Ref ID: 8428

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Reply To: 1630

Date: January 2, 1990

Mr. Glenn Phillips
Water Pollution Control Office
Cogswell Bldg., Room A-206
Helena, MT 59620

Dear Mr. Phillips:

I have finally finished my doctorate, thus I can finally send you the information you requested last July. Chapters II through IV have been published in the Canadian Journal of Fisheries and Aquatic Sciences (II) and the Transactions of the American Fisheries Society (III, IV). Chapter V is being reviewed for publication in Northwest Science, and Chapters VI and VII are to be submitted to CJFAS and the North American Journal of Fisheries Management, respectively. If you would prefer the published papers (which differ slightly from the dissertation chapters), please let me know. If and when the other chapters are published, I would be happy to send you those as well.

If you'd like any other information, feel free to write or call (307) 742-6621.

Sincerely,

MICHAEL K. YOUNG
Research Fisheries Biologist

Young, Michael K., Effect of Substrate Composition on the Survival to Emergence of Colorado River Cutthroat Trout and Brown Trout, Ph.D., Department of Zoology and Physiology, December 1989.

Various physical, chemical and biological factors influence the survival of trout embryos during their incubation in the substrate. Substrate composition directly or indirectly affects these factors and the intragravel environment. My objectives were to develop models to assess survival to emergence for Colorado River cutthroat trout and brown trout from knowledge of substrate composition. First, I considered including permeability as a variable in the models. But using the MARK VI standpipe to measure permeability in a substrate-filled flume under constant-flow conditions, I found significant differences in permeability readings made by different people at four of five sites. The measurement of substrate composition also posed problems. Part of this difficulty included the failure of biologists to select a single measure of substrate composition and to use statistically valid techniques to relate it to survival to emergence. I questioned Chapman's (1988) conclusion that the fredle index should be the preferred measure of substrate composition. Reanalysis of the data used by Chapman led me to suggest the geometric mean particle size as an appropriate statistic. With data obtained from laboratory experiments, I regressed survival to emergence of brown trout on several measures of substrate composition and found that the geometric mean particle size accounted for the greatest proportion of variation in survival to emergence. Furthermore, I noted that as the geometric

mean of a substrate decreased, the days to first emergence decreased and the length of the emergence interval increased. The geometric mean was also the best predictor of survival to emergence for Colorado River cutthroat trout. Using field data, I discovered that the percentage of sediment less than 0.85 mm was more sensitive to changes in substrate composition in streams than was the geometric mean. Substrate samples are collected using a variety of techniques, so I compared samples collected by two freeze-core samplers, a McNeil sampler, and a shovel, and found that samples collected by different methods significantly differed from test substrates for individual particle sizes. The McNeil sampler produced samples that approximated the test substrate composition more frequently than did the other devices.

EFFECT OF SUBSTRATE COMPOSITION ON THE SURVIVAL TO EMERGENCE OF COLORADO RIVER CUTTHROAT TROUT AND BROWN TROUT

by
Michael K. Young

A dissertation
submitted to the Department of Zoology and Physiology
and the Graduate School of the University of Wyoming
in Partial Fulfillment of Requirements for the Degree of

DOCTOR OF PHILOSOPHY
in
ZOOLOGY AND PHYSIOLOGY

Laramie, Wyoming
December, 1989

TO THE OFFICE OF THE GRADUATE SCHOOL:

The members of the Committee approve the dissertation of Michael K. Young presented on December 8, 1989.

Wayne A. Hubert, Chairman

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ACKNOWLEDGMENTS

I thank P. Anderson, J. Bobbitt, L. Dolan, R. Grost, P. Guenther, C. Klingen, D. Lanning, B. Rhodine, and S. Wolff for assisting with the laboratory and field studies, L. McDonald for statistical advice, and T. Annear, H. Bergman, T. Bjornn, M. Bozek, D. Chapman, F. Everest, P. Eschmeyer, W. Hubert, K Koski, R. Marston, F. Rahel, D. Reiser, N. Schmal, M. Stone, T. Wesche, and R. Wiley for reviewing all or portions of the dissertation.

I also thank H. Bergman of the University of Wyoming Department of Zoology and Physiology, V. Hasfurther of the University of Wyoming Department of Civil Engineering, and J. Dodd of the University of Wyoming Department of Range Management for making research facilities available to me. Thanks also to C. Goertler of the Wyoming Water Research Center and D. Logan of the University of Wyoming Department of Civil Engineering for designing and constructing the freeze-core apparatus.

Special thanks to J. Hall for contributing data from Phillips et al. (1975) that was used in Chapter 3.

Special thanks also to my advisors, W. Hubert and T. Wesche, and to the rest of my committee, H. Bergman, R. Marston, F. Rahel, and R. Wiley, for valid criticism and sound advice.

Funding for this project was provided by the Wyoming Game and

Fish Department, the U.S. Forest Service, the U.S. Fish and Wildlife Service, and the Wyoming Water Research Center.

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CHAPTER I

INTRODUCTION

Various physical, chemical and biological factors influence the survival of trout embryos during their incubation in the substrate (Reiser and Bjornn 1979). Physical factors include intragravel water flow, substrate composition, porosity, permeability, temperature, and redd disturbance. The key chemical factor is dissolved oxygen; however, ammonia, pH, and heavy metals are also important. Biotic interactions include predation, redd superimposition, and the oxygen demand of other stream organisms. The introduction of sediment to a stream channel alters the intragravel conditions by affecting all of the aforementioned parameters.

Sediment generally has been regarded as detrimental to the survival of trout embryos (Cordone and Kelly 1961, but see Everest et al. 1987). Increases in fine sediment have led to decreases in porosity, permeability, and apparent water velocity in stream substrates (Reiser and White 1981, Sowden 1983). Field and laboratory studies have demonstrated that as the proportion of fine sediment increases, the survival to emergence of trout embryos decreases (Phillips et al. 1975, Bjornn 1969, Hausle and Coble 1976, Tappel and Bjornn 1983).

Incubation of salmonid embryos occurs in two roughly defined

stages: eggs and alevins. The egg stage lasts from spawning to hatching. The alevin stage begins at hatching and continues until the juvenile fish has emerged from the substrate, usually coinciding with the absorption of the yolk sac (Phillips 1971). Both stages are subject to mortality from unfavorable substrate conditions caused by sediment. However, sediment impacts vary with the stage of development.

Both dissolved oxygen concentration and intragravel flow directly determine survival-to-emergence (McNeil 1966, Iwamoto et al. 1978). Coble (1961) suggested survival would be higher in areas of high intragravel flow compared to areas of low flow, even if both contained identical concentrations of dissolved oxygen. Perhaps the rate of oxygen delivery to the egg periphery is the key determinant of survival (Daykin 1965, Witzel and MacCrimmon 1983). Since increased levels of sediment decrease intragravel flow (Reiser and White 1981), this delivery rate would be decreased.

