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## Critical Review of Variables Used to Define Effects of Fines in Redds of Large Salmonids

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*Abstract.* — Laboratory studies have not duplicated the structure and composition of egg pocket centrums in redds of large salmonids, and thus have not accurately modeled survival of embryos and alevins in natural egg pockets. Field studies of capped natural redds have related survival to conditions in the redds or surrounding areas but not demonstrably in egg pockets. These data probably do not accurately reflect conditions faced by embryos or emerging alevins. The few data on egg pocket characteristics indicate that geometric mean particle diameter, fredle index, and permeability are higher in gravel surrounding the embryos than elsewhere. Survival to alevin emergence usually regresses positively on each of these factors separately and on dissolved oxygen in intragravel water. Survival to emergence usually relates negatively to percentages of small fines. Quantitative predictors depend upon careful definition of egg pocket structure through field surveying of egg pocket centrum locations and on intensive study of pocket conditions. Laboratory duplication of egg pocket structure and physical variables will permit more accurate modeling of effects of fines on survival to emergence. Redd capping in natural redds can provide estimates of survival to emergence, which one may relate to average egg pocket conditions and to variates in the redd. After appropriate modeling, it may become possible to relate conditions outside of the egg pocket to the environment within it and to survival-to-emergence.

Here I review critically the variates used to evaluate effects of fine sediments on survival to alevin emergence in redds of large salmonids in streams. I have divided the main body of the review into sections on the structure of the salmonid redd and physical variables within it, on the relationships between substrate particle sizes, permeability, and survival, on the effects of fines on incubation and emergence success, and on the utility of survival predictors. I conclude with some research recommendations.

Work on effects of fine sediment on salmonid reproductive success began with Harrison (1923), who reported low survival of sockeye salmon *Oncorhynchus nerka* in gravels with high percentages of fine sediment. Hobbs (1937) found that fine

sediments reduced the survival of salmonid embryos in the substrate in some New Zealand streams. Shapovalov and Berrian (1940) and Shaw and Maga (1943) reported that high fractions of small sediment particles increased mortality of salmonid embryos. Stuart (1953) experimented in the laboratory on effects of silt on early life stages of brown trout *Salmo trutta* in Scotland, and found that survival decreased as fines increased. Shelton (1955), in simulated field conditions, showed that fine sediments reduced the emergence success of chinook salmon *Oncorhynchus tshawytscha*. Fine sediments, or fines, as discussed by these and later authors, include particles smaller than about 6 mm in diameter, although some researchers may use smaller diameters to bound the category.

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Numerous laboratory and field studies on effects of fines on salmonid survival soon supplemented these early efforts (Wickett 1954; McDonald and Shepard 1955; Alderdice et al. 1958; Terhune 1958; Coble 1961; Cordone and Kelley 1961; McNeil 1962; Phillips and Campbell 1962; Vaux 1962; Bianchi 1963; Silver et al. 1963; McNeil and Ahnell 1964; Shumway et al. 1964; Cooper 1965; Koski 1966; Mason 1969). These studies led to consensus that low dissolved oxygen and reduced water exchange increase embryo mortality in laboratory environments and in nature. They also showed that incubation success could decline in natural intragravel environments in which fines accreted. Furthermore, laboratory and field studies demonstrated that emergence of alevins declined as percentage of fines increased in experimental mixtures of substrate or in spawning gravels. Since 1969, research on fine sediment in the redd environment tended toward corroboration and refinement of the relationship between emergence success and percentage of fines (Koski 1975, 1981; Phillips et al. 1975; Tagart 1976, 1984; Cederholm et al. 1981; Tappel and Bjornn 1983; Irving and Bjornn 1984; Sowden and Power 1985).

Some work has addressed the difficult task of defining criteria for "healthy" and degraded intragravel environments (Platts and Megahan 1975; Shirazi et al. 1981; Stowell et al. 1983; Everest et al. 1987). Laboratory studies and single-factor analyses underlie most of these criteria.

The difficulty inherent in determining which environmental variables act as limiting factors has made it difficult, in turn, to establish the effects of intragravel conditions on fish ecology. For example, excessive fines in spawning gravels may not lead to smaller populations of adult resident salmonids if the amount of winter hiding space controls the number of juveniles that reach adulthood. However, criteria suitable for evaluation of watershed management practices may not necessarily relate directly to limiting factors. That is, a habitat criterion for best land management practices may only indicate streambed composition in areas used for salmonid spawning. Any criterion couched in terms of effects on salmonids should have demonstrable quantitative reproductive requirements. I concentrate in my review on the utility of quantitative predictors of salmonid responses.

## Structure of Salmonid Redds

The structure of salmonid redds mitigates the effects of fine sediment on survival of incubating embryos and on fry emergence. Many field and laboratory investigators have overlooked redd structure in formulating their sampling and experimental designs, reducing the utility of their reported data. The difficulty of locating and sampling the egg pocket, the small area that actually contains embryos or alevins within the relatively large spawning site disturbed by each female, has impeded research on the way fines affect emergence success of salmonids. The following material pertains to the redds constructed by large female salmonids, such as Pacific salmon of the genus *Oncorhynchus*, rainbow trout *Salmo gairdneri* and steelhead (anadromous rainbow trout), and brown trout.

### Redd Development

The salmonid redd in a stream begins as a pocket from which the female has removed fines and small gravels. She accomplishes this by the lifting action created when she turns on her side and vigorously and repeatedly flexes her body. Currents help carry the lifted materials; the finest particles travel well downstream and the small to medium gravels and larger sands move into a pile or ridge, called the tailspill, below the pocket (Burner 1951; Chapman et al. 1986; Figure 1). Gravels and cobble (or rubble) usually include particles with diameters of 6.3–76 and 76–254 mm, respectively. The size of the particles moved and left by a female depends on her size and the makeup of the substrate.

The female cannot or does not lift the largest particles in the substrate within the initial pocket; these form the clean egg pocket centrum, commonly a grouping of two to four large gravel or cobble particles that lie on the undisturbed substrate that forms the floor of the redd (Hobbs 1937; Burner 1951; Jones and Ball 1954; Vronskiy 1972). The female deposits the first group of eggs into this centrum and the male simultaneously fertilizes them. The eddying currents within the pocket help retain sperm in contact with the eggs. Currents at the bottom of the pocket deposit most eggs around the upstream bottom edges of large centrum components (Hobbs 1937).

The female quickly begins digging again directly and obliquely upstream from the first pocket. Current again carries the finer materials downstream from the redd, and gravels and some sands lifted from this newly excavated area drop into the first egg pocket or onto the tailspill, depending upon size of the excavated material. The female then prepares a new egg pocket with a centrum of sev-
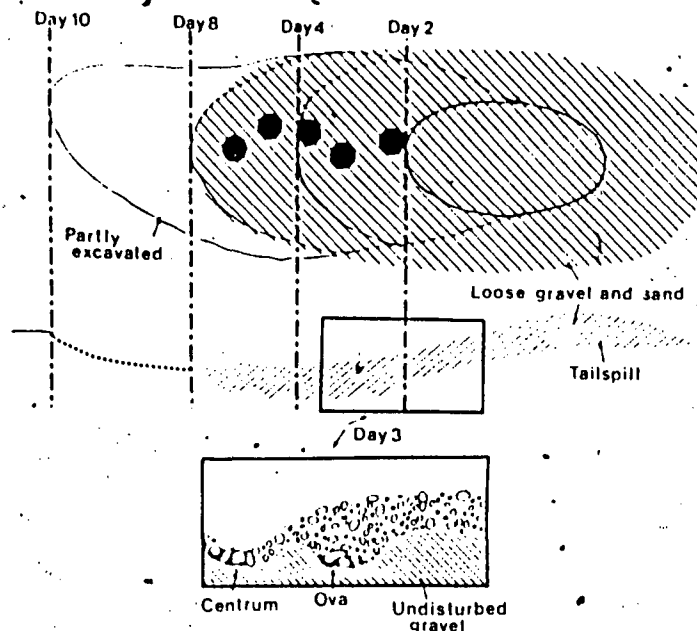
FIGURE 1.—Diagram of a salmonid redd in plan view (top) and longitudinal section (middle), showing redd development during the days after redd construction begins; upstream is to the left. Solid black circles represent locations and relative sizes of egg-pocket centrums. (Figure was adapted from Burner 1951 and Hawke 1978.) An expanded section of the redd with two egg pockets on day 3 is shown at the bottom of the figure.

eral large gravel or cobble particles cleaned of fine materials, and the egg deposition and fertilization process continues.

Understanding of redd construction evolved slowly. Hobbs (1937) described redds of chinook (quinnat) salmon and brown trout. Burner (1951) described the shape and size of redds constructed by chinook salmon, coho salmon *O. kisutch*, and sockeye salmon and also the locations of ova well upstream from the crest of the tailspill. Redds of other large salmonids cover smaller areas (Hobbs 1937; Burner 1951; Stuart 1953; Jones and Ball 1954; Hardy 1963) but have similar configurations.

Burner (1951) described the bottom of the egg pocket by noting that "there remain in the pot large stones too heavy for the fish to move far, and the crevices between these rocks provide excellent lodgement for the eggs." Jones and Ball (1954) reported that large rocks lie in the bottom of the egg pockets of brown trout. Vronskiy (1972) confirmed characteristics of the egg pocket centrum of chinook salmon by noting, "One interesting structural feature of most chinook redds is the presence of one or two large stones (15–23 cm

in diameter) lying on the bottom of the redd; the bulk of the eggs are concentrated around them." He excavated redds to reach this conclusion. Gustafson-Marjanen and Moring (1984) stated that redds of Atlantic salmon *Salmo salar* contain one or more large rocks in the egg pit. These authors prepared artificial egg pockets with large centrum components, among which they introduced eyed ova of Atlantic salmon.

