Assessing Physical Quality of Spawning Habitat

G. MATHIAS KONDOLF*

Department of Landscape Architecture and Environmental Planning University of California, Berkeley, 202 Wurster Hall, Berkeley, California 94720, USA

> JOHN G. WILLIAMS 875 Linden Lane, Davis, California 95616, USA

TIMOTHY C. HORNER Department of Geology, California State University Sacramento 6000 J Street, Sacramento, California 95819, USA

DAVID MILAN

Department of Natural & Social Sciences, University of Gloucestershire Cheltenham, GL50 4AZ, UK

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 suitable 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

^{*} Corresponding author: kondolf@berkeley.edu

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.

Physical Conditions that Affect Spawning, Incubation, and Emergence

The spawning gravel requirements of salmonids differ during redd construction, 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.

Dye studies in the field and laboratory

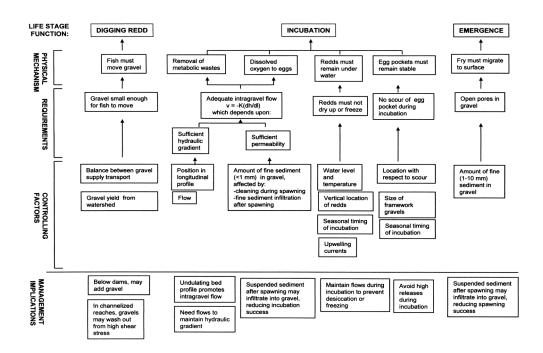


Figure 1. Flow chart showing gravel requirements of salmonids during redd construction, incubation, and emergence. The intergravel flow equation is defined in Figure 3.

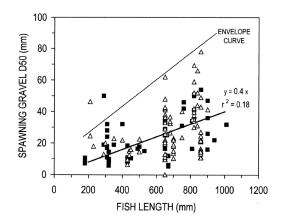


Figure 2. Median diameter (D_{50}) of spawning gravel plotted against body length of a spawning salmonid. Solid squares denote samples from redds; open triangles are unspawned gravels, which are potential spawning gravels sampled from the undisturbed bed near redds. (Modified from Kondolf and Wolman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

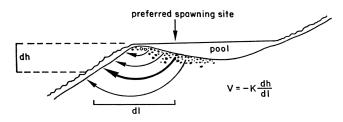


Figure 3. Diagram of groundwater flow through the tail of a pool. The lower elevation of the water surface in the riffle creates a hydraulic gradient that induces downwelling at the tail of the pool; *V* is Darcy velocity, and *K* is hydraulic conductivity. Vertical scale is greatly exaggerated. (From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

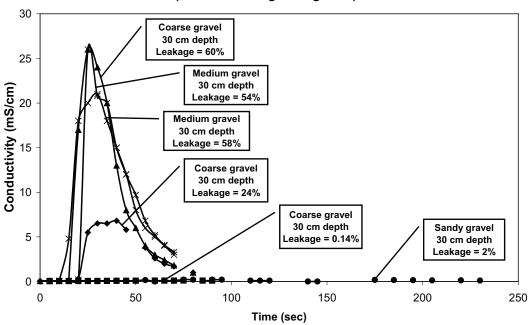
Several sampling strategies can minimize contamination by atmospheric oxygen. Dissolved oxygen should be measured in situ or immediately after samples are collected in the field whenever possible. Samples that are transported to the laboratory for analysis should be analyzed the same day. If a portable 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



Leakage along annulus of piezometer (estimated using mixing lines)

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.

