

Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival

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Abstract: Bed scour, egg pocket depths, and alteration of stream-bed surfaces by spawning chum salmon (*Onchorhynchus keta*) were measured in two Pacific Northwest gravel-bedded streams. Close correspondence between egg burial depths and scour depths during the incubation period suggests an adaptation to typical depths of bed scour and indicates that even minor increases in the depth of scour could significantly reduce embryo survival. Where egg burial depths are known, expressing scour depth in terms of bed-load transport rate provides a means for predicting embryo mortality resulting from changes in watershed processes that alter shear stress or sediment supply. Stream-bed alteration caused by mass spawning also may influence embryo survival. Theoretical calculations indicate that spawning-related bed surface coarsening, sorting, and form drag reduce grain mobility and lessen the probability of stream-bed scour and excavation of buried salmon embryos. This potential feedback between salmon spawning and bed mobility implies that it could become increasingly difficult to reverse declines in mass-spawning populations because decreased spawning activity would increase the potential for bed scour, favoring higher embryo mortality. Further analysis of this effect is warranted, however, as the degree to which spawning-related bed loosening counteracts reduced grain mobility caused by surface coarsening, sorting, and redd form drag remains uncertain.

Résumé : Des chercheurs ont mesuré l'affouillement du lit, la profondeur de la ponte et l'altération de la surface du lit de gravier de deux cours d'eau causée par le saumon kéta (*Onchorhynchus keta*) sur la côte nord-ouest du Pacifique. L'étroit rapprochement entre la profondeur d'enfouissement des oeufs et celle de l'affouillement pendant la période d'incubation pourrait pointer vers une adaptation à des profondeurs caractéristiques d'affouillement et pourrait signifier que même un léger approfondissement de l'affouillement pourrait nuire sensiblement à la survie des embryons. Lorsqu'on connaît la profondeur d'enfouissement des oeufs, l'expression de la profondeur d'affouillement en termes de charge de fond constitue un moyen de prévoir la mortalité des embryons attribuable à des changements dans les conditions dynamiques du bassin hydrographique à l'origine d'une modification de la force de cisaillement exercée par l'eau ou de l'apport en sédiments. Altération de la surface du lit de gravier causée par l'activité de fraye en masse influence peut-être la survie des embryons. Des calculs théoriques indiquent que la rugosité du lit, que le tri des matériaux à sa surface ainsi que la microtopographie des nids, attribuables à l'activité de fraye des saumons, devraient diminuer la mobilité des grains et abaisser la probabilité d'un affouillement du lit ainsi que de l'excavation des embryons de saumon enfouis. L'existence possible d'une telle boucle de rétroaction entre la fraye du saumon et la mobilité du lit signifie qu'il pourrait être de plus en plus difficile de renverser la tendance chez des populations en déclin qui fraient en masse puisque toute diminution de l'activité de fraye devrait correspondre à une hausse de la possibilité pour l'affouillement des nids, ce qui favorise une hausse du taux de mortalité chez les embryons. L'analyse plus poussée de cet effet paraît justifiée puisqu'on ignore dans quelle mesure l'ameublissement du lit associé à la fraye enraye la perte de mobilité des grains attribuable au durcissement de la surface du lit, au tri et à la traînée causée par la forme du nid.

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Introduction

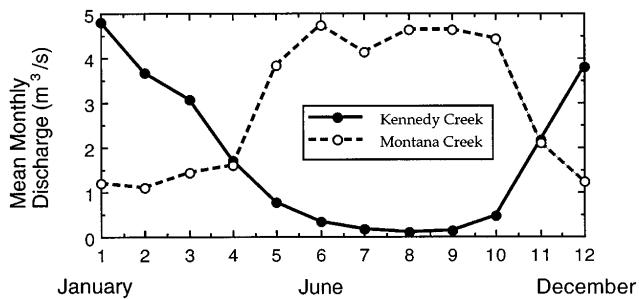
Dramatic declines of Pacific salmon (*Oncorhynchus* spp.) in the northwestern United States led to the application of the Endangered Species Act to certain populations (Federal Register 1991, 1992) and concern that many other populations are either in jeopardy or already extinct (Nehlsen et al. 1991). Declines in salmon populations reflect the combined influences

of dam construction, overfishing, habitat degradation, and other factors, but it has proven extremely difficult to isolate specific influences, in part because of difficulties in linking habitat change to population-level response (Holtby and Scrivener 1989; Bisson et al. 1992). We hypothesize that an important factor in salmon population biology is the active role that salmon play in the creation and maintenance of their own habitat. Beaver dams are probably the most widely recognized

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Fig. 1. Annual hydrographs of mean monthly flows for Kennedy Creek (1960–1971) and Montana Creek (1965–1987).



example of animal–habitat interactions (e.g., Ives 1942; White 1979; Naiman et al. 1988), but burrowing activity (e.g., Grinnell 1923; Cox 1987; Black and Montgomery 1991) and grazing (e.g., McNaughton et al. 1988) provide additional examples. It is well known that spawning salmonids construct redds for their eggs and that in the process they sort and coarsen stream-bed gravels (e.g., Everest et al. 1987; Chapman 1988; Young et al. 1989; Kondolf et al. 1993) and influence the invertebrate community (Field-Dodgson 1987), but neither fisheries biologists nor geomorphologists have explored how spawning activity influences bed mobility and reproductive success.

