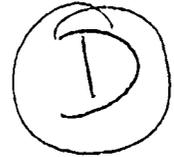


# Effects of Sediment Transport on Survival of Salmonid Embryos in a Natural Stream: A Simulation Approach

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A model is presented that simulates the effects of streamflow and sediment transport on survival of salmonid embryos incubating in spawning gravels in a natural channel. Components of the model include a 6-yr streamflow record, an empirical bedload-transport function, a relation between transport and infiltration of sandy bedload into a gravel bed, effects of fine-sediment infiltration on gravel properties, and functions relating embryo survival to gravel properties. High-flow events drive temporal variations in survival; cross-channel variations in bedload transport cause spatial variations. Expected survival, as a result, varies widely from year to year and between spawning runs in a single year. Alternative functions from previous research that relate survival to fine-sediment concentration in spawning gravel and to intergravel rates of flow yield categorically different results. The relative uncertainty of the components of this model indicates that the greatest research needs are to understand how sediment transport affects the intergravel environment and how these changes affect embryo development and survival.

Nous présentons un modèle qui simule les effets de l'écoulement d'un cours d'eau et du transport des sédiments sur la survie des embryons de salmonidés en incubation dans des frayères de gravier dans un chenal naturel. Les composantes du modèle incluent un relevé du débit du cours d'eau pendant 6 ans, une fonction empirique de transport des sédiments de fond, une relation entre le transport et l'infiltration de la charge de fond sableuse dans une couche de gravier, les effets de l'infiltration de sédiments fins sur les propriétés du gravier et des fonctions mettant en relation la survie des embryons et les propriétés du gravier. Les épisodes de débit élevé entraînent des variations temporelles de la survie; les variations à travers le chenal du transport des sédiments de fond causent des variations spatiales. Par conséquent, la survie prévue varie considérablement d'une année à l'autre et d'une montaison de fraie à l'autre au cours de la même année. D'autres fonctions établies lors d'études précédentes qui mettent en relation la survie et la concentration de sédiments fins dans le gravier de la frayère ou l'écoulement entre les graviers donnent des résultats totalement différents. L'incertitude relative des composantes de ce modèle indique que le besoin le plus pressant sur le plan de la recherche est la compréhension de la manière dont le transport des sédiments influe sur l'environnement du gravier et des répercussions de ces changements sur le développement et la survie des embryons.

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Survival of salmonid embryos to emergence from the streambed has been related to substrate and flow conditions in many experiments (Phillips et al. 1975; Tappel and Bjornn 1983; among others) and field studies (Koski 1966; Tagart 1984; Scrivener and Brownlee 1989). The suitability of incubation habitat ultimately depends on how much, what size, and when sediment is transported. Almost regardless of the original condition of gravel, the spawning female can alter the grain size and porosity of gravel to ensure that the ova begin with an adequate flow of oxygenated water (Burner 1951; Cordone and Kelley 1961; among others). For many regions and species, however, incubation coincides with seasonal high flows that carry sediment. Accumulated fine sediment in the gravel can restrict intergravel flow and block emergence of fry. Therefore, the key to embryo survival is not the condition of spawning gravel before or immediately after spawning but during the several weeks or months of incubation. Moreover, stream temperature can control the rate of development and thereby determine the period of incubation (Heggberget 1988). Processes that change gravel conditions vary widely in time and space because they are driven by climatic events and modified

by the complexity of natural channels.

Are effects of sediment transport sufficiently intensive, pervasive, and frequent to significantly affect embryo survival? To answer this question, we need to know how a hierarchy of processes leading from (1) water discharge to (2) sediment transport to (3) changes in gravel conditions to (4) physiologic functions of embryos are linked. We also need to know how the variability of processes affects survival of the population of embryos incubating in a stream. This problem can be approached effectively by modeling if relationships between processes are quantifiable and data are available.

We present a model that links variations in flow and sediment transport to the fraction of salmonids that survive in a natural channel. We do not intend it to serve as a management tool, but as a framework to build more accurate and comprehensive models, reveal gaps in understanding, and explore the temporal and spatial variability of sediment effects on embryo survival in a natural stream. Furthermore, we do not presuppose that quality of incubation habitat limits fish production. Rather, we offer a mechanistic approach to deciphering the physical-biological linkage for one critical life stage of salmonids in streams.

## Study Site

We constructed the model with data primarily from one natural stream. Some site-specific relations are included pro tem until more general relations can be found. We applied the model to one reach where data are available; thus the model does not evaluate embryo survival rates for the entire stream.

Jacoby Creek is a small gravel-bed stream that drains into Humboldt Bay near Arcata, California. It supports populations of steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) and has been the site of life-history studies of salmonids (Harper 1980), fluvial geomorphology (Lisle 1986), and sediment transport and its effects on spawning gravels (Lisle 1989). Mean bankfull channel width at the primary study reach is 17.2 m, median grain size of the bed surface is 22 mm, and channel gradient is 0.0063. Drainage area is 36.3 km<sup>2</sup>, and peak discharges can exceed 40 m<sup>3</sup>/s during the rainy season from October through April. Clastic sediment yield (180 tons (t)·km<sup>-2</sup>·yr<sup>-1</sup>), of which approximately 15% is bedload (Lehre and Carver 1985), is moderate compared with other basins in northwestern California (Janda and Nolan 1979). Large fluxes of sediment during stormflow periods in Jacoby Creek can cause extensive scour and fill and fine-sediment infiltration (Lisle 1989).