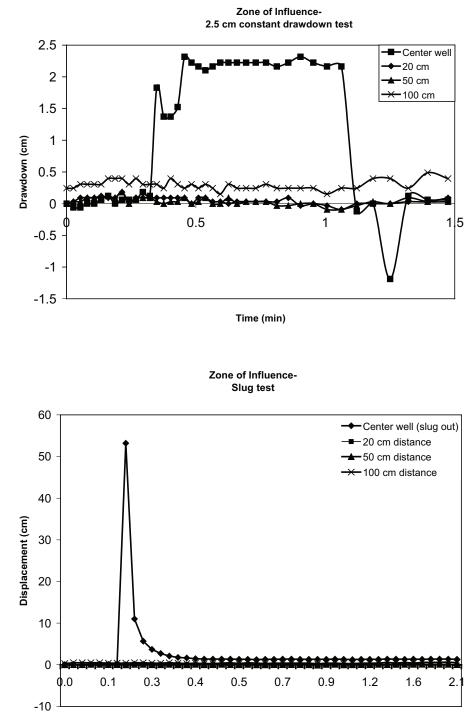
The small zone of influence encompassed by each test creates similar problems during assessment of a heterogeneous stream environment. A small number of permeability tests may not accurately characterize a habitat zone such as a riffle, and the number of these tests required to accurately characterize 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 hvporheic 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



Time (min)

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.

B

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 direction 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 intragravle 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 fastmoving, 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 Mc-Neill 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 meterscale 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

Sampling method	Details	Advantages	Disadvantages	Papers considering error and sample size
Visual sampling Bovee (1982)	 Visual/subjective estimate used to assess relative percentages of different size fractions required. 	 Rapid assessment of grain size. No data processing. Data are not comparable to grain-size distributions normally presented in geomorphic and enginnering literature. 	 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)	 Gravel surface photographed, size determined from scale-bar. Image analysis involves automated derivation of DEMs from image, or grey-level histogram segmentation. 	 Possible to recover complete grain-size distribution. Provide data on percentage of fines present on surface. Bed surface is not disturbed. 	 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)	 Random selection and measurement of 100 clasts from specific geomorphic features on the bed surface. Variants include the zigzag count (Bevenger and King 1995) and the transect method (Rosgen 1996). 	 Data are normally presented as cumulative grain-size curves, able to compare data presented in engineering, and geomorphic literature 	 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	 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). 	 Better approximation of true substrate than shovel and freeze-core sampling 	 Very large samples >200 kg) required in order to represent all grain size present. 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)

12

Table 1.

KONDOLF ET AL.

· · · · · · · · · · · · · · · · · · ·				
); et al. 7); 11); (2000);		Advantages	Disadvantages	rapers considering error and sample size
• • • • • • • • • • • • • • • • • • •	Steel or copper probe driven into bed substrate. Liquid CO_2 or N_2 is injected to the base of the probe. Sediment and water freezes to the outside of the probe.	 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. 	 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 	Thoms (1992); Milan et al. (1999)
Levasseur et al. (2006) cables attached to the me rim are stretched to the b surface. Clean gravel is th placed on top of bag. Fin that infiltrate voids can b sampled by pulling bag u via cables. Variants inclu permeable pots and wire baskets.	• 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.	 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) 	 Packing character of clean gravel placed on top of bag may not reflect natural packing. 	

Table 1. Continued

ASSESSING PHYSICAL QUALITY IF SPAWNING HABITAT

	Maxi	mum percent fii	ner than grain size	(mm)
Source	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

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

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.

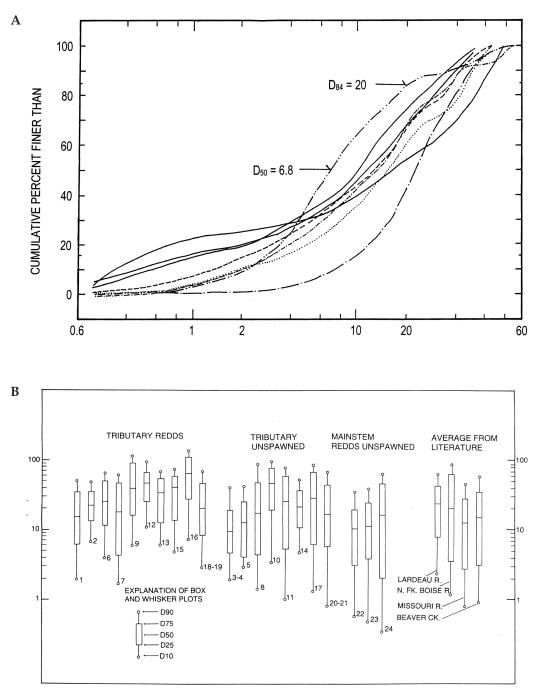


Figure 6. Multiple gravel-size distributions, presented as cumulative frequency curves (A) and (B) boxand-whisker plots (for rainbow trout spawning gravels in the Colorado River and tributaries downstream of Glen Canyon Dam, along with averages for other rainbow trout spawning gravels). For each sample, 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).