Hawke (1978) excavated chinook salmon redds in New Zealand. Although he did not explicitly describe the tailspill, his definition of a redd, as the total area excavated by a fish and the area in which ova lie, implicitly means that he did not include the tailspill in the term "redd." His diagrams show that deposited embryos lie not beneath the tailspill crest, but upstream in a series of five to six egg pockets within the disturbed area of the substrate. His observations supplement the findings of Hobbs (1937) during excavations of redds of chinook salmon, brown trout, and rainbow trout in New Zealand.

Pocket placement progresses upstream, but excavation also extends perpendicular to streamflow and to the pocket line, because of oblique digging

to cover the egg pocket centrum (Hawke 1978). Not all digging in the redd serves to cover earlier egg pockets or even to construct new ones. Females apparently also dig to test the substrate for suitability. They do not place eggs in all initial pockets, and may move to a new area for actual spawning.

When the female has prepared the final, most upstream egg pocket, she digs upstream but excavates no identifiable new single pocket. Rather, several shallow excavations often appear directly and obliquely upstream. Some material from these areas falls into the most recently excavated egg pocket. The female removes fines from an area much wider than the pockets themselves as she digs obliquely and at the next pocket location (Figure 1).

Hobbs (1937) described the "floor" of the redd by noting that the substratum of undisturbed material underlying the redd falls in elevation steadily from the upstream end of the redd down to the point where the female commenced work. He stated that embryos of chinook salmon in egg pockets lay about 25 cm beneath the surface of the redd. The first egg pockets have deeper floors than later ones (Hawke 1978). Much disturbed gravel from the last pockets tends to deposit toward the lower end of the redd because of the more upstream location of the last pockets and perhaps because of waning energy of the female and effects of the tailspill on water velocity over the redd.

Egg pocket depth ranges from 18 to 43 cm for chinook salmon redds (Hawke 1978; Chapman et al. 1986), and from 8 to 22 cm for brown trout redds (Hardy 1963). Ova tend to concentrate at the bottom of the egg pocket (Hawke 1978) in the centrum. Freeze-core samples taken from chinook salmon redds in the Rogue River, Oregon, revealed that the eggs lay in a stratum 2–3 cm thick just above the undisturbed streambed at the bottom of the egg pocket (F. Everest, U.S. Forest Service, personal communication). Although stray eggs lay higher in the redd matrix, most ova lay in the deepest portion of the redd. Chapman et al. (1986) reported that the shallowest chinook salmon eggs in redds excavated at Vernita Bar, on the Columbia River in Washington, lay 10 cm beneath the gravel surface in the redd, but 19 cm was the mean depth at which the first eggs lay. The mean depth of egg pockets (bottom of pocket) was 29 cm (range, 19–37 cm), close to that reported by Hawke (1978).

Hobbs (1937) found that redds of brown and rainbow trout had structures similar to those of chinook salmon, although they were smaller. Brown trout redds had one to four egg pockets, the number a function of redd size, and most eggs lay 20 cm beneath the gravel surface. Hobbs stated that rainbow trout eggs also lay in well-defined egg pockets at a depth of about 20 cm beneath the gravel surface. In redds of small salmonids, the egg pocket, even where singular, very likely has the same physical characteristics, although it is shallower and contains smaller particles.

*Removal of Fines*

The female salmonid removes fines from an area much wider than the pockets themselves. Her completed redd contains less fine silt and sand than the surrounding undisturbed substrate. Where spawners use the same areas year after year, they may maintain the area in a coarser condition than surrounding gravels, that remain unused. Large numbers of spawners in the same area should engender a "mass cleaning," as fines removed from one redd deposit downstream, only to be lifted and passed along by females working downstream. Large annual spawning populations of sockeye salmon, pink salmon *O. gorbuscha*, chum salmon *O. keta*, chinook salmon, and coho salmon probably help maintain high-quality spawning habitat. When spawning populations decrease, the overall quality of spawning habitat can decline (Everest et al. 1987).

McNeil and Ahnell (1964) found that pink salmon significantly reduced the percentage of solids in the substrate that passed through sieve openings of 0.833 and 0.104 mm, and that a portion of the removed materials consisted of light organic material. The fraction with the greatest amount of organic matter formed part of the smallest size components, the portion females could most easily remove during redd construction. This should apply to spawning gravels used by other salmonid species as well.

New redds can contain as much as 32% less organic material than old redds constructed in the previous year (Ringler 1970). Everest et al. (1987) summarized reports that demonstrated reductions in fines in the substrate as a result of spawning. Although the criteria for fines have differed among researchers, the evidence for substantial cleaning is clear.

*Intrusion of Fines into Gravel*

After the female has partially cleansed fines from the redd, small particles inevitably move back into the relatively clean gravel. Hobbs's (1937) pi-

oncering report stated that "Sediment tended to lodge and to cake firstly amongst the surface material of the redds, forming a silt 'crust' overlying cleaner material. In some cases, but subsequently, silt penetrated to egg-pockets, virtually restoring the bed to its original state." Hobbs stated that it was unusual for silt to penetrate to the egg pocket while ova or alevins remained in the pocket. Everest et al. (1987) noted that clean and smaller gravels overlie the egg pocket.

Depth of intrusion of fines into clean gravels tends to be greater for smaller-diameter particles and less for larger ones (Beschta and Jackson 1979). In flume tests of intrusions of fines of 0.5-mm diameter into an initially clean gravel bed with a median particle size of 15 mm, Beschta and Jackson (1979) noted that the uper 10 cm of the gravel bed trapped the fines and formed a barrier, or "seal," against further intrusions. Intrusion amounted to 2–8% of total bed voume.

Froude numbers ($F_r$) help characterize flow conditions that influence intrusion of fines. Beschta and Jackson (1979) described this dimensionless variable, which represents the ratio of inertial to gravitational forces in fluid flow (Streeter and Wylie 1975):

$$F_r = V^2/gy;$$

$V$ = mean velocity, m/s;
$g$ = acceleration due to gravity, 9.8 m/s²;
$y$ = depth of flow, m.

For subcritical flow ($F_r < 1.0$), water flows relatively slowly and deeply. At a critical flow ($F_r = 1.0$), the specific energy ($E = V^2/[2g + y]$) is at a minimum. Standing waves in a stream indicate critical flow conditions. Supercritical flow ($F_r > 1.0$) typically occurs in relatively shallow, rapid flows.

Beschta and Jackson (1979) showed that, when $F_r$ is low, 0.5-mm sands added to flow over clean gravel quickly established a sand seal in the upper 5 cm of the clean gravel bed; the larger sand particles "bridged" the openings between adjacent gravel particles and prevented downward movement of additional sands. At higher $F_r$ (higher velocity and turbulence), flow characteristics began to alter the sealing process, and most deposition and intrusion occurred within the 5–10-cm depth zone in the bed. Higher water velocities (associated with higher $F_r$) led to greater bed shear and "jiggling" of surface gravels, inhibiting formation of a sand seal near the gravel surface. Hence, the sand seal still formed, but deeper within the bed, where it would prevent still deeper intrusion.

In a study of even finer sediment than 0.5-mm sand, Beschta and Jackson (1979) used 0.2-mm sands in two tests. They found that the sand seal in the upper level in the bed did not develop. Instead, the finer material moved down through the gravels by gravity and began to fill the test gravels from the bottom up. Particle size thus influences depth of intrusion. The amount of intrusion by 0.2-mm sands decreased as $F_r$ increased from 0.6 to 1.1.

Hydraulic dynamics tend to pull surface water through the redd (Stuart 1953; Vaux 1962; Cooper 1965). Stuart (1953) demonstrated with potassium permanganate crystals that water moves downward into the egg pocket as well as longitudinally through it. With dyes, Cooper (1965) showed penetration of surface water to depths as great as 46 cm. Cooper (1965) demonstrated that a salmon redd, with its peculiar shape, draws surface water deeper than does a gravel bed with relatively flat surface. Cooper (1965) studied the effect of this "pulling" on intrusion of fines into gravels in an experimental environment. He confirmed that silt is drawn into the gravel even though high surface water velocities (high $F_r$) prevent deposition on the gravel surface. The intrusion of fines reduced gravel permeability. Gravel composition affects the depth to which surface water circulates in the substrate (Cooper 1965). Very coarse gravel retained the least fines and finer gravel retained the most.

Meehan and Swanston (1977) introduced fines smaller than 2 mm into the flow in an artificial stream channel and measured their deposition in test baskets a given distance downstream; deposition was greater among rounded gravels than among angular gravels at very low flows, but the outcome was reversed at higher flows. The authors believed that more low-velocity areas existed in rounded gravels at low flows, which permitted fines to intrude and settle. In angular gravels, more tractive force was needed to carry sediments downstream, but more zones of low velocity were associated with angular particles at high flows, permitting more accumulation of sediment under those conditions.

Koski (1975) showed that the percentage of silt (<0.105 mm in diameter) retained in gravels in experimental stream channels correlated inversely with the amount of sand particles between 0.105 and 3.327 mm in diameter. The relationship appears to show that voids filled with sand cannot subsequently fill with silt.