## Model

The following provides a brief conceptual overview of our model. We assume that adult fish are equally likely to enter Jacoby Creek to spawn each day that discharge is between 0.85 and 4.8 m<sup>3</sup>/s during the period from January 1 to April 5. In the process of burying the eggs, the females reduce the fraction of fine sediment in the spawning gravel. The embryos then incubate for 40 d, during which periodic high flows transport fine sediment over the bed surface. Some sediment infiltrates into the interstices of the gravel that overlies the embryos, reducing intergravel flow velocities and plugging gravel interstices. These changes increase mortality of the embryos. Our observations in Jacoby Creek suggest that redd topography is planned off by flows large enough to transport significant quantities of sediment. We assume, therefore, that redd topography does not affect infiltration of fine sediment.

## Water Discharge

Water discharge drives changes in spawning gravels and is the source of temporal variability of factors that affect embryo survival. We used water stage, recorded continuously at a gauging station at the downstream end of the study reach, to construct a record of discharge from 1979 to 1985. Discharge during the rainy season ranged from 0.4 to 62 m<sup>3</sup>/s, and associated sediment transport ranged from a trace to hundreds of tons per day. We used data for the period from January 1 to May 15, which includes most of the rainy season. Calculations were initiated after discharge first exceeded 0.85 m<sup>3</sup>/s each winter, when it was assumed that adults entered the stream to spawn.

## Sediment Transport

Sand and granules (0.25 < *D* < 4 mm, where *D* is particle diameter) are the predominant sizes that infiltrate spawning gravels in Jacoby Creek (Lisle 1989). These particle sizes are large enough to be transported in frequent contact with the bed and small enough to enter interstices of spawning gravels.

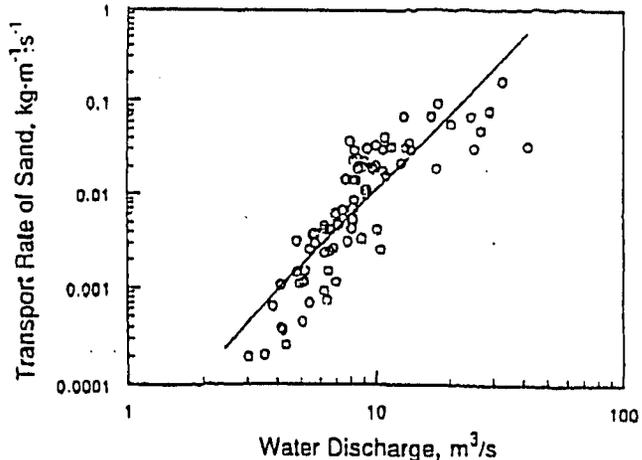


FIG. 1. Relation between transport rate of sand (0.25 < *D* < 2 mm) and water discharge, Jacoby Creek.

Transport rates of this fine bedload were measured directly from a bridge at the gauging station with a Helley-Smith bedload sampler that had a mesh size of 0.20 mm. Fine-bedload transport rate increased steeply with discharge and had wide scatter (Fig. 1) typical of bedload data from natural streams (Gomez 1991). As a point of reference, a transport rate of 0.023 kg·m<sup>-1</sup>·s<sup>-1</sup> equates to 1 t·m<sup>-1</sup>·d<sup>-1</sup>.

We used a power function of transport rate versus water discharge to compute fine-bedload fluxes every hour during the modeled period:

$$(1) \quad q_b = (2.19 \times 10^{-5})Q^{2.72} \quad r^2 = 0.71$$

where  $q_b$  is mean bedload transport rate per unit channel width (kilograms per metre per second) and  $Q$  is water discharge (cubic metres per second). We computed mean unit flux of fine bedload (kilograms per metre) by summing equation (1) for each 40-d incubation period.

## Infiltration of Fine Sediment

The volume of fine sediment that accumulates in spawning gravels in Jacoby Creek is related to the flux of fine bedload (Lisle 1989). Cans filled with gravel devoid of fine sediment were buried in spawning areas to measure rates and grain sizes of fine-sediment infiltration. After periods in which sediment transport was measured continuously, we emptied the cans and sieved their contents. For the model, infiltrated sediment was considered to range between 0.12 and 4.0 mm in diameter, which represents 93% of the material finer than 4 mm collected in the cans. We considered this as the maximum size range that we could use to determine infiltration rates from transport rates of sediment between 0.25 and 4 mm.