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

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

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 grainsize 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_{s4} (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).

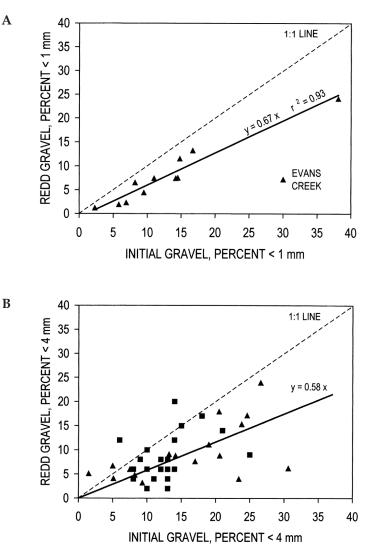


Figure 7. (A) Percentage of sediment finer than 1 mm in redds and potential (comparable, unspawned) gravels. The data point for Evans Creek is excluded from the regression. (See Kondolf et al. 1993 for sources of data.) (B) Percentage of sediment finer than 4 mm from pairs of redd and potential spawning 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 subsurface), 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 then 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 cobbleand 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 spawning 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 freezecore 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 140-240kg 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 tripodmounted 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 CO_2 cylinders, N_2 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 freezecores 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 freezecores. 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

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

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 grainsize 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 grainsize 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, intergravel 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?

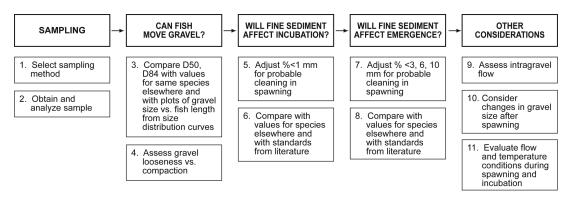


Figure 8. Flow chart illustrating nine discrete steps in evaluating quality of potential salmonid spawning gravel.

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 exces*sive for emergence (steps 7–8).* – While the finesediment (<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 watergroundwater 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 stepbackwater 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.

References

- Adams, J. 1979. Gravel size analysis from photographs. Journal of the Hydraulics Division of the American Society of Civil Engineers 105:1247–1285, New York.
- Adams, J. N., and R. L. Beschta. 1980. Gravel bed composition in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 37:1514–1521.
- Bams, R. A. 1969. Adaptations in sockeye salmon associated with incubation in stream gravels. Pages 71–88

in T. G. Northcote, editor. Symposium on salmon and trout in streams. University of British Columbia, Vancouver.

- Barnard, K., and S. McBain. 1994. Standpipe to determine permeability, dissolved oxygen, and vertical particle size distribution in salmonid spawning gravels. U.S. Forest Service, Region 5, Fish Habitat Relationships Technical Bulletin 15, Eureka, California.
- Beer, W. N., and J. J. Anderson. 1997. Modeling the growth of salmonid embryos. Journal of Theoretical Biology 189:297–306.
- Bernier-Bourgault, I., F. Guillemette, C. Vallé, and P. Magnan. 2005. A new incubator for the assessment of hatching and emergence success as well as the timing of emergence of salmonids. North American Journal of Fisheries Management 25:16–21.
- Bevenger, G. S., and R. M. King. 1995. A pebble count procedure for assessing watershed cumulative effects. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Paper RM-RP-319, Fort Collins, Colorado.
- Bouwer, H., and R. C. Rice. 1976. A slug test for determining hydraulic conductivity of unconfined aquifers with completely or partially penetrating wells. Water Resources Research 12:423–428.
- Bovee, K. D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. U.S. Fish and Wildlife Service, Office of Biological Services, FWS/OBS-82/86, Instream Flow Information Paper 12, Fort Collins, Colorado.
- Briggs, J.C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. California Department of Fish and Game Fish Bulletin 94.
- Buer, K., R. Scott, D. Parfitt, G. Serr, J. Haney, and L. Thompson. 1981. Salmon spawning gravel enhancement studies on northern California rivers. Pages 149–154 *in* T. J. Hassler, editor. Proceedings of the propagation, enhancement, and rehabilitation of anadromous salmonid populations and habitat in the Pacific Northwest. Humboldt State University, Cooperative Fishery Research Unit, Arcata, California.
- Bunte, K., and S. R. Abt, 2001, Sampling surface and subsurface particle-size distributions in wadable gravel- and cobble-bed streams for analyses in sediment transport, hydraulics, and streambed monitoring. U.S. Forest Service, Rocky Mountain Research Station, RMRS-GTR-74, Fort Collins, Colorado.
- Bush, N. J. 2006. Natural water chemistry and vertical hydraulic gradient in the hyporheic zone of the Cosumnes River near Sacramento, California. M.S. thesis. California State University, Sacramento.
- Carbonneau, P. E., N. E. Bergaron, and S. N. Lane. 2005. Texture-based segmentation applied to the quantification of superficial sand in salmonid river gravels. Earth Surface Processes and Landforms 30:121–127.
- Carling, P. A., and C. P. McMahon. 1987. Natural siltation of brown trout (*Salmo trutta* L.) spawning gravels during low flow conditions. Pages 229–244 *in* J. F. Craig and J. B. Kemper, editors. Regulated streams. Plenum Press, New York.