Although one cannot project the findings of

Cooper (1965) and Beschta and Jackson (1979) to every salmonid redd in exact detail, some conjecture seems reasonable. From the moment when fertilized eggs fall into the cobble or large-gravel centrum of the egg pocket, digging by the female spawner results in a bridging of smaller gravels among centrum components, and then in a mix of gravels over the centrum. Finally a seal of finer sediments develops somewhere in the redd, the depth and composition of the seal depending on sediment transport in the surface flow. The seal may develop partly during the completion of the redd.

Hawke (1978) described the gravels above the egg pocket centrum as mainly fine, but containing a high proportion of coarse sand. In some pockets, a loose core of pebbles ran from the egg pocket to the surface, probably an example of bridging. Platts et al. (1979) used multiple probes to freeze and extract part of a chinook salmon redd that included an egg pocket. The lower part of the egg pocket had a "tunneled" appearance (W. Platts, U.S. Forest Service, personal communication). Bridging of small particles among larger particles leads to this condition. Both inorganic particles and salmonid eggs must bridge across voids in the substrate. The smaller the spawner, the smaller will be the average particle size in the redd and the smaller should be the average diameter of the "seal" components. Of course, egg and alevin size tend to relate directly to fish size as well.

Gravel composition varies widely over time in many streams (Adams and Beschta 1980). The complex interactions among $F_x$ freshet events, and sediments in transport strongly influence conditions in the redd during incubation and emergence. However, the configuration of the egg pocket and placement of embryos by the female appear to lead to optimal physical conditions for egg incubation and alevin emergence.

### Internal Characteristics of the Egg Pocket

One can find many references to substrate composition and intragravel conditions in salmonid spawning areas, or even in redds, but few directly concern the individual egg pocket. Platts et al. (1979) removed an entire egg pocket from a chinook salmon redd in the South Fork Salmon River in November 1978 with "freeze cores." One freezes cores in the substrate by placing probes in the bottom materials and passing liquid gas, such as carbon dioxide or nitrogen, through the probes (Walkotten 1976; Lotspeich and Reid 1980). The extracted cores can be analyzed by depth stratum.

Platts et al. (1979) used a battery of such probes for the extraction, then kept the egg pocket, which weighed 620 kg, frozen until they could dissect it in the laboratory.

Mean diameter of particles in gravel samples serves as one descriptor of substrate composition. Platts et al. (1979) defined geometric mean diameter $(d_g)$ as

$$d_g = (d_{16} d_{84})^{1/2};$$

$d_{16}$ = particle diameter corresponding to the 16th percentile; $d_{84}$ = particle diameter corresponding to the 84th percentile. The $d_g$ of particles in the egg pocket extracted by Platts et al. (1979) differed markedly from that of the surrounding substrate. The $d_g$ of the entire extracted pocket, 45 cm deep, was 23 mm. The sample may have included some sediment from outside the egg pocket, hence may have had a bias toward a lower $d_g$. The average $d_g$ in the Poverty area of the South Fork Salmon River, where the egg pocket was extracted, was 13 mm. Shirazi et al. (1981) provided some additional estimates of $d_g$ in the area of the pocket taken by Platts et al. (1979), and they stated that the $d_g$ of the area near the egg pocket was 23 mm. However, the data, obtained with a 25-cm McNeil sampler, were analyzed with sieves that had a maximum mesh diameter of 25 mm. Extrapolation of these data beyond 25 mm to obtain the $d_g$ of samples that included particles as large as 152 mm misleads, and one should not rely on the comparison. Shirazi et al. (1981) reported analyses of single-probe freeze cores taken from 15 egg pockets in the South Fork Salmon River in 1977. The average of the 15 $d_g$s was 35 mm. Although the standard deviation was 21 mm, largely because single probes yield high variability, the data show that $d_g$ was high in egg pockets.

A gravel descriptor developed by Lotspeich and Everest (1981), the fredle index, also demonstrates the difference between the egg pocket sampled by Platts et al. (1979) and the surrounding substrate. The fredle index $(f_i)$ incorporates elements that integrate gravel permeability and pore size.

$$f_i = d_g / S_o;$$

$S_o = (d_{75}/d_{25})^{1/2}$, $d_{75}$ and $d_{25}$ being diameters of grains at the 75th and 25th percentiles of cumulative gravel sample weight. In the egg pocket dissected by Platts et al. (1979), the fredle index equaled 7.5; in surrounding spawning gravels, $f_i$ was only 1.8. Both $d_g$ and $f_i$ provide evidence that the spawning female coarsened the substrate within the egg pocket.

In the previous section on intrusion of fines into gravels cleansed by the female, I noted that some workers described a crust or seal of fines in the egg pocket. This shallow intrusion did not appear in the egg pocket that Platts et al. (1979) described, but $d_c$ of the middle pocket stratum, at a depth of 15–30 cm, was less than that of the top or bottom 15 cm of the pocket. The middle stratum may have captured more sands as the female excavated upstream of the pocket. Flows steadily declined in the fall of 1978 in the South Fork Salmon River after chinook salmon spawned. Egg pocket structure for a stream subjected to freshets during the incubation period probably would differ as a result of bed load movement.

Permeability of the egg pocket greatly exceeds that of the surrounding substrate and that of redd areas outside the pocket. Permeability is a function of hydraulic gradient, apparent velocity, and temperature (Pollard 1955), and it describes the ability of gravel to pass water per unit of time. It increases with increased $d_c$ (Platts et al. 1979). One can estimate permeability in the field by measuring the water volume pulled into a volumetric cylinder per unit of time from a standpipe well point 25 cm deep in the substrate under constant rapid suction of water through a small tube whose entrance lies 2.5 cm deeper than the water surface outside the pipe (Terhune 1958). Chapman et al. (1986) observed progressive construction of redds of chinook salmon in the Columbia River at Vernita Bar. We recorded exact locations of egg pockets as females prepared them in 15 redds in 1980. After the females completed the redds, we drove truncated standpipes into the centrum of the pockets and left them there. The median permeability of the pockets equalled 10,500 cm/h (range, 3,700–18,000 cm/h). We also drove standpipes into the substrate every 5 m along an upstream–downstream axis in a nearby zone of heavy spawning. Median permeability of six locations in this zone equaled 1,300 cm (range, 180–3,000 cm/h). Median permeability of six locations in an adjacent zone of light spawning was 395 cm/h (range, 190–400 cm/h). In 1981, we measured permeability in 15 locations 10 m apart along an upstream–downstream axis in a zone of almost continuously overlapping redds, and found a median permeability of 910 cm/h (range, 460–6,200 cm/h). In 1980 we also attempted to create egg pockets by digging with shovels in the substrate in current, then covering the pocket by digging upstream as we thought the female chinook salmon did. Median permeability of 12 such artificial

pockets was 5,000 cm/h (range, 1,400–18,000 cm/h). We concluded that the egg pocket constructed by the female had a much higher permeability than the surrounding substrate, and that spawners cleansed the substrate more effectively than we did. Female chinook salmon create relatively high $d_c$ and permeability in egg pockets by the way in which they excavate and cover egg pockets. Other large salmonids almost certainly perform similarly in streams.

## Ecology of Salmonid Embryos

A very large body of literature deals with intragravel ecology of incubating embryos. Although these studies generally have not provided accurate analogs for the environment within the egg pocket, they demonstrate that survival relates positively to dissolved oxygen and apparent velocity of intragravel water that moves past the embryos. They also show that survival relates positively to gravel permeability and gravel size, and negatively to proportions of fine particles.

### Apparent Velocity and Dissolved Oxygen

Alderdice et al. (1958) found that the lower incipient median lethal concentration of dissolved oxygen rose with embryo development, from about 0.4 mg/L early in development to 1.0–1.4 mg/L before hatching. Alderdice et al. (1958) tested survival of chum salmon eggs exposed to constant levels of dissolved oxygen for 7 d at various developmental stages. Exposure to low dissolved oxygen caused premature hatching, and rate of oxygen uptake increased steadily from fertilization to hatching.

Alderdice et al. (1958) calculated the critical oxygen concentration, the concentration at which respiratory demand is just satisfied, for various stages of development. They found that oxygen need rises with development and, by the stage of development at 250 degree-days (a degree-day equals 1°C above 0°C for 1 d), oxygen need reaches 5 mg/L at 10°C. Alderdice et al. (1958) recommended that one should regard the critical level of dissolved oxygen as a measure of oxygen requirement for successful incubation, and that studies should determine if theoretically estimated critical levels of oxygen equate to empirical limiting levels.

Coble (1961) demonstrated that survival of steelhead embryos related directly to apparent velocity of intragravel water. However, when he adjusted his data to normalize the dissolved oxygen level to 6 mg/L, he found that survival no longer

was obviously related to apparent velocity. Coble noted that incubating embryos require oxygen, not water velocity, and that water movement mainly delivers oxygen to the embryo and carries away waste. His graph of the relationship between dissolved oxygen and apparent velocity in artificially dug redds that contained steelhead embryos showed a direct relationship of oxygen concentration to velocity. He stated that survival of embryos was related to apparent velocity, but only indirectly through dissolved oxygen concentrations.