Anadromous salmon are spawned in fresh water, migrate to sea after a variable period of freshwater residence, spend several years at sea, then return to their natal stream and spawn. Each female constructs a redd consisting of several egg pockets dug in the channel bed by turning on her side and rapidly undulating her tail and body. This action sweeps finer particles into the water column where they are transported downstream (e.g., Kondolf et al. 1993). After eggs are released and fertilized, the female buries them while simultaneously excavating another egg pocket immediately upstream (Groot and Margolis 1991). So long as they are alive, females defend these nests from encroachment, but high spawning densities may result in superimposition of nests, which is widely accepted as a major cause of density-dependent mortality (Hunter 1959; McNeil 1964). In the absence of substantial superimposition, most embryo mortality is thought to occur from poor water circulation associated with the filling of intergravel pore spaces by fine sediment (Tappel and Bjornn 1983; Chapman 1988; Lisle and Lewis 1992) and scour during high-flow events (McNeil 1964; Holtby and Healey 1986; Lisle 1989). Although high salmon densities can reduce survival, we report evidence that mass spawning activity alters channel morphology in ways that may reduce the vulnerability of eggs to scour. We further show that nested embryos are quite vulnerable to increases in the average depth of bed scour.

Study areas

The study sites are low-gradient, gravel-bedded channels used by spawning chum salmon (*Oncorhynchus keta*). Kennedy Creek is located at the south end of Puget Sound, Washington, and Montana Creek is near Juneau, Alaska. The Kennedy Creek study reach is a pool–riffle type channel with a bank-full width and depth of approximately 10.8 and 0.42 m, and a reach-average slope of 0.0047. Flow convergence and diver-

gence associated with accumulations of large woody debris (LWD) locally influence the bed morphology. The Montana Creek study reach is a plane-bed type channel (Montgomery and Buffington 1993) with a bank-full width and depth of 18.4 and 0.72 m, and a reach-average slope of 0.0037. The Montana Creek reach has little cross-channel topography and a very low LWD loading (i.e., 0.01 pieces/m²). The annual hydrograph of Kennedy Creek is rainfall dominated with the greatest average discharges occurring from November through March (Fig. 1), a period coinciding with incubation of salmonid embryos in the stream-bed gravel. In contrast, summer high flows dominate the annual hydrograph of Montana Creek, with a relatively uniform high discharge period from May through October (Fig. 1). Chum salmon typically spawn in Montana Creek during July in the middle of this high discharge period.

Methods

Paired pebble counts (Wolman 1954) of 100 grains were conducted in each reach in unspawned locations proximal to redds and in tailspill or tailout portions of redds immediately downstream of egg pockets. Redds (spawned sites) were readily discerned by a change in the texture and patina of the bed surface. Pebble counts were conducted during spawning activity in the fall of 1991 in Kennedy Creek and in the summer of 1993 in Montana Creek. A pebble count (Wolman 1954) records the intermediate axis length of clasts randomly selected during a traverse across the channel bed. Characterization of the bed surface material is preferable to bulk samples of the channel substrate for examining bed stability because the size of material in the surface layer governs bed mobility.

Channel cross sections and slopes were surveyed using a digital theodolite in Kennedy Creek and a hand level and stadia rod in Montana Creek. Redd dimensions and frequencies estimated at each study site characterized alteration of bed topography during spawning activity. Repeated topographic mapping of the entire study reach immediately prior to and after spawning further quantified effects on channel morphology at Kennedy Creek.

A total of 104 scour chains placed throughout the Kennedy Creek site gauged the depth of bed scour and fill during the winter season following spawning. Scour monitors consisted of an anchored chain with a series of 4 cm diameter perforated plastic balls, a variant on the sliding bead scour monitors developed by Nawa and Frissell (1993). Scour monitors were distributed throughout the study reach both at redd locations and at sites not used by spawning fish. Egg pocket depths in 40 redds were measured after visual identification immediately following spawning (see Peterson and Quinn (1996) for further details). Field observations of discharge and channel scour at Kennedy Creek were made from November 1991 to February 1992 during the time of both peak flows and incubation of salmonid embryos within stream gravels.