- Castleberry, D. T., J. J. Cech, Jr., M. K. Saiki, and B. A. Martin. 1993. Growth, condition and physiological performance of juvenile salmonids from the American River. U.S. Fish and Wildlife Service, Dixon, California.
- Cederholm, C. J., and E. O. Salo. 1979. The effects of logging road landslide siltation on the salmon and trout spawning gravels of Stequaleho Creek and the Clearwater River basin, Jefferson County, Washington, 1972–1978. University of Washington, Fisheries Resources Institute, FRI-UW-7915, Seattle.
- Chambers, J. S., R. T. Pressey, J. R. Donaldson, and W. R. McKinley. 1954. Research relating to study of spawning grounds in natural areas. Annual Report to U.S. Army Corps of Engineers, Contract No. DA.35026-Eng-20572. Available from Washington State Department of Fisheries, Olympia.
- Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117:1–21.
- Chow, V.T. 1959. Open-channel hydraulics. McGraw-Hill, New York.
- Church, M. A., D. G. McLean, and J. F. Wolcott. 1987. River bed gravels: sampling and analysis. Pages 43–87 in C. R. Thorne, J. C. Bathurst, and R. D. Hey, editors. Sediment transport in gravel-bed rivers. Wiley, New York.
- Constantz, J., A. E. Stewart, R. Niswonger, and L. Sarma. 2002. Analysis of temperature profiles for investigating stream losses beneath ephemeral channels. Water Resources Research 38:52–1–52–13.
- Cooper, A. C. 1965. The effect of transported stream sediments on the survival of sockeye and pink salmon eggs and alevins. International Pacific Salmon Committee, Bulletin 18, New Westminster, BC.
- Crisp, D. T. 1993. The ability of U.K. salmonid alevins to emerge through a sand layer. Journal of Fish Biology 43:656–658.
- Einum, S., A. P. Hendry, and I. A. Fleming. 2002. Eggsize evolution in aquatic environments: does oxygen availability constrain size? Proceedings of the Royal Society of London, Series B 269:2325–2330.
- Elliott, J. M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. Journal of Animal Ecology 44:805–821.
- Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Functional Ecology 9:290–298.
- Everest, F. L., R. L. Beschta, J. C. Scrivener, K. V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmind production – a paradox. Pages 98–142 *in* E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. University of Washington, College of Forest Resources, Seattle.
- Everest, F. L., C. E. McLemore, and J. F. Ward. 1980. An improved tri-tube cryogenic gravel sampler. U.S. Forest Service, Northwest Forest and Range Experiment Station, Research Note PNW-350, Portland, Oregon.