The survival and condition of alevins are also dependent on oxygen and intragravel flow (Shumway et al. 1964, Witzel and MacCrimmon 1981). Furthermore, alevins must migrate through the substrate to reach the surface waters. If insufficient interstitial space exists in the substrate, the alevins will become entrapped and starve. Decreases in substrate porosity have been linked to increases in sediment content. Decreases in alevin survival have also been attributed to increases in fine sediment (Bjornn 1968).

Numerous attempts have been made to model survival to emergence of salmonid embryos (Shirazi and Seim 1981, Tappel 1981, Stowell et

al. 1983). However, these models have suffered from several drawbacks. Shirazi and Seim (1981) suggested the use of the geometric mean particle size of the substrate to determine survival. However, different substrates with various proportions of different size classes of material can possess the same geometric mean (Lotspeich and Everest 1981). Tappel (1981) generated curves explaining over 90% of the variation in survival to emergence in his experiments with steelhead and chinook salmon. However, his test substrates and test statistic did not represent natural redds (Everest et al. 1982). Finally, the model of Stowell et al. (1983) relied on the percentage of material below 6.35 mm to determine survival. This characteristic suffered from the same problem as the geometric mean i.e., many substrates could have identical proportions of material below 6.35 mm, yet the distribution of sizes both above and below this size may vary. Furthermore, much of the variance in survival was not explained by this variable.

Most models have suffered from an oversimplification of the conditions present in a redd. Note that they all rely solely on measures of substrate, yet the importance of dissolved oxygen and intragravel flow have been demonstrated in the laboratory and in the field (Alderdice et al. 1958, Coble 1961, Silver et al. 1963, McNeil 1966). Sowden and Power (1985) reported no correlation between survival to emergence and substrate measures, but found significant correlations between survival and intragravel flow and dissolved oxygen. However, the technology to measure intragravel dissolved oxygen and intragravel flow has presented problems, especially in

conjunction with attempts to validate these models in the field (R. Grost, Hosey and Associates, Seattle, Washington, personal communication).

SPECIES OF INTEREST

The Cheyenne Water Project has diverted water from many streams in the North Fork Little Snake River drainage (Jespersen 1981). On several occasions, large amounts of sediment have been introduced to the streams in this watershed due to road construction, diversion failures, and channel rerouting (R. Schmal, Medicine Bow National Forest, Laramie, Wyoming, personal communication). This drainage contains the largest known population of genetically pure Colorado River cutthroat trout (Oncorhynchus clarki pleuriticus) in Wyoming (Binns 1977). This subspecies has a very restricted range in Colorado and Wyoming (Behnke and Zarn 1976) and has been recognized as a species of special concern by the Wyoming Game and Fish Department (M. Stone, Wyoming Game and Fish Department, Cheyenne, Wyoming, personal communication). Additional mortality caused by sediment introductions is likely to cause further declines in the populations of this rare subspecies.

The status of brown trout (Salmo trutta) populations is also of concern, due to the recreational popularity of this species (R. Wiley, Wyoming Game and Fish Department, Laramie, Wyoming, personal communication). Numerous streams containing this species across Wyoming are affected by land uses, such as logging, livestock grazing, mining, or road construction, which increase sediment loads.

PROJECT OBJECTIVES

There were two primary goals for this project. The first was the development of a field-validated model predicting the survival to emergence of Colorado River cutthroat trout. The second was the development of a laboratory model predicting the survival-to-emergence of brown trout. The following chapters present my work that addressed these goals. The chapters focus on laboratory and field experiments of survival to emergence and the sampling and measuring of characteristics of the intragravel environment.

The importance of intragravel flow in affecting survival to emergence is evident. One index of intragravel flow is permeability; this has been measured using a bicycle pump to suck water through a perforated standpipe (Terhune 1958). In Chapter 2, I evaluate the variation in measurements of permeability when using the MARK VI standpipe, which I found to produce significantly different results when used by different people. To reduce the variability and bias associated with this technique, I replaced the bicycle pump with an electric vacuum pump capable of producing constant vacuum pressure (Appendix B). Though the variation in permeability measurements declined, substrate composition alone was a better predictor of survival to emergence than was permeability.

The inadequacy of permeability measurements, as well as problems associated with direct measures of intragravel water velocity (R. Grost, Hosey and Associates, Seattle, Washington, personal communication), led me to focus on the effects of substrate composition on survival to emergence (Grost et al. 1988).

Oversimplification has led to the creation of unrealistic models that attempt to predict survival to emergence (Stowell et al. 1983). Chapman (1988) believed the problem was largely due to the lack of understanding of redd structure. Based on analyses of previously published data, he proposed measuring a certain set of variables in egg pockets of redds. In Chapter 3, I present data suggesting that biologists have overlooked a number of variables that may influence predictions of survival to emergence. Furthermore, through reanalyses of the data used by Chapman, I reach different conclusions about how certain variables are related to survival to emergence.

A reduction in survival to emergence is only one potential consequence of concentrations of fine sediment in redds. For example, changes in emergence timing may increase the mortality of swim-up fry due to predation or to increased competition for suitable microhabitats. Chapter 4 explains the development of a laboratory model of survival to emergence for brown trout. In addition, I found that increasing amounts of fine sediment decreased the time to first emergence and increased the length of the emergence interval. I also observed no difference in the survival to emergence between two stocks of brown trout, though differences might become apparent in more extensive tests.

In Chapter 5, I compare several measures of substrate composition to determine which measure may be the best predictor of survival to emergence. For both brown trout and cutthroat trout, the geometric mean particle size accounted for the greatest proportion of the variation in survival to emergence. However, in analyses of two

sets of field data (contained in Appendices A and C), I found that the percentage of fine sediment less than 0.85 mm in diameter was more sensitive to changes in substrate composition.

Biologists have devised several techniques for sampling substrate composition in streams. Unfortunately, they have also assumed that these techniques produced samples of identical composition. Using laboratory tests, I demonstrate that four devices collected samples that significantly differed from one another and from the substrates from which they were collected (Chapter 6).

Chapter 7 presents a summary of my findings. Included are guidelines for designing a strategy to sample and measure substrate composition and to estimate its impact on survival to emergence.

The appendices contain information that did not directly address the goals of this project or were not substantial enough to warrant a separate chapter. The appendices include an assessment of the modification of substrate composition by spawning brook trout (Appendix A). I concluded that brook trout significantly altered substrate composition during spawning and that substrates containing eggs had less fine sediment than other locations both inside and outside the redd. Appendix B contains analyses of the relation between survival to emergence and permeability as measured by the electric vacuum permeability technique. I collected substrate samples from 41 egg pockets in redds of Colorado River cutthroat trout; these data are tabulated in Appendix C. Finally, I attempted to validate the laboratory models of survival to emergence of Colorado River cutthroat trout in 1988 and 1989. The results of these attempts are

given in Appendix D. Though largely unsuccessful, the tests revealed possible relations between certain aspects of substrate composition and survival to emergence, and they represent a starting point for future attempts to measure survival to emergence in the field.

To assist other researchers, the data sets for all experiments are available from myself, the Wyoming Cooperative Fish and Wildlife Research Unit, the Medicine Bow National Forest, and the Wyoming Game and Fish Department.