Results

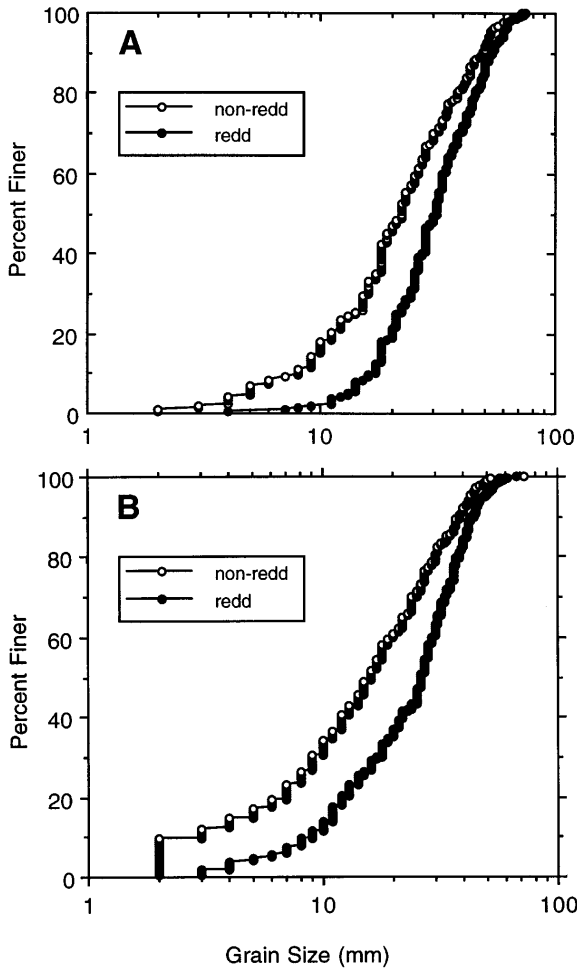
Spawning occurred throughout the entire study reach at Kennedy Creek during fall 1990, coarsening the bed surface, partially filling pools, and excavating bar margins. Similar spawning effects on channel morphology were documented the following year through repeated topographic surveying before and after spawning activity. Redds formed a distinctive microtopography on the channel bed with an amplitude of 10–20 cm and a wavelength of about 2.0 m. These bed forms persisted until the bed surface was reworked during high winter flows. At Montana Creek, half of the bed surface had been disturbed by spawning at the time of the survey. Redd

Table 1. Median surface grain sizes and sorting coefficients of paired unspawned and spawned samples.

Sample	d_{50} (mm)			σ_1 (ϕ)		
	Unspawned	Spawned	% difference	Unspawned	Spawned	% difference
Kennedy Creek						
1	23	32	+39	1.18	0.61	-48
2	21	28	+33	0.94	0.75	-20
Montana Creek						
1	12	20	+67	1.70	0.93	-45
2	16	25	+56	1.35	1.18	-13
3	15	26	+73	1.48	0.70	-53
4	18	29	+61	1.11	0.99	-11

Note: σ_1 is the inclusive graphic standard deviation defined as $(\phi_{95} - \phi_{16})/4 + (\phi_{95} - \phi_5)/6.6$ (Folk 1974), where ϕ is the standard log base 2 unit of grain size measurement and the subscripts represent percentiles of a given grain size distribution in ϕ units. Lower values of σ_1 indicate better sorting.

Fig. 2. (A) Composite cumulative size distributions of bed surface sediment for non-redd and redd locations sampled on October 28, 1991, at Kennedy Creek. (B) Composite cumulative size distributions of bed surface sediment for non-redd and redd locations sampled on July 21 and 22, 1993, at Montana Creek.



microtopography was comparable to that observed in Kennedy Creek.

Bed-surface grain size

Spawning activity visibly coarsened the channel bed in both

Table 2. *t* tests of all possible groupings of spawned (S) and unspawned (U) samples from Kennedy Creek.

Sample grouping	Probability of similarity
1U/2U	0.528
1U/1S	0.000
1U/2S	0.016
2U/1S	0.000
2U/2S	0.002
1S/2S	0.083

Note: Unpaired, two-tailed *t* tests were used assuming unequal and unknown variances.

study reaches, as demonstrated by grain size distributions of unspawned and postspawning samples (Table 1). Spawning caused a 33–39% increase in median surface grain size d_{50} in Kennedy Creek, and a 56–73% increase in d_{50} in Montana Creek. While the coarse end of each composite grain size distribution was similar, the percentage of fine particles on the redd surfaces decreased (Fig. 2). Body undulations during redd construction cause fine particles to be suspended and transported downstream (e.g., Kondolf et al. 1993), producing coarser and better sorted gravels. Fine sediment from portions of the bed surface disturbed by spawning in Kennedy Creek collected downstream on channel margins and in pools. Bed surface sorting, defined by the inclusive graphic standard deviation (Folk 1974), σ_1 , increased by 20–48% in Kennedy Creek and by 11–53% in Montana Creek as a result of spawning (Table 1).

Statistical similarity among the mean grain sizes of spawned and unspawned portions of Kennedy Creek was evaluated through *t* tests (Table 2). Differences among unspawned samples were not significant at a 0.05 probability level. The same was true of postspawning samples. However, differences between spawned and unspawned grain size distributions were significant ($P < 0.05$). Composite grain size distributions indicate that spawning activity locally increased d_{50} from 22 to 30 mm in Kennedy Creek (Fig. 2).

Similarity among the postspawning and unspawned locations in Montana Creek also was evaluated using *t* tests (Table 3). While each of the paired samples differed significantly, one of the postspawning samples (1S) was not different from the unspawned samples of the other paired pebble counts (2U, 3U, and 4U). Except for sample 1, all spawned samples were similar, as were all unspawned samples. These observations

Table 3. *t* tests of all possible groupings of spawned (S) and unspawned (U) samples from Montana Creek.