Phillips and Campbell (1962) buried newly fertilized steelhead and coho salmon ova among glass beads within perforated stainless steel boxes; the boxes surrounded short standpipes in shovel-dug redds in tributaries of Drift Creek, Oregon. Steelhead survived very poorly to a time about 3 weeks after hatching in these artificial redds when dissolved oxygen levels averaged below 7 mg/L. Eggs of coho salmon survived well at oxygen levels above 8 mg O₂/L and alevin size correlated with the amount of dissolved oxygen. Steelhead alevin size had no relationship to oxygen level. These authors concluded that incubating embryos required more oxygen than had previously been suspected.

Silver et al. (1963) demonstrated that water velocities must be high enough within the redd not only to support the oxygen requirements of all the embryos, but also to deliver sufficient oxygen to the surface of the chorion around each embryo. Steelhead and chinook salmon embryos, held at 9.5 and 11°C, respectively, all died at an oxygen concentration of 1.6 mg/L. Silver et al. (1963) concluded that the theoretical critical oxygen levels calculated for salmonid embryos by Alderdice et al. (1958) were far below the true limiting oxygen levels throughout most of development at temperatures of 10–12.5°C. Silver et al. (1963) ascribed the discrepancy to assumptions underlying the models used by Alderdice et al. (1958). One such assumption was that the periphery of the chorion defines the limiting respiratory surface before blood circulation is established, whereas it probably is defined by the surface of the embryo itself. Another error may be associated with the posthatch period. Alderdice et al. (1958) assumed that the perivitelline fluid was anoxic after blood circulation began. The embryo could not survive without oxygen in the fluid, however, which means that real tensions are less than assumed by Alderdice et al., and that higher oxygen concentrations are needed in the water to support embryo development. Sil-

ver et al. (1963) suggested that one cannot assume, realistically, a critical oxygen concentration in water surrounding the embryos that is very much lower than the critical concentration for newly hatched sac-fry.

Silver et al. (1963) followed this suggestion by showing that all tested oxygen concentrations less than 11.7 mg/L restricted growth of chinook salmon embryos before the 24th day after fertilization. For steelhead, all tested oxygen concentrations below 11.2 mg/L restricted development before the 30th day. Growth of coho salmon at 11°C is restricted before the seventh day after fertilization at concentrations of dissolved oxygen at least as high as 6 mg/L, and before the 28th day at concentrations slightly below 11.9 mg/L. Other data showed restricted growth of embryonic steelhead at 12.5°C before the 11th day at oxygen levels slightly below 10.4 mg/L.

Shumway et al. (1964) established that both the velocity of water moving past embryos and the dissolved oxygen concentration directly affected survival of embryos. Cooper (1965) showed that apparent velocity strongly influenced survival of eyed sockeye salmon eggs to emergence. But these workers noted that very low water velocities can meet the oxygen requirements of embryos if oxygen concentrations remain high. Dissolved oxygen concentration has relatively more influence than apparent velocity on embryonic survival and development.

Development of embryos often proceeds at temperatures of less than 10°C. For example, winter water temperatures during incubation of eggs laid by fall spawners often reach 3–5°C (Columbia River mainstem), or even less than 1°C (tributaries at high elevation and northern latitudes). Hobbs (1937) noted that the oxygen requirement per unit of tissue and per unit of time at 3°C was about one-third, and at 7°C about one-half, that at 12°C. Wickett (1954) tabulated data obtained at about 5°C for Atlantic salmon (Lindroth 1942) that indicated a critical dissolved oxygen level of 5.8 mg/L just before hatching. Wickett's (1954) own data for chum salmon suggest a critical level of less than 5 mg/L for 85-d eggs (faintly eyed) at 3.6–4.9°C. The limited data indicate that an assumption that critical oxygen levels decrease at low temperature is reasonable. Critical levels for dissolved oxygen at low temperatures are not established, but may be somewhat less than those reported by Silver et al. (1963).

The convincing results of Silver et al. (1963) and Shumway et al. (1964) showed that any reduction

of dissolved oxygen could reduce length of fry at hatching. Length and strength of sac fry from embryos reared at high oxygen concentrations exceeded those of sac fry reared in low and intermediate oxygen concentrations. Length of steelhead fry was positively related to water velocity at given oxygen concentrations, but water velocity was more important at low than at high oxygen levels (Silver et al. 1963).

Dissolved oxygen has relatively more influence on steelhead fry size than water velocity (Silver et al. 1963). The velocities measured by Silver et al. approached true pore velocity (the actual velocity past the surface of the embryo) because of conditions in the experimental apparatus. Apparent velocities in the substrate, as measured in field studies, are lower than actual velocities, and one cannot compare them absolutely with these laboratory studies. However, the results of Silver et al. (1963) demonstrated the combined effects of dissolved oxygen and velocities, regardless of absolute values for velocity.

Shumway et al. (1964) incubated embryos among glass beads in the laboratory, and found that the embryos grew larger for a given water flow and oxygen concentration than they did when grown on a porous plate such as that used by Silver et al. (1963); the effect was especially pronounced in a mix of large and small beads. True pore velocities were higher in the substrate mix, and one may conclude that velocities in redd pores exceed those indicated by apparent velocity measurements.

Embryos hatch earlier at larger total weight in media with high dissolved oxygen concentrations. Brannon (1965) reported that newly hatched embryos incubated at 3, 6, and 12 mg $O_2$/L had average respective lengths and wet weights of 16, 19, and 20 mm and 22, 30, and 42 mg. Embryos incubated in 3 mg $O_2$/L required 2 weeks longer to absorb yolk material than those held at 6 mg/L, and 3 weeks longer than those held at 12 mg/L. Subsequent growth of alevins with the 3 mg/L hypoxial history was slower than that of alevins incubated at 12 mg/L.

McNeil (1966) stated that oxygen requirements of embryos rise to a maximum just before hatching, and that larvae tolerate lower dissolved oxygen levels than do embryos. He attributed this change to availability of vastly increased respiratory areas (gills) after hatching. Hays et al. (1951) reported that the oxygen concentration that would limit metabolism of Atlantic salmon decreased after hatching.

Mason (1969) exposed coho salmon embryos and alevins to dissolved oxygen levels of 11, 5, and 3 mg/L. Mortalities to time of yolk absorption amounted to 17, 23, and about 41%, respectively. Embryos subjected to the lower oxygen levels were smaller at hatching (22.9, 25.4, and 28.1 mm for oxygen concentrations of 3, 5, and 11 mg/L, respectively). Alevins subjected to 3 mg/L were about 33 mm long at yolk absorption, whereas alevins subjected to the higher oxygen levels were over 37 mm long. Fry exposed to the most severe hypoxial conditions subsequently tended to emigrate into downstream traps after emergence because of competition during the postemergence period. Mason (1969) compensated for low dissolved oxygen levels by increasing temperatures so that fish would emerge from all three groups at the same time. Had he maintained all groups at the same temperature, the social disadvantage faced by fry with hypoxial histories would have been exacerbated because they would emerge both later and smaller.

Any reduction in size at emergence as a result of hypoxial incubation history can have important effects on the subsequent social success of postemergent coho fry (Mason 1969). Fry with hypoxial history did not compete successfully with larger fry. Only by emigrating to unoccupied habitats could they achieve normal growth. In habitat in which early emerging fry have occupied the environment, or even just the most favorable portions of it (Puckett and Dill 1985), fry with hypoxial history would inevitably suffer higher mortality than larger fry. I discuss effects on emergence itself later in this review.

Wells and McNeil (1970) noted that the largest and fastest-developing embryos and alevins of pink salmon found in Sashin Creek, Alaska, had incubated in spawning gravels with high levels of dissolved oxygen in intragravel water. Koski (1975) showed that survival of chum salmon to emergence was about one-third as high for embryos subjected to dissolved oxygen levels below 3 mg/L than for embryos subjected to levels over 3 mg/L. Oxygen concentrations below 3 mg/L delayed emergence. Sowden and Power (1985) found that survival of rainbow trout embryos in a groundwater-fed streambed depended upon mean dissolved oxygen content and velocity of groundwater in redds. Survival increased directly as oxygen content rose above 6 mg/L.

The key inference from the body of work described above is that deprivation of dissolved oxygen leads to subtle problems often not detectable

in tests of survival in various oxygen concentrations. It appears incorrect to set critical oxygen levels at any arbitrary point, or to assume that survival to time of emergence is sufficient evidence of ecological success. Any decremental reduction in dissolved oxygen levels from saturation probably reduces survival to emergence or postemergent survival.

Davis (1975) extensively reviewed the oxygen requirements of salmonids, including anadromous forms. He showed a mean threshold of incipient oxygen response for hatching eggs and larval salmonids as 8.1 mg/L and 76% saturation, and he suggested three levels of protection against effects of low dissolved oxygen concentrations. The highest of these, one standard deviation above the incipient response level, would represent ideal conditions. The lowest, one standard deviation below the incipient response, would be applied only to populations of little value.

Low dissolved oxygen concentrations tend to occur in substrates with high percentages of fines (Tagart 1984) and low permeabilities. However, Koski's (1966) data indicate only a loose negative relationship between fines smaller than 3.3 mm in diameter and the dissolved oxygen concentration in intragravel water.

*Permeability, Mean Particle Size, and Indices of Pore Size*

Sediment texture does not directly control survival to emergence of salmonid embryos (Lotspeich and Everest 1981). Permeability and pore size, influenced by sediment texture, directly influence survival by controlling water movement for embryo irrigation, and ease of alevin emergence. Wickett (1958) related percent survival (to emergence) of pink and chum salmon fry to average permeability in the streambed. McNeil and Ahnell (1964) showed that permeability was inversely related to the percentage of substrate particles that passed through a 0.833-mm sieve, and that the more productive pink salmon spawning streams, among those they examined, had high permeability coefficients. Wells and McNeil (1970) found that the largest embryos of pink salmon in Sashin Creek, Alaska, came from a stream segment with a relatively steep grade and coarse materials in the bed.