CHAPTER II

AN EVALUATION OF VARIATION IN PERMEABILITY MEASUREMENTS WHEN USING THE MARK VI STANDPIPE

The impact of fine sediment on salmonids has been studied for more than 60 years (Harrison 1923). In a relation that is not precisely understood, increases in fine sediment lead to decreases in the embryonic intragravel survival of numerous species (Cordone and Kelly 1961; Iwamoto et al. 1978). Among the suggested influences of fine sediment on spawning substrates is a reduction in permeability (Cooper 1965).

Permeability and hydraulic head directly determine intragravel water velocity, as demonstrated by Darcy's Law (Pollard 1955). Estimates of permeability have focused on two methods, laboratory estimates based on permeameters (McNeil and Ahnell 1964) and field estimates based on the use of standpipes (Gangmark and Bakkala 1958). Because the laboratory estimates require that substrate be removed from a streambed, the true permeability cannot be measured because the substrate loses its in-stream arrangement and compaction (Pollard 1955). Consequently in-stream measurement of permeability is preferred.

Wickett (1954), Pollard (1955), and Terhune (1958) developed the standpipe method to measure permeability of the spawning substrates of salmonids. By applying suction in the standpipe at a point 2.5 cm

below the surface of the water inside the pipe, the operator draws water through the perforated tip buried in the substrate. The volume of water collected is an index of the permeability of the substrate. Terhune (1958) demonstrated remarkable precision with this technique; coefficients of variation (c(v) = standard deviation/mean x 100) ranged from 1% to 5%. In contrast, Pollard (1955) found greater scatter about the predicted mean permeabilities, and his test substrates seemed much more representative of salmonid redds than those of Terhune.

After evaluating the available techniques for directly or indirectly evaluating intragravel flow in salmonid redds, Chapman and McLeod (1987) suggested that the standpipe measurement of permeability was the most desirable method. Previous studies of salmonid spawning habitats have relied on this method of permeability estimation (Wickett 1958; Turnpenny and Williams 1980). Several investigators (e.g. Coble 1961; Hansen 1975) failed to demonstrate a relation between permeability and survival of salmonid embryos to emergence, despite the theoretical support for this relation (Shumway et al. 1964; Vaux 1968). Few researchers have reported means and variances for their measurements, apparently assuming that single readings were adequate descriptors of permeability (Koski 1966; Reiser and Wesche 1977). My field observations of this technique made us less certain of its precision and led to the present laboratory study.

I wished to assess the variability in permeability estimates made by different people, at different sites, and through time under laboratory conditions. By replicating measurements by individuals at

given sites, I hoped to estimate the precision of this technique.

METHODS

I conducted the experiment from 0800 to 1200 on 18 May 1987. I used a 21.3-m flume, containing a substrate typical of that found in the Big Laramie River of southeastern Wyoming, in the Hydraulics Laboratory of the University of Wyoming Department of Civil Engineering. The materials and technique used for determining permeability closely followed those used by Terhune (1958). I drove a standpipe 25 cm into the substrate once at each of five randomly selected sites that had different substrate compositions and hydraulic characteristics (i.e. pools or riffles). Flow through the flume was 0.07 $m^3 \cdot s^{-1}$. Water temperature was held constant (at 18 °C), since changes in water temperature alter viscosity and hence permeability (Terhune 1958).

Five people, with varying physical abilities and differing amounts of experience in using this technique, collected the samples. To collect a sample, a person pumped water for 5 or 10 seconds through a copper tube (inside the standpipe) into a graduated cylinder using a modified bicycle pump (Terhune 1958). The workers usually took three samples at each site; the sequence of sampling for each person and each site was randomized. Because one person took only one reading at site 3 and two readings at site 1, the total number of readings was 72. All analyses were performed on a standardized sample of discharge ($mL \cdot s^{-1}$) into the graduated cylinder, less the 25 mL introduced by the sampling technique. I used two-way ANOVA, performed by the GANOVA-4 program (Courtesy of D. G. Bonett, Department of Statistics,

University of Wyoming, Laramie), to assess differences between people and sites; pairwise comparisons were made between all individual sampler combinations within sites and across all sites. Tests for runs up and down and binomial probabilities (Mosteller and Rourke 1973) were used to determine if permeability changed at each site through time. Finally, I calculated estimates of the sample sizes needed to detect possible changes of 10, 20, or 30% in the permeability means at each site (Sokal and Rohlf 1981). $P \leq 0.05$ was accepted as indicating significance.

RESULTS

Mean permeability readings ranged from 3 to 43 $mL \cdot s^{-1}$ over the five sites; coefficients of variation at each site ranged from 27 to 79%. Means between individuals varied greatly within and between sites (Table 1). I was unable to detect overall differences among people by applying two-way analysis of variance, but I did identify significant differences among sites. A significant interaction between people and sites suggested that people performed differently at different sites. Nonetheless, when I transformed the measured values to ranks, I found the majority of people gave the same rank to a given site.

Pairwise comparisons of samples withdrawn by different people across all sites yielded only one significant difference (between samples collected by persons I and II), but pairwise comparisons of samples taken by different people at each site revealed several significant differences (Table 2). Only for site 1 did I find no significant differences between the samples removed by all possible

pairs of individuals, which may be attributable to the variance associated with samples at this site rather than to a lack of differences between people. At site 3, seven of the 10 pairwise comparisons were significant, but a low single reading by sampler I influenced this result. Nonetheless, the samples withdrawn by each individual differed significantly from those taken by at least one other person at one or more sites.

Permeability did not exhibit a directional shift at any site during the experiment (test for runs, $P > 0.05$). The probabilities that readings by specific samplers at each site had successively increased (sample 1 < sample 2 < sample 3) or decreased (sample 1 > sample 2 > sample 3) were not significant. The number of samples needed to detect a 10% change in the mean permeabililty of a site varied from 34 to 90, to detect a 20% change, from 9 to 23, and to detect a 30% change, from 4 to 10 (Table 3).

DISCUSSION

I demonstrated the need to take replicate samples for permeability estimates. Yet single samples taken at various intervals have been used to evaluate temporal variation in permeability (e.g. Reiser and White 1981). Typically, researchers attributed this variation to fluctuation in permeability, rather than to imprecision of the technique and the individual sampler (Moring 1982). Furthermore, sampling by different people at a single site should be interpreted cautiously, and I question the comparison of permeabilities between different streams when readings are collected

Table 1. Means of Permeability Readings ($mL \cdot s^{-1}$) for each Combination of Person and Sampling site. All Cell Means Are Based on Three Observations per Cell Except Cells I-3 (one observation) and V-1 (two observations). Sample Standard Deviations Are Given in Parentheses.