Sample grouping	Probability of similarity
1S/2S	0.016
1S/3S	0.003
1S/4S	0.000
2S/3S	0.988
2S/4S	0.316
3S/4S	0.238
1U/2U	0.015
1U/3U	0.051
1U/4U	0.015
2U/3U	0.682
2U/4U	0.888
3U/4U	0.770
1S/1U	0.000
1S/2U	0.290
1S/3U	0.144
1S/4U	0.196
2S/1U	0.000
2S/2U	0.001
2S/3U	0.000
2S/4U	0.000
3S/1U	0.000
3S/2U	0.000
3S/3U	0.000
3S/4U	0.000
4S/1U	0.000
4S/2U	0.000
4S/3U	0.000
4S/4U	0.000

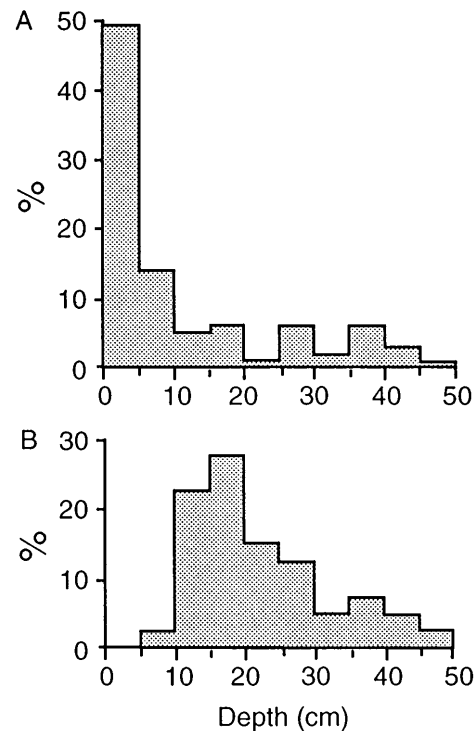
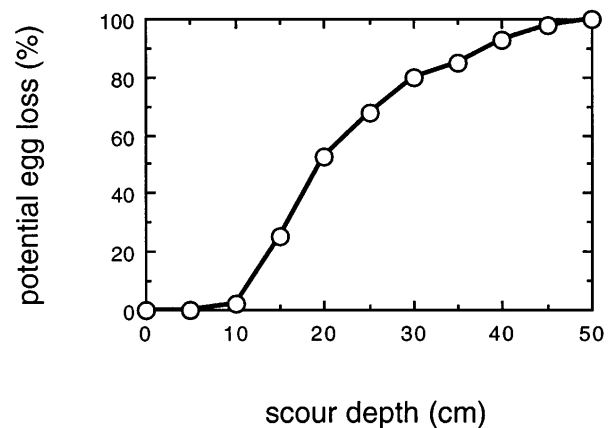
Note: Unpaired, two-tailed *t* tests were used assuming unequal and unknown variances.

are consistent with Kondolf et al.'s (1993) finding that the best predictor of the postspawning concentration of fine sediment in redds is the prespawning concentration. Composite grain size distributions from Montana Creek showed that d_{50} increased from 15 mm before spawning to 25 mm after spawning (Fig. 2).

In addition to coarsening and sorting bed surface grains, spawning activity also changed bed material packing. Although we did not quantify bed packing, we noted that in both Kennedy Creek and Montana Creek, gravels disturbed by spawning were more loosely packed than unspawned portions of the bed. Postspawning gravels were typically overloose in the terminology introduced by Church (1978), whereas prespawning gravels were underloose (imbricated) to normally loose. Application of these qualitative terms, however, is highly subjective.

Bed scour and egg pocket depths

The peak discharge observed in Kennedy Creek from November 1991 to February 1992 slightly exceeded bank-full stage. During this approximately bank-full event, scour depths recorded by 104 scour chains distributed throughout the reach exhibited a roughly exponential distribution ranging from 0 to 60 cm, with a mean of 13.4 cm (Fig. 3A). Forty measured egg-pocket depths ranged from 9.8 to 48.9 cm, with a mean of 22.6 cm (Fig. 3B). Comparison of bed scour and egg pocket

Fig. 3. Normalized histograms of (A) scour and (B) egg burial depths for Kennedy Creek in 1991–1992. Scour depths ($n = 104$) were determined from scour chains monitored through the winter season. Egg burial depths ($n = 40$) were measured during spawning activity.**Fig. 4.** Percent survival versus scour depth for Kennedy Creek derived from Fig. 3B.

distributions revealed that only a small proportion of the channel bed scoured to egg-pocket depths during this approximately bank-full event. Sixty-five percent of the scour chains recorded scour of less than 10 cm, while less than 5% of the egg pockets were less than 10 cm deep. Distributions of scour and egg-pocket burial depths, however, indicated that even a slight increase in scour depths would significantly affect the integrity of many egg pockets. A doubling of the mean scour depth to 26.8 cm, for example, would jeopardize the majority of egg pockets (Fig. 4).

Discussion

Salmonid reproductive success depends in part on egg burial depths exceeding the depth of scour during the incubation period. Successful reproduction thus requires adjustment to the typical timing and depth of bed scour. The observed distribution of egg burial depths below scour depths during a bank-full flood both suggests such an adjustment and indicates that an increase in the average depth of bed scour would significantly affect salmon populations. A strong correlation between mortality and peak seasonal discharge (Holtby and Healey 1986) suggests a direct link to bed scour. Therefore, conceptual models that relate bed scour to discharge and bed-load transport rates provide a framework for predicting embryo mortality caused by changes in watershed processes and grain size.

