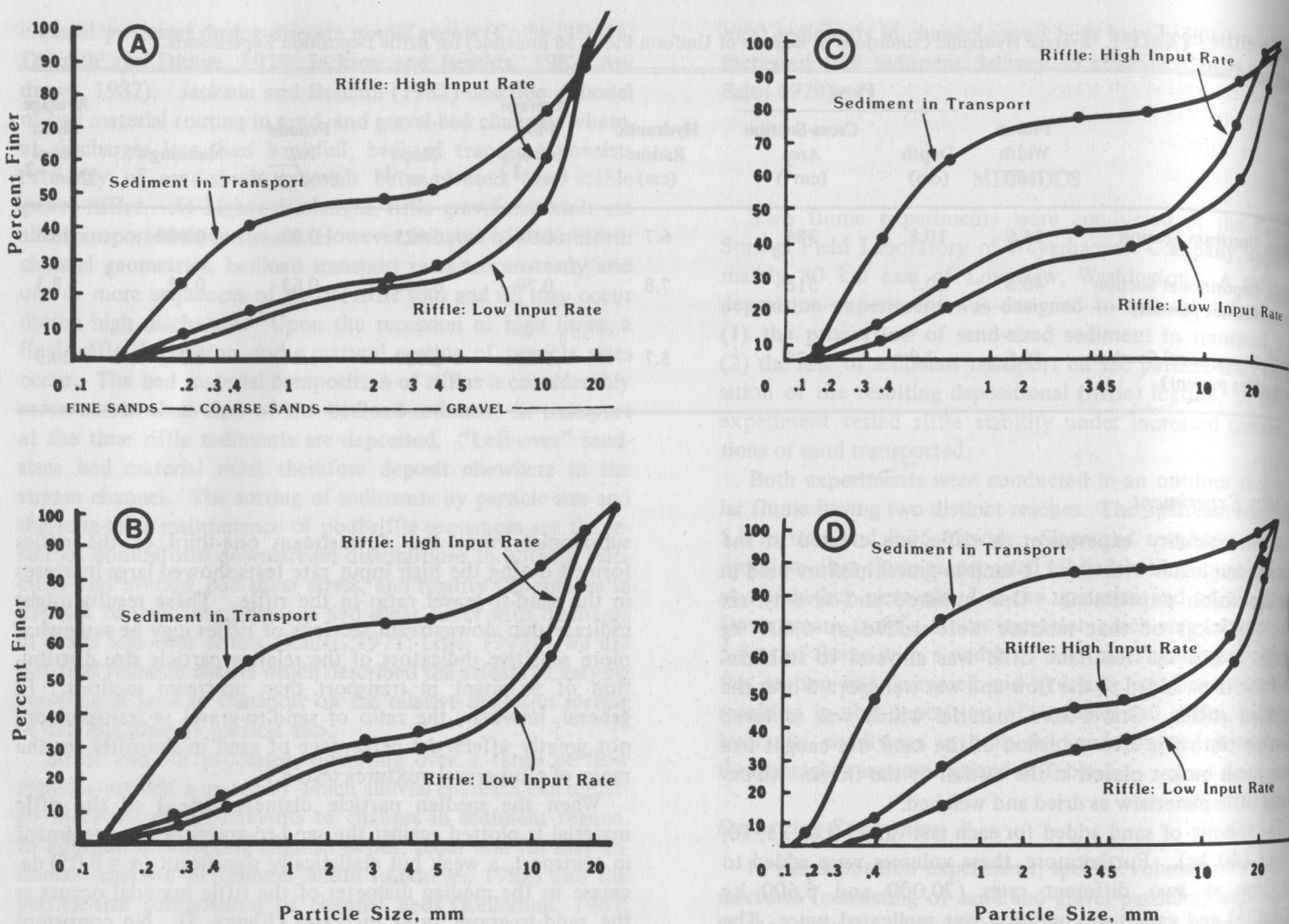


Figure 1. Particle-Size Distributions of Four Sediment Mixtures (A, 1:1 sand-to-gravel ratio; B, 2:1, C, 3:1; D, 5:1) and Average Distributions of the Resultant Test Riffles Formed Under High ($20,000 \text{ kg hr}^{-1}\text{m}^{-1}$) and Low ($6,600 \text{ kg hr}^{-1}\text{m}^{-1}$) Rates of Sediment Transport.

