A NEW METHOD OF RELATING SPAWNING GRAVEL SIZE COMPOSITION TO SALMONID EMBRYO SURVIVAL

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by

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AUTHORIZATION TO PROCEED WITH THE FINAL DRAFT:

A preliminary draft of the thesis titled "A New Method of Relating Spawning Gravel Size Composition to Salmonid Embryo Survival" by Paul David Tappel has been reviewed and found adequate for the Master of Science degree with a major in Fishery Resources. Permission is hereby granted for preparation of the final thesis copy incorporating suggestions made by the committee.

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ABSTRACT

A new method for describing the size composition of salmonid spawning gravel was developed. For spawning gravel samples from Idaho, Washington, and Wyoming streams, cumulative particle size distributions for material smaller than 25.4 mm consistently plotted as straight lines on log-probability paper. Because of the lognormal distribution of particle sizes in this range, the size composition of material smaller than 25.4 mm was closely approximated by two points on the cumulative particle size distribution. The two particle size classes which best reflected spawning gravel size composition were the percentage of the substrate smaller than 9.50 mm and the percentage smaller than 0.85 mm.

Laboratory experiments related these two particle size classes to salmonid embryo survival. In these tests, 90 to 93 percent of the variability in embryo survival was correlated with changes in substrate size composition. Equations were developed to quantify the effect of spawning gravel size composition on chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Salmo gairdneri*) survival-to-emergence in a wide range of spawning gravel mixtures.

Gravel mixtures containing high percentages of fine sediment produced slightly smaller steelhead fry than gravels containing low percentages of fine sediment. The inverse relationship between fine sediment and steelhead fry size was not significant (alpha = 0.05) over the range of experimental gravel mixtures. There was no relationship between changes in gravel size composition and the size of chinook salmon emergents. In gravels containing large amounts of fine sediment, steelhead and salmon fry frequently emerged before yolk sac absorption was complete.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

INTRODUCTION

A new method of describing the size composition of salmonid spawning gravel provided a more reliable, useful, and comprehensive measure of spawning gravel quality than "percent fines" or geometric mean. In laboratory experiments, 90 to 93 percent of the variability in chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Salmo gairdneri) embryo survival was correlated with changes in substrate size composition. Equations were developed to quantify the effect of spawning gravel size composition on chinook salmon and steelhead trout survival-to-emergence in a wide range of spawning gravel mixtures.

Successful incubation of salmon, steelhead, and trout embryos in streams requires spawning gravels that are relatively free of silt and sand. Laboratory studies and field experiments have repeatedly shown that salmonid embryo survival is inversely related to the amount of fine sediment in the spawning substrate. The detrimental effects of excessive amounts of fine sediment on salmonid embryo survival are well documented and have been summarized by Cordone and Kelley (1961), Gibbons and Salo (1973), and Iwamoto et al. (1978).

Although the effect of substrate size composition on salmonid embryo survival has been intensively studied, there is little agreement on which particle size classes should be classified as fine sediment. Fine sediment generally includes silt- and sand-sized particles. When used in this thesis, fine sediment refers to sediment particles that are predominantly silt- and sand-sized but may be as large as 12.7 mm (1/2 inch). The reason for this inexact definition of fine sediment will become apparent later in the thesis.

Two other terms need to be defined. Spawning gravel refers to the total mixture of sediment sizes in the spawning substrate and is not limited to any particle size range. Survival-to-emergence is the percent survival of salmonid embryos from the time they are placed in the gravel until they emerge from the substrate as alevins or fry.

In gravels containing excessive amounts of fine sediment, most researchers cited by Cordone and Kelley (1961), Gibbons and Salo (1973), and Iwamoto et al. (1978) attribute low embryo survival to decreased gravel permeability and/or entrapment of alevins and fry. Reduced permeability restricts the flow of water around incubating salmonid embryos. This results in a decreased supply of oxygen to the embryos and also allows accumulation of toxic metabolic wastes (free carbon dioxide and ammonia). Entombment of embryos and alevins occurs when fine material lodged in gravel interstices prevents their emergence. Cooper (1965) suggested that embryos could be crushed when the weight of overlaying material was transferred to the embryos via fine material.

McNeil and Ahnell (1964) were among the first to compare a specific size class of sediment to salmonid embryo survival. In pink salmon (Oncorhynchus gorbuscha) spawning areas of Alaska, they found that fry emergence was inversely related to the percentage of the spawning substrate smaller than 0.833 mm in diameter. McNeil and Ahnell (1964) suggested that spawning gravel quality could be quantified by determining the percentage of the substrate (by weight or volume) that was finer than a particular particle size. Fisheries biologists adopted this technique and "percent fines" became the standard measure of spawning gravel quality.

Relationships between "percent fines" and salmonid embryo survival have been investigated using several salmonid species and various combinations of particle sizes. Koski (1966) found that coho salmon (Oncorhynchus kisutch) embryos survived best in stream channels that contained low percentages of material less than 3.3 mm in diameter. Bjornn (1969) demonstrated that emergence of chinook salmon and steelhead trout fry was impeded by a high percentage of material finer than 6.35 mm. In laboratory tests, Hall and Lantz (1969) found a significant inverse relationship between the amount of fine sediment from 1 to 3 mm and the ability of coho salmon and steelhead fry to emerge. Koski (1975) observed that increased percentages of fine sediment from 0.105 to 3.327 mm in diameter decreased survival-to-emergence of chum salmon (Oncorhynchus keta). Tagart (1976) reported that survival-to-emergence of coho salmon in natural redds decreased when more than 20 percent of the substrate was composed of particles finer than 0.85 mm. Cederholm et al. (1981) determined that material finer than 0.85 mm was the most detrimental particle size class for coho salmon embryo survival in the Clearwater River system, Washington. In a study to determine the effects of logging on the quality of salmonid spawning areas, Scrivener and Brownlee (1981) have classified material less than 9.55 mm in diameter as "fines".

Depending on the study, embryo survival has been negatively correlated with fine sediment of various sizes: <0.85 mm, 1 to 3 mm, <3.3 mm, and <6.35 mm. This nebulous definition of "fine" material has made it difficult for fisheries biologists to evaluate the quality of spawning areas based on gravel size composition.

An inescapable problem with using "percent fines" as a measure of spawning gravel quality is determination of which particular particle size classes are harmful to incubating salmonid embryos. It may be impossible to isolate a single size class of material that is detrimental to embryo survival. Different salmonid species can probably tolerate different levels of fine sediment, depending on embryo size and inherited adaptations to substrate conditions. "Percent fines" is an inadequate measure of spawning gravel quality. A better method of relating gravel size composition to salmonid embryo survival is presented.

PART 1: DEVELOPMENT OF A NEW TECHNIQUE FOR DESCRIBING SPAWNING SUBSTRATE SIZE COMPOSITION

Salmonid mortality and survival during embryo incubation and alevin emergence depends largely on the total size composition of the spawning substrate, not just the amount of substrate finer than a particular size. An ideal measure of the quality of spawning substrate would completely describe the sediment matrix. Unfortunately, a single parameter which completely describes spawning gravel mixtures does not exist.

Platts et al. (1979) suggested the geometric mean particle diameter (d_g) as a companion measurement to "percent fines". Geometric means are computed as:

$$d_g = \sqrt{d_{84}\ d_{16}}$$

where: d_{84} = particle size that 84 percent of substrate is smaller than
d_{16} = particle size that 16 percent of substrate is smaller than

They proposed the use of d_g primarily because (1) d_g is commonly used in other disciplines to describe stream substrate size composition, (2) d_g describes streambed size composition better than "percent fines", and (3) statistical comparison of spawning areas is easier when using d_g instead of "percent fines".

Using data from a number of studies, Shirazi and Seim (1979) demonstrated a good relationship between salmonid embryo survival and the geometric mean diameter of spawning gravel.

Lotspeich and Everest (1980) proposed a "Fredle index" to relate substrate size composition to embryo survival. They noted that d_g alone was inadequate to describe spawning gravel. Several spawning areas could have the same d_g but quite different properties, depending on how large and small sediment particle size classes were distributed about the mean particle size.

Fredle numbers use d_g/s_o as a measure of pore size and permeability. Lotspeich and Everest (1980) suggested that Fredle numbers be calculated as:

$$\text{Fredle number} = d_g/s_o$$

where: s_o = sorting coefficient = $\sqrt{d_{75}/d_{25}}$

d_{75} = particle size that 75 percent of substrate is smaller than

d_{25} = particle size that 25 percent of substrate is smaller than

In this ratio, d_g increases as average grain size increases. The sorting coefficient, s_o, is inversely related to permeability of the substrate. An increase in the Fredle number may indicate an increase in the average particle size or an increase in permeability and average pore size. Correlation of Fredle numbers with embryo survival-to-emergence data would indicate if Fredle numbers are a good measure of spawning gravel quality.

Lognormal Particle Size Distribution of Spawning Gravel

Stream substrate size composition can be described by plotting the cumulative distribution of sediment particle sizes on log-probability paper (Figure 1). Geologists and hydraulic engineers frequently assume the cumulative distribution of natural stream sediments will approximate

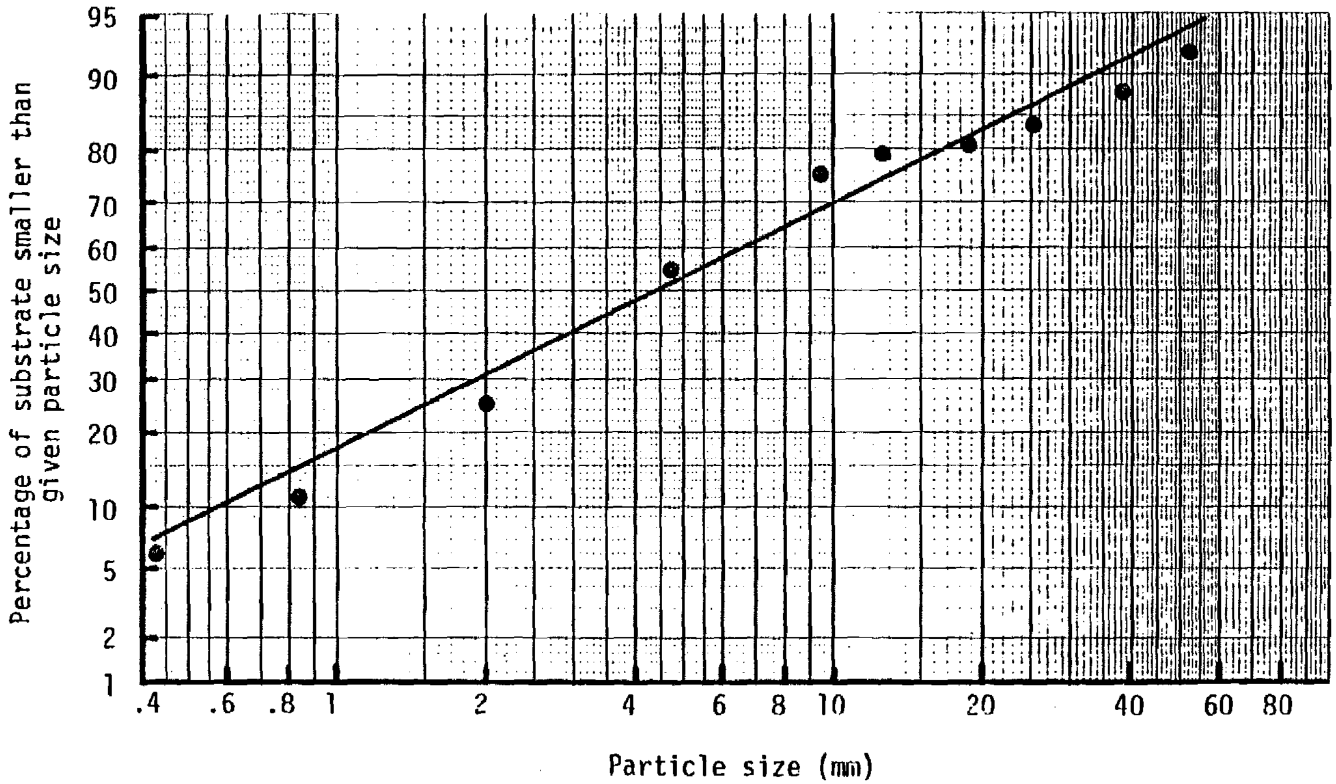

Figure 1. Log-probability plot of spawning gravel sample with a particle size distribution close to lognormal (r^2 = 0.99).

a straight line on log-probability paper (Shen 1971). Sediment represented by a straight line on log-probability paper has a lognormal distribution of particle sizes.