I used data of Koski (1966) and McCuddin (1977) to calculate permeabilities of redd and laboratory gravels in relation to embryo survival to emergence for coho and chinook salmon. Survival

of both species was positively and significantly related to permeability (Figure 2).

Shirazi et al. (1981) compared percentage embryo survival, as reported in several studies, to geometric mean particle size ($d_g$) in spawning substrates, laboratory gravel mixes, and redds used for spawning. Their report included studies that measured survival of several species for parts of the incubation period and data for survival to emergence. High survivals tended to occur in association with high $d_g$s (Shirazi et al. 1981). I plotted their model for survival in relation to $d_g$ together with linear regressions of survival to emergence on $d_g$ for Koski's (1966) data from natural coho salmon redds and for laboratory data on sockeye salmon (Cooper 1965) and steelhead and chinook salmon (Tappel and Bjornn 1983). The regressions (Figure 3), all significant ($r^2 = 0.46$–$0.83$), did not conform to the model of Shirazi et al. (1981). I also regressed coho salmon survival data of Tagart (1976), as developed in net-capped natural redds, on $d_g$ but the relationship was not significant. Use of the Shirazi et al. (1981) model to depict survival of salmonids in relation to $d_g$ does not appear appropriate.

Lotspeich and Everest (1981) calculated $d_g$ as

$$d_g = d_1{}^{w_1} \times d_2{}^{w_2} \times \ldots \times d_n{}^{w_n};$$

$d_1 \ldots d_n$ = particle diameters in percentiles 1 ... $n$; $w_1 \ldots w_n$ = weight fractions in percentiles 1 ... $n$. They showed with empirical data from the Rogue River in Oregon that this formulation provided a somewhat more accurate estimate of $d_g$ than the formula of Platts et al. (1979).

Lotspeich and Everest (1981) related the fredle index to survival to emergence of coho salmon and steelhead placed into laboratory mixes of gravels (Phillips et al. 1975). These data included only the intragravel period of "swim-up" fry to emerging fry, the period after nearly complete yolk absorption. The index appeared sensitive to pore size as the latter influences emergence and merited further study. I calculated $f_i$ for the data of Tappel and Bjornn (1983), and found highly significant regressions ($r^2 = 0.85$ for chinook salmon and 0.95 for steelhead) of survival on $f_i$ between $f_i = 1.0$ and $f_i = 4.0$ (Figure 4). At $f_i = 5.0$ and above, survival to emergence exceeded 90% for both chinook salmon and steelhead, and survival did not increase at higher $f_i$ values (Figure 4). These data pertained to the entire incubation period through emergence. Tappel and Bjornn (1983) noted that their gravel mixes had more particles 12.7–25.4 mm in diameter than would natural gravels. Near-
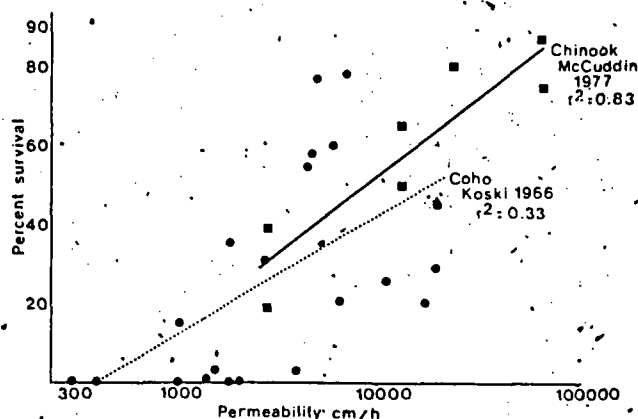
FIGURE 2.—Survival to emergence of coho salmon in natural redds (solid circles) (Koski 1966), and of chinook salmon in laboratory gravel mixes (solid squares) (McCuddin 1977) in relation to gravel permeability.

ly 100% of the particles in their experimental mixes were smaller than 51 mm, and thus did not include larger sediments normally found in the egg pocket centrum. Survival of sockeye salmon in laboratory studies (Cooper 1965) also related significantly to $f_i$ (Figure 4). Survival data of Tagart (1984) from capped coho salmon redds did not regress significantly on $f_i$.



FIGURE 3.—Survival to emergence in relation to geometric mean particle size $(d_g)$ for natural coho salmon redds (Koski 1966), and for other salmonids in laboratory gravels (Cooper 1965; Tappel and Bjornn 1983). The composite model of Shirazi et al. (1981) is plotted in the same $d_g$ range (3–17 mm).

The somewhat greater survival to emergence for steelhead at intermediate $f_i$ (2.5–5.0) in the study of Tappel and Bjornn (1983) may have occurred because the alevins had to move vertically through only about 15–20 cm. Alevins in the studies used by Lotspeich and Everest had to emerge through about 25 cm of gravel (Phillips et al. 1975).

Tappel and Bjornn (1983) concluded that the usefulness of the $d_g$ is limited because gravel mixtures with the same geometric mean can have different size compositions. They noted, after an analysis of 100 samples of spawning gravels from the South Fork Salmon River, that some samples had substantial deviations from lognormality. These deviate samples curved upward in the upper end of cumulative distribution plots. The correlation improved if particles larger than 25.4 mm were deleted from the plot. Elimination of such large particles from any study of the incubation medium of large salmonids; however, would distance the test environment from real conditions in the egg pocket.

Sowden and Power (1985) evaluated survival of rainbow trout embryos to 1 week after hatch in relation to gravel statistics. They reported correlation coefficients of 0.41, 0.36, and 0.36 for survival in 19 redds in relation to $d_g$, $f_i$, and permeability, respectively. When they examined only redds with mean dissolved oxygen levels greater than 5.3 mg/L and similar hydraulic gradients, the same respective correlation coefficients equaled 0.85, 0.90, and 0.98. In this case, the relationships for the fredle index and permeability were significant at $P = 0.05$ and $P = 0.01$, respectively. Sowden and Power (1985) excluded particles larger
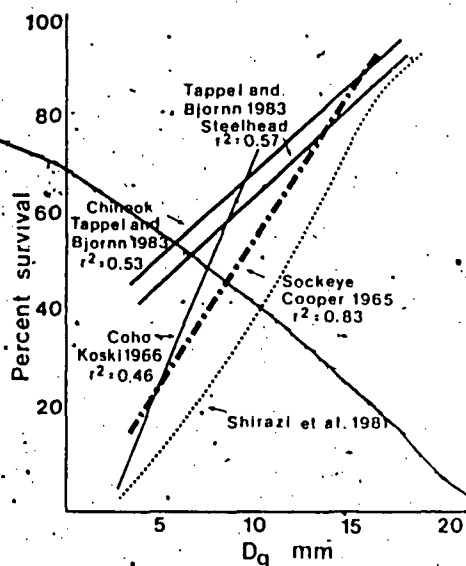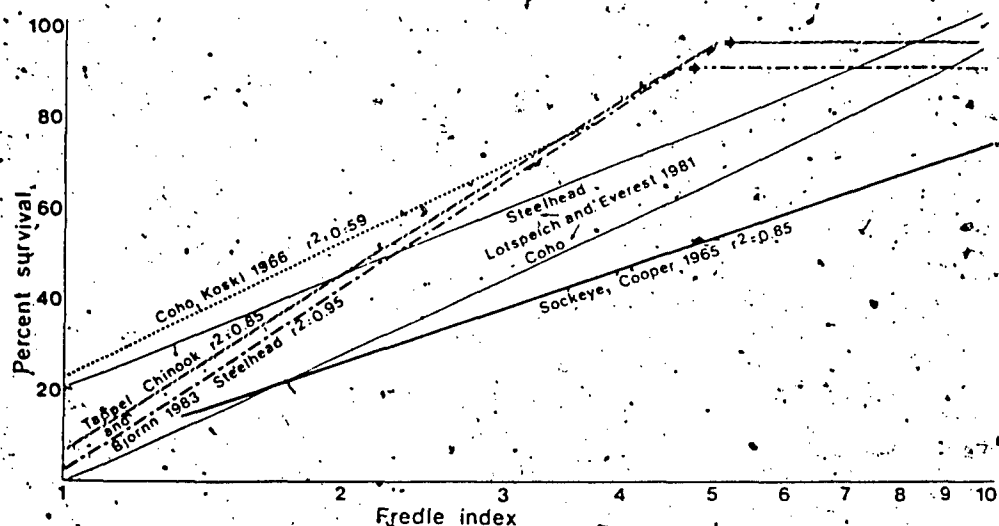
FIGURE 4.—Survival to emergence in relation to the fredle index for natural coho salmon redds (Koski 1966) and for chinook salmon and steelhead (Tappel and Bjornn 1983) and sockeye salmon (Cooper 1965) in laboratory gravel mixes. Heavy arrows indicate the upper ends of regressions for the Tappel and Bjornn data; at higher fredle indexes, survival exceeded 90%. Regression lines for steelhead and coho salmon are also plotted from Lotspeich and Everest (1981) for the late part of the incubation period in laboratory gravels. (Lotspeich and Everest 1981 used data from Phillips et al. 1975.)

than 48 mm from their freeze-core samples for reasons of weight bias (Adams and Beschta 1980), and thus may have excluded some or all particles of the egg pocket centrum.