Bed scour

The depth of scour in gravel-bedded channels reflects the rate of bed-load transport, which is a function of boundary shear stress (and thus flow stage) relative to the critical shear stresses of both the surface and subsurface material (e.g., Emmett and Leopold 1963; Leopold and Emmett 1984; Carling 1987; Hassan et al. 1991). In armored gravel-bedded streams, mobility of the surface layer is followed by a rapid rise in bed-load transport (Jackson and Beschta 1982) resulting from exposure and scour of the finer and more easily mobilized subsurface material. The rate of bed-load transport is also a function of sediment supply. Increased sediment loads cause bed surface fining and thus higher transport rates for a given shear stress (e.g., Dietrich et al. 1989). Finer bed surfaces likely cause more frequent and greater depths of scour.

The depth of scour can be determined from the bed-load transport rate as

$$(1) \quad d_s = Q_b / (u_b \rho_s (1 - \gamma))$$

where d_s is the mean depth of scour, Q_b is the bed-load transport rate per unit channel width, u_b is the average bed-load velocity, ρ_s is sediment density, and γ is bed porosity (Carling 1987). Bed-load transport rates vary substantially between channels and thus primarily control average scour depths.

Numerous expressions describe bed-load transport as a nonlinear function of shear stress, discharge, velocity, or stream power (see review by Gomez and Church 1989). One conceptually simple equation expresses the bed-load transport rate per unit channel width as a function of the difference between the effective basal shear stress (τ') and the critical shear stress (τ_c):

$$(2) \quad Q_b = k(\tau' - \tau_c)^{1.5}$$

where k is an empirical constant. Together eqs. 1 and 2 provide a simple framework for quantifying scour depth and potential embryo mortality owing to changes in watershed processes. Changes in either the effective or critical shear stresses can alter bed-load flux and should influence the depth of scour and thereby embryo survival. Changes in sediment supply can alter τ_c (e.g., Dietrich et al. 1989), while changes in discharge and LWD loading can affect τ' (e.g., Buffington 1995). Furthermore, the observed stream-bed modifications caused by spawning chum salmon also have the potential to alter both τ' and τ_c and thus influence bed scour and embryo mortality.

Influence of spawning on stream-bed mobility

Salmonid-induced modifications of grain size, sorting, packing, and bed topography all potentially affect bed surface mobility, and thereby the vulnerability of embryos to fluvial excavation. In gravel-bedded channels of mixed grain sizes, the mobility of the median surface grain size provides an indicator of general bed mobility. Many gravel-bedded rivers exhibit equal grain mobility at incipient motion (Parker et al. 1982), owing in part to surface armoring (Jackson and Beschta 1982), friction angle distributions (Buffington et al. 1992), and hiding effects (Einstein 1950), which together cause a threshold condition of general bed surface mobility. Consequently, the critical boundary shear stress required to mobilize the surface grains of a gravel-bedded channel can be estimated from Shields' (1936) equation written in terms of the surface d_{50} :

$$(3) \quad \tau_{c50} = \tau_{c50}^* (\rho_s - \rho_w) g d_{50}$$

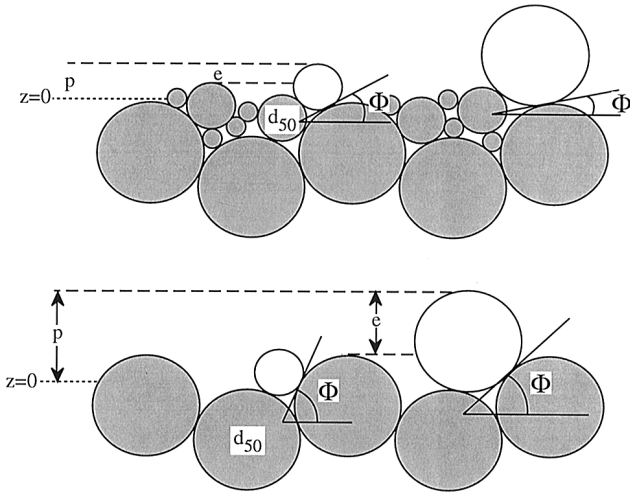
where τ_{c50} and τ_{c50}^* are the dimensional and dimensionless critical shear stresses for the median surface grain size, ρ_s and ρ_w are the densities of sediment and water, and g is gravitational acceleration. Numerous and disparate values reported in the literature complicate determining τ_{c50}^* (see reviews by Church 1978 and Buffington 1995). Here we use Parker and Klingeman's (1982) value of 0.035, as it represents bed surface characteristics of mixed grain sizes typical of gravel-bedded streams and is derived from a study reach with subdued bed-form roughness (Milhous 1973). Regardless of the specific τ_{c50}^* value used, inspection of eq. 3 shows that τ_{c50} is linearly proportional to d_{50} , implying that surface coarsening increases the shear stress necessary to initiate general bed mobility.