	Site				
Person	1	2	3	4	5
I	2 (1)	23 (5)	12 (0)	27 (16)	38 (12)
II	4 (2)	15 (7)	57 (5)	45 (4)	38 (3)
III	5 (5)	21 (7)	42 (3)	39 (2)	23 (10)
IV	2 (2)	12 (9)	42 (6)	30 (15)	33 (6)
V	4 (0)	25 (2)	40 (4)	39 (2)	32 (5)
Means	3 (3)	19 (7)	43 (12)	36 (11)	33 (9)

Table 2. Pairwise Comparisons of Samples Taken by Different Individuals at Each Site Based on F-tests (* Indicates Significance at $P \leq 0.05$; ** Indicates Significance at $P \leq 0.01$). Site 1 Had No Significant Differences and Was Excluded.

Site	Person	Person I	Person II	Person III	Person IV
2	II				
	III				
	IV				
	V				*
3	II	**			
	III	**	*		
	IV	**	*		
	V	**	**		
4	II	**			
	III	*			
	IV		**		
	V	*			
5	II				
	III	*	*		
	IV				
	V				

by different people whose sampling biases are unknown (e.g. Moring 1982).

Terhune (1958) stated that the probable error in predicting mean permeability when using his calibration curve was 1.1%, and that a liberal allowance for error would be 10%. Conversion of my samples to permeability estimates by using the figure published by Terhune (1958) exacerbated the variability, since the calibration curve is based on a log-log plot and one performs the conversion graphically. Thus I believe that the standpipe technique is best adapted to assessing relative differences or changes, rather than providing precise estimates of permeability. Replicated readings by one person taken at various sites or times will probably reflect true changes in permeability.

Pollard (1955) suggested that permeability readings did not change over the course of sampling. My results confirm this conclusion and suggest that individual samplers behaved consistently during the test, despite the strenuous sampling effort. From these perspectives, the standpipe method has potential for detecting temporal or spatial changes in permeability.

PROPOSED SAMPLING STRATEGY

I demonstrated limitations of the standpipe technique for measuring permeability, but I also identified advantages of this method and believe it can be successfully used to assess permeability. I offer the following sampling strategy:

1) Drive a single standpipe into the specific location of interest, e.g. the egg pocket of a salmonid redd. If spatial differences are of

Table 3. The Number of Permeability Samples Necessary to Detect Potential Changes of 10, 20, or 30% in the Mean Permeability (Alpha = 0.05) at the Five Sites.

Potential change (percent)	Sites 1	2	3	4	5	Mean
10	90	68	38	44	34	55
20	23	17	9	11	9	14
30	10	8	4	5	4	6

interest, the standpipe can be removed after sampling. If temporal changes are of concern, then the standpipe should not be removed or disturbed because doing so could alter future readings.

2) Select the percentage change in the mean permeability that one wishes to be able to detect. My results suggest that about 15 samples should enable one to recognize a 20% change in mean permeability at an alpha of 0.05, but variability among sites may require a different number of samples to detect a similar change.

3) One person should collect all the readings, following the technique developed by Terhune (1958). Intervals between sampling may vary, but all samples should be collected at similar water temperatures and flows.

4) Results should be interpreted as an index of permeability, rather than as an accurate estimator.

CHAPTER III

COMMENT ON "CRITICAL REVIEW OF VARIABLES USED TO DEFINE EFFECTS OF FINES IN REDDS OF LARGE SALMONIDS" BY D. W. CHAPMAN

Chapman (1988) noted that the relation between the survival to emergence (STE) of embryonic salmonids and several measures of substrate composition was not quantitatively consistent. He stated that fisheries biologists cannot accurately and precisely predict STE from the existing data on the intragravel environment. He largely attributed these problems to a lack of understanding of the structure of the egg pocket, which is the exact location of the eggs in a salmonid redd. To address these deficiencies, he proposed an intensive study of egg pocket structure, followed by laboratory assessment of STE from simulated egg pockets and field assessment of STE in natural redds.

I agree that current predictions of STE in natural redds are unreliable, but the unreliability is only partly due to the lack of understanding of egg pockets. Although the research proposed by Chapman on the structure of egg pockets can only improve our understanding of the effects of fine sediment on STE, certain problems remain. Specifically, fisheries biologists have overlooked several other sources of variation that may produce inaccurate predictions of STE, such as variation in egg viability and egg deposition and the

inappropriate analysis of STE data.

Researchers tend to assume that egg viability equals 100%, but in response to environmental or genetic causes, egg viability may vary substantially among stocks or individuals of a single stock. Furthermore, the fecundity of a salmonid of a given size varies with location, age, and time. The imprecision of fecundity estimates based on fish size, as well as the difficulty of estimating egg loss and fertilization success during spawning, seriously reduces the accuracy of estimates of egg deposition. The selection and computation of measures of substrate composition lack uniformity and thus hamper comparisons of the effects of substrate on STE. Unfortunately, the inappropriate selection and application of independent variables in regressions involving STE have compounded this problem and have produced spurious relations between STE and substrate measures.

EGG VIABILITY

Assessments of STE (or survival during a portion of the intragravel phase) in relation to simulated redd characteristics have been conducted with brook trout (Salvelinus fontinalis) (Hausle and Coble 1976; Witzel and MacCrimmon 1983), brown trout (Harshbarger and Porter 1979; Witzel and MacCrimmon 1983), bull trout (Salvelinus confluentus) (Shepard et al. 1984), cutthroat trout (Bianchi 1963), rainbow trout (O. mykiss) (Witzel and MacCrimmon 1981; NCASI 1984), chinook salmon (O. tshawytscha) (Tappel and Bjornn 1983), chum salmon O. keta (Scrivener 1988), coho salmon (O. kisutch) (Phillips et al. 1975), pink salmon (O. gorbuscha) (Meehan and Swanston 1977), and kokanee (O. nerka) (Irving and Bjornn 1984). Among these studies,

only Witzel and MacCrimmon (1981, 1983) and Irving and Bjornn (1984) estimated survival in non-gravel treatments, thus creating a laboratory control. Implicit in studies lacking a laboratory control is the assumption that survival equals 100% under ideal conditions, but I contend that this belief is unjustified.

Embryonic survival may vary between stocks, years, and individual females. Morrison et al. (1985) reported significant differences in survival to hatch among different Great Lakes stocks of coho salmon. Furthermore, they presented data demonstrating that survival to hatch of coho salmon eggs from the Lake Michigan stock fluctuated between 45% and 90% from 1972 to 1982. Survival to hatch of coho salmon eggs from a Lake Erie stock was significantly greater for eggs taken from large females than for those taken from small females (Morrison et al. 1985). Springate and Bromage (1985) noted that large females tended to produce large eggs but that the relation between egg size and survival was often significant but equivocal i.e., egg size was negatively correlated with survival to later stages for chinook salmon (Fowler 1972) and chum salmon (Beacham and Murray 1985) and positively correlated for Arctic char Salvelinus alpinus (Wallace and Aasjord 1984).

More striking is the variation in survival of eggs from individuals of a single stock. The survival to swim-up stage of the eggs from six 2-year-old rainbow trout varied from 14% to 88% (Springate and Bromage 1985), and survival to the eyed stage varied from 40% to 98% for the eggs of nine 3-year-old rainbow trout (Bruhn and Bowen 1973).