Sediment infiltration rates were related to bedload transport rates by a power function (Lisle 1989) modified to include a wider range of grain size than used originally:

$$(2) \quad I = 2.03(q_b)_T^{0.412}$$

where  $I$  is mean fine-sediment infiltration (kilograms per square metre of spawning gravel) and  $(q_b)_T$  is fine-bedload flux per unit width (kilograms per metre). Data from two other streams were also used to derive the original function (Lisle 1989). All three streams have unimodal bed material and each shows no systematic deviation from the common relationship between

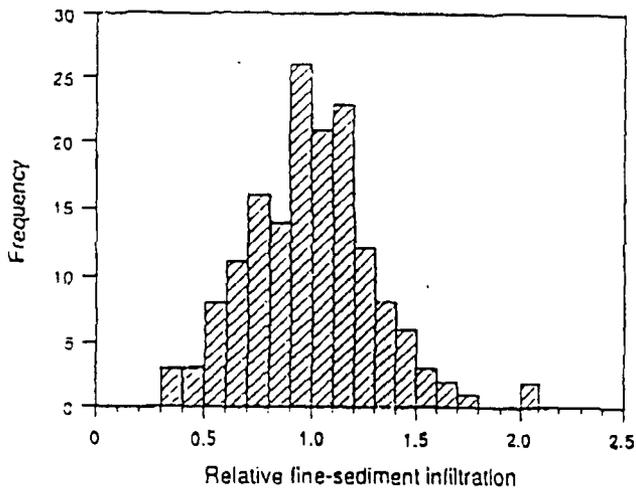


FIG. 2. Frequency distribution of relative fine-sediment infiltration rates (fine-sediment content in each gravel can divided by the mean of all cans for corresponding measurement periods) during stormflows, Jacoby Creek.

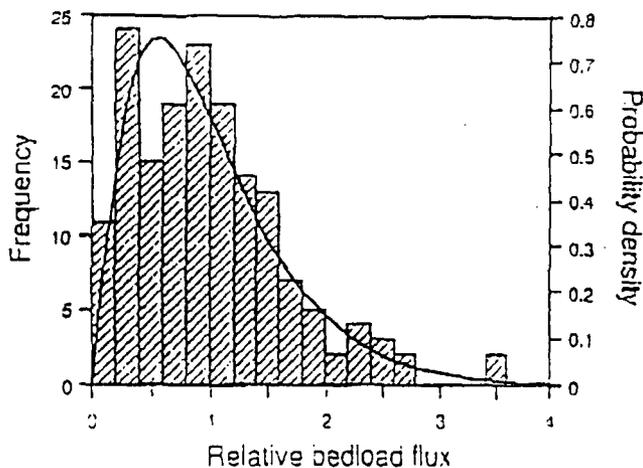


FIG. 3. Frequency and probability density distribution of relative bedload fluxes (local flux divided by mean flux), Jacoby Creek.

sediment infiltration and transport. Equation (2) was used to compute fine-sediment infiltration for each incubation period.

Fine-sediment infiltration into the gravel cans varied widely within each stormflow period (Fig. 2). To explicitly incorporate this variation in the model, we assumed that it was caused solely by spatial variation in bedload transport. Bedload transport characteristically varies widely across channels (Carey 1985; Emmett, cited in Gomez 1991; Gomez et al. 1991). Equation (2) indicates that infiltration rate for a given sediment transport rate decreases as total sediment flux increases. The physical explanation is that surficial interstices are free of fine sediment during initial stages of infiltration and become plugged as infiltration progresses, thereby inhibiting further infiltration. A greater proportion of transported sediment can infiltrate areas of the bed with low accumulated sediment fluxes more readily than areas where high fluxes have previously plugged many surficial interstices. This tends to dampen differences between areas of the streambed in total sediment infiltrated.

We inverted equation (2) to compute local bedload fluxes from values of infiltration measured in 153 cans that were

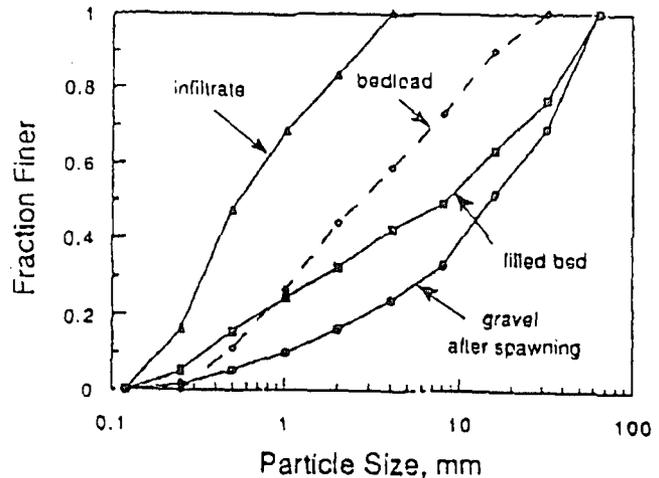


FIG. 4. Cumulative size distributions by weight of fine-sediment infiltrate, bedload, spawning gravel whose interstices are completely filled with fine sediment, and spawning gravel immediately after spawning, Jacoby Creek.

recovered from five transects after six measured stormflow periods. Values of local flux were normalized by dividing by the mean value of flux for each measurement period, and the probability density distribution of normalized fluxes was fit to a gamma distribution (Fig. 3):

$$(3) \quad f[(q_B)_T] = 5.351[(q_B)_T]^{1.232} e^{-2.232(q_B)_T}$$

The discharge record and equations (1) through (3) could be used to generate local sediment fluxes and infiltration rates for each incubation period.