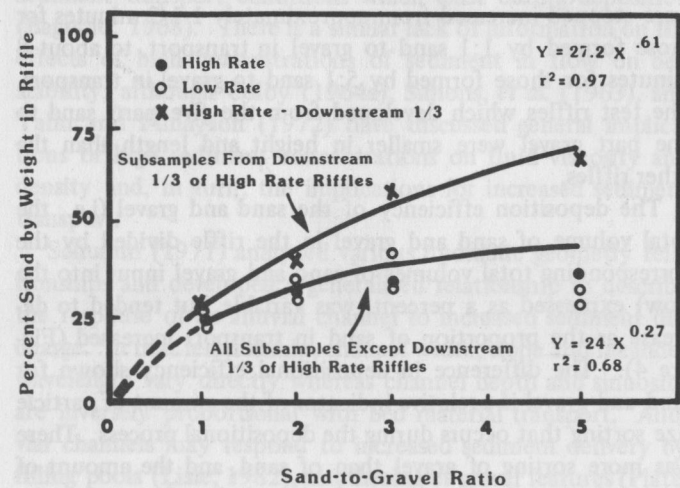


Figure 2. Relationship Between Percentage of Sand by Weight in Test Riffles, and Ratio of Sand-to-Gravel for High ($20,000 \text{ kg hr}^{-1}\text{m}^{-1}$) and Low ($6,600 \text{ kg hr}^{-1}\text{m}^{-1}$) Transport Rates.

which occurs as gravel riffles locally scour and redeposit downstream.

Stability Experiment

Relatively high rates of sand in transport resulted in initiating scour of riffles which were stable under conditions of no sand transport when shear stresses acting on the bed averaged 21 N.m^{-2} . The weight of material exported from each riffle increased with the increase in volume of sand transported over the riffle (Figure 5). No significant differences ($\alpha = 0.05$) between gravel export for different rates of sand transport (i.e., $20,000$ vs. $6,600 \text{ kg hr}^{-1}\text{m}^{-1}$) were detected.

Measurement and analysis of fluid mechanics variables affecting the transport capacity of the flows at the riffle was beyond the scope of this study, hence the mechanisms by which gravel movement was initiated are not known. However, we hypothesize that the increased capacity of the sand-water mixture to transport bed gravels compared to that of pure water may be caused in part by the higher density of the

and-water mixture. Possible increases in fluid viscosity and changes in the turbulent structure of the flow caused by high sand concentrations in transport near the streambed may also have affected the bedload transport capacity of flows. Finally, the large amounts of sand moving on the bed may have effectively reduced the mean particle diameter of the bed material, thus reducing the shear stress required to initiate motion (Andrews, 1983).

was to decrease the volume of gravel which ultimately deposited in the riffle. This, combined with the fact that there was only a small increase in the percentage of sand in the test riffles, means that most of the increased volume of sand in transport and a larger percentage of the gravel in transport did not deposit in the test riffles, but was transported through the flume. In addition, high rates of sand in transport caused the stable gravel riffles to undergo scour and caused the transport of gravel-sized materials.