Considering the number of factors that influence the fitness of salmonids, one should expect egg viability to come under the influence of natural selection. Artificial selection of hatchery fish can increase egg viability over that in wild fish (see Leitritz and Lewis 1976). Perhaps wild stocks balance reductions in egg viability with increases in egg number, female survival, or some other trait that increases fitness. Beacham and Murray (1987), who found variation in the embryonic survival of different chum salmon stocks in British Columbia, concluded that it was a consequence of selection imposed by an array of environmental conditions.

EGG DEPOSITION

Most estimates of STE in natural redds rely on a regression of fecundity on body size (measured as length) and the use of fry traps. Consequently, precise and accurate measurement of STE depends on the size-related variation in fecundity. Chapman (1988) noted that fecundity for fish of a given size may vary, but that estimates of STE would simply require a greater number of fry traps. I believe that the variation in egg deposition caused by variation in fecundity and other sources, combined with the variation in egg viability, may prevent meaningful estimates of STE in the field.

Tagart (1976) found significant differences among the length-fecundity equations for three stocks of coho salmon, and these equations accounted for only 47% to 78% of the variation in fecundity. This observation suggests that an equation developed for one stock should not be extrapolated to other stocks. But Healey and Heard (1984) also found significant changes between years in the size-

specific fecundity of four stocks of chinook salmon, and speculated that these changes might have been related to food availability. Rounsefell (1957) found that only 12% of the variation in fecundity was explained by length for pink salmon when data for several years were combined. Female age also influences the variation in fecundity. When Healey and Heard (1984) pooled the fecundity data for eight populations of chinook salmon and standardized it for fish size, they found that age was significantly related to fecundity. Thus, fecundity of fish of a given size can fluctuate randomly if influenced by environmental conditions (Wooton 1973) or undergo directional change if older fish are selectively removed by exploitation (Ricker 1981).

To demonstrate the potential difficulty of accurately estimating fecundity, I used the length-fecundity data of Tagart (1976; p. 12), which were also used by Chapman (1988; p. 15) to try to demonstrate a precise relation between fecundity and length; however his results actually pertain to the estimation of fecundity from a subsample of egg mass. I found a significant relation between fecundity and length ($r^2 = 0.69$, $P = 0.002$). Next, I found that the mean predicted fecundity for a female coho salmon 628 mm long (roughly one standard deviation below the mean size) was 3019 eggs. However, the 95% prediction interval for fecundity was 2002 to 4036 eggs. I concluded that meaningful estimates of STE based on fecundity-length relations must rely on fish from a small size range, from a single stock, and from a single year. Unfortunately, these restrictions reduce the generality of any relation between intragravel conditions and STE.

Other sources of variability in estimating egg deposition focus on monitoring redd construction. In high-density spawning areas, redd superimposition may be common. If late-spawning females use previously constructed redds, the unique structure of egg pockets may be altered and of little importance to STE. Ironically, such modified egg pockets may closely resemble the homogeneous substrate mixes used in many studies (e.g., Meehan and Swanston 1977) that were criticized by Chapman (1988). A less common problem involves multiple redds. Within a redd, female salmonids may construct one or more egg pockets (Hawke 1978). But MacKenzie and Moring (1988) watched an Atlantic salmon construct egg pockets and deposit eggs in at least two redds. If not detected, the division of one female's eggs into more than one redd would distort the estimate of egg deposition in a single redd. But multiple redds may be relatively rare in semelparous species if females are concentrated in spawning areas and defend redds (M. R. Gross, University of Toronto, Toronto, Ontario, personal communication).

Despite its potential importance to STE predictions, the estimation of unfertilized (but viable) eggs has been ignored; I know of no study quantifying the proportion of eggs deposited by females that are not fertilized. Nonetheless, I have found egg pockets containing few or no live eggs shortly after spawning, though the substrate appeared adequate for survival. And I have observed egg losses caused by water currents during oviposition and covering of the egg pocket, but I am unaware of any research on this topic.

All these problems lead to difficulties in estimating the STE of

salmonids in the field. Even if large numbers of fry traps could be used to obtain reliable information, the costs (up to US$300 per trap; S. Wolff, EA Engineering, Seattle, Washington, personal communication) and time for installation (up to 4 h per trap; Phillips and Koski 1969) and monitoring may deter fisheries researchers and managers from using this approach.

As an alternative, I propose constructing artificial egg pockets and redds. Planting eggs in known locations might be less costly and time-consuming than capping redds of wild fish, and it should produce more precise results. Ideally, the eggs and sperm that are used in field tests should be collected from the stream where the test is being conducted. But, as Chapman suggested, I must intensively investigate the structure and function of egg pockets before attempting these tests.

SUBSTRATE ANALYSIS AND STE

Fisheries biologists have not adopted a single measure of substrate composition in studies of STE. Instead, STE has usually been related to one of four substrate measures: the percentage of fine sediment less than a given size (size varying from 0.8 to 6.3 mm in diameter); the percentage of fine sediment less that 0.85 mm and 9.5 mm (Tappel and Bjornn 1983); the geometric mean particle size of a substrate (Platts et al. 1979); and the fredle index (Lotspeich and Everest 1981). Chapman (1988) preferred the fredle index to the geometric mean, and recommended that researchers that conduct laboratory and field investigations of egg pockets and redds should focus on the fredle index, on the percentage of sediment less than

both 0.85 mm and 9.5 mm, and on permeability.

Chapman (1988), who calculated the relation between STE and both the log of the fredle index and the untransformed geometric mean using data from several published studies, concluded that the transformed fredle index was a better correlate with STE than was the geometric mean. However, his analyses of the two measures were flawed. Using data from Tappel and Bjornn (1983), he found that the geometric mean accounted for 57% of the variation in STE for steelhead and 53% for chinook salmon. However, a plot of these data (Tappel and Bjornn 1983; Figure 9, p. 132) suggested that the geometric mean should be transformed or that the analysis should include only substrate treatments with a geometric mean of less than 10 mm i.e., the STE-geometric mean particle size curve becomes asymptotic at values greater than 10 mm. Chapman acknowledged this problem for the fredle index, because he examined only substrates with a fredle index of less than 4.0.

I reanalyzed these data, and came to different conclusions about the relation of the fredle index and geometric mean to STE (Table 4). For chinook salmon, the log of the fredle index accounted for slightly more of the variation in STE than did the log of the geometric mean for both the entire range of substrates and the substrates below a geometric mean of 10 mm (roughly corresponding to a fredle index less than 5). But for steelhead, the log of the geometric mean accounted for slightly more of the variation in STE for the substrates from the restricted range, and nearly as much from the entire range.

I also examined the relation between these two substrate

statistics and the survival of alevins of steelhead and coho salmon to swim-up stage from data published by Phillips et al. (1975). Again, I found very little difference in the amount of variation in survival accounted for by the log transformations of the fredle index and the geometric mean and the untransformed geometric mean (Table 5). From these results, I concluded that the fredle index and the geometric mean are both adequate descriptors of the effects of substrate composition on STE.