#### Changes in Spawning Gravel Conditions

We modeled effects of fine-sediment infiltration on gravel properties that decrease embryo survival by two alternative approaches: (1) an increase in the fraction of fine sediment in the gravel, which affects both the rate of flow of oxygenated water to the embryos and the ability of emerging fry to penetrate the gravel interstices, and (2) a reduction in permeability of the gravel, which decreases intergravel flow velocities.

In both approaches, we start with the average grain size distribution of Jacoby Creek spawning gravels, which contain a small residual fraction of fine sediment, and recalculate gravel properties at the end of each incubation period. We do not, therefore, distinguish between adverse conditions that may prevail throughout most of an incubation period and those that may accrue only near the end of the period. The particle-size distribution of gravel overlying freshly spawned eggs is the average distribution obtained from freeze-core samples at five spawning areas (Lisle 1989) minus a proportion of the fraction finer than 4 mm such that the fraction finer than 1 mm equals 10% (Fig. 4). Initial porosity of the gravel is 0.35. The thickness of the gravel layer is 0.2 m, which approximates the average burial depth of eggs of steelhead trout and coho salmon (Shapalov and Taft 1954; Van den Berghe and Gross 1984).

The framework of the gravel bed after spawning is assumed to remain intact as fine sediment fills the interstices. That is, neither scour and fill nor expansion of the gravel framework occurs. Particle-size distribution of fine sediment between 0.12 and 4 mm was obtained from the average distribution of material collected in the cans (Fig. 4). The disregarded fraction finer

than 0.12 mm constituted only 7% of the material finer than 4 mm. Particle-size distribution of bedload material does not equal that of infiltrated fines, partly because the distributions are not truncated at the same minimum values. Also, fine bedload particles can more easily enter gravel interstices than coarse particles and are thus disproportionately represented in sediment infiltrating the gravel (Einstein 1970; Carling 1984; Lisle 1989).

The introduction of fines changes the value of grain-size parameters used in the model. In approach 1, bed-material fractions finer than 1 mm and finer than 8 mm were calculated for increasing values of accumulation. These grain-size ranges correspond approximately to those used by Tappel and Bjornn (1983) to relate survival to emergence of four species of salmonids.

In approach 2, effective diameter, which is used in calculations of permeability, is reduced by fine-sediment infiltration. Effective diameter is defined by

$$(4) D_e = [\sum(p_i / \psi_i D_i)]^{-1}$$

where  $p_i$  is the volume fraction and  $\psi_i$  is the sphericity of particles of size  $D_i$  (Johnson 1980). Sphericity is given a value of 0.7.

Porosity is also reduced as interstices are filled with sediment. Given initial conditions, porosity ( $E$ ) is calculated as a function of fine-sediment infiltration ( $I$ , kilograms per square metre):

$$(5) E = E_0 - E_0(1 - E_0)(I/I_{max})$$

where  $E_0 = 0.35$  is initial porosity,  $E_r = 0.40$  is porosity of fine sediment, and  $I_{max} = 0.042 \text{ kg/m}^2$  is fine-sediment accumulation to the point where interstices are completely filled. Mass of sediment was converted to volume by dividing by a particle density of  $2.5 \text{ g/cm}^3$  that was measured from Jacoby Creek sediment. Using these values, equation (5) simplifies to

$$(6) E = 0.35 - 5.0I$$

$E = 0.14$  when interstices are completely filled. This value corresponds closely to those for undisturbed gravel beds measured by Carling and Reader (1982).

Permeability ( $K$ ) is calculated from the Kozeny-Cozeny equation (Scheidegger 1960):

$$(7) K = g f(E) D_e^3 / 36 \nu$$

where  $K$  is in centimetres per second,  $g$  is gravitational acceleration,  $f(E) = E^3 / (1 - E)^2$ , and  $\nu$  is kinematic viscosity.  $\kappa$  is an empirically derived permeability constant and is given a value of 5.4, which Johnson (1980) found suitable for spawning gravel.

Apparent intergravel flow velocity ( $u_a$ ) is calculated from Darcy's Law:

$$(8) u_a = K(dh/dl)$$

where  $u_a$  is in centimetres per second. Head loss ( $dh/dl$ ) over riffle crests where fish commonly spawn is given a value of 0.005. Channel gradient of the study reach equals 0.0062. We use values of  $u_a$  to compute expected survival.

#### Embryo Survival

We use the two approaches for evaluating changes in gravel properties (described above) and corresponding relations to embryo survival (described below) to explicitly evaluate uncertainty in relating survival to gravel properties.