### Survival of Embryos in Relation to Percentage of Fines

Several investigators have examined the effects of fine sediments on salmonid incubation through emergence. Koski (1966) trapped coho salmon fry emerging from 21 natural redds in three Oregon streams. Survival was inversely related to percentage of fines. Fines smaller than 3.3 mm gave the highest correlation. Koski (1975) reported a similar relationship for chum salmon survival to emergence in gravels placed in a spawning channel in Washington, though his gravel data came from the channel cell in which chum salmon spawned, not from the redd.

For the nine redds from which he obtained data on minimum and mean dissolved oxygen concentrations, Tagart (1976, 1984) showed that dissolved oxygen was related inversely to the percentage of fines under 0.85 mm in diameter. The reason for the relationship is not clear, but biochemical oxygen-demand in the substrate may have reduced oxygen levels where permeability was low

(high percentage of fines), or low permeability may have prevented interchange of oxygenated surface waters with intragravel water. Tagart's (1976) data indicated 32% survival to emergence from redds in which less than 20% of fines were smaller than 0.85 mm, whereas survival was only 18% from redds that had more than 20% of such fines; the difference was significant at $P = 0.05$.

McCuddin (1977) tested the ability of chinook salmon and steelhead to survive and emerge in troughs of various gravel–sand mixtures that simulated the substrate mix in natural spawning areas. Survival decreased as the proportion of sand in the substrate increased above 10–20%. For tests with newly fertilized eggs placed in the substrate, any percentage of 6–12-mm particles above about 10–15% appeared to reduce survival, as did any percentage of fines (<6 mm) above about 20–25%. Whether or not the gravel beds in artificial channels are typical of natural beds is always an issue; in McCuddin's work, the structure of the incubation environment did not appear similar to that in a natural redd. The effect of this on his results is uncertain, Cederholm et al. (1981) summarized studies of coho salmon survival from green egg to emergence in artificial stream troughs, and found an inverse relationship between percentage of fines

smaller than 0.85 mm and survival. The mixture and stratification of gravels in these experiments was chosen to provide an analog of actual conditions in various streams of the Clearwater basin in Washington State, but "actual conditions" refers in part to conditions within spawning gravels (the areas used by fish) and in part to conditions within the redd periphery (Cederholm et al. 1981). Cederholm et al. (1981) demonstrated that increased fines smaller than 0.85 mm reduced survival of coho salmon to emergence in both artificial and natural redds. Elements in Figure 5 illustrate the difference between laboratory gravel mixes and conditions in the redd. Coho salmon survival, as reported by Cederholm et al. (1981), was 30% at about 10% fines (<0.85 mm) in the trough mixes and at 15% fines in natural redds. Survival of 15% occurred at about 13% fines in the trough and 25% fines in natural redds. Although the overall gravel mixture in troughs duplicated natural gravels, survival was lower in troughs at a given percentage of f■■■■■■■re of the trough mixes to duplicate arra■■■■■■■f fines in redds may have been at least ■■■■■■sible for the differences.

Survival of coho salmon in natural redds in both the Alsea River, Oregon (Koski 1966), and the Clearwater River, Washington (Cederholm et al. 1981), declined as the percentages of fines smaller than 0.85 mm increased (Figure 5). However, survival at given percentages of fines was considerably higher in the Oregon study. For example, at 20% fines, survival to emergence was about twice as great in Koski's work (45%) as in that of Cederholm et al. (20%). Factors other than these fine particles must have affected survival in one or both of these coho salmon studies. Chinook salmon survival to emergence (Tappel and Bjornn 1983) varied widely at given percentages of fines less than 0.85 mm (Figure 5), depending upon the percentage of fines smaller than 9.5 mm in diameter. For example, graphs in Tappel and Bjornn (1983) show that survival at 10% fines smaller than 0.85 mm varied from 20 to 80% as the amount of fines 9.5 mm or less varied from 60 to 25%.

Peterson and Metcalfe (1981) measured emergence of Atlantic-salmon eggs that had incubated in various gravel and sand mixtures. Fine sand (0.06–0.5 mm) reduced emergence success more effectively than coarse sand (0.5–2.2 mm). Strong upwelling water current in the gravel bed mitigated effects of sand to some degree (sand tends to reduce porosity, hence permeability) and induced earlier fry emergence. These workers showed that
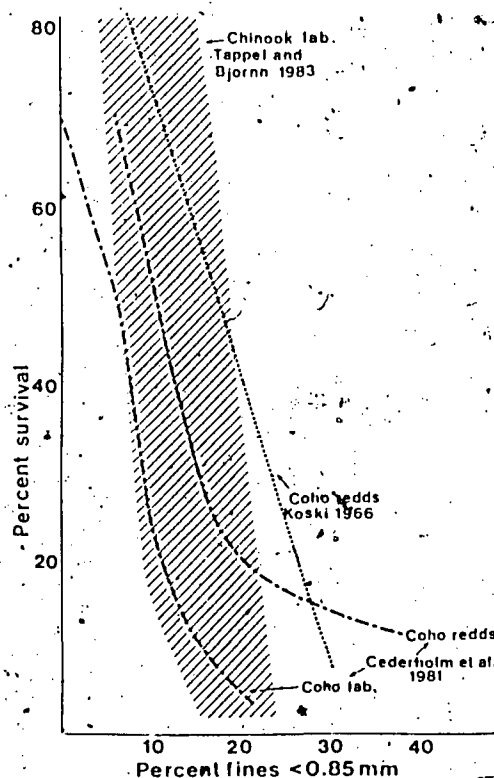


FIGURE 5.—Survival of salmonid embryos to emergence in relation to fines smaller than 0.85 mm in diameter. Data provide comparisons of coho salmon survivals in laboratory (lab.) and field (Cederholm et al. 1981), of coho salmon in two different streams (Koski 1966; Cederholm et al. 1981), and of chinook salmon in gravels with a range of percentages of particles less than 9.5 mm in diameter (shaded area; Tappel and Bjornn 1983).

where the percentage of fine sand rose above about 12%, survival declined sharply. Where the percent of coarse sand rose above about 22%, emergence dropped sharply. The gravel mix used by Peterson and Metcalfe had a high ratio of small:medium gravels (particles 22–62 mm had a 5:3 ratio to smaller particles of 2.3–22 mm), a mix that would be unusual for most gravels used by Pacific salmon and steelhead.

MacCrimmon and Gots (1986) investigated the effects of fines smaller than 4 mm on survival of rainbow trout from eyed egg to emergence. Survivals were 51–74% in gravels with 40–100% fines, although more fines led to earlier emergence of smaller alevins. Alevins apparently responded to

high percentages of fines by leaving the substrate early, independent of dissolved oxygen levels. Survivals equaled 87–92% in 0–20% fines. Incubation cells had vertical water movement adjusted to 130·mL/min regardless of substrate composition; thus, actual pore velocities should have increased in mixtures with more fines.

Tappel and Bjornn (1983) examined various gravel mixes and concluded that two particle categories, diameters less than 0.85 mm and less than 9.5 mm, adequately described linear particle size distribution. They provided isolines of survivals of chinook salmon and steelhead in relation to percentages of fines in these two categories. Irving and Bjornn (1984) extended the laboratory techniques of Tappel and Bjornn (1983) to investigate survival of kokanee (landlocked sockeye salmon), cutthroat trout *Salmo clarki*, and rainbow trout. These workers also prepared isoline graphs for 0–80% survival in relation to percentage of fines smaller than 0.85 and 9.5 mm. These lines show that chinook salmon embryos and alevins tolerate higher percentages of such fines than do cutthroat and rainbow trout and kokanee. The difference may be related in part to embryo size and alevin strength. Laboratory mixes of gravels are not packed tightly by substrate shifts or intrusion of additional sediments during the incubation process. The relatively large chinook salmon alevins may bull their way to the surface more successfully in these mixes. The explanation for the difference more probably lies in the different depths of burial of embryos in the laboratory channels. The channel diagram provided by Irving and Bjornn (1984) indicates a burial depth of about 20 cm for embryos, rather deeper than burial depths in natural redds for small trout and kokanee; but less than the natural depth of ova in chinook salmon egg pockets. The chinook salmon data used by Irving and Bjornn (1984) were obtained from Tappel and Bjornn (1983). The total depth of gravels in the troughs used by Tappel and Bjornn (1983) ranged from 15 to 20 cm, and the center of the Vibert boxes that contained experimental lots of ova lay about 12–15 cm below the gravel surface. The alevins first encountered the experimental gravel mixes at the top of the Vibert boxes. Chinook salmon and steelhead alevins must emerge from considerably greater depths in natural egg pockets. The relationships shown by Irving and Bjornn (1984) are consistent with my explanation.

Research by NCASI (1984) showed that the survival of rainbow trout embryos to emergence was inversely related to the percentage of fines smaller than 0.8 mm. For each 1% increase in fines over the range of 10–30%, survival declined 1.3%. In a second study, each 1% increase over the range of 10–40% decreased survival 1.1%. The work also showed a negative relationship between survival and percentage of fines smaller than 6.4 mm. The authors stated that failure to emerge was probably associated with physical entrapment, because the dissolved oxygen content of the intragravel water was similar for all gravel mixes. No information on apparent velocities was obtained. The high survival (near 90%) at 20% fines (<6.4 mm) is of interest. The authors speculated that these particles prevented smaller fines and organic debris from entering the incubation environments. This bridging effect would also occur in the egg pocket. I infer, from this and other information, that some fines aid survival, and that the particular mix and stratification in the egg pocket govern emergence success.