In multiple regression equations predicting STE, Chapman (1988) included the geometric mean, the log of the fredle index, and permeability. Unfortunately, equations in which these variables are used may suffer from high multicollinearity. If these variables are highly intercorrelated, the regression coefficients for each variable depend on the variables already included in the model, and the precision of the estimates of the coefficients is reduced (Zar 1984; pp. 338, 344). An informal technique for detecting multicollinearity is inspection of a correlation matrix of independent variables (Neter et al. 1983; p. 390). A correlation matrix for several substrate statistics, based on data from Tappel and Bjornn (1983), indicated that most measures of substrate composition were highly correlated (Table 6). And Platts et al. (1979) found that permeability was highly correlated ($r > 0.9$) with the geometric mean and several measures of "percent fines." Consequently, if errors associated with multicollinearity are to be avoided, perhaps estimates of STE should include only one independent variable representing substrate composition.

Table 4. Relation Between Survival to Emergence of Steelhead and Chinook Salmon and Several Measures of Substrate Composition, Based on Data From Tappel and Bjornn (1983). F_s is the Fredle Index, D_g is the Geometric Mean Particle Size, N is the Number of Substrate Treatments Examined, and r^2 is the Coefficient of Determination. Where N = 15, All Substrates Are Included; Where N = 7, Only Substrates with a D_g of Less Than 10.0 mm Are Included. All Regressions Are Significant ($P < 0.05$).

N	Equations	r^2
	Steelhead	
15	$21.4 + 68.9[\log F_s]$	0.79
15	$-38.9 + 111.1[\log D_g]$	0.77
7	$-1.5 + 134.0[\log F_s]$	0.94
7	$-133.4 + 233.1[\log D_g]$	0.96
	Chinook Salmon	
15	$25.4 + 69.3[\log F_s]$	0.76
15	$-33.7 + 110.2[\log D_g]$	0.71
7	$-1.4 + 149.8[\log F_s]$	0.93
7	$-141.0 + 250.3[\log D_g]$	0.85

Table 5. Relation Between the Arcsine Transformation of Survival of Alevins of Steelhead and Coho Salmon to Emergence and Several Measures of Substrate Composition, Based on Data from Phillips et al. (1975). F_1 is the Fredle Index, D_g is the Geometric Mean Particle Size (mm), and r^2 is the Coefficient of Determination. For All Equations, $N = 48$ and $P < 0.05$.

Equations	r^2
Steelhead	
$16.4 + 65.4[\log F_1]$	0.78
$-34.5 + 92.0[\log D_g]$	0.76
$9.4 + 4.3[D_g]$	0.78
Coho Salmon	
$2.6 + 70.0[\log F_1]$	0.83
$-50.5 + 97.0[\log D_g]$	0.77
$-4.5 + 4.6[D_g]$	0.82

Finally, I question the use of mean STE from a given substrate to calculate regression statistics. Freund (1971) suggested that this process artificially reduces the variation in the data and tends to inflate the coefficient of determination. All of the equations calculated by Chapman for the data of Tappel and Bjornn (1983) and Phillips et al. (1975) apparently relied on the means from those data, as did my reassessment of the data from Tappel and Bjornn (1983)[1]. For comparison, I regressed the arcsine transformation of the proportion of successfully emerging coho salmon alevins on the log of the fredle index (as in Table 5) but used only the mean survival for each substrate from Phillips et al. (1975). This reduced the sample size from 48 to 8, but did not alter the regression coefficients. However, the coefficient of determination increased from 0.83 (all data) to 0.99 (means only). Additionally, the precision of the estimate of the regression coefficients was reduced when the means were used. I concluded that the use of means tended to conceal the variation in the relation between STE and substrate composition and that this form of analysis should be avoided.

CONCLUSIONS

Chapman (1988) concluded that fisheries biologists must measure conditions in the egg pocket to accurately estimate STE. However, the importance of egg pockets to STE for the eggs and alevins of all large salmonids was extrapolated from data on the substrate composition of

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[1]Based on identical results obtained between his analyses and mine when I used the means. I contacted the authors in an attempt to obtain the entire data sets, but these data were unavailable.

Table 6. Correlation Matrix Between Several Measures of Substrate Composition, Based on Data from Tappel and Bjornn (1983). F_1 is the Fredle Index, D_g is the Geometric Mean Particle Size (mm), %<9.5 is the Percentage of Sediment Less Than 9.5 mm in Diameter, and %<0.85 is the Percentage of Sediment Less Than 0.85 mm in Diameter. All Correlations Are Significant ($P < 0.05$).

Substrate measures	log F_1	log D_g	D_g	%<9.5	%<0.85
log F_1	1.000				
log D_g	0.996	1.000			
D_g	0.959	0.976	1.000		
%<9.5	-.944	-.940	-.943	1.000	
%<0.85	-.899	-.904	-.826	0.760	1.000

16 egg pockets and the permeability of 15 egg pockets (Chapman 1988; p. 17). I suggest that researchers collect numerous samples throughout incubation from the redds of several species of large salmonids from many different streams to elucidate the structure and function of egg pockets. But based on the sources of variation and error associated with egg viability and deposition in the field, I question the utility of capping redds to accurately estimate STE in the field.

I concur with Chapman that information on the structure of egg pockets should be incorporated in laboratory experiments evaluating the relation between STE and intragravel conditions. Unlike Chapman, I suspect that much of the current information on STE derived from laboratory studies could be applied to the field, but only when embryonic survival characteristics and intragravel conditions in laboratory tests match those in the field. The suggested investigations of egg pockets should resolve this problem.

Finally, fisheries researchers should be aware of statistical problems that can cause misleading results. Realism in simulating intragravel conditions must be matched with rigorous analyses of the data from experiments involving STE.

CHAPTER IV

EFFECT OF SUBSTRATE COMPOSITION AND STOCK ORIGIN ON THE SURVIVAL TO EMERGENCE OF BROWN TROUT

The survival of salmonid eggs and alevins during incubation in the stream bed is affected by several chemical and physical characteristics, including dissolved oxygen concentration (Silver et al. 1963), intragravel water velocity (Shumway et al. 1964), water temperature (Beacham and Murray 1985), and interstitial pore space (Chapman 1988). Fine sediment in substrates can directly or indirectly alter these variables and influence survival to emergence (STE) of embryonic salmonids. Because many land management practices e.g., logging (Megahan and Kidd 1972), increase fine sediment in streams, managers have wished to quantify the relation between fine sediment and STE. Laboratory models predicting STE have been developed for several native salmonids in the western U. S., including steelhead and chinook salmon (Stowell et al. 1983), but no models have been developed for introduced resident salmonids such as brown trout.

The percentage of fine sediment less than a given diameter is frequently used to represent substrate composition in STE models (see Reiser and White 1988). But fine sediment has been inconsistently defined; it has been measured as being from less than 6.3 mm (Sheridan et al. 1984) to less than 0.83 mm (McNeil and Ahnell 1964). Other measures of substrate composition, such as the geometric mean particle

size (Platts et al. 1979) and the fredle index (Lotspeich and Everest 1980), have also been related to STE. Rarely have the three measures of substrate composition and their relation to STE been simultaneously compared (but see Tappel and Bjornn 1983).