By plotting sediment data on log-probability paper, Shirazi and Seim (1979) found that spawning gravel samples from Oregon and Washington had particle size distributions close to lognormal. For 100 samples, they obtained an average coefficient of determination (r^2) of 0.93 for the least squares regression lines through the data. I did a similar analysis with 100 samples of spawning gravel from the South Fork Salmon River in Idaho. All samples were collected by U.S. Forest Service personnel from salmon spawning areas. R-squared values for these data averaged 0.95 and ranged from 0.62 to 1.00.

Spawning gravel size composition could be completely and accurately described by regression line equations if the entire range of particle sizes in substrate samples were consistently linear when plotted on log-probability paper. However, some sediment samples from the South Fork Salmon River had substantial deviations from lognormality and were not accurately represented by regression line equations.

Generally, sediment samples with substantial deviations from lognormality curved up in the upper end of cumulative distribution plots (Figure 2). The solid line in Figure 2 represents the regression through all data points with the r^2 value being 0.89. By ignoring material larger than 25.4 mm (1 inch) in diameter, a regression line with an r^2 value of 0.97 was obtained. The dashed line in Figure 2 shows the regression for material less than 25.4 mm in diameter.

The average r^2 value for the 100 South Fork Salmon River samples

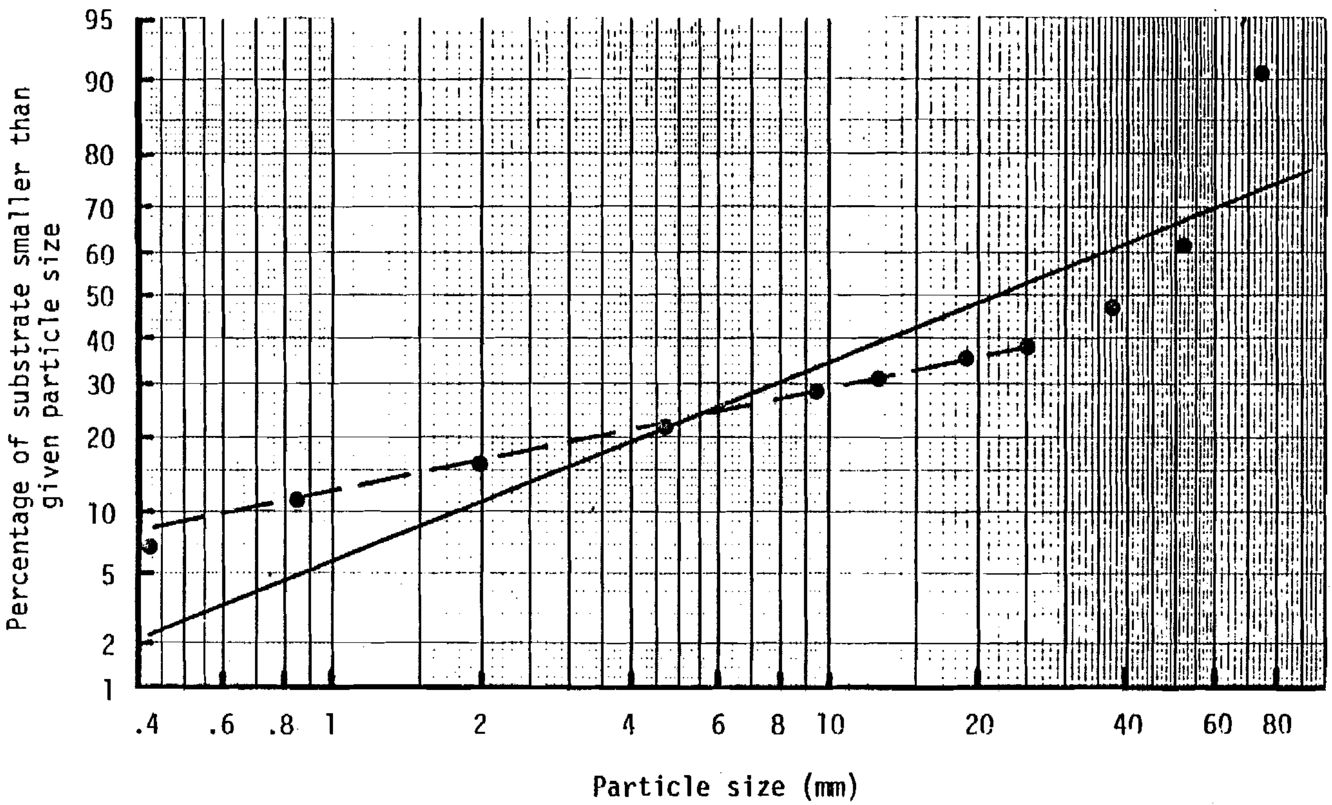

Figure 2. Typical deviation from lognormal particle distribution in spawning gravels from the South Fork Salmon River, particularly in upper end (right side) of cumulative distribution plot. Solid line is for all particle sizes ($r^2 = 0.89$). Broken line is for material smaller than 25.4 mm in diameter ($r^2 = 0.97$).

increased from 0.95 to 0.97 when material larger than 25.4 mm was not included in the analysis. In almost all samples, a straight line on log-probability paper accurately represented the material less than 25.4 mm ($r^2 = 0.97$). Only three samples had r^2 values less than 0.90.

Similar results were obtained from an analysis of sediment from 50 brown trout redds and 50 brook trout redds. These substrate samples were collected in small Wyoming streams by Reiser and Wesche (1977). For these samples, the average r^2 value for material finer than 25.4 mm was 0.97; r^2 values ranged from 0.87 to 1.00.

Data from 126 salmon spawning areas sampled by Cederholm et al. (1977) in the Clearwater River drainage, Washington, were similarly analyzed. For these data, straight lines on log-probability paper closely approximated the composition of material finer than 26.9 mm (about 1 inch). The average r^2 value for these samples was 0.97. R-squared values ranged from 0.85 to 1.00.

Proposed Method of Describing Sediment Size Composition

Since the size composition of spawning gravel less than 25.4 mm can be accurately described by straight lines on log-probability paper, regression line equations could be used to describe gravel size composition in this particle range. Regression equations would be of the form:

$$\text{PERCENT} = C + K\log_e \text{SIZE}$$

where: PERCENT = inverse probability transform of percentage of substrate smaller than a given sieve size.

C = intercept of regression line

K = coefficient of variable $\log_e$SIZE

SIZE = sieve size in mm

Rather than determine regression equations for sediment samples, I simplified the description of spawning gravel size compositions with an approximation. For particle sizes less than 25.4 mm in diameter, particle size distributions on log-probability paper were almost linear. Because of the good correlation in this size range (r^2 values close to 1.0), lines passing through data points for two sieve sizes closely approximated lines determined by the least squares regression procedure.

For data from the South Fork Salmon River, a line passing through data points for the 9.50 mm and 0.85 mm particle sizes closely approximated the line calculated by the least squares procedure for material smaller than 25.4 mm. For the gravel sample presented in Figure 2, the least squares regression line for material less than 25.4 mm was almost identical to the line drawn between 9.50 mm and 0.85 mm data points.

Using an analysis of residuals, I found that lines extended through the 9.50 mm and 0.85 mm data points consistently over-estimated the amount of material smaller than 0.25 mm in diameter. However, this particle size class rarely comprised more than five percent of the substrate samples (usually one or two percent), so a small over-estimation should not invalidate the technique.

Application of Proposed Method

The size range of spawning substrate from several river systems was graphically illustrated by plotting the percentage of particles smaller than 9.50 mm versus the percentage less than 0.85 mm. Each point in

Figure 3 represents one sample of spawning gravel from the South Fork Salmon River (Idaho), the Clearwater River (Washington), or Wyoming trout streams. Interpretation of Figure 3 is best accomplished by example. Points A and B (Figure 3) represent two different spawning gravel samples. A vertical line passing through A and B would represent a continuum of gravel size compositions, all with 50 percent of the substrate less than 9.50 mm in diameter. If particles less than 9.50 mm were considered "fines", then any data points falling on the line AB would represent spawning gravel samples with the same "percent fines" yet different particle size distributions.

If samples represented by points A and B (Figure 3) had lognormal particle size distributions (Figure 4), the geometric mean of both mixtures would be equal.

For A, $d_g = \sqrt{d_{84}\ d_{16}}$ $\qquad d_{84} = 96$ mm

$d_{16} = 0.94$ mm

$$d_g = \sqrt{(96)\ (.94)}$$

$$d_g = 9.50 \text{ mm}$$

For B, $d_g = \sqrt{d_{84}\ d_{16}}$ $\qquad d_{84} = 41$ mm

$d_{16} = 2.2$ mm

$$d_g = \sqrt{(41)\ (2.2)}$$

$$d_g = 9.50 \text{ mm}$$

In the past, researchers relating salmonid embryo survival to d_g or "percent fines" would have considered samples A and B identical. However, as shown in Figure 4, samples A and B would have different particle size distributions, implying that embryo survival could differ in the two mixtures.