Where groundwater instead of surface water irrigates the substrate, the relationship between fines and survival provides a poor predictor of survival. Sowden and Power (1985) reported that survival of rainbow trout was not significantly related to the percentage of sediments smaller than 2.0 mm. Rather, it was strongly related to dissolved oxygen level and water velocity; oxygen content was determined by groundwater conditions rather than by factors causing biological oxygen demand within the redd. Sowden and Power measured survival to the sac-fry stage, not to emergence. They noted that further studies that measure survival to emergence would be desirable, but urged cautious application of survival models based on substrate particle sizes.

### Emergence from Gravels

Incubation success depends not only upon conditions through the development from fertilized egg to alevin, but also upon emergence of fry from the substrate. Egg pocket structure and composition influence survival during the emergence phase.

White (1942) reported that where Atlantic salmon incubated in areas with high quantities of sand, 80% of the eggs died and 20% of the surviving larvae could not emerge through the compact sand layer. He found entombed fry even in redds where emergence had occurred. Shelton (1955) placed chinook salmon eggs in various gravel mixes in screened bags in a natural stream and recorded emergence success. He noted much lower survival to emergence through small gravels

(a mix of particles less than 2.5 cm in diameter) than through larger particles. Koski (1966) excavated coho salmon redds that had been surrounded with netting. He found 260 emaciated dead fry several centimeters below the surface of the gravel in one redd.

Phillips et al. (1975) examined effects of fines on emergence success. They prepared eight mixtures of sand and gravel, then inserted coho salmon and steelhead fry into the substrate through a vertical standpipe. Emergence success of both species declined (from near 100%) when fines exceeded about 10% (1–3 mm). Presence of 20% fines reduced emergence success about 60–70%. The amount of fines (<3.3 mm) in spawning gravels used by coho salmon in 15 unlogged Oregon watersheds varied from 27 to 55% (Koski 1966; Moring and Lantz 1974). One might infer from the laboratory studies of Phillips et al. (1975) that survival of coho salmon and steelhead from the preemergent state to emergence would be 25–50% in undisturbed environments. Because they only tested survival of alevins to emergence, the incremental effects of incubation from egg deposition to the preemergent state would be subtracted from these percentages. However, the data of Phillips et al. (1975) only illustrate that emergence success declined in laboratory mixes of gravel that contained high percentages of fines. They do not permit quantitative predictions in field situations.

Data from natural redds as reported by Koski (1966) and Tagart (1976, 1984) support a mean survival from deposition to emergence of about 27 and 30%, respectively, in undisturbed (Alsea watershed) and partially logged (Clearwater River) drainages. These data from net-capped redds, although they integrate responses to several physical variables in the redd, may contain errors caused by the procedures used to estimate deposition in each redd. Estimates of egg placement were obtained by recovering the carcass of the spawned-out female, estimating fecundity from length, and deducting eggs retained in the carcass. This presumes that an individual female has an egg complement that is average for her length. Tagart (1976) provided estimated and actual egg complements for 15 coho salmon at a Washington hatchery that used a stock of fish very similar to the one he studied in the field. He reported a mean error of only 0.5% (range, 0.05–1.94%). Koski's (1966) regression of fecundity on coho salmon length suggests a much larger variability.

Phillips and Koski (1969) tested the efficiency of net caps in capturing emerging coho salmon fry

and reported a mean efficiency of over 99%, based on releases within the gravel of fry ready to emerge. They also showed that the net caps did not significantly alter dissolved oxygen or permeability in 25 coho salmon redds.

Hausle and Coble (1976) showed that emergence success of brook trout alevins *Salvelinus fontinalis* declined significantly as the percentage of sand in laboratory mixes of gravel increased. The NCASI (1984) study showed significant negative relationships between survival of rainbow trout embryos and percentages of fines smaller than 0.8 mm in test mixes of gravels, probably because of interference of sands with emergence. Dissolved oxygen content did not change in various mixes of sand, although apparent velocity might have differed.

Bams (1969) reported that when alevins of sockeye salmon confronted a sand barrier near the surface of an experimental gravel bed, they "butted" upward with repeated short thrusts. This action loosened the sand grains, which fell down and past the butting fish, and formed an open passage through which the fish moved upward. Thus bridges within the egg pocket may be breached by such butting behavior, and the particle gradation, caused as larvae move about and fines drop into the deeper sediment pores, may be an important component of intragravel ecology. Pores in the egg pocket centrum result from the large size of centrum components, bridging by small gravels and large sand particles (NCASI 1984), and bridging of small particles on the embryos themselves. Pore volume and configuration probably change after alevins hatch, change shape as they absorb their yolk, and begin to move about. Some fines probably redistribute from above to beneath groups of alevins as hatching and development proceed and as alevins move upward to emerge.

The effect of fine sediments on size of emergent fry has been reported by several workers. Koski (1966) found that the size of coho salmon at emergence related directly to permeability of the substrate. Gravels with high proportions of fines and low permeability tend to have low dissolved oxygen levels, which delay embryo development. In such contexts, size of emergent fry decreases, with the potential subsequent ecological disadvantages noted by Mason (1969).

Phillips et al. (1975) reported that coho salmon fry that emerged from high percentages of sand were smaller than those from gravels with low percentages, but that steelhead fry were similar in size after emergence from substrata with different

percentages of sand. Hausle and Coble (1976) were unable to find a relationship between percentages of sand and size of emerging brook trout fry that did not have fully absorbed egg sacs.

Koski (1981) showed that chum salmon that emerged from gravels with high proportions of sand were smaller. He attributed this to restriction by sand of the size of fish that could physically emerge. Tappel and Bjornn (1983) found that the size of steelhead fry that emerged from gravels with low percentages of fines slightly exceeded that of fry from gravels with high percentages of fines, but that the size of chinook salmon fry varied little through the range of experimental gravel mixtures. The effects of different incubation histories (steelhead were placed in gravels as newly fertilized ova, whereas chinook salmon were placed in gravels as eyed embryos) and shallow gravel depths are unknown. The burial depth of chinook salmon embryos in the laboratory mixes of gravel was shallow. Had the alevins emerged through 25–30 cm, the results might have differed.

Bams (1969) described the behavior of sockeye salmon fry as they emerged from a glass-walled observation chamber by upward swimming motions, presumably oriented to gravitational force. Normal emergence movements were slow and appeared restrained, and there were long periods of rest between movements. However, in favorable substrata, movements of 5 cm/min were frequently recorded. Bams (1969) described the field of movement of fish released from a given point as an inverted cone with a vertical axis. Fry dropped backward or pulled themselves backward by flexion and a pulling action provided by tail leverage.

Koski (1966) reported that mean total duration of emergence from 21 coho salmon redds was 30–39 d, and that 90% of fry emerged from redds in 15–20 d. The number of days to first emergence was not significantly related to the amount of fines smaller than 3.3 mm in redds of coho salmon, but the total period of emergence was greatest in redds with highest percentages of fines.

For chum salmon, Koski (1975) noted that the number of temperature units required for the first 5% of emerging fry to reach the surface decreased with increasing percentages of fines. Hausle and Coble (1976) recorded increases, rather than the decreases reported by most workers, in the time required for emergence of brook trout in gravels that contained higher percentages of fines (<2.0 mm). McCuddin (1977) stated that he found no relationship between timing of fry emergence for chinook salmon or steelhead and percentages of

sand in the substrate. However, his data show considerable differences. Emergence of steelhead through 0–22% sand peaked earlier than emergence through 41–52% sand. On the contrary, emergence of chinook salmon peaked earlier from 52% sand. Although McCuddin's data do not shed light on the cause for the difference, it may relate to stress level in the two species. The behavior of chinook salmon seemed to parallel that recorded for chum salmon by Koski (1975), a study in which higher percentages of fines correlated inversely with the number of temperature units required for emergence. Steelhead observed by McCuddin (1977) seemed to behave in a manner opposite to Koski's (1975) chum salmon. The degree to which laboratory circumstances affected the results is unknown.

## Utility of Existing Studies as Predictors of Survival

The laboratory studies of survival of embryos, as reviewed in this report, employed various gravel mixtures and depths and stages of embryonic development. Investigations of survival in natural redds have related survival, either through emergence or to posthatch, to conditions within the periphery of the salmonid redd, but not necessarily to conditions in the egg pocket. These studies did not specifically attempt to duplicate the arrangement, depth, and composition of sediments as they occur in the salmonid egg pocket.

Evaluations of geometric mean particle size, fredle index, and effects on survival of various percentages of fines in the incubation medium have produced results that are quantitatively inconsistent among and usually within fish species. Research generally supports the hypothesis that survival declines in substrates as quantities of fine sediments increase. Fines tend to reduce gravel permeability and pore space, as well as dissolved oxygen in water available to embryos, thus influencing incubation success.

The limited information specific to the salmonid egg pocket strongly indicates that the permeability and particle sizes in egg pockets considerably exceed the same variates in the surrounding spawning gravels and within the periphery of redds. Some of Koski's (1966) samples from capped redds may have included some data from egg pockets. His investigation approached survival to emergence directly, and his survivals integrate conditions within the redd. However, one cannot determine how closely his independent variates reflected conditions in the egg pocket.