Incorporating sediment and water densities of 2650 and 1000 kg/m³ into eq. 3 predicts that spawning-related bed coarsening (i.e., 22–30 mm) increased the critical shear stress from 12.5 to 17.0 Pa in Kennedy Creek. Comparison of these shear stresses with the bank-full shear stress allows the significance of this increase in τ_{c50} to be estimated. The reach-average bank-full shear stress calculated from the depth–slope product ($\tau_0 = \rho_w g D S$, where τ_0 is the total boundary shear stress and D and S are the flow depth and slope, respectively) is approximately 19.4 Pa. This predicts that spawning-related surface coarsening therefore increased the critical shear stress from about 64 to 88% of the bank-full shear stress. However, these theoretical (i.e., calculated) critical shear stresses underestimate the effects of bar form and LWD roughness that dissipate shear stress, effectively lowering the basal shear stress available for sediment transport (i.e., τ') and increasing the total shear stress required for grain mobility (see Buffington 1995 for further discussion). Hence, τ_{c50} for redd surfaces is likely to exceed 88% of the bank-full shear stress.

Similar critical shear stress calculations for Montana Creek indicate that spawning-related bed coarsening increased τ_{c50} from approximately 33 to 54% of the bank-full shear stress. Roughness effects associated with LWD and bar forms are minimal in Montana Creek. Equation 3 thus predicts that spawning-related bed surface coarsening significantly increases the critical shear stress in both Kennedy and Montana creeks.

Sorting of bed surface material during spawning likely further reduces grain mobility. Increased sorting raises friction angles (Φ) between the bed surface and particles moving over the bed (Fig. 5), causing greater resistance to motion (Miller

Fig. 5. Diagram illustrating the increase in friction angles, Φ , owing to increased sorting. Grains composing the bed surface are shaded, while particles traversing the bed are unshaded. Removal of finer grains during spawning activity produces better sorted bed surfaces that present deeper intergranular pockets and higher friction angles. Protrusions of particles equivalent in size to the d_{50} of the bed surface are also shown. Protrusion is defined by a particle's projection, p , above the local datum, $z = 0$, and by its exposure, e , above upstream grains (Kirchner et al. 1990).



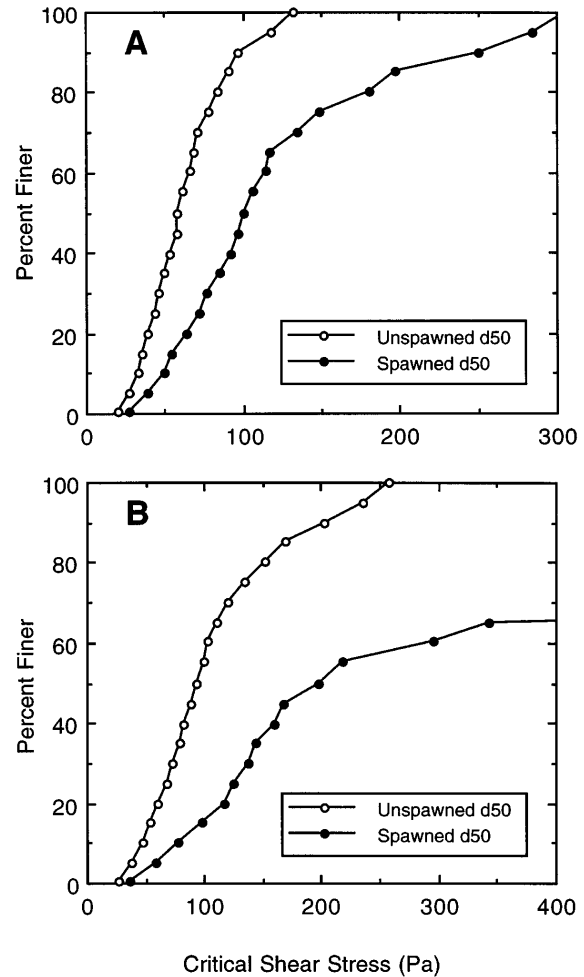
and Byrne 1966; Buffington et al. 1992). The varied arrangement of grain sizes composing a heterogeneous bed surface results in a distribution of friction angles for a given particle size on that surface (Kirchner et al. 1990; Buffington et al. 1992). Distributions of Φ for unspawned and spawned values of d_{50} were determined empirically as functions of grain size and sorting (σ_1) (Buffington et al. 1992). In addition to friction angle, grain mobility depends on projection (p) and exposure (e) (Fig. 5) (Fenton and Abbott 1977). As with Φ , distributions of p and e characterize each particle size on a bed surface and can be determined empirically as functions of grain size and Φ (Kirchner et al. 1990).

The combined effects of bed surface coarsening and sorting on grain mobility are examined by calculating critical shear stresses of unspawned and postspawning gravels using Kirchner et al.'s (1990) theoretical critical shear stress formulation. In this model, the critical shear stress for incipient grain motion is expressed as

$$(4) \quad \tau_c = (\rho_s - \rho_w) g \pi d^3 \kappa^2 (\tan \Phi \cos \alpha - \sin \alpha) / \left(3 \left(C_D \int_{p-e}^p f^2(z) (d^2 - (2z - (2p - d))^2)^{1/2} dz + \frac{C_L \pi d^2}{4} f^2(z) \Big|_{p-d}^p \tan \Phi \right) \right)$$

where d is grain size, von Kármán's constant κ equals 0.407 (Wiberg and Smith 1987), α is the inclination of the bed, C_D (≈ 0.45) is the drag coefficient for a sphere at high-particle Reynolds numbers (i.e., 10^3 – 10^5) (Rouse 1946), z is the height above the bed, $f(z)$ is a velocity profile function of the law of the wall, and C_L (≈ 0.2) is the lift coefficient for a sphere (Wiberg and Smith 1987) (see Kirchner et al. 1990 for further details). Inspection of eq. 4 shows that τ_c is inversely propor-

Fig. 6. Calculated critical shear stress distributions of d_{50} grain sizes on unspawned and spawned bed surfaces in (A) Montana Creek and (B) Kennedy Creek.



tional to grain protrusion ($p - e$), and directly proportional to d and Φ (and thus σ_1).