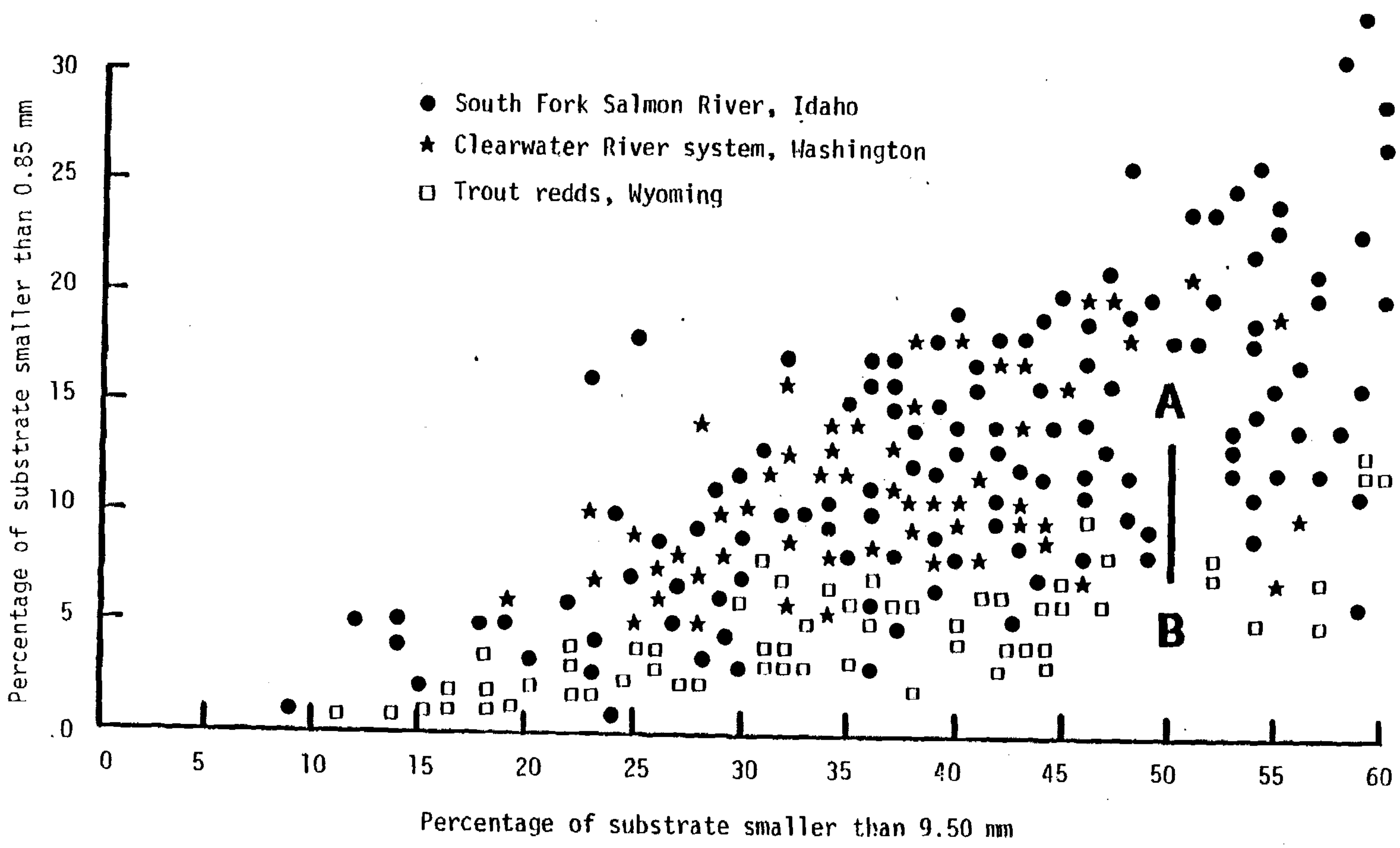

Figure 3. Range of spawning gravel size composition for samples from several river systems. Line AB represents mixtures with the same "percent fines" (50% smaller than 9.50 mm) and geometric mean but different size compositions.

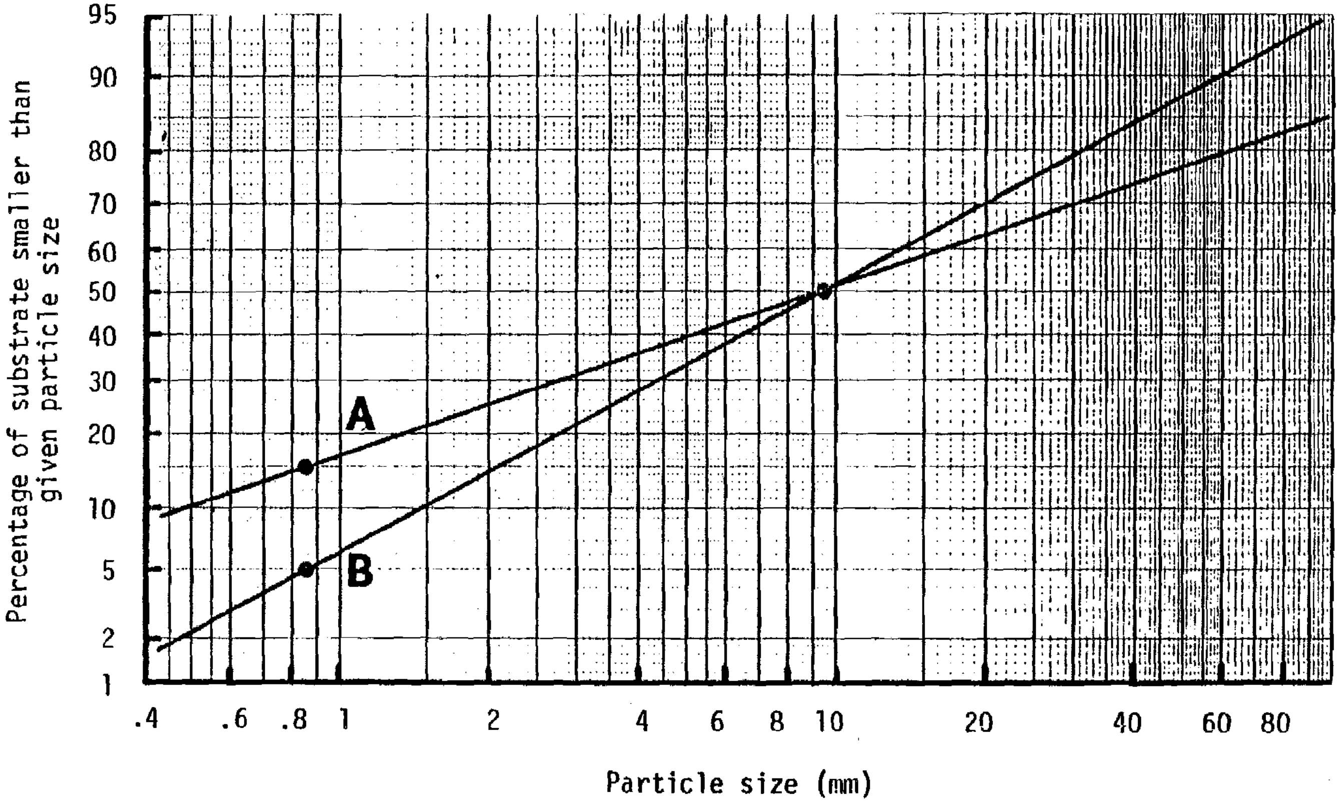

Figure 4. Lognormal particle size distributions of gravel samples A and B (from Figure 3).

Spawning gravels sampled from the Clearwater River, Washington, and the South Fork Salmon River, Idaho, had similar ranges of size distributions (Figure 3). Samples from these two rivers were collected from typical spawning areas that had not been used by salmon for almost one year. Wyoming substrate samples, collected directly from trout redds soon after spawning occurred, had a distinctly different range of size compositions than spawning gravel samples taken from the Clearwater and South Fork Salmon Rivers (Figure 3). Trout redd samples contained only small amounts of fine sediment compared to samples from salmon spawning areas which had not been recently used for spawning. The relatively small amount of fine sediment found within redds (e.g. Wyoming trout redd samples, Figure 3) may reflect the ability of salmonids to flush fine sediment from the gravel during spawning.

Summary of New Method for Describing Spawning Gravel Size Composition

For gravel mixtures in natural stream spawning areas, the size composition of material finer than 25.4 mm can consistently be approximated by straight lines when cumulative particle size distributions are plotted on log-probability paper. By knowing two points on this line, the size composition of material finer than 25.4 mm can be accurately described. The two points which best approximate spawning gravel size composition are the percentage of the substrate smaller than 9.50 mm in diameter and the percentage of the substrate smaller than 0.85 mm.

By using gravel size mixtures similar to those found in streams, salmonid embryo survival could be implicitly related to the entire range of material less than 25.4 mm. This could be accomplished by comparing embryo survival to two substrate variables (percentage of the substrate smaller than 9.50 mm and percentage less than 0.85 mm). This technique would eliminate the need to define exactly which particle sizes are detrimental to salmonid embryos and only requires the assumption that material larger than 25.4 mm is not harmful to incubating salmonids. The second part of this thesis describes laboratory experiments in which this new technique was used to quantify the effects of gravel size composition on chinook salmon and steelhead trout embryo survival.

PART 2: EFFECTS OF SPAWNING GRAVEL SIZE COMPOSITION ON SALMONID EMBRYO SURVIVAL

METHODS

Laboratory tests were designed to correlate salmonid embryo survival with mixtures of sediment sizes like those found in stream spawning areas. Obtaining a wide range of gravel mixtures similar to natural mixtures was a difficult task.

A large amount of granitic streambed sediment from an alluvial deposit in central Idaho was transported to the University of Idaho where material larger than 12.7 mm (1/2 inch) was removed by sieving. The remaining material was sluiced, sorted into size groups, and then combined with 12.7 to 76.1 mm gravel (1/2 to 3 inches) to provide a range of gravel mixtures for embryo incubation tests (Table 1).

Each experimental gravel mixture was given a label which corresponded to the percentage of the gravel smaller than 9.50 mm and the percentage smaller than 0.85 mm (Table 1). As an example, for the gravel mixture labeled 30:2, 30 percent of the mixture was smaller than 9.50 in diameter and 2 percent was smaller than 0.85 mm. Gravel mixture labels do not include fractions since all percentages were rounded to the nearest whole number.

Gravel mixture labels were plotted in Figure 5 corresponding to the size composition of respective experimental gravel mixtures. The shaded area of Figure 5 delineates the range of gravel size compositions found in salmon spawning areas in the Clearwater River, Washington, and the South Fork Salmon River, Idaho (Figure 3). As shown on Figure 5, the range of experimental gravel mixtures was similar to the range of gravel

Table 1. Size composition of gravel mixtures used in steelhead and chinook salmon embryo survival tests.