- Flosi, G., S. Downie, J. Hopelain, M. Bird, R. Coey, and B. Collins. 1998. California salmonid stream habitat restoration manual. California Department of Fish and Game, Inlands Fisheries Division, Sacramento.
- Freeze, R. A., and J. A. Cherry. 1979. Groundwater. Prentice Hall, Englewood Cliffs, New Jersey.
- Fripp, J. B., and P. Diplas. 1993. Surface sampling in gravel streams. Journal of Hydraulic Engineering 119:473–490.
- Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall Chinook salmon: the importance of geomorphic features in large rivers. Environmental Management 22:655–669.
- Geist, D. R., T. P. Hanrahan, E. V. Arntzen, G. A. Mc-Michael, C. J. Murray, and Y. J. Chien. 2002. Physiochemical characteristics of the hyporheic zone affect redd site selection by chum salmon and fall Chinook salmon in the Columbia River. North American Journal of Fisheries Management 22:1077–1085.
- Greig, S. M., D. A. Sear, and P. A. Carling. 2007. A review of factors influencing the availability of dissolved oxygen to incubating salmonid embryos. Hydrological Processes 21:323–334.
- Greig, S. M., D. A. Sear, and P. A. Carling. 2005b. The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. Science of the Total Environment 344:241–258.
- Greig, S. M., D. A. Sear, P. A. Carling, and L. J. Whitcombe. 2005a. Refinement and application of a conductiometric standpipe technique for measuring interstitial flow velocity in salmonid spawning gravels. Hydrobiologia 545:249–256.
- Gustafson-Marjanen, K. I., and J. R. Moring. 1984. Construction of artificial redds for evaluating survival of Atlantic salmon eggs and alevins. North American Journal of Fisheries Management 4:445–461.
- Harvey, J. W., and B. J. Wagner. 2000. Quantifying hydrologic interactions between streams and their subsurface hyporheic zones. Pages 3–44 in J. B. Jones and P. J. Mulholland, editors. Streams and ground waters. Academic Press, San Diego, California.
- Harvey, J. W., B. J. Wagner, and K. E. Bencala. 1996. Evaluating the reliability of the stream tracer approach to characterize stream-subsurface water exchange. Water Resources Research 32:2441–2451.
- Hey, R. D., and C. R. Thorne. 1983. Accuracy of surface samples from gravel bed material. Journal of Hydraulic Engineering 109:842–851.
- Horner, T. C. 2005. Physical and geochemical characterization of American River spawning gravels. Report to the U.S. Bureau of Reclamation Sacramento Office. Available: www.csus.edu/indiv/h/hornert (April 2008).
- Horner, T. C., R. Titus, and M. Brown. 2004. Phase 3 gravel assessment on the lower American River: report to the U.S. Bureau of Reclamation Sacramento Office. Availablet: www.csus.edu/indiv/h/hornert (April 2008).
- Horton, J. L., and D. W. Rogers. 1969. The optimum streamflow requirements for king salmon spawn-

ing in the Van Duzen River, Humboldt County, California. California Department of Fish and Game, Water Projects Branch, Administrative Report 69–2, Sacramento.