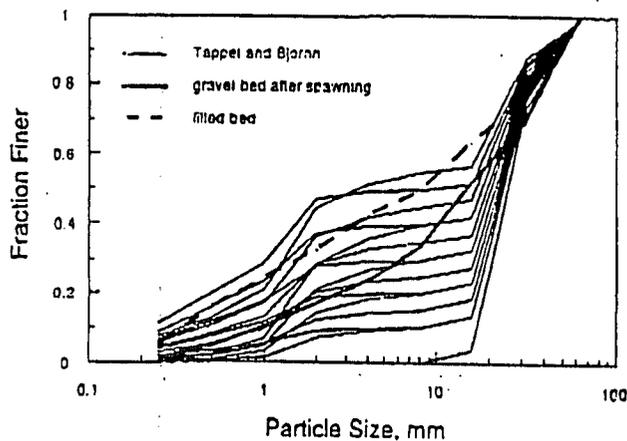


FIG. 5. Cumulative frequency distributions of particle sizes used in our model and in experiments by Tappel and Bjornn (1983).

In the first approach, we use Tappel and Bjornn's (1983) empirical relation between survival of steelhead embryos and the percentages of spawning gravel finer than 0.85 mm and finer than 9.5 mm:

$$(9A) S = 94.7 - 0.1P_{0.85}P_{9.5} + (P_{9.5})^2$$

where  $S$  is expected percent survival to emergence and  $P_{9.5}$  and  $P_{0.85}$  are the percent volume of sediment finer than 9.5 and 0.85 mm, respectively, in the overlying gravel. We substitute  $P_8$  for  $P_{0.85}$  and  $P_1$  for  $P_{9.5}$ . Although Tappel and Bjornn's (1983) empirical relation fits specific laboratory conditions, we justify its use in our model by comparing their gravel properties with those used in our model. First, we both use a burial depth of 0.2 m. Second, their particle-size distributions of gravel-sand mixtures overlap our starting distribution and the distribution corresponding to maximum infiltration (Fig. 5).

Expected survival computed for a range of values of fine-sediment infiltration fits a linear relation well:

$$(9B) S = 67.9 - 0.648I \quad r^2 = 0.999$$

which, when combined with equation (2), yields

$$(9C) S = 67.9 - 1.10(q_B)_T^{0.412}$$

In our second approach, survival is a function of intergravel flow velocity according to an empirical relation derived from data for sockeye salmon (J. Pyper, cited in Cooper 1965):

$$(10A) S = 167.0 + 46.3 \log(u_a) \quad r^2 = 0.96$$

The wall thickness and diameter of steelhead eggs are usually smaller than those of sockeye salmon; thus, demands for oxygen concentration for steelhead should be greater (Wickett 1975; Beacham and Murray 1989). Consequently, equation (10A) should overestimate survival of steelhead embryos.

Survival then approximates a linear function of infiltration which is substituted for  $u_a$  using equations (4), (6), (7), and (8):

$$(10B) S = 56.8 - 0.918I \quad r^2 = 0.999$$

Then by using equation (2) to substitute  $(q_B)_T$  for  $I$ :

$$(10C) S = 56.8 - 1.864(q_B)_T^{0.412}$$

For a given sediment flux, the survival function generated from the Tappel and Bjornn (1983) relation (9C) yields higher rates of survival than that generated from the intergravel-flow function (10C) (Fig. 6). This discrepancy is especially large for

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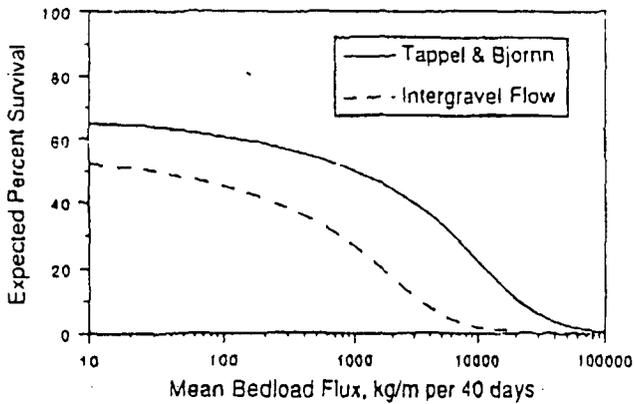


FIG. 6. Functions of embryo survival versus bedload flux (equations (9C) and (10C)) using the intergravel flow function and Tappel and Bjornn's (1983) relation.

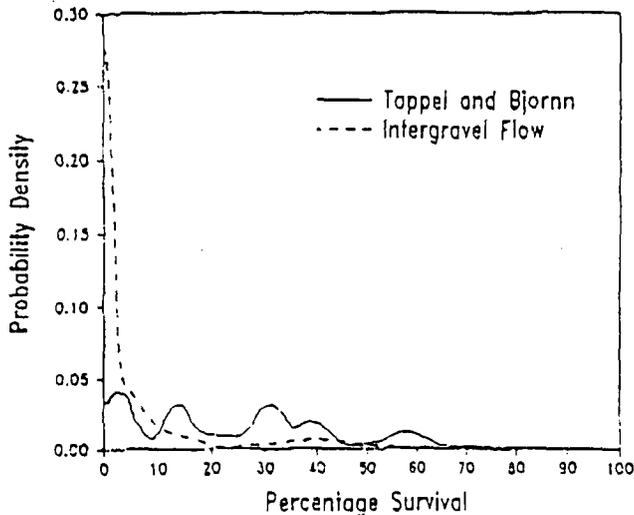


FIG. 7. Probability density distribution of embryo survival for all 40-d incubation periods over a 6-yr period using the intergravel-flow function and Tappel and Bjornn's (1983) relation.

fluxes between 5000 and 20 000 kg/m, a range that was commonly achieved during the 40-d periods.