Gravel mixture label	Percentage of mixture smaller than given particle size (size in mm)									Geometric mean	Fredle number
	50.8	25.4	12.7	9.50	6.35	4.76	1.70	0.85	0.42		
0:0	99.4	73.7	4.2	0	0	0	0	0	0	21.5	17.6
10:4	99.5	76.3	13.8	10.0	9.9	9.4	5.9	3.9	2.2	19.1	14.8
20:8	99.5	79.0	23.4	20.0	19.8	18.7	11.7	7.8	4.4	11.8	8.7
30:12	99.6	81.6	32.9	30.0	29.6	28.1	17.6	11.7	6.6	6.6	3.0
40:16	99.6	84.2	42.5	40.0	39.5	37.5	23.4	15.6	8.8	4.7	1.6
50:20	99.7	86.8	52.1	50.0	49.4	46.8	29.3	19.5	11.0	4.0	1.1
15:4	99.5	77.6	18.6	15.0	14.1	12.2	5.7	3.5	2.0	16.4	12.5
25:6	99.6	80.3	28.2	25.0	23.4	20.3	9.5	5.8	3.4	10.4	6.5
35:8	99.6	82.9	37.7	35.0	32.8	28.4	13.3	8.2	4.8	7.6	3.5
45:10	99.7	85.5	47.3	45.0	42.2	36.5	17.1	10.5	6.2	6.1	2.4
55:13	99.7	88.2	56.9	55.0	51.6	44.7	20.9	12.9	7.5	5.0	1.7
10:1	99.5	76.3	13.8	10.0	9.0	7.1	1.8	0.7	0.4	19.1	14.8
20:1	99.5	79.0	23.4	20.0	18.0	14.2	3.5	1.4	0.9	13.9	9.6
30:2	99.6	81.6	32.9	30.0	26.9	21.3	5.2	2.0	1.3	10.7	6.0
40:3	99.6	84.2	42.5	40.0	35.9	28.4	7.0	2.7	1.7	9.1	4.5

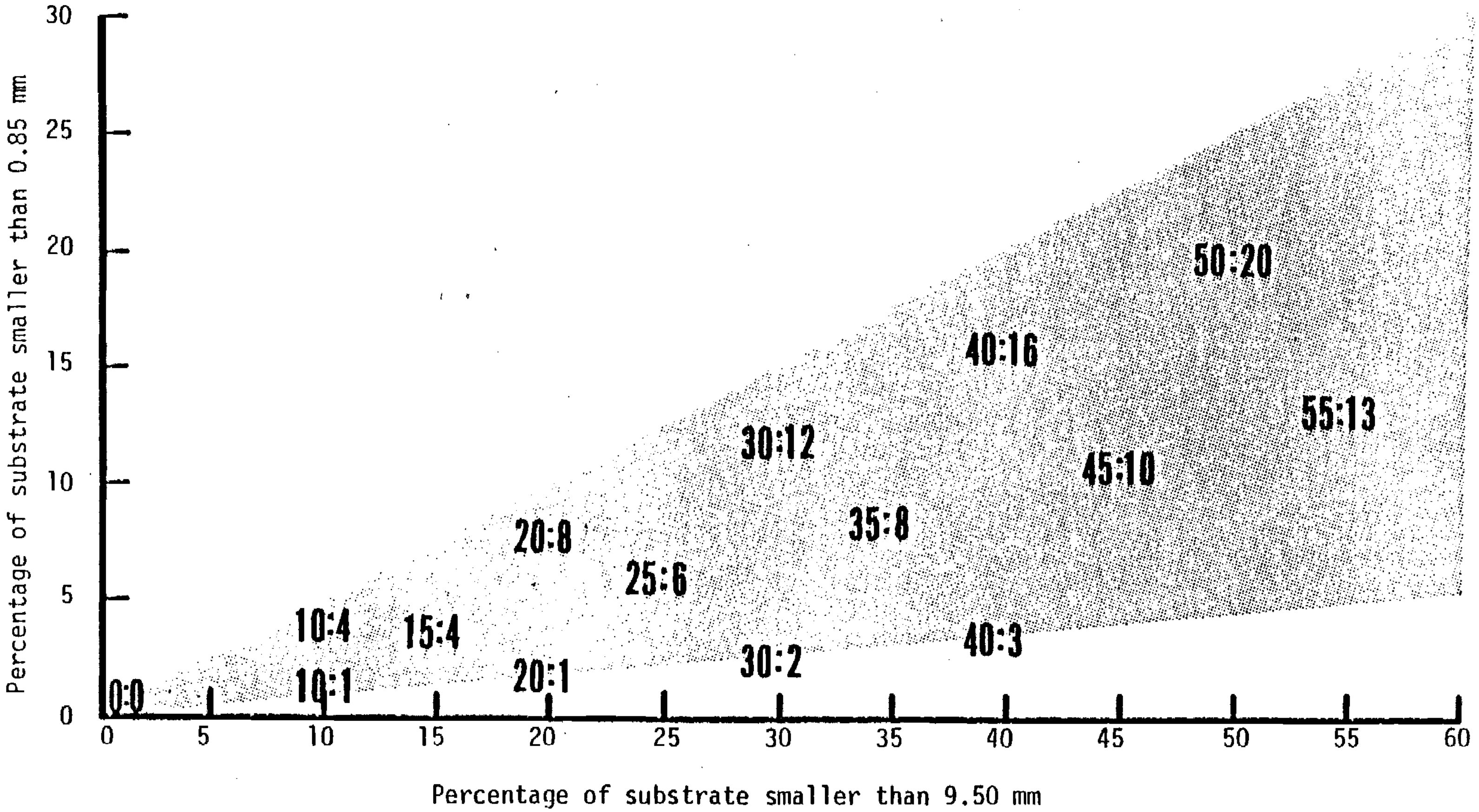

Figure 5. Experimental gravel mixture labels overlying range of natural spawning substrate. Placement of labels (0:0, 20:8, 40:3, etc.) corresponds to respective experimental gravel compositions.

size compositions found in these two rivers.

Because of the way experimental gravel mixtures were produced, they did not exactly duplicate natural mixtures. Each experimental gravel mixture contained more material from 12.7 to 25.4 mm than its natural counterpart. This deviation would be significant only if material from 12.7 to 25.4 mm was detrimental to incubating salmonid embryos. I found no evidence in the literature that this particle range was harmful to salmonid embryos, so I assumed this deviation from natural gravel size composition would not substantially affect experimental results.

Experimental gravel mixtures were put into 40 incubation troughs at the University of Idaho (Figure 6). There were two or three replicates of each of the 15 gravel mixtures. Water flow and gradient through each trough could be regulated by a valve at the water inlet (Figure 6).

In Spring of 1980, approximately 10,000 fertilized steelhead eggs were obtained from Dworshak National Fish Hatchery, Idaho. At the University of Idaho, these water-hardened embryos were counted into Vibert boxes which had been filled with appropriate gravel mixtures. Each box received 50 embryos. Four Vibert boxes were placed in each incubation trough and buried to a depth of 15 to 20 cm (6 to 8 inches). Care was taken to surround the 200 embryos in each trough with a homogeneous mixture of gravel. Vibert box lids were left open so emerging fry would not be impeded by the plastic mesh (Figure 7).

Chilled, unchlorinated water flowing through each trough kept water temperatures between 10 and 13 C (50-55 F). Throughout the experiment, dissolved oxygen levels remained near saturation. Before the embryos hatched, water levels were kept below the surface of the gravel (Figure 7) so the gradient of water could be maintained at two percent in each incubation trough.

After 35 days of incubation, fry began to emerge and water levels in each trough were raised above the gravel. Steelhead fry were collected over a 3-week period as they emerged from each experimental gravel mixture. Numbers collected indicated percent survival in each incubation trough. Fifty fry from each gravel mixture were weighed to the nearest milligram on a Mettler balance, and fry fork lengths were recorded to the nearest millimeter.

During Fall of 1980, a similar experiment was done with chinook salmon

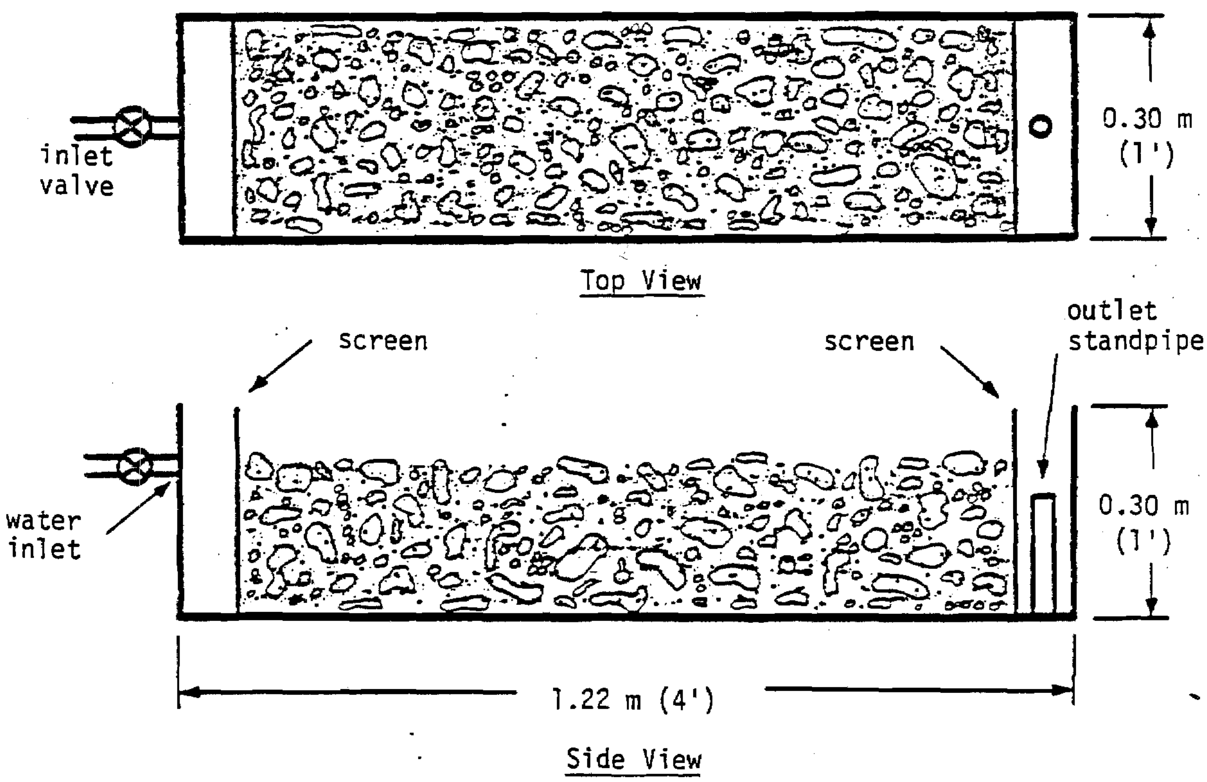

Figure 6. One of 40 incubation troughs used to evaluate steelhead and chinook salmon survival-to-emergence in various gravel mixtures.

embryos. Because chinook salmon embryos were sensitive to handling stress before the "eyed" stage, "eyed" chinook salmon embryos were used in the experiments. Embryos were flown from Carson National Fish Hatchery (Washington) to the University of Idaho. These 6,000 embryos were incubated for 52 days in the hatchery and were subjected to 624 temperature units (Leitritz and Lewis 1976) before they were placed in experimental incubation troughs.

Chinook salmon embryos were handled and placed in gravel mixtures exactly as steelhead embryos in the previous test, except that only 25 chinook salmon embryos were placed in each Vibert box. Each incubation trough contained 100 "eyed" chinook salmon embryos. Thirty days of incubation at 10 to 13 C elapsed before fry emergence began. As with the steelhead experiment, water levels in each trough were raised when fry were ready to emerge. Emerging fry were captured, counted, weighed, and measured.