- Inman, D. L. 1952. Measures for describing the size distribution of sediments. Journal of Sediment Petrology 22:125–145.
- Kondolf, G. M. 1997. Application of the pebble count: reflections on purpose, method, and variants. Water Resources Bulletin 33:79–87.
- Kondolf, G. M. 2000. Assessing salmonid spawning gravels. Transactions of the American Fisheries Society 129:262–281.
- Kondolf, G. M. 2005. Expert report of Professor G. Mathias Kondolf, PhD. Expert report submitted in Natural Resources Defense Council et al. vs. Kirk C. Rogers et al., Civ. No. S-88-1658 LLK/GGH (E.D. Cal.).
- Kondolf, G. M., and A. Adhikari. 2000. Weibull vs. lognormal distributions for fluvial gravels. Journal of Sedimentary Research 70:456–460.
- Kondolf, G. M., G. F. Cada, M. J. Sale, and T. Felando. 1991. Distribution of potential salmonid spawning gravels in steep, boulder-bed streams of the eastern Sierra Nevada. Transactions of the American Fisheries Society 120:177–186.
- Kondolf, G. M., S. S. Cook, H. R. Maddux, and W. R. Persons. 1989. Spawning gravels of rainbow trout in the Grand Canyon, Arizona. Journal of the Arizona-Nevada Academy of Science 23:19–28.
- Kondolf, G. M., and S. Li. 1992. The pebble count technique for quantifying surface bed material in instream flow studies. Rivers 3:80–87.
- Kondolf, G. M., T. E. Lisle, and G. M. Wolman. 2003. Bed sediment measurement. Chapter 13 in G. M. Kondolf and H. Piégay, editors. Tools in fluvial geomorphology. Wiley, New York.
- Kondolf, G. M., M. J. Sale, and M. G. Wolman. 1993. Modification of gravel size by spawning salmonids. Water Resources Research 29:2265–2274.
- Kondolf, G. M., and M. G. Wolman. 1993. The sizes of salmonid spawning gravels. Water Resources Research 29:2275–2285.
- Koterba, M. T., F. D. Wilde, and W. W. Lapham. 1995. Ground-water data-collection protocols and procedures for the National Water-Quality Assessment program: collection and documentation of waterquality samples and related data. U.S. Geological Survey Open File Report 95-399.
- Lane, S. N. 2001. The measurement of gravel-bed river morphology. Pages 291–320 in M. P. Mosley, editor. Gravel-bed rivers V. New Zealand Hydrological Society, Wellington.
- Lee, D. R., and J. A. Cherry. 1978. A field exercise on groundwater flow using seepage meters and minipiezometers. Journal of Geological Education 27:6– 10.
- Levasseur, M., F. Berube, and N. E. Bergeron. 2006. A field method for the concurrent measurement of fine sediment content and embryo survival in artificial salmonid redds. Earth Surface Processes and Landforms 31:526–530.
- Libelo, E. L., and W. G. MacIntyre. 1994. Effects of sur-

face-water movement on seepage meter measurements of flow through the sediment-water interface. Applied Hydrogeology 2:49–54.

- Lisle, T. E., and R. E. Eads. 1991. Methods to measure sedimentation of spawning gravels. U.S. Forest Service, Pacific Southwest Research Station, Resources Note PSW- 411, Berkeley, California.
- Lorenz, J. M., and J. H. Eiler. 1989. Spawning habitat and redd characterization of sockeye salmon in the glacial Taku River, British Columbia and Alaska. Transactions of the American Fisheries Society 118:495–502.
- MacFarlane, R. B., and E. C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and the Gulf of the Farallones, California. Fishery Bulletin 100:244–257.
- Malcolm, I. A., C. Soulsby, A. F. Youngson, and J. Petry. 2003a. Heterogeneity in ground water-surface water interactions in the hyporheic zone of a salmonid spawning stream. Hydrologic Processes 17:601–617.
- Malcolm, I. A., A. F. Soulsby, and C. Youngson. 2006. High-frequency logging technologies reveal statedependent hyporheic process dynamics: implications for hydroecological studies. Hydrological Processes 20:615–622.
- Malcolm, I. A., A. F. Youngston, and C. Soulsby. 2003b. Survival of salmonid eggs in a degraded gravelbed stream: effects of groundwater-surface water interactions. River Research and Applications 19:303–316.
- McNeil, W. J., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U.S. Fish and Wildlife Service, Special Scientific Report Fisheries 469.
- Meehan, W. R. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.
- Merz, J. J., J. D. Setka, G. B. Pasternack, and J. M. Wheaton. 2004. Predicting benefits of spawning-habitat rehabilitation to salmonid (*Oncorhynchus* spp.) fry production on a regulated California river. Canadian Journal of Fisheries and Aquatic Sciences 61:1433–1446.
- Meyer, C. B., M. D. Sparkman, and B. A. Klatte. 2005. Sand seals in coho salmon redds: do they improve egg survival? North American Journal of Fisheries Management 25:105–121.
- Milan, D. J., G. L. Heritage, A. R. G. Large, and C. F. Brunsdon. 1999. Influence of particle shape and sorting upon sample size estimates for a coarsegrained upland stream. Sedimentary Geology 128:85–100.
- Milan, D. J., G. L. Heritage, A. R. G. Large, and M. E. Charlton, M. E. 2001. Stage-dependent variability in shear stress distribution through a riffle-pool sequences. Catena 44:85–109.
- Moyle, P. B. 2005. Expert report of Professor Peter B. Moyle, PhD. Expert report submitted in Natural Resources Defense Council et al. vs. Kirk C. Rog-

ers et al., defendants. US Court Eastern District of California.