Finally, many models predict STE of a generic stock of a given salmonid species (e.g., Stowell et al. 1983). Yet Morrison et al. (1985) found significant differences in the survival to hatch of different stocks of coho salmon from the Great Lakes, and Beacham and Murray (1987) noted variation in STE among stocks of chum salmon from British Columbia. Furthermore, females from the same stock but of different ages may produce eggs differing in viability. For example, Springate and Bromage (1985) noted that large females tended to produce large eggs and Bagenal (1969) implied that large eggs had yielded higher STE.

In the present study, I had three objectives: (1) to develop a laboratory model of STE for brown trout based on substrate composition; (2) to determine which of the three measures of substrate composition accounted for the greatest proportion of variation in STE of brown trout; and (3) to assess the differences in STE between two stocks of brown trout.

METHODS

I conducted experiments at the Red Buttes Environmental Biology Laboratory, 16 km south of Laramie, Wyoming, in experimental aquaria equipped with a horizontal flow system (Figure 1). Test substrate was placed between porous baffles in glass-walled, plexiglass-bottomed aquaria 50.8 cm long, 25.4 cm wide, and 30.5 cm deep. Baffles,

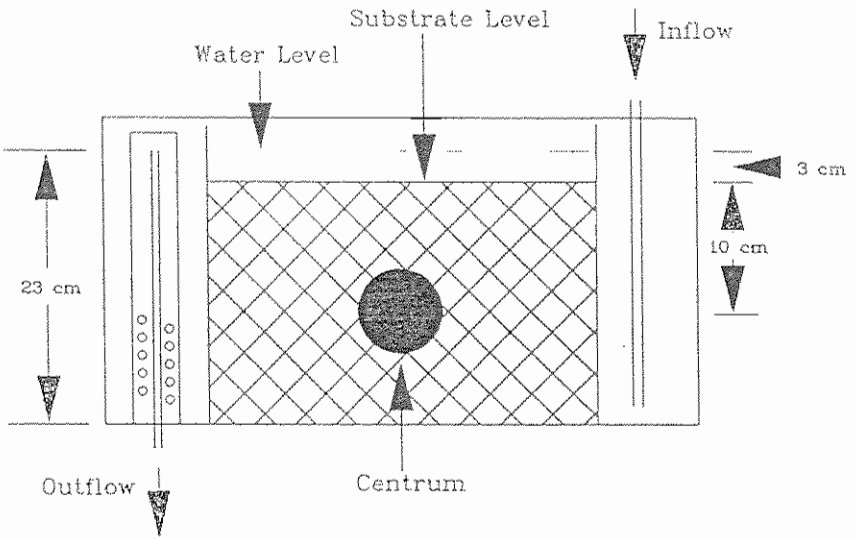

Figure 1. Side View of an Experimental Aquarium. Water Flows Through the Substrate from Right to Left.

consisting of a plexiglass frame covered with fiberglass screen, werepositioned 7.5 cm from each end of an aquarium. Flow splitters (Mount and Brungs 1967) maintained constant flows of 1 L/min of 9°C well water at or near oxygen saturation to each aquarium. An adjustable standpipe inside a venturi standpipe controlled water depth; the venturi standpipe drew water from the lower one-third of the aquarium.

I filled each aquarium with substrate to a depth of 10 cm and constructed a centrum of 3 or 4 gravel particles more than 25 mm in diameter (Chapman 1988). Next, I began filling each tank with water; when the water level exceeded the depth of the substrate, I poured 100 eggs onto the centrum and then gently added the remaining substrate and continued filling each tank with water. The rear standpipe was adjusted to maintain a water depth of 3 cm over the substrate.

I monitored the aquaria weekly until emergence began, then collected emerging fry with a suction device every 1 to 3 days until emergence ended. Each year, 300 eggs from each stock were placed in Heath incubator trays to estimate STE in a non-gravel control. All alevins from the substrate treatments were preserved in 70% alcohol. The first 10 fry to emerge from each treatment were later measured to the nearest 0.1 mm (total length).

I conducted two STE experiments, the first from 20 November 1987 to 6 April 1988 and the second from 16 November 1988 to 31 March 1989. I devised 24 test substrates of various compositions (Table 7). I used three replicates of each of 15 different test substrates in 1987, and six replicates of each of nine additional substrate mixtures in

Table 7. Percentages of Each Substrate Size Class in the Treatment Substrates. Type is the General Description of Each Treatment Substrate; the First and Second Numbers Define the Approximate Percentage of Substrate Less Than a Given Size (mm) and the Letter Defines the Distribution of this Fine Substrate as Skewed (s), Uniform (u), or Geometric (g). D_g is the Geometric Mean Particle Size (mm), F_s is the Fredle Index, and F_m is the Modified Fredle Index. The First Nine Treatment Substrates Were Used in the 1988 Tests and the Remaining 15 Treatment Substrates Were Used in the 1987 Tests.

	Sieve size (mm)										
Type	50	25	12.5	9.5	6.3	3.35	1.70	0.85	0.42	0.21	0.0
7.5-0.85-s	1.8	26.5	34.8	7.7	11.0	4.0	5.2	6.0	2.7	0.2	0.0
7.5-0.85-u	1.8	26.5	34.8	7.7	11.0	4.0	5.1	3.0	1.8	2.6	1.7
7.5-0.85-g	1.8	26.5	34.8	7.7	11.0	4.0	5.1	4.2	2.4	1.5	1.0
15-1.70-s	1.8	24.9	32.7	7.1	10.4	3.7	7.6	11.3	0.4	0.0	0.0
15-1.70-u	1.8	24.9	32.7	7.1	10.4	3.7	5.2	5.0	2.6	3.7	2.4
15-1.70-g	1.8	24.9	32.7	7.1	10.4	3.7	6.1	8.5	2.3	1.5	0.9
25-3.35-s	1.6	22.7	30.0	6.7	9.5	3.6	26.0	0.1	0.0	0.0	0.0
25-3.35-u	1.6	22.7	30.0	6.7	9.5	3.5	7.2	6.8	3.5	5.0	3.3
25-3.35-g	1.6	22.7	30.0	6.7	9.5	3.5	15.5	6.9	1.8	1.3	0.8
5-0.85-s	2.0	27.2	35.8	7.8	11.2	4.2	5.2	4.6	1.8	0.2	0.0
5-0.85-u	2.0	27.2	35.8	7.8	11.2	4.2	5.2	2.6	1.2	1.7	1.1
5-0.85-g	2.0	27.2	35.8	7.8	11.2	4.2	5.2	3.2	1.5	1.1	0.7
10-0.85-s	1.8	25.7	34.0	7.3	10.7	3.9	5.0	7.5	3.6	0.3	0.0
10-0.85-u	1.8	25.7	34.0	7.3	10.7	3.9	5.0	3.4	2.3	3.4	2.2
10-0.85-g	1.8	25.7	34.0	7.3	10.7	3.9	5.0	4.9	3.0	2.2	1.4
10-1.70-s	1.8	26.2	34.7	7.5	10.8	4.0	6.9	7.6	0.3	0.0	0.0
10-1.70-u	1.8	26.2	34.7	7.5	10.8	4.0	5.3	3.5	1.8	2.6	1.7
10-1.70-g	1.8	26.2	34.7	7.5	10.8	4.0	5.9	5.7	1.5	1.0	0.6
20-1.70-s	1.7	23.3	30.8	6.7	9.7	3.5	8.4	15.1	0.5	0.0	0.0
20-1.70-u	1.7	23.3	30.8	6.7	9.7	3.5	5.1	6.9	3.6	5.1	3.3
20-1.70-g	1.7	23.3	30.8	6.7	9.7	3.5	6.4	11.4	3.1	2.0	1.3
30-3.35-s	1.5	21.2	28.0	6.2	8.8	3.3	30.9	0.1	0.0	0.0	0.0
30-3.35-u	1.5	21.2	28.0	6.2	8.8	3.2	8.4	8.3	4.3	6.1	4.0
30-3.35-g	1.5	21.2	28.0	6.2	8.8	3.2	18.2	8.2	2.2	1.5	1.0