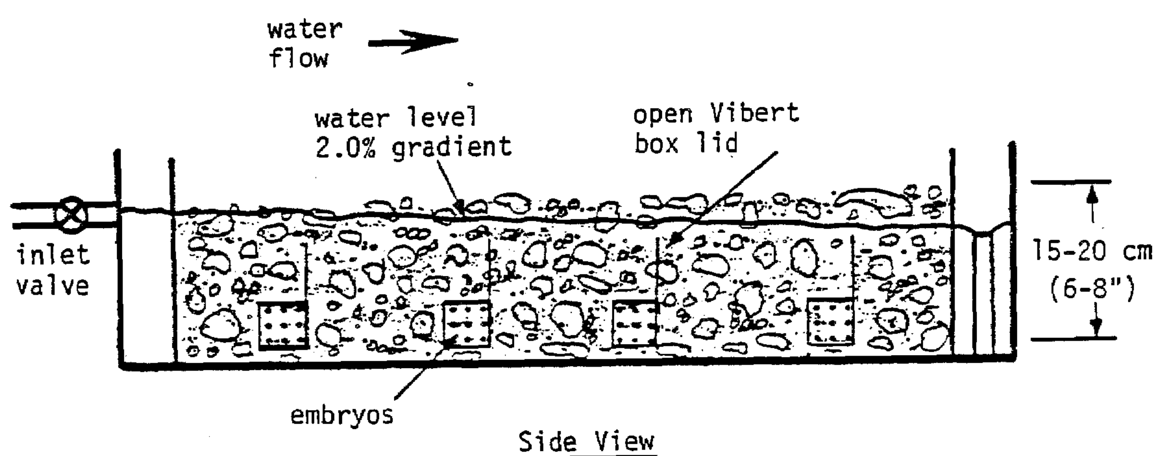

Figure 7. Incubation trough after placement of salmonid embryos and adjustment of water level.

Stepwise regression was used to develop the best second-order equations relating steelhead trout and chinook salmon survival-to-emergence to gravel size composition. Survival was correlated with two substrate variables: the percentage of the substrate smaller than 9.50 mm ($S_{9.5}$) and the percentage less than 0.85 mm ($S_{.85}$). Second-order terms [$(S_{9.5})^2$, $(S_{.85})^2$] and a cross-product term [$(S_{9.5})(S_{.85})$] were included as variables in the regression analysis to detect curvilinear relationships between embryo survival and gravel size composition.

Survival-to-emergence was also related to geometric means and Fredle numbers for all gravel mixtures. Fredle numbers were calculated as suggested by Lotspeich and Everest (1980).

Average steelhead and chinook salmon fry lengths and weights were calculated for each experimental gravel mixture. A Duncan's multiple range test was performed on each data set to detect significant relationships between fry size and gravel size composition.

RESULTS AND DISCUSSION

Embryo Survival

Survival-to-emergence of steelhead and chinook salmon embryos ranged from 6 to 99 percent (Table 2). As the amount of fine material increased in experimental gravel mixtures, embryo survival of both species decreased (Table 2).

The relationship between embryo survival and gravel size composition was best described by showing steelhead and chinook salmon embryo survival overlaying the range of spawning gravel size compositions (Figures 8 and 9). The location of embryo survival values in Figures 8 and 9 correspond to the gravel mixture in which the embryos were buried.

The best second-order equation relating steelhead survival to gravel size composition was:

$$\text{Percent Survival} = 94.7 - 0.116(S_{9.5})(S_{.85}) + 0.007(S_{9.5})^2$$

This equation had an R^2 value of 0.90.

The best equation relating chinook salmon embryo survival to gravel size composition was:

$$\text{Percent Survival} = 93.4 - 0.171(S_{9.5})(S_{.85}) + 3.871(S_{.85})$$

The chinook salmon equation had an R^2 value of 0.93.

These equations were used to predict steelhead and chinook salmon embryo survival for gravel mixtures like those used in the incubation

Table 2. Average survival-to-emergence of steelhead and chinook salmon embryos in experimental gravel mixtures.

Gravel[a] mixture label	Average percent survival-to-emergence in each gravel mixture (number of replicates)	
	Steelhead	Chinook salmon
0:0	93 (n=2)	96 (n=2)
10:4	87 (n=3)	99 (n=3)
20:8	86 (n=3)	97 (n=3)
30:12	59 (n=3)	88 (n=3)
40:16	14 (n=3)	32 (n=3)
50:20	10 (n=3)	6 (n=3)
15:4	92 (n=3)	95 (n=3)
25:6	91 (n=3)	93 (n=3)
35:8	67 (n=3)	77 (n=3)
45:10	59 (n=3)	61 (n=3)
55:13	30 (n=2)	18 (n=3)
10:1	94 (n=2)	95 (n=2)
20:1	93 (n=2)	92 (n=2)
30:2	95 (n=2)	88 (n=2)
40:3	90 (n=2)	87 (n=2)

[a]First number in gravel mixture label is percentage of substrate smaller than 9.50 mm. Second number is percentage of substrate smaller than 0.85 mm.

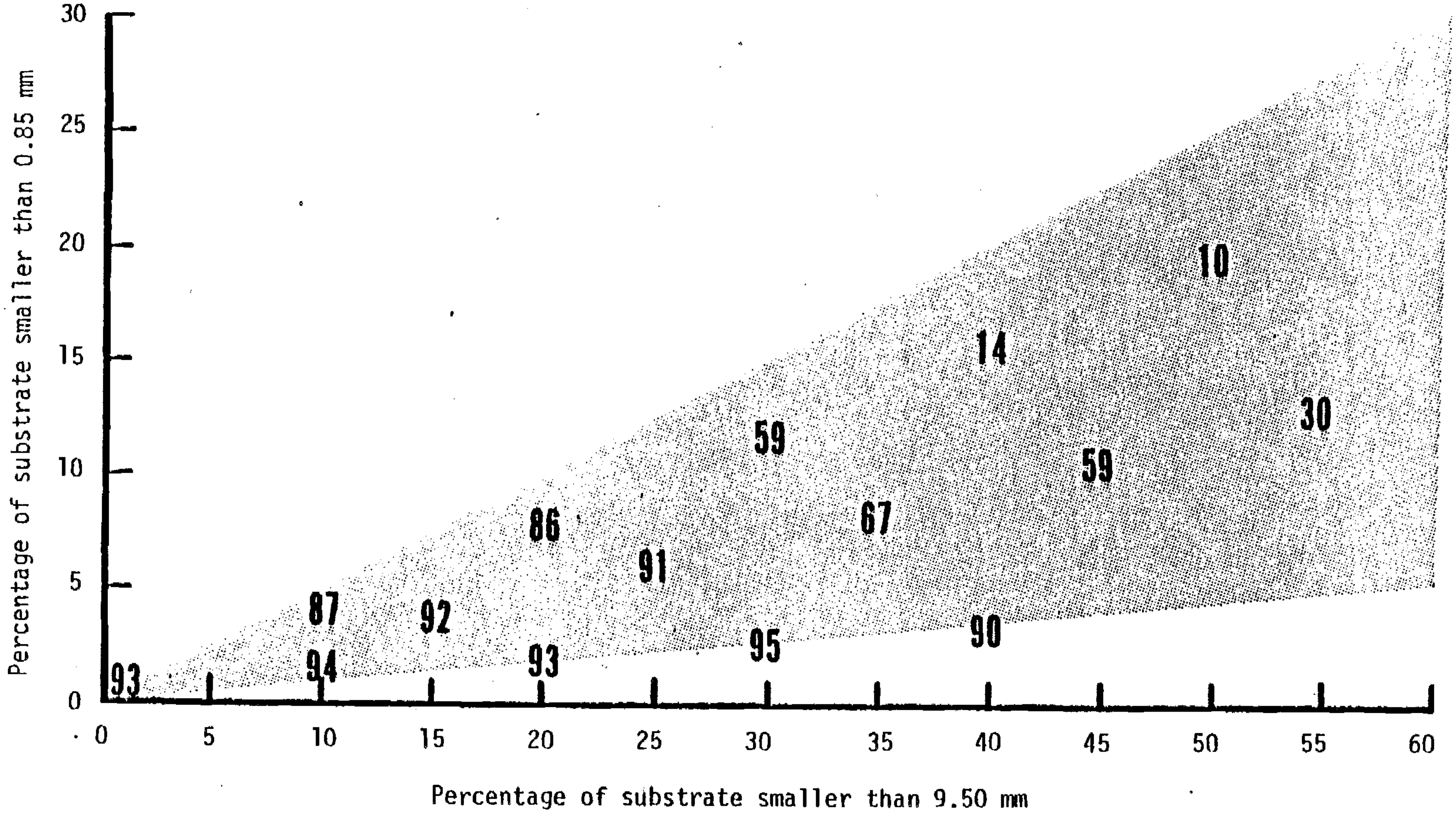

Figure 8. Average percent survival of steelhead embryos. Placement of survival percentages corresponds to gravel mixture embryos were buried in.

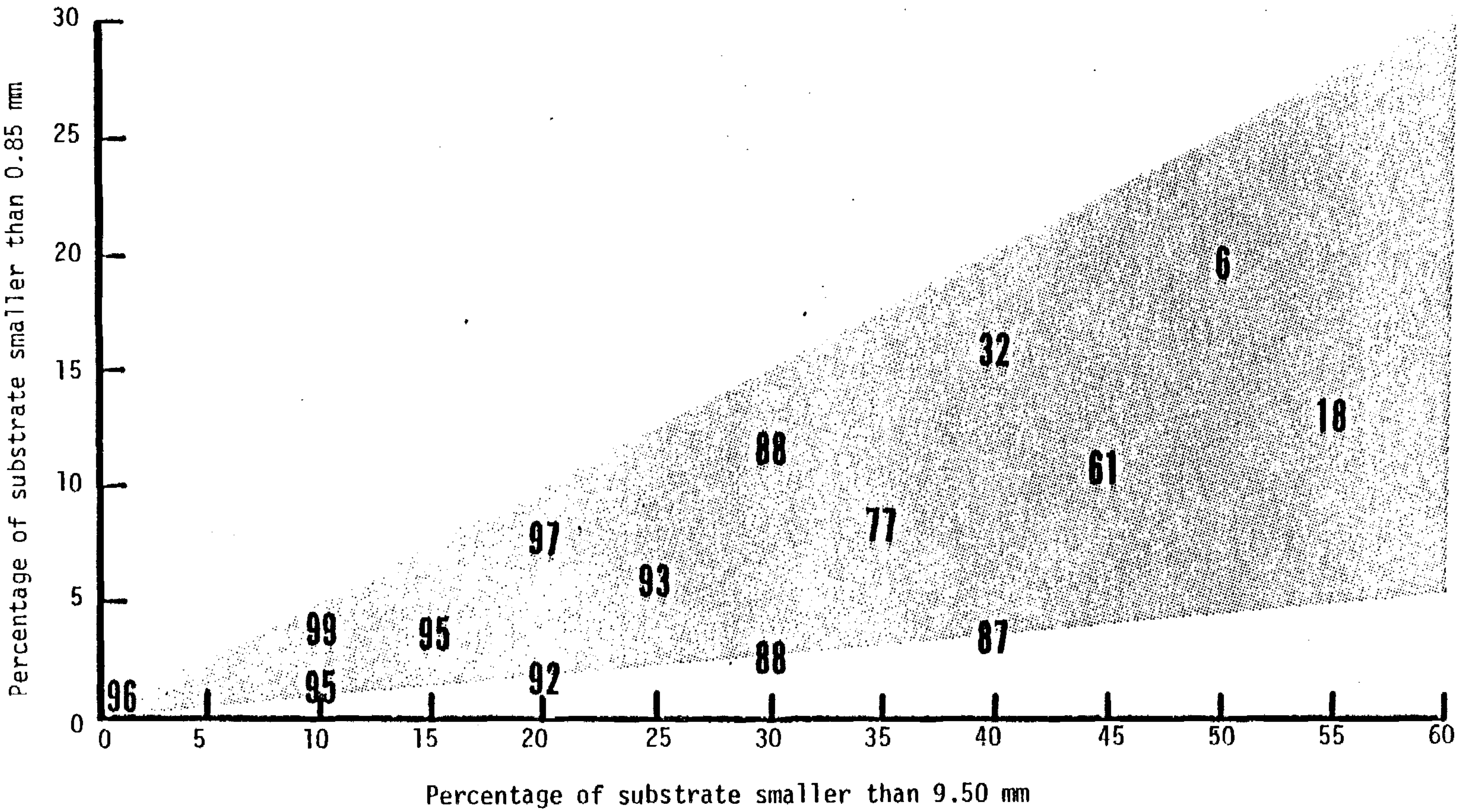

Figure 9. Average percent survival of chinook salmon embryos. Placement of survival percentages corresponds to gravel mixture embryos were buried in.

experiments. For most gravel mixtures, predictions of steelhead embryo survival using the equation were close to survival percentages observed in the incubation experiment (Table 3). Observed steelhead survival values were in all cases within the 90 and 95 percent confidence ranges for equation predictions (Table 3).