Because each 40-d summation of mean sediment flux from equation (1) is associated with a distribution of values of local flux, expected survival must be integrated over equation (3) using equations (9C) and (10C). This results in a distribution of survival rates for each value of mean flux.

## Results

Probability density distributions of expected embryo survival were compiled for the entire period of record using the Tappel-Bjornn and intergravel-flow functions (Fig. 7). Expected survival for each 40-d incubation period is the mean value resulting from mean sediment flux and spatial variations in sediment flux and infiltration. Variations in expected survival arise from temporal variation in sediment transport due to climatic events. The salient feature of both distributions is the high variability of survival rates.

The two survival functions yield categorically different survival rates. Results from the Tappel-Bjornn function indicate

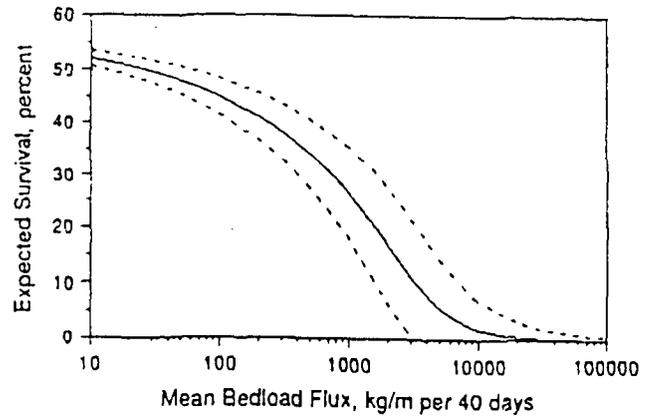


FIG. 8. Integrated relation computed from the intergravel-flow function between expected embryo survival and mean bedload flux with  $\pm 1$  SD in survival about the mean due to spatial variations in fine-sediment transport and infiltration.

that survival rates for each day eggs are deposited would most often exceed 10%. In contrast, most of the distribution of survival rates computed from the intergravel-flow function falls below 5%. Depending on critical embryo survival rates necessary to maintain fish populations, one could conclude that the quality of incubation habitat does or does not limit populations, depending on the choice of survival functions.

Spatial variations in sediment transport and infiltration create high variations in expected survival, particularly for high values of sediment flux. The standard deviation of expected survival, expressed as either an absolute value or a ratio to mean expected survival (coefficient of variation), increases with increasing mean sediment flux computed from the intergravel-flow function (Fig. 8). The coefficient of variation is greatest for mean values of flux exceeding approximately 5000 kg/m and corresponding to mean survival rates of less than 10%. Given that such low survival rates are realized most of the time according to this function (Fig. 7), high spatial variations typify expected survival in Jacoby Creek.

Temporal variations in expected survival are also high. Embryo survival rates can be expected to vary widely from year to year because of the episodic nature and strong influence of stormflows that punctuate the spawning and incubation season (Fig. 9). In some years, e.g. 1983, high-flow events are frequent, while in others, e.g. 1985, only one event may occur. Even in a relatively dry year, e.g. 1980, survival may be low if all eggs are laid over a short period and a single high-flow event happens to occur during incubation.

## Discussion

### Evaluation of Uncertainty and Variability

One of the most useful immediate results of modeling a system of natural processes is an evaluation of the relative uncertainty and variability of individual processes. As more knowledge of a process is gained and uncertainty diminishes, our awareness of its variability often increases. Among the hierarchy of processes between sediment transport and salmonid embryo survival, variability is high and uncertainty relatively low in the driving processes (streamflow and sediment transport), and uncertainty is high in the response processes (changes in gravel conditions and embryo mortality).