Table 7, continued.

Type	Statistics D_σ	F_s	F_m
7.5-0.85-s	13.20	7.16	4.41
7.5-0.85-u	12.32	6.67	3.40
7.5-0.85-g	12.69	6.87	3.78
15-1.70-s	11.91	6.05	3.85
15-1.70-u	10.31	5.28	2.40
15-1.70-g	11.15	5.66	3.08
25-3.35-s	11.30	4.12	4.02
25-3.35-u	8.33	2.98	1.70
25-3.35-g	10.00	3.60	2.80
5-0.85-s	14.19	7.87	5.11
5-0.85-u	13.56	7.50	4.23
5-0.85-g	13.79	7.65	4.54
10-0.85-s	12.24	6.49	3.81
10-0.85-u	11.21	5.95	2.78
10-0.85-g	11.58	6.14	3.11
10-1.70-s	13.32	7.20	4.71
10-1.70-u	12.07	6.53	3.29
10-1.70-g	12.73	6.88	3.97
20-1.70-s	10.45	4.26	3.12
20-1.70-u	8.58	3.50	1.74
20-1.70-g	9.55	3.89	2.36
30-3.35-s	10.18	3.67	3.49
30-3.35-u	7.04	2.14	1.31
30-3.35-g	8.78	3.04	2.32

1988. Three replicates of each mixture were used in tests of the STE of each of two stocks of brown trout.

In 1987 I obtained eyed eggs from the Daniel (Wyoming) State Fish Hatchery that had been taken from wild brown trout of various ages inhabiting Soda Lake in western Wyoming. This population was established from brown trout taken from Big Sandy Reservoir in southwestern Wyoming in the late 1950's; that population is speculated to have originated from the Plymouth Rock (Massachusetts) State Fish Hatchery (Richard Cheeney, Wyoming Game and Fish Department, Daniel, Wyoming, personal communication). In 1988 I obtained brown trout eggs from both Soda Lake and from a hatchery-reared stock at the Saratoga (Wyoming) National Fish Hatchery. These eggs were taken from 3-year-old hatchery fish spawning for the first time. This stock descended from brown trout at the Crawford (Nebraska) National Fish Hatchery, which had come from the Plymouth Rock Hatchery in 1980 (Jim Hammer, U. S. Fish and Wildlife Service, Saratoga, Wyoming, personal communication). The brown trout eggs from Soda Lake stock averaged 9,670 per liter and the smaller eggs from the Saratoga Hatchery stock averaged 20,830 per liter.

To assess the relation of the various measures of substrate composition to STE, I created skewed, uniform, and geometric distributions of sediment less than 3.35 mm in diameter in each test substrate (Table 7). For example, the test substrates consisting of about 30% sediment less than 3.35 mm in diameter contained essentially no sediment less than 1.7 mm in diameter (skewed), roughly equal proportions of sediment from 1.7 mm to less than 0.212 mm (uniform),

or increasing proportions of sediment from less than 0.212 mm to 1.7 mm (geometric).

To obtain substrates of different size classes, I sorted material on a mechanical shaker through sieves of 10 mesh sizes (mm): 50, 25, 12.5, 9.5, 6.3, 3.35, 1.70, 0.85, 0.425, and 0.212; smaller particles were collected on a pan attached to the last sieve. Particles larger than 6.3 mm consisted largely of alluvial material and those less than 6.3 mm largely of angular silica.

Lotspeich and Everest (1981) calculated the geometric mean particle size for each treatment using the formula:

$$D_g = D_a^{P_a} * D_b^{P_b} * \ldots D_i^{P_i}$$

where

D_g = the geometric mean, in mm;

D_i = the mean diameter, in mm, of material retained on sieve i, and

P_i = the proportion of the entire sample made up of material retained on sieve i.

To calculate the fredle index of each substrate, I used the formula:

$$F_i = D_g/S_o$$

where

S_o = a sorting coefficient, $(D_{75}/D_{25})^{0.5}$, and

D_{75}, D_{25} = the substrate diameter below which 75% and 25% of the sample lies.

Finally, Beschta (1982) suggested that the fredle index should be modified by using the standard deviation of the geometric mean rather than a sorting coefficient. Shirazi and Seim (1979) provided a

formula for the geometric standard deviation. I used the notation F_m to indicate the modified fredle index.

I assessed the effect of stock origin of eggs and substrate composition on STE, fry length at emergence, days to first emergence, days to 50% emergence, and the length of the emergence interval. Prior to any analyses, I applied the arcsine transformation (Zar 1984; p. 286) to normalize STE. To assess the effect of stock origin and the interaction between stock origin and substrate composition on the dependent variables, I conducted two-way analysis of variance using the GANOVA-4 program (Courtesy of D. G. Bonett, Department of Statistics, University of Wyoming, Laramie, Wyoming). I performed regression analyses using SPSS* (SPSS Inc. 1986) to assess the relation between STE and substrate composition for all substrate treatments. In addition, I evaluated this relation for skewed, uniform, and geometric treatments separately. I used indicator variables in regression analyses (Neter et al. 1983; p. 343) of STE and substrate composition to compare the slopes and intercepts of regression lines calculated separately for the 1987 Soda Lake stock, the 1988 Soda Lake stock, and the 1988 Saratoga National Fish Hatchery stock. I decided from the start to pool the data from both stocks and both years if I failed to reject the null hypothesis of no difference in the regression coefficients between stocks or years or both. Using only data from 1988, I conducted separate regression analyses for the two different stocks on the relation between the different measures of substrate composition and alevin size, days to first and 50% emergence, and length of the emergence interval. $P \leq 0.05$ was

accepted as indicating significance.

RESULTS

The STE did not differ significantly between the eggs from two stocks of brown trout, nor did days to first emergence (Table 8). Nor was the interaction between stock origin and substrate composition on STE significant. However, stock origin was significantly related to fry length at emergence ($P < 0.001$), days to 50% emergence ($P < 0.001$), and length of the emergence interval ($P