One cannot, with the existing information on survival of embryos and alevins in the redds of large salmonids, predict survival quantitatively and with known accuracy on the basis of physical factors measured in field or laboratory studies. It will remain impossible until researchers measure survival to emergence in simulated egg pockets appropriately constructed to model actual egg pocket conditions in the substrates used by the species of interest. Tappel and Bjornn (1983) and Irving and Bjornn (1984) suggested that the greatest applicability of their model functions for survival in relation to two classes of fines lies in predicting the relative change in embryo survival rates that may occur if changes occur in the spawning and incubation substrate. But the greatest applicability of their laboratory data, in spite of the elegance of the laboratory approach and resultant data, is to conditions in the laboratory. One cannot assume, for example, that a 10% incremental increase in particles smaller than 0.85 mm will result in a predictable decline in embryo survival of a given salmonid in a field environment.

Laboratory studies have not taken into account the internal structure of the egg pocket for the species of salmonid used for test animals. One should regard laboratory studies of embryo survival in relation to percentages of fines as models useful in assessing mechanistic responses rather than as analogs of nature that permit accurate assessment of quantitative biological responses in actual redds. With appropriate egg pocket simulations, it may become possible to relate conditions and survival in the pocket to characteristics and survival within the redd. Researchers may find that physical data from within the redd periphery or from laboratory studies provide suitable predictors.

Some variables examined in field and laboratory studies may better predict survival than others. I used stepwise multiple regressions to examine the two most complete data sets, one obtained from capped redds (Koski 1966) and the other from laboratory gravel mixes (Tappel and Bjornn 1983). Independent variables in the regressions for Koski's 21 capped redds of coho salmon included $d_g$, percentage of fines smaller than 0.85 and than 2.0 mm, permeability, dissolved oxygen, and the logarithm of $f_i$. Survival regressed significantly on log $f_i$ ($P = 0.001$) and permeability ($P = 0.07$); $r^2 = 0.63$. I used $d_g$ and log $f_i$ for independent variables in the regressions for laboratory survivals of steelhead and chinook salmon (Tappel and Bjornn 1983). Permeability information

was not available. Tappel and Bjornn (1983) had already calculated $r^2$ values of 0.90 and 0.93 for steelhead and chinook salmon, respectively, with percentages of substrate with diameters smaller than 0.85 and than 9.5 mm as independent variates.[1] Steelhead survival regressed with high significance on log $f_i$ ($P = 0.001$) and $d_g$ ($P = 0.03$); $r^2 = 0.86$ ($P = 0.001$). Chinook salmon survival regressed on log $f_i$ ($P = 0.001$) and $d_g$ ($P = 0.02$); $r^2 = 0.84$.

Survival correlated much better with the fredle index $f_i$ than with $d_g$ in multiple regressions for both field and laboratory data. Earlier, I showed significant single-factor regressions of survival on the log of permeability for coho salmon survival in the field (Koski 1966) and for a laboratory study of chinook salmon survival (McCuddin 1977; Figure 2). If permeabilities were available for the laboratory work that Tappel and Bjornn (1983) carried out under conditions similar to those used by McCuddin (1977), they would very likely also correlate well with survival. Future data obtained on egg pockets and redds, both in the field and in laboratory modeling, should certainly include the fredle index, permeabilities, percentages of fines (<0.85 and <9.5 mm), and dissolved oxygen concentrations, for these all tend to integrate conditions in the incubation medium.

## Research Requirements

Specific techniques for securing data on fines in and on the substrate can be found in Brusven and Prather (1974), Walkotten (1976), Platts et al. (1979), Lotspeich and Reid (1980), Lotspeich and Everest (1981), and Shirazi et al. (1981) and in the summaries by Levinski (1986). Terhune (1958) provided details on the Mark VI standpipe, used to assess permeability and apparent velocity in gravels within and outside of redds.

• Conditions "in the redd" may serve as indices, and even predictors, of conditions in the egg pocket. Sediment composition and stratification have been reported from only 16 identified egg pockets (Platts et al. 1979; Shirazi et al. 1981), and permeabilities from 15. The relationship between average conditions within the redd periphery and those in the egg pocket must be established before hypothesis progresses to fact.

The first research phase should establish the particle sizes, arrangement, permeability, and dissolved oxygen concentration over time in natural egg pockets as incubation proceeds. With these data, one can calculate pocket characteristics such as geometric mean particle diameter by vertical

stratum and fredle index. One can also construct laboratory analogs of egg pockets.

In the first phase, researchers will have to locate egg pockets precisely. One can do this by intensive field observation from blinds of redd progress in clear, relatively shallow water. Redds in water deeper than about 1 m or distant from shore would require more complex observational techniques. Depth of the centrum should be measured, which may require temporary disturbance of the spawning female. Either range stakes, for triangulation on pockets, or data obtained with surveying instruments should permit researchers to find the pockets after females complete redd construction. Freeze-probes (Walkotten 1976; Lotspeich and Reid 1980) can extract some cores of pockets to the bottom of the centrum, and analysis of these cores can define vertical stratification and particle compositions. Freeze-cores should also be obtained at other points in several redds where egg-pocket cores are obtained. Core sampling should include efforts to determine changes in stratification and proportions of fines over the incubation season as fines intrude in the cleansed egg pocket and redd periphery. Intrusion of organic fines also may require attention in some environments.

A truncated Mark VI standpipe (Terhune 1958) can be inserted in undisturbed pockets so that permeability and dissolved oxygen can be tracked through the incubation period. At the same time, standpipes should be inserted at randomly selected locations within the redd periphery, permitting comparison of data from within the redd with information from egg pockets. Also, permeabilities obtained through the entire incubation period in egg pockets and the surrounding redds will provide information for modeling gradual intrusion of fines into the redd.

McNeil samplers (McNeil 1962) will not provide information on vertical stratification, although they may serve, with appropriate core diameter and excavation depth, to assess gravel composition in egg pockets. Shirazi et al. (1981) compared McNeil and freeze-core systems, and found that triple-probe freeze-cores and McNeil samples yielded similar results in spawning gravels. One should not interpret these results as pertaining to vertical stratification in the egg pocket. Unlike samples from McNeil cylinders, frozen cores can be placed horizontally to thaw into separate bins designed to provide data on vertical stratification.

Where spawning is extremely dense, as in certain pink, chum, and sockeye salmon spawning areas, condition of the spawning gravels may more truly reflect conditions in egg pockets. I cannot find data that permit me to examine the validity of this argument; but I think the egg pocket will have conditions different from "spawning gravel" or "redd" even in zones of dense spawning.

In the second research phase, one should relate survival through emergence to conditions in egg pockets. I suggest that laboratory environments should simulate egg pocket conditions determined as described above, including centrum depth, particle sizes and locations, permeability, and dissolved oxygen. The proportion of sediment made up by fine particles can be varied in different treatments, but basic pocket structure should simulate nature. This requires inclusion of large particles as found in actual egg pockets. Accurate modeling of temporal changes in field conditions may require that fine particles, possibly including organic fractions, be added during the incubation period.

A third research phase should encompass estimation of survival to emergence with redd capping. The field investigator should follow the procedures suggested in phase one for location of egg pockets, and should incorporate truncated standpipes in egg pockets and elsewhere in the redd. Redd caps (Phillips and Koski 1969) can be emplaced 2 or 3 weeks before anticipated fry emergence as estimated from temperature data. This minimizes possible ice or debris damage to caps and accumulation of fines or organic matter on and beneath cap netting.

Phase three also requires a length–fecundity regression appropriate for the stock of fish. This can be developed from hatchery or fishery data, and should probably involve standard length rather than fork length because of tail erosion during spawning. One may estimate fecundity and assess egg retention from carcasses of females associated with certain redds. Alternatively, one might use photographic techniques to measure females on the redd, estimate fecundity from that length, and correct for a percentage of egg retention based on a sample of carcasses. Variability in fecundity for fish of given lengths may, for some stocks, demand a large sample of capped redds. For example, Healey and Heard (1984) reported that fish length explained somewhat less than 50% of the variation in fecundity between individuals within chinook salmon populations. The net caps must surround the redd, rather than individual pockets, to integrate survival from all pockets.

Behavior of some species and races of salmonids, as well as environmental circumstances, will

permit all three phases of work. For other stocks, only the first two phases may be feasible. For example, spring-spawning rainbow trout and steelhead may pose more difficulties for redd capping than fall-spawning chinook salmon in streams with a snow-melt hydrograph. Data for even a few egg pockets on centrum depth, composition, and stratification may permit improved laboratory simulation. Where extended observation of egg-pocket locations cannot occur, examination of many frozen cores may reveal details necessary for simulation. The samples used to characterize egg pockets should include only cores that contained several ova.

Variability of data about the regressions of survival on certain categories of fines, $d_r$, $f_r$, and permeability should decrease for information obtained within the egg pocket and applied to laboratory modeling and redd capping. One may not entirely overcome variability caused by temporal changes in sediment composition in some streams, but one can reduce variability that results from inaccurate sampling procedures. It may become feasible to relate conditions within the redd to survival within the egg pocket. Quantitative models and predictive tools could then be developed for field environments. Even if redd capping in adequate sample sizes proves economically and physically infeasible, knowledge of structure and composition of the egg pocket can be applied to laboratory experimental conditions, making for better analogs of egg pockets in the field.

Determination of conditions in the egg pocket and survival to emergence requires labor-intensive, expensive procedures. The alternative is to continue to use data of unknown accuracy and to extrapolate inappropriate experimental and sample data to natural incubation environments.

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