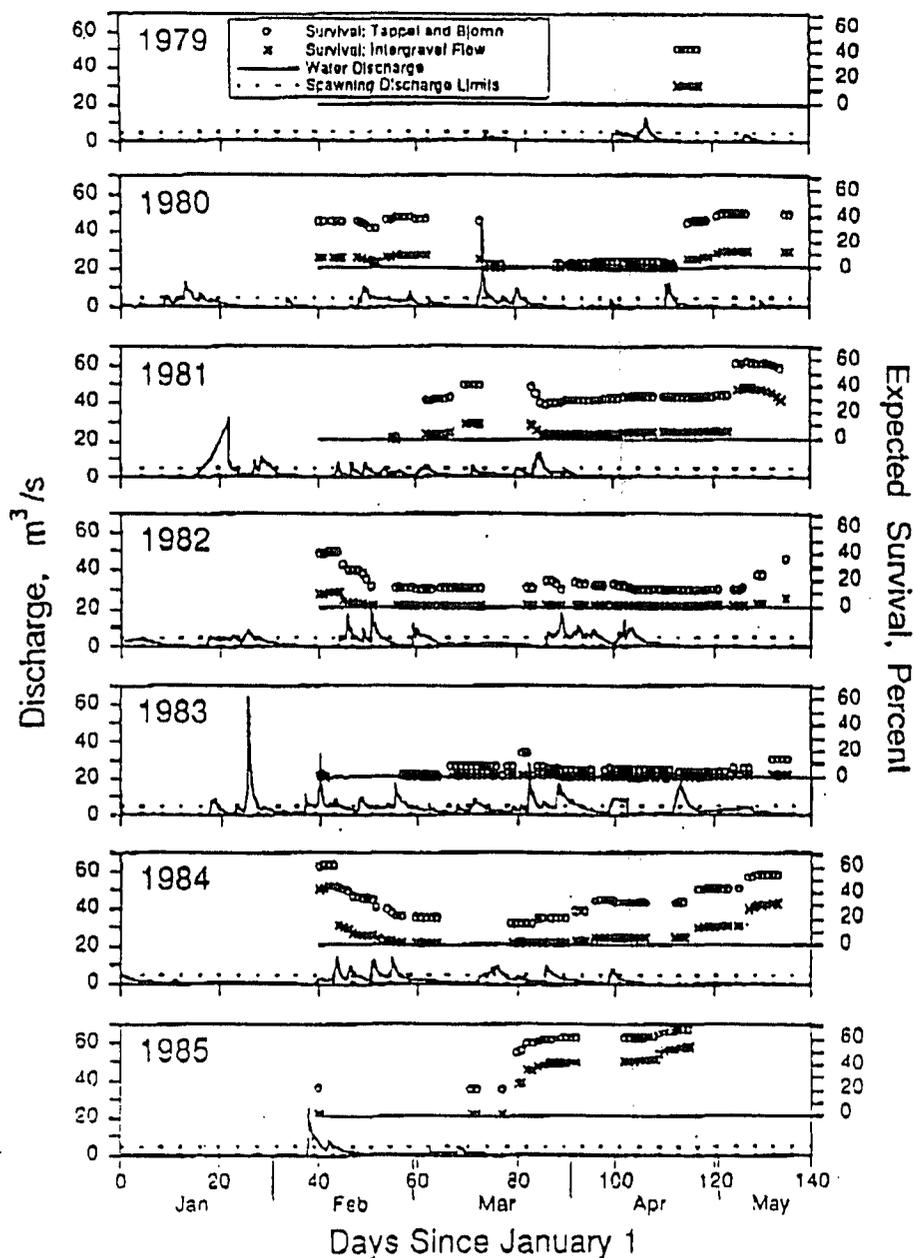


FIG. 9. Hydrographs and expected survival of embryos for the period of January 1 to May 15 for the years 1979-85. Plots of survival correspond to the day of emergence of alevins after a 40-d incubation period following spawning which occurs within discharge limits of 0.85 and 4.8  $m^3/s$ .

Streamflow is highly variable but measured routinely with little uncertainty. Bedload transport varies approximately with streamflow, and varies considerably laterally and longitudinally during a stormflow event (see Gomez 1991). Bedload transport rates can be measured directly with careful attention to sampling strategies and limitations of samplers or predicted with an expected accuracy of within an order of magnitude (Gomez and Church 1989). Considerable investment in measurement and modeling is required to quantify spatial variation in bedload transport. Compared with its effects on gravel properties and embryo survival, however, variability in bedload transport outweighs its uncertainty.

Uncertainty in effects of sediment transport on spawning gravel is high because of a lack of understanding of the variation of fine-sediment infiltration and scour and fill with hydraulic and sedimentological properties of streams. Scour and fill of streambeds can alter streambed composition as much as sediment infiltration (Lisle 1989) and can also result in fatal entrainment of embryos (Gangmark and Broad 1956). Although mean depths of scour and fill in gravel-bed channels have been modeled (Ziemer et al. 1991), such models are crude and do not adequately incorporate spatial variations. Relations between sediment transport and fine-sediment infiltration are either empirical, and thus applicable only to channels similar to those

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where relations were developed, or fit stringent sedimentological criteria. Where sand is abundant, rates of infiltration are influenced by plugging of gravel interstices near the bed surface early in the infiltration process, which inhibits further infiltration into deeper layers (Beschta and Jackson 1979; Carling 1984; Lisle 1989; Diplas and Parker 1992). Alonso et al. (1988) developed a model of sediment infiltration and its effects on gravel properties in a channel containing abundant silt and clay, but little sand. Under these conditions, silt and clay are able to penetrate all but the smallest interstices and thus fill beds from the bottom up (Einstein 1968).