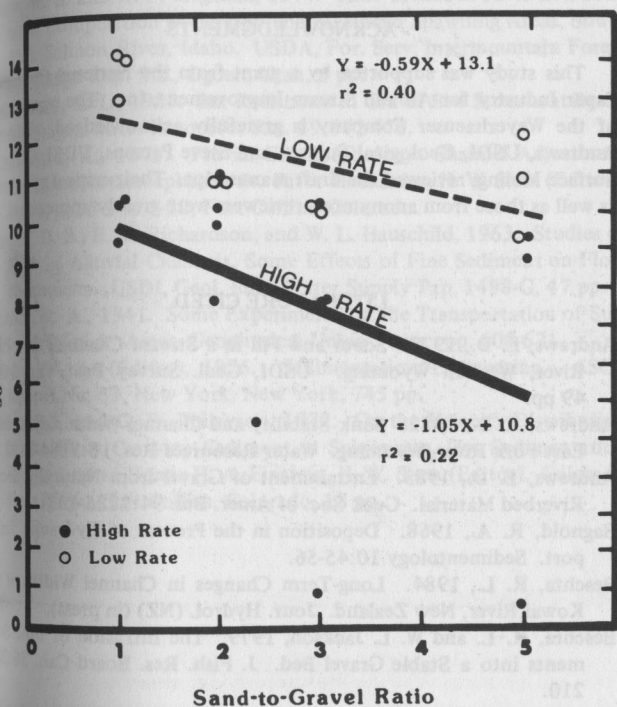


Figure 3. Relationship Between Median Particle Diameter (d_{50}) of Riffle Sediments and Ratio of Sand-to-Gravel in Transport for High ($20,000 \text{ kg hr}^{-1}\text{m}^{-1}$) and Low ($6,600 \text{ kg hr}^{-1}\text{m}^{-1}$) Transport Rates.

CONCLUSIONS

The results indicate that the particle size gradation of the riffles was not sensitive to increased proportions of fine bed material in transport at the time of deposition for the range of bed material mixtures tested. However, extrapolation of these results to lower sand-to-gravel ratios (i.e., ratios < 1, Figure 2) indicates changes in bed composition would be influenced by the size distribution of sediment in transport. Within the scope of this study, however, the rate of bedload transport and the range of bed material sizes (as determined by the largest particles in transport) appear to be more important variables affecting the particle size composition of riffle features than the proportion of fine bed material in transport at the time of deposition.

Possibly the most important effect of increasing the ratio sand-to-gravel in transport, while holding total bedload transport rates and total gravel volumes in transport constant,

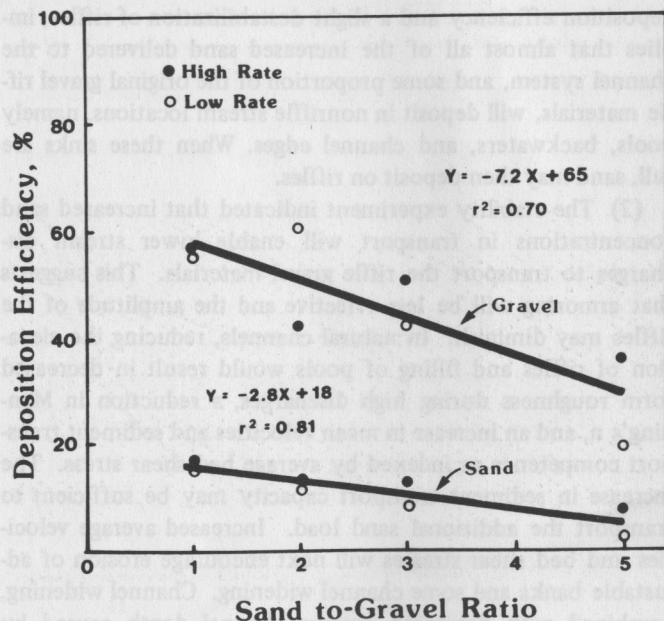


Figure 4. Average Deposition Efficiency of Sands and Gravels (each relationship significant at $\alpha = 0.05$).