Predictions for chinook salmon embryo survival using the chinook salmon equation were also close to observed values, reflecting the equation's high R^2 value (Table 4). In all instances, observed chinook salmon embryo survival values were within the 90 and 95 percent confidence ranges for equation predictions (Table 4). Predicted survival values less than zero or greater than 100 were unrealistic and were interpreted as 0 or 100 percent, respectively (Tables 3 and 4).

Using the equation relating steelhead embryo survival to gravel size composition, steelhead embryo survival was predicted for a wide range of spawning substrate. A "three-dimensional" graph was used to visualize the relationship between gravel size composition and equation predictions for steelhead embryo survival (Figure 10). The equation for steelhead predicted the same embryo survival for all gravel mixtures along any single line in Figure 10. For example, the equation predicted 80 percent survival in gravel mixtures corresponding to points B and C (Figure 10). As in Figure 3, points A and B in Figure 10 represent two different gravel mixtures with the same "percent fines" and geometric mean. The equation developed for steelhead embryo survival predicted 20 and 80 percent embryo survival in gravel mixtures corresponding to points A and B, respectively (Figure 10). Survival of steelhead embryos could vary widely in gravel mixtures with the same "percent fines" and geometric mean.

Table 3. Observed values, equation predictions, and confidence intervals for steelhead survival-to-emergence in gravel mixtures. Survival values are expressed as percentages.

Gravel mixture label	Observed steelhead embryo survival	Predicted survival-to-emergence using equation	Equation confidence range 95% low	Equation confidence range 95% high	Equation confidence range 90% low	Equation confidence range 90% high
0:0	93	95	74	115	78	112
10:4	87	91	70	111	74	108
20:8	86	79	59	100	62	96
30:12	59	60	40	81	43	77
40:16	14	33	12	54	16	50
50:20	10	-1	-23	20	-19	17
15:4	92	90	70	111	73	107
25:6	91	82	62	102	65	99
35:8	67	70	50	90	53	87
45:10	59	54	33	74	37	71
55:13	30	33	11	55	15	51
10:1	94	95	74	115	77	112
20:1	93	94	74	115	77	111
30:2	95	94	73	115	77	111
40:3	90	93	71	115	75	111

Table 4. Observed values, equation predictions, and confidence intervals for chinook salmon survival-to-emergence in gravel mixtures. Survival values are expressed as percentages.

Gravel mixture label	Observed chinook salmon embryo survival	Predicted survival-to-emergence using equation	Equation confidence range 95% low	95% high	90% low	90% high
0:0	96	93	75	112	78	109
10:4	99	102	84	120	87	117
20:8	97	97	78	115	82	112
30:12	88	78	60	97	63	94
40:16	32	47	28	65	32	62
50:20	6	2	-17	21	-14	18
15:4	95	98	80	116	83	113
25:6	93	91	73	109	76	106
35:8	77	76	58	94	61	91
45:10	61	53	35	71	38	68
55:13	18	22	3	40	6	37
10:1	95	95	77	113	80	110
20:1	92	94	76	112	79	109
30:2	88	91	73	109	76	106
40:3	87	85	67	103	70	100

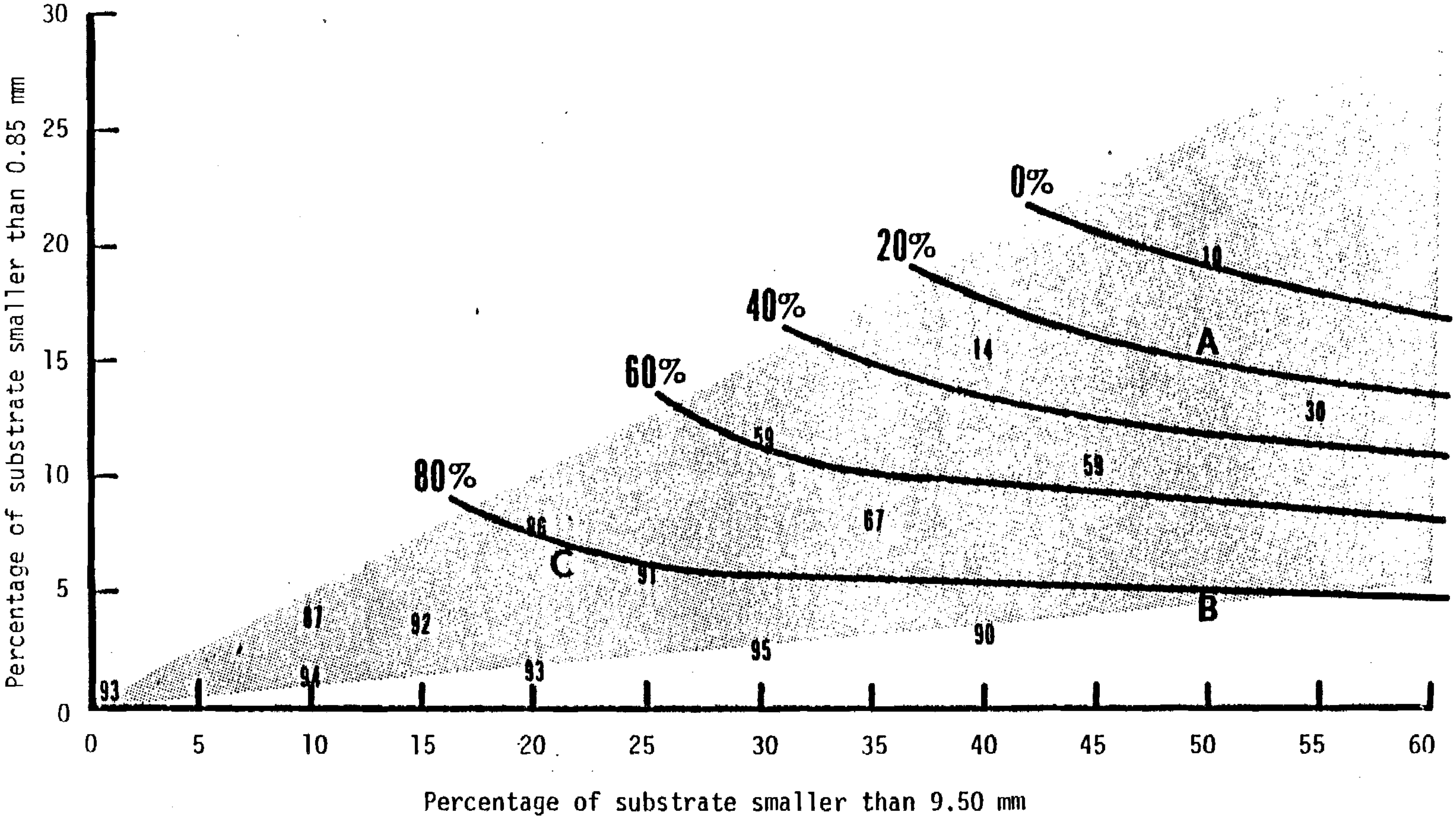

Figure 10. Bands showing steelhead embryo survival predictions (80%, 60%, 40%, 20%, 0%) overlying range of natural spawning gravel. Scattered numbers are percent survival values from laboratory incubation tests.

The equation relating chinook salmon embryo survival to gravel size composition produced a similar pattern of embryo survival overlaying the range of natural spawning substrate (Figure 11). For gravel mixtures along any single line in Figure 11, the chinook salmon equation predicted equal survival of chinook salmon embryos ("eyed" stage to emergence).

Comparison of the patterns of "lines of equal survival" for steelhead (Figure 10) and chinook salmon (Figure 11) revealed how various particle sizes affected survival of steelhead and chinook salmon embryos. "Lines of equal survival" for steelhead were almost horizontal, implying that steelhead embryo survival was strongly related to material less than 0.85 mm and only weakly related to the percentage of the substrate finer than 9.50 mm. "Lines of equal survival" for chinook salmon embryos (Figure 11) were neither vertical or horizontal. Compared to steelhead, this demonstrated that chinook salmon embryo survival was more strongly affected by material from 0.85 to 9.50 mm.

As noted in the introduction, "percent fines" is the most commonly used measure of spawning gravel quality. Numerous researchers have tried to isolate which particle sizes are most harmful to salmonid embryos by analyzing which particle size classes have the strongest inverse relationship with embryo survival. I used this approach to gain additional insights into how steelhead and chinook salmon embryos responded to different particle sizes.

In the incubation experiments with steelhead, linear relationships between particle size classes and survival-to-emergence were strongest for particle size classes smaller than 1.70 mm (Table 5). If steelhead embryo survival was related to a single particle size (e.g. "percent