Results from this analysis predict a shift in the τ_{c50} distributions for unspawned and postspawning surfaces (Fig. 6). In Montana Creek the median value of τ_{c50} increases by 73% as a result of surface coarsening and sorting. Moreover, there is a threefold increase in the overall range of stresses required to entrain d_{50} grain sizes in Montana Creek. In Kennedy Creek the median critical shear stress for d_{50} increases by 111%. Additionally, there is a severe expansion in the range of critical shear stresses, with about 10% of the distribution characterized by friction angles in excess of 90° , indicating virtual immobility of this percentage of the d_{50} sizes. Because these calculations employ friction angle and protrusion data derived from grains placed on bed surfaces, they provide conservative estimates of the stresses required to mobilize the actual stream-bed surface; grains composing the bed surface likely will be characterized by lower protrusions and higher friction angles (Buffington et al. 1992; Jiang and Haff 1993), resulting in critical shear stresses greater than those estimated here.

Grain mobility and susceptibility to scour may be further reduced by redd microtopography that introduces form drag that decreases bed shear stresses (i.e., lowers τ). Bar-form

Table 4. Effects of spawning activity on grain mobility: percent change in τ_{c50} relative to the unspawned value and percentage of bank-full shear stress represented by this change.

	Surface coarsening (eq. 3)		Surface coarsening and sorting combined (eq. 4) ^a		Redd form drag (eq. 5)	
	% change in τ_{c50}	% of bank-full τ	% change in τ_{c50}	% of bank-full τ	% change in τ_{c50}	% of bank-full τ
Kennedy Creek	36	23	111	na	17–62	11–40
Montana Creek	67	22	73	na	26–89	8–29

^aEvaluated using median critical shear stresses of calculated stress distributions (Fig. 6). τ_c values calculated from eq. 4 may represent instantaneous turbulent sweeps and so may not be comparable to the time-averaged values of unspawned τ_{c50} and bank-full τ used here (Buffington et al. 1992).

resistance in gravel-bedded rivers varies with stage and bed morphology but may comprise 10–75% of the total channel roughness (Parker and Peterson 1980; Prestegard 1983; Hey 1988). Nelson and Smith (1989) presented a theoretical model that describes the shear stress dissipated by flow over regularly spaced channel-spanning bedforms as

$$(5) \quad \tau_{bf} = \tau_g \frac{C_D}{2\kappa^2} \frac{H}{\lambda} \left(\ln \left(\frac{H}{z_0} \right) - 1 \right)^2$$

where τ_{bf} and τ_g are the shear stresses dissipated by bed-form and grain roughness, respectively, C_D is approximately equal to 0.21 for fully separated flow (Smith and McLean 1977), and H and λ are the bed-form amplitude and wavelength, respectively. Shear stress dissipated by redd topography decreases the basal shear stress available for sediment transport, effectively increasing the total shear stress required for grain mobility. The additional shear stress necessary to overcome redd form drag and initiate particle motion can be calculated from eq. 5, recognizing that at incipient motion $\tau_g = \tau_{c50}$ as defined by eq. 3.

Using τ_g equal to the postspawning τ_{c50} values calculated from eq. 3 together with $\lambda = 2.0$ m, $H = 0.10$ – 0.20 m, and $z_0 = 0.1d_{84}$ (of postspawning gravels), eq. 5 predicts that at incipient grain motion, redd topography dissipates 2.1–7.8 Pa of channel shear stress in Kennedy Creek and 2.2–7.6 Pa in Montana Creek. In Kennedy Creek, these τ_{bf} values increase the critical shear stress of unspawned gravels (12.5 Pa) by 17–62% and constitute 11–40% of the bank-full shear stress (19.4 Pa). Similarly in Montana Creek, redd form drag increases the unspawned τ_{c50} value (8.5 Pa) by 26–89% and represents 8–29% of the bank-full shear stress (26.1 Pa). Our analyses indicate that the combined influence of redd form drag, surface coarsening, and sorting more than doubles τ_{c50} in Kennedy and Montana creeks (Table 4).

Spawning-related changes in packing of bed material, however, may also affect grain mobility. Redd construction loosens the stream bed, likely causing it to be less imbricated (i.e., have lower friction angles) and thus more easily mobilized (e.g., Church 1978; Reid et al. 1985; Li and Komar 1986). However, loose packing of the surface layer is unlikely to persist for long, as its deep intergranular pockets provide high friction angle locations that will trap fine material (e.g., Kirchner et al. 1990) that is normally in motion at flows less than critical (e.g., Jackson and Beschta 1982). These finer grains partially bury the larger loosely packed ones, likely decreasing their mobility by lowering grain protrusion and increasing friction angles (Buffington et al. 1992).