Uncertainty in the depth of fine-sediment infiltration complicates modeling of changes in gravel conditions and their effect on embryo survival. Empirical relations between survival of eggs to emergence and the volume of fine sediment deposited in redds vary considerably depending on grain size distributions of fines and redd material, distribution of fines with depth in the bed, and other conditions imposed in the laboratory or in the field (Everest et al. 1987; Chapman 1988). As a result, there are no clear criteria to choose between relations for a model such as ours:

Chapman (1988), for example, objected to the application of relations developed under laboratory conditions to field situations on the grounds that gravel conditions in natural egg pockets are poorly understood and not replicated by the uniform distributions of fines with depth imposed in laboratory experiments. The implication, however, that the greater permeability that has been observed in an egg pocket (Platts and Penton 1980) translates to a greater rate of intergravel flow than indicated by the material surrounding the pocket may also be erroneous. Subsurface streamlines do converge into a permeable volume, but only when inflow and outflow conduits exist. Thus, intergravel flow through a permeable egg pocket may be governed more by conditions in the surrounding material than those in the pocket itself. As Chapman (1988) admonished, the true nature of bed material structure associated with redds and the effects of sedimentation on embryo survival in natural channels are not well understood and need to be improved before accurate, predictive modeling can proceed. The categorically different results from our model resulting from two applicable survival functions highlight this need.

The issue is further complicated by multiple causes of mortality, as well as adaptations of ova and alevins that increase survival under low rates of intergravel flow and low levels of dissolved oxygen (reviewed in Everest et al. 1987). Even if intergravel flow is adequate for embryo development, sand that plugs near-surface interstices can prevent alevins from emerging from the gravel (Koski 1966; Phillips et al. 1975). Degradation of incubation conditions can also lead to smaller size of alevins (Silver et al. 1963; Shumway et al. 1964; Bams 1969), which may decrease chances for survival of fry. The immediate cause of mortality from reduced intergravel flow is the reduction of oxygen available to the embryos. Oxygen concentration of intergravel water does not necessarily depend on intergravel flow velocity, but they usually correlate (Chapman 1988). Fine sediment in Jacoby Creek gravel contains abundant fine particulate organic matter. Subsurface samples of gravel whose interstices were filled with fine sand and silt smelled of decaying organics, suggesting that low oxygen concentrations are associated with high concentrations of fine sediment.

#### Influence of Diversity and Size of Spawning Runs

The strong influence of individual stormflow events suggests that young-of-the-year fish populations would vary less widely

if spawning were spread out in time over the rainy season. This is most likely to result from a diversity of species, races, and genotypes, as well as high escapement. Steelhead, for example, spawn late in the season during the onset of drier weather in many streams, and their embryos would have an advantage if high flows became less frequent. Reductions in diversity of genotypes that lead to concentrated spawning over a short period would seem to threaten fish populations because even in relatively dry years the annual recruitment could be threatened by a single stormflow. The number of embryos surviving each year to provide annual fry recruitment is more likely to affect the dynamics of fish populations than the composite survival rate over a period of years.

Similarly, wide spatial variations in sediment effects suggest that a diversity of redd sites can promote stability in fry recruitment. If a large number of redds are constructed, the few located in zones of low sediment flux and infiltration may produce enough fry to compensate for high mortality elsewhere. Steelhead do not appear to select low-risk spawning sites in Jacoby Creek but instead choose loose gravel of the appropriate size often in the thalweg. Our measurements have shown that sediment transport and scour and fill are high in such areas (Lisle 1989).

Fewer redds, resulting from reduced size and diversity of spawning runs, would lead to increased variability in embryo survival and a greater risk of dangerously low populations even in the most favorable of seasons. As populations of emerging fry become less, embryo survival rates become critical for fish populations if the available rearing habitat for juveniles is not adequately filled. At the same time, spawning success becomes less predictable on the basis of the quality of incubation habitat for embryos.

#### Conclusions

Despite a considerable degree of uncertainty and inherent variability, the effects of flow and sediment transport on salmonid embryo survival can be modeled. Spatial and temporal variability of water discharge, sediment transport, and fine-sediment infiltration can be explicitly incorporated. Relations between driving and response variables can be quantified to various degrees of generality, precision, and accuracy. The resulting model is sufficiently comprehensive to explore variability, highlight research needs, and perhaps evaluate relative effects of changes in sediment transport regime.

Regardless of the uncertainties in many of the processes we modeled, it is clear that the fraction of embryos surviving to emerge from spawning gravels each year can be expected to be extremely variable in streams like Jacoby Creek, where fish spawn during the high-flow season and the channel bed is at least moderately mobile. In these cases, and especially where adult escapement is low (Everest et al. 1987), the nature of the linkage between the sediment transport regime and embryo mortality may be to limit fish production in some years but not others.

Some research needs are clear. The further we move down the hierarchy of processes from water discharge to embryo mortality the more we find is unknown. Relations between sediment transport and gravel conditions need to become more general, include scour and fill, and adequately treat variations in depth and grain size of fine-sediment infiltration. More crucially, the subsurface structure of natural redds and the response of embryos in conditions in spawning gravels need to be quantified better. Progress in the problems outlined above will move

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us closer to predicting embryo survival under changing watershed conditions and improve our understanding of factors influencing population dynamics of stream fishes.

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