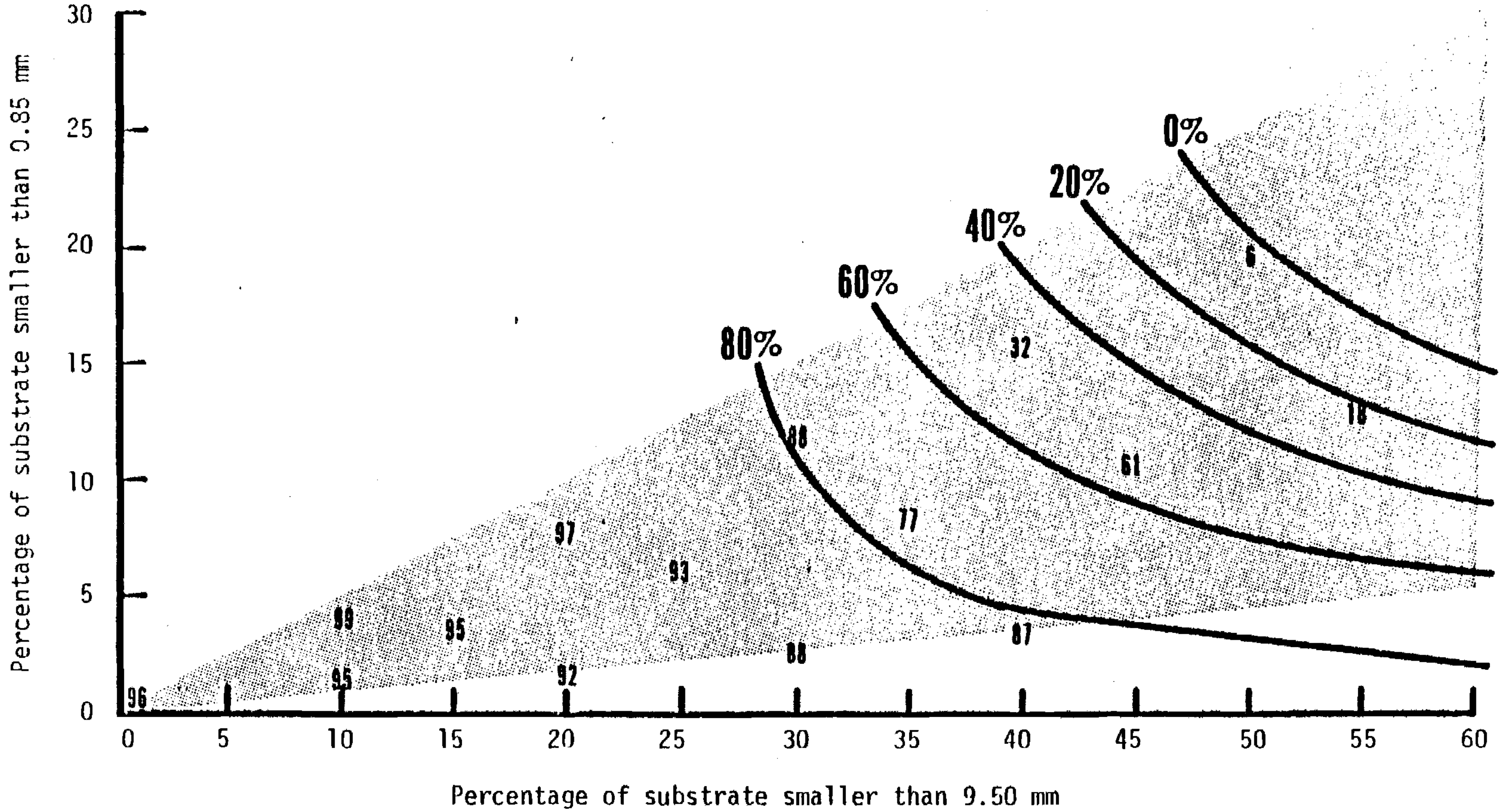

Figure 11. Bands showing chinook salmon embryo survival predictions (80%, 60%, 40%, 20%, 0%) overlying range of natural spawning gravel. Scattered numbers are percent survival values from laboratory incubation tests.

Table 5. R-squared values for linear regressions between individual particle size classes and survival of steelhead and chinook salmon embryos.

	R-squared values	
Particle size class[a]	Steelhead	Chinook salmon
<9.50 mm	0.56	0.66
<6.35 mm	0.62	0.70
<4.76 mm	0.71	0.74
<1.70 mm	0.86	0.74
<0.85 mm	0.86	0.70
<0.42 mm	0.86	0.71

[a]Particle size class defined as percentage of substrate smaller than given sieve size.

fines"), a particle size class of 1.70 mm or smaller would provide the best relationship.

Individual particle size classes were also correlated with chinook salmon embryo survival using linear regressions (Table 5). If chinook salmon embryo survival was correlated with a single size class, a particle size class of 4.76 mm or smaller would provide the best relationship. Material from 1.70 to 4.76 mm in diameter was more harmful to chinook salmon embryos than steelhead embryos.

The ability of steelhead embryos to tolerate a finer particle size class of material than chinook salmon was not surprising considering the observations of Bjornn (1969) and Hall and Lantz (1969). In gravels with a high percentage of sand, Bjornn (1969) reported that steelhead fry emerged more readily than larger chinook salmon fry. In a similar study, Hall and Lantz (1969) placed steelhead and coho salmon fry in various mixtures of sand and gravel. Steelhead were able to emerge through the restricted gravel interstices better than the larger coho salmon fry. Relative to embryo size, void spaces in identical gravel mixtures would be larger for steelhead than chinook salmon. The smaller size of steelhead embryos inherently allows them to tolerate smaller particles in the spawning substrate than chinook salmon.

In most gravel mixtures tested, chinook salmon embryos survived at higher percentages than steelhead embryos (Table 2). This unexpected result seemingly contradicts evidence that smaller embryos (i.e. steelhead) survive better than larger embryos (i.e. chinook salmon) in gravels with the same level of fine sediment.

The use of "eyed" chinook salmon embryos probably increased chinook salmon survival relative to survival if newly fertilized ("green") embryos had been used. Bjornn (1969) placed "green" steelhead trout and chinook salmon embryos in gravel mixtures along with swim-up fry of both species. In almost all gravel mixtures tested, swim-up fry emerged at a higher rate than "green" embryos. In the experiments I conducted, chinook salmon embryo survival was enhanced because embryos were at an advanced stage of development when placed in gravel mixtures.

If "green" chinook salmon embryos had been used instead of "eyed" embryos in these experiments, chinook salmon survival would have probably been lower in most gravel mixtures; equation predictions for chinook salmon survival would have also been lower. To relate gravel size composition to newly fertilized chinook salmon embryos instead of "eyed" embryos, the "lines of equal survival" in Figure 11 should be shifted towards the origin. Unfortunately, I have no way to quantify such a shift.

Percent survival of steelhead and chinook salmon embryos was also compared to the geometric mean (Figure 12) and Fredle number (Figure 13) of each experimental gravel mixture. Curves showing the relationships between geometric mean, Fredle number, and embryo survival were drawn by eye to best fit experimental data (Figures 12 and 13). Statistical analyses of these data were not done.

Steelhead and chinook salmon embryos both had survival rates of approximately 90 percent when the geometric mean exceeded 10 mm. As geometric means of gravel mixtures decreased below 10 mm, percent survival dropped precipitously (Figure 12). Using a number of studies, Shirazi and Seim (1979) showed that salmonid embryo survival was generally less than 90 percent unless the geometric mean exceeded 15 mm. In gravels with identical geometric means, I observed higher survival rates than those reported by Shirazi and Seim (1979). As shown earlier, gravel mixtures can have much different size compositions even with the same geometric mean. Therefore, the discrepancy between survival values presented here and those reported by Shirazi and Seim (1979) could have resulted from differences in gravel size composition.

The relationship between Fredle numbers and embryo survival resembled the relationship between geometric means and survival. Embryo survival was about 90 percent when Fredle numbers exceeded 5; survival was decreased as Fredle numbers decreased below 5 (Figure 13).

Geometric means and Fredle numbers both correlated well with embryo survival (Figures 12 and 13). However, the new method of describing spawning gravel size composition I have developed has advantages over both geometric mean and Fredle number as a measure of spawning gravel quality.

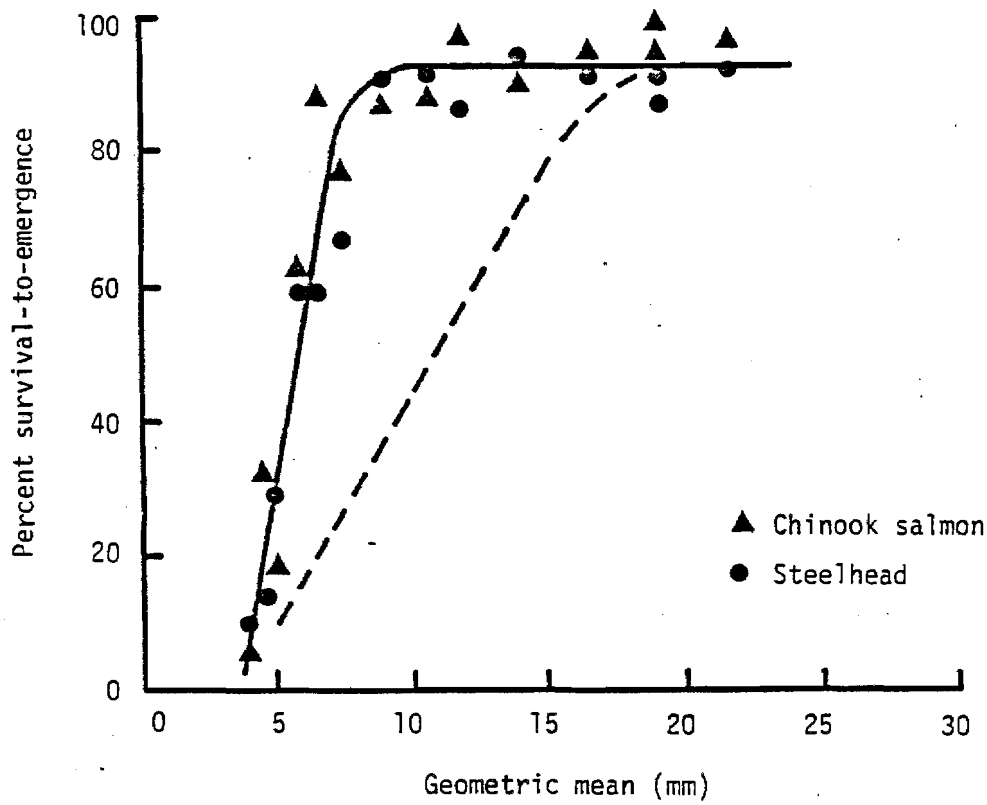

Figure 12. Relationship between geometric mean and steelhead and chinook salmon embryo survival. Solid line fitted by eye to data from laboratory tests. Broken line represents survival curve presented by Shirazi and Seim (1979) for other data.

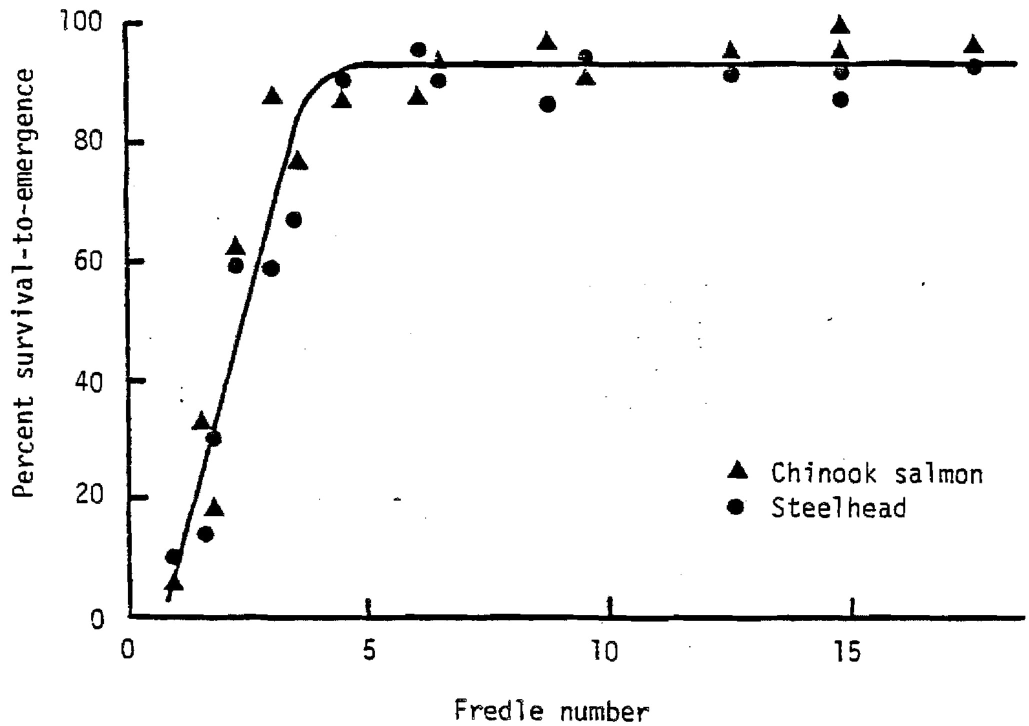

Figure 13. Relationship between Fredle numbers and embryo survival-to-emergence. Curve fitted by eye to data from laboratory experiments.