- Murdoch, L. C., and S. E. Kelly. 2003. Factors affecting the performance of conventional seepage meters. Water Resources Research 39:2-1–2-10.
- Nicola, G. G., and A. Almodóvar. 2004. Growth pattern of stream-dwelling brown trout under contrasting thermal conditions. Transactions of the American Fisheries Society 133:66–78.
- Orcutt, D. R., B. R. Pulliam, and A. Arp. 1968. Characteristics of steelhead trout redds in Idaho streams. Transactions of the American Fisheries Society 97:42–45.
- Osenberg, C. W., R. J. Schmitt, S. J. Holbrook, K. E. Abu-Aba, and A. R. Flegal 1994. Detection of environmental impacts; natural variability, effect size, and power analysis. Ecological Applications 4:16–30.
- Parfitt, D., and K. Buer. 1980. Upper Sacramento River spawning gravel study. California Department of Water Resources, Northern Division, Red Bluff.
- Peterson, N. P., and T. P. Quinn. 1996. Persistence of egg pocket architecture in redds of chum salmon, *Oncorhynchus keta*. Environmental Biology of Fishes 46:243–253.
- Petts, G. E. 1987. Accumulation of fine sediment within substrate gravels along two regulated rivers, UK. Regulated Rivers 2:141–362.
- Phillips, R. W., and K. V. Koski. 1969. A fry trap method for estimating salmonid survival from egg deposition to fry emergence. Journal of the Fisheries Research Board of Canada 26:133–141.
- Pollard, W. P. 1955. The oxygen supply to salmon eggs in spawning beds. Journal of Fisheries Research Board of Canada 12:706–741.
- Radtke, D. B., J. K. Kurklin, and F. D. Wilder, editors. 1998. Techniques of water-resources investigations, book 9, handbooks for water resources investigations, section 6.2. National field manual for the collection of water-quality data. U.S. Geological Survey, Reston, Virginia.
- Reiser, D. W., and T. C. Bjornn. 1979. Habitat requirements of anadromous salmonids. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-96, Portland, Oregon.
- Rice, S. 1995. The spatial variation and routine sampling of spawning gravels in small coastal streams. British Columbia Ministry of Forests, Research Branch Working Paper 06/1995, Victoria.
- Rice, S., and M. Church. 1996. Sampling surficial gravels: the precision of size distribution percentile estimates. Journal of Sedimentary Research 66:654–665.
- Rombough, P. J. 1985. Initial egg weight, time to maximum alevin wet weight, and optimal ponding times for Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 42:287–291.
- Rombough, P. J. 1988. Growth, aerobic metabolism, and dissolved oxygen requirements of embryos and alevins of steelhead, *Salmo gairdneri*. Canadian Journal of Zoology 66:651–660.
- Rosgen, D. 1996. Applied river morphology. Wildland

Hydrology, Pagosa Springs, Colorado.