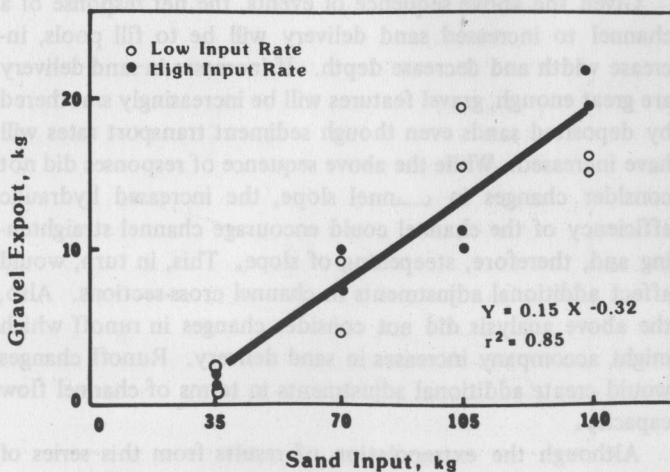


Figure 5. Gravel Export from Established Riffles in Relation to Total Sand Inputs (significant at $\alpha = 0.05$). High and low rates of transport correspond to $20,000$ and $6,500 \text{ kg hr}^{-1}\text{m}^{-1}$, respectively.

When the results of these experiments are combined with descriptive process of nonuniform bedload transport in sand and gravel-bedded stream channels with sequences of pools and riffles (Jackson and Beschta, 1982), it is possible to suggest a series of events which occur as part of the morphologic response of such channels to increased sand delivery:

(1) The deposition experiments indicated that increased sand concentrations in transport (for sand-to-gravel ratios of greater than 1:1) will not greatly increase the percent sand composition in riffles. This, combined with reductions in gravel deposition efficiency and a slight destabilization of riffles, implies that almost all of the increased sand delivered to the channel system, and some proportion of the original gravel riffle materials, will deposit in nonriffle stream locations, namely pools, backwaters, and channel edges. When these sinks are full, sand may then deposit on riffles.

(2) The stability experiment indicated that increased sand concentrations in transport will enable lower stream discharges to transport the riffle gravel materials. This suggests that armoring will be less effective and the amplitude of the riffles may diminish. In natural channels, reducing the elevation of riffles and filling of pools would result in decreased form roughness during high discharges, a reduction in Manning's n , and an increase in mean velocities and sediment transport competence as indexed by average bed shear stress. The increase in sediment transport capacity may be sufficient to transport the additional sand load. Increased average velocities and bed shear stresses will next encourage erosion of adjustable banks and some channel widening. Channel widening, combined with decreased average channel depth caused by filling of pools, will result in an overall increase in width-to-depth ratio. Some additional aggradation of the bed will occur until velocities and shear stresses are sufficient to transport the stream's increased sediment load. Overall channel stability will be reduced.

Given the above sequence of events, the net response of a channel to increased sand delivery will be to fill pools, increase width and decrease depth. If increases in sand delivery are great enough, gravel features will be increasingly smothered by deposited sands even though sediment transport rates will have increased. While the above sequence of responses did not consider changes in channel slope, the increased hydraulic efficiency of the channel could encourage channel straightening and, therefore, steepening of slope. This, in turn, would affect additional adjustments in channel cross-sections. Also, the above analysis did not consider changes in runoff which might accompany increases in sand delivery. Runoff changes would create additional adjustments in terms of channel flow capacity.

Although the extrapolation of results from this series of flume experiments to changes in the morphology of natural channels will need further study, these changes are in general agreement with the channel adjustment concepts of Schumm (1971, 1977). Evidence from other studies is generally supportive of these concepts. This is particularly true with regard to channel width changes (Grant, 1977; Lyons and Beschta,

1983; Beschta, 1984) and the tendency for channel form roughness to decrease during high flows by the partial filling of pools and scouring of riffles (Andrews, 1979). Measurements of changes in channel depths have been less common than changes in channel widths for channels where accelerated sediment inputs have occurred, although Megahan, *et al.* (1980) documented increases in channel depths following reductions in sediment delivery.

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