As demonstrated by points A and B in Figure 3, the usefulness of geometric mean is limited because gravel mixtures with the same geometric mean can have different size compositions.

Fredle numbers theoretically provide a good measure of spawning gravel size composition but are not as convenient as the method I developed. When increased deposition of fine sediment is anticipated in spawning areas, predicted changes in spawning substrate are usually expressed as changes in the percentage of the substrate smaller than specified particle sizes. Predictions of this nature could be directly used in the equations I have developed for embryo survival, whereas the use of Fredle numbers would be more complicated.

Size of Emergent Fry

In the range of gravel mixtures tested, steelhead fry lengths and weights varied little. The smallest fry averaged only 0.8 mm and 22 mg smaller than the largest (Table 6). Although the trend was indistinct and not statistically significant (alpha = 0.05), steelhead fry emerging from gravels with high percentages of fine material were generally smaller than fry from gravels containing low percentages of fine sediment (Table 7). Fry emerging from gravel mixture 55:13 weighed significantly less (alpha = 0.05) than all other steelhead fry (Table 7). There was no significant relationship (alpha = 0.05) between chinook salmon fry size and gravel size composition (Table 8).

Somewhat in contrast with my results, Phillips et al. (1975) found that coho salmon fry emerging from gravels with high percentages of sand were smaller than those from gravels with low percentages of sand. In the

Table 6. Average lengths and weights of steelhead and chinook salmon fry after emergence from experimental gravel mixtures. Averages are for 50 fry unless otherwise noted.

Gravel mixture label	Steelhead Length (mm)	Steelhead Weight (mg)	Chinook salmon Length (mm)	Chinook salmon Weight (mg)
0:0	27.0	208	30.8	348
10:4	26.9	211	31.3	369
20:8	26.9	210	31.0	362
30:12	26.4	203	30.9	355
40:16	26.4	203	30.8	343
50:20	26.5	203	30.8[a]	335[a]
15:4	26.8	206	30.8	338
25:6	26.9	214	31.2	356
35:8	26.9	208	31.0	358
45:10	26.7	210	30.2	328
55:13	26.3	193	30.5	344
10:1	27.1	207	31.0	351
20:1	27.1	215	30.6	339
30:2	27.0	208	30.9	352
40:3	26.6	210	30.7	345

[a]Average of 17 chinook salmon fry.

Table 7. Duncan's multiple range test results for steelhead lengths and weights. Means with the same grouping were not significantly different (alpha = 0.05).

Gravel mixture label	Mean length (mm)	Grouping
20:1	27.1	A
10:1	27.1	A
30:2	27.0	A
0:0	27.0	A
20:8	26.9	A B
25:6	26.9	A B
35:8	26.9	A B
10:4	26.9	A B
15:4	26.8	A B
45:10	26.7	A B C
40:3	26.6	B C D
50:20	26.5	B C D
30:12	26.4	C D
40:16	26.4	C D
55:13	26.3	D
	Mean weight (mg)	
20:1	215	A
25:6	214	A
10:4	211	A B
20:8	210	A B
40:3	210	A B
45:10	210	A B
30:2	208	A B
0:0	208	A B
35:8	208	A B
10:1	207	A B
15:4	206	A B
50:20	203	B
30:12	203	B
40:16	203	B
55:13	193	C

Table 8. Duncan's multiple range test results for chinook salmon lengths and weights. Means with the same grouping were not significantly different (alpha = 0.05).

Gravel mixture label	Mean length (mm)	Grouping
10:4	31.3	A
25:6	31.2	A B
10:1	31.0	A B C
35:8	31.0	A B C
20:8	31.0	A B C
30:2	30.9	A B C
30:12	30.9	A B C
15:4	30.8	A B C D
40:16	30.8	A B C D
50:20	30.8	A B C D
0:0	30.8	A B C D
40:3	30.7	B C D
20:1	30.6	B C D
55:13	30.5	C D
45:10	30.2	D
	Mean weight (mg)	
10:4	369	A
20:8	362	A B
35:8	358	A B
25:6	356	A B
30:12	355	A B C
30:2	352	A B C
10:1	351	A B C
0:0	348	A B C
40:3	345	A B C
55:13	344	A B C
40:16	343	A B C
20:1	339	B C
15:4	338	B C
50:20	335	B C
45:10	328	C

same tests (Phillips et al. 1975), steelhead fry size was similar in all gravel mixtures. Koski (1966) found that coho salmon fry size was inversely related to the amount of fine sediment in the substrate. In a later study, Koski (1975) reported that chum salmon fry from gravels with high percentages of sand were up to 3.0 mm shorter than fry from gravels with low percentages of sand. However, Koski (1975) observed several discrepancies in this trend and the relationship was not consistent.

The effect of fine sediment on salmonid fry size remains unresolved. Koski (1975) speculated that selective mortality of larger embryos and increased environmental stress could both result in reduced average fry size in gravels containing high percentages of fine sediment. Selective entombment of larger fry would occur because smaller fry would have a better chance of squirming through restricted gravel interstices during emergence. Koski (1975) also suggested that stress caused by fine sediment increased the metabolic rate of salmonid embryos, resulting in a loss of growth.

Whether or not excessive deposition of fine sediment in spawning gravel areas reduces salmonid fry size enough to affect later survival is unclear. If fine sediment does substantially reduce fry size, it is probable that the smaller fry have a disadvantage after emergence. Relatively small fry might experience higher mortality due to selective predation (Parker 1971) or competition with larger fry of the same or similar species.

Timing of Fry Emergence

Several researchers (Koski 1975, Phillips et al. 1975) observed that fry emergence was accelerated in gravels containing large amounts of fine sediment, sometimes to the point where fry emerged before completely absorbing the yolk sac. I observed the same phenomena. In gravels with large proportions of fine material, steelhead and chinook salmon fry tended to emerge before yolk sac absorption was complete. Fry emerging from gravels with low percentages of fine sediment emerged only after total absorption of the yolk sac. This phenomena was not sufficiently quantified for a statistical analysis.

Deposition of excessive amounts of fine sediment in spawning gravels may result in embryo stress and cause early emergence of salmonid embryos (Bams 1969). Fry that emerge prematurely would be more susceptible to predation than fully developed fry. The residual yolk sac would impair their swimming ability (Thomas et al. 1969, Koski 1975) and their relatively small size could increase predation (Parker 1971). In some species, a bright red or orange yolk sac probably makes premature fry particularly vulnerable to predation.

SUMMARY AND CONCLUSIONS

The effects of fine sediment deposition on salmonid embryo survival must be understood and quantified. In the past, efforts to correlate gravel size composition with embryo survival have been hampered by inadequate measures of spawning gravel quality (i.e. "percent fines" and geometric mean).

A single parameter which completely describes gravel mixtures does not exist. In spawning gravels, however, the size composition of material smaller than 25.4 mm in diameter follows a consistent pattern. Because of the lognormal distribution of particle sizes in this range, the size composition of material smaller than 25.4 mm can be closely approximated knowing only two points in the cumulative particle size distribution. The two particle size classes which best reflect spawning gravel size composition are the percentage of the substrate smaller than 9.50 mm and the percentage smaller than 0.85 mm.

By comparing steelhead and chinook salmon embryo survival to these two particle size classes in laboratory experiments, embryo survival was indirectly related to the entire range of material less than 25.4 mm in diameter. This particle size range includes all particle sizes that are potentially harmful to incubating salmonid embryos.

In laboratory experiments, changes in substrate size composition accounted for 90 to 93 percent of the variation in embryo survival. Equations were developed to predict steelhead and chinook salmon embryo survival in a wide range of gravel mixtures. Because "eyed" chinook salmon embryos were used instead of newly fertilized eggs, survival predictions generated by the chinook salmon equation were probably higher than survival would be in natural redds.

Correlations of individual particle size classes and embryo survival indicated that material from 1.70 to 4.76 mm in diameter was less harmful to steelhead than chinook salmon embryos. Apparently, the smaller size of steelhead embryos allowed them to tolerate smaller particles in the spawning substrate than chinook salmon embryos.

The effect of gravel size composition on emergent fry size was not clear. Steelhead fry emerging from gravels with low percentages of fine sediment were slightly larger than those from gravels containing high percentages of fine material. There was little variation in chinook salmon fry size throughout the range of experimental gravel mixtures.

A large percentage of steelhead and chinook salmon fry from gravels containing high percentages of fine sediment emerged before complete yolk sac absorption. In streams, these premature emergents would be susceptible to predation because of their impaired swimming ability, smaller size, and the bright red or orange color of the yolk sac.

The effects of fine sediment on fry size and timing of emergence seemed minor compared to the effects of gravel size composition on embryo survival.

The most important outcome of my research was the development of a new method for quantifying the effects of substrate size composition on salmonid embryo survival. By considering two particle sizes (i.e. 9.50 mm and 0.85 mm), salmonid embryo survival was implicitly related to a continuum of particle sizes in natural gravel mixtures. This approach is much better than trying to isolate which particular particle size classes are harmful to incubating salmonid embryos.

Of secondary importance was the development of equations which related steelhead and chinook salmon embryo survival to gravel size composition. Because both equations were developed in a laboratory environment, predictions of embryo survival generated by the equations may be inaccurate when applied to field conditions. The experimental gravel mixtures contained only small amounts of organic material. In spawning areas where organic material was abundant, survival of salmonid embryos would probably be lower than predicted by the equations I developed. Because salmonids disturb the spawning substrate in the process of redd digging, the percentage of fine material in the substrate after egg deposition is usually less than the percentage of fine sediment before spawning. The equations presented do not consider the ability of salmonids to change the size composition of gravel in spawning areas. For reasons outlined above, embryo survival in natural situations may be different than equation predictions.

Although embryo survival in streams may not exactly parallel equation predictions, the equations should provide a good index of relative changes in survival. As an example, suppose the steelhead equation predicts that embryo survival in a stream would decrease from 80 to 60 percent as a result of increases in fine sediment in the spawning substrate. Even if survival was not 80 percent before increases in fine sediment occurred, the 20 percent reduction in embryo survival predicted by the equation should be close to the decrease in embryo survival in the stream. If embryo survival was originally 50 percent instead of 80 percent, survival of steelhead embryos should still decrease by 20 percent as a result of increases in fine sediment.

Predicting the consequences of increased fine sediment deposition in spawning areas is an important application of my research. In watersheds affected by human activities (e.g. road-building), sediment transport models are sometimes used to predict changes in stream substrate size composition. In the past, it has been difficult to quantify how salmonid embryo survival would be affected by predicted changes in stream substrate. The relationships developed between embryo survival and gravel size composition in this thesis could be used to fill this void. In combination with existing sediment transport models, the equations presented could be used to predict the effects of human activities on steelhead and chinook salmon embryo survival.

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