- Rubin, J.-F. 1995. Estimating the success of natural spawning of salmonids in streams. Journal of Fish Biology 46:603–622.
- Savant, S. A., D. D. Reibleand, and L. J. Thibodeaux. 1987. Convective transport within stable river sediments. Water Resources Research 23:1763–1768.
- Scrivener, J. C. 1988. Two devices to assess incubation survival and emergence of salmonid fry in an estuary streambed. North American Journal of Fisheries Management 8:248–258.
- Sear, D. A. 1993. Fine sediment infiltration into spawning beds within a regulated river experiencing floods: ecological implications for salmonids. Regulated Rivers Research & Management 8:373–390.
- Sear, D. A. 1995. Morphological and sedimentological changes in a gravel-bed river following 12 years of flow regulation for hydropower. Regulated Rivers Research and Management 10:247–264.
- Shaw, R. D., and E. E. Prepas. 1989. Anomalous, shortterm influx of water into seepage meters. Limnology and Oceanography 34:1343–1351.
- Shincariol, R. A., and J. D. McNeil. 2002. Errors with small volume elastic seepage meter bags. Groundwater 40:649.
- Shinn, E. A., C. D. Reich, and T. D. Hickey. 2002. Seepage meters and Bernoulli's revenge. Estuaries 25:126– 132.
- Silver, S. J., C. E. Warren, and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and Chinook salmon embryos and different water velocities. Transactions of the American Fisheries Society 92:327–343.
- Sowden, T. K., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Transactions of the American Fisheries Society 114:804–812.
- Springer, A. E., W. D. Petroutson, and B. A. Semmens. 1999. Spatial and temporal variability of hydraulic conductivity in active reattachment bars of the Colorado River, Grand Canyon. Groundwater 37:338–344.
- Stonestrom, D. A., and J. Constantz. 2003. Heat as a tool for studying the movement of ground water near streams. U.S. Geological Survey Circular, Denver, Colorado.
- Sutton, S. G., Built, T. P., and R. L. Jaedrocj. 2000. Relationships among fat weight, body weight, water weight, and condition factor in wild Atlantic salmon parr. Transactions of the American Fisheries Society 129:527–538.
- Terhune, L. D. B. 1958. The Mark VI groundwater standpipe for measuring seepage through spawning gravel. Journal of the Fisheries Research Board of Canada 15:1027–1063.

- Theurer, F. D., Harrod, T. R. and M. Theurer. 1998. Sedimentation and salmonids in England and Wales. Environment Agency, R&D Technical Report P194, Bristol, England.
- Thibodeaux, L. J., and J. D. Boyle. 1987. Bedform-generated convective transport in bottom sediment. Nature(London) 325:341–343.
- Thoms, M. C. 1992. A comparison of grab- and freezesampling techniques in the collection of gravel-bed river sediment. Sedimentary Geology 78:191–200.
- Tukey, J. W. 1977. Box-and-whisker plots. Pages 39-43 in J. W. Tukey, editor. Exploratory data analysis. Addison-Wesley, Reading, Massachusetts.
- Vanoni, V. A. 1975. Sedimentation engineering. American Society of Civil Engineers, Manual 54, Reston, Virginia.
- Vaux, W. G. 1968. The flow and interchange of water in a streambed. U.S. Fish and Wildlife Service Fishery Bulletin 66:479–489.
- Vibert, R. 1949. De repeuplement en truites et saumons par enforissement de "boites d"alevinage" ganies d'oeuf dans les graviens. Bulletin Francais de la Peche et del Pisciculture 153:125–150.
- von Schalburg, K. R., M. L. Rise, G. D. Brown, W. S. Davidson, and B. F. Koop. 2005. A comprehensive survey of the genes involved in maturation and development of the rainbow trout ovary. Biological Reproduction 72:687-699.
- Weight, D., and J. L. Sonderegger. 2001. Manual of applied field hydrogeology. McGraw-Hill, New York.
- Wilcock, P. R., G. M. Kondolf, W. V. G. Matthews, and A. F. Barta. 1996. Specification of sediment maintenance flows for a large gravel-bed river. Water Resources Research 32:2911–2921.
- Wolman, M. G. 1954. A method of sampling coarse river-bed material. Eos, Transactions of the American Geophysical Union 35:951–956.
- Young, M. K., W. A. Hubert, and T. A. Wesche. 1990. Fines in redds of large salmonids. Transactions of the American Fisheries Society 119:156–162.
- Young, M. K., W. A. Hubert, and T. A. Wesche. 1991. Biases associated with four stream substrate samplers. Canadian Journal of Fisheries and Aquatic Sciences 48:1882–1886.
- Zamora, C. 2006. Estimating rates of exchange across the sediment/water interface in the lower Merced River, CA. Master's thesis. California State University, Sacramento.
- Zellweger, G. W. 1994. Testing and comparison of four ionic tracers to measure stream flow loss by multiple tracer injection. Hydrologic Processes 8:155–165.
- Zimmerman, A. E., and M. Lapointe. 2006. Intergranular flow velocity through salmonid redds: sensitivity to fines infiltration from low intensity sediment transport events. River Research and Applications 21:865–881.