While we observed that redd gravels were typically more loosely packed than non-redd surfaces, the significance of bed

loosening relative to that of surface coarsening and sorting is unknown. As we are unaware of any studies that have thoroughly quantified the influence of packing on grain mobility, we cannot estimate the importance of bed loosening by salmonids. Nevertheless, the influence of changes in packing on bed surface mobility would likely counteract the other spawning-related effects to some degree. Although critical shear stress calculations for Kennedy Creek indicated that postspawning bed mobility, and thus scour, should occur at stages significantly in excess of bank-full, field observations show that the postspawning bed surface mobilized during an approximately bank-full event. This bed mobility and scour at roughly the bank-full stage implies that loosening of the bed surface offsets approximately 32–44% of the increase in critical shear stress indicated by our calculations, implying that the net effect of spawning is reduced bed mobility, despite loosening of the bed surface.

Another issue remaining to be investigated is the longevity of salmonid modifications of the channel. Well-sorted bed surfaces tend to be hydraulically rough and have deep intergranular pockets that readily trap fine material. Salmonid-altered gravels may progressively decrease in size and become more poorly sorted in channels with high sediment supply that transport fine sediment at low to moderate stages. P.E. Porter (cited by Everest et al. 1987), for example, found that the percentage of fine particles (<1 mm) in stream-bed gravels of Montana Creek returned to prespawning levels within 1–2 months. Redd topography, however, may discourage fine sediment deposition above egg pockets by forcing both upstream deposition within redd pits and downstream suspension over tailspills (e.g., Everest et al. 1987). Nevertheless, persistence of redd forms is unlikely in streams that normally lack such microtopography as part of their bed morphology.

Implications

The close correspondence between egg burial depths and scour depths during typical annual high flows implies a finely tuned adaptation to long-term rates of sediment transport and implies high salmonid population sensitivity to variations in scour depths. The greater than 60% embryo survival for a bank-full flood inferred from Fig. 3 may define a reasonable minimum estimate of long-term mortality, as bank-full flows represent a predictable minimum annual peak discharge. The lower survival rate at higher discharges noted by Holtby and Healey (1986) may simply reflect scouring deeper into the population of embryos buried in the stream bed. Our data imply that changes in processes influencing scour depths could have dramatic impacts on salmonid population dynamics. Higher bed-load transport rates resulting from increased sediment supply

and consequent bed surface fining (Dietrich et al. 1989), for example, should directly increase scour depths. Many human activities (e.g., logging, road construction, urbanization) may increase bed scour by increasing the discharge and (or) the sediment supply to streams. Although numerous processes contribute to the ongoing decline of salmonid populations, changes in the depth of bed scour may be a key factor in the decline of certain species.

Our calculations indicate that spawning-related bed modifications may also influence scour and embryo survival by decreasing bed mobility. Bank-full flows for many rivers have recurrence intervals of roughly 1 or 2 years (Wolman and Leopold 1957; Wolman and Miller 1960; Dury 1973; Williams 1978). Hence, salmonid modifications that increase the critical shear stress may help protect embryos from scour during typical annual to biennial flows. The potential for spawning activity to reduce bed surface mobility may be particularly important at our study sites because of the coincidence of spawning timing and the highest monthly average discharges. Spawning activity in both channels may decrease bed mobility during periods when embryos are most susceptible to disruption and scour by high flows, implying that spawning alters the channel in a way that may enhance the probability of offspring survival. Spawning-related bed modifications will decrease as a mass-spawning salmonid population declines, potentially resulting in more frequent scour to egg-pocket depths, decreased embryo survival, and hence further population decline. Such feedback would make it increasingly difficult to reverse a declining population trend, especially if the decline coincided with changes in land use that lead to more frequent or higher discharges (e.g., Harr 1986; Booth 1991) or to bed surface fining and thus greater bed mobility (e.g., Dietrich et al. 1989) and scour. The influence of spawning-related bed modifications on scour and embryo survival warrants further investigation, however, because of the unquantified effect of bed loosening.

Fishing patterns that decrease fish size (e.g., Ricker et al. 1978; Ricker 1980) could also increase embryo mortality from bed scour. Smaller fish bury their eggs less deeply, leaving them more vulnerable to scour during bed-mobilizing events (e.g., van den Berghe and Gross 1984). Consequently, management practices that tend to reduce fish size might increase embryo mortality and would exacerbate any positive feedback between a declining population and bed mobility.

Examples of biological influences (other than the pervasive impact of human activity (Turner et al. 1990)) on physical environmental processes are relatively uncommon, and many ecological models assume that animals passively respond to environmental constraints. Our observations, however, suggest a potential feedback mechanism between spawning-related habitat modification, bed mobility, and embryo survival. This feedback is likely to be significant only for mass-spawning species using low-gradient gravel-bedded channels in which bed scour typically involves a fraction of the full thickness of the alluvium composing the stream bed. This mechanism is unlikely to significantly affect dispersed-spawning species inhabiting steep cobble and boulder-bedded channels in which frequent scour incorporates most of the available spawning gravel. In such channels the timing of spawning may represent a fundamental adaptation to channel-bed mobility (Montgomery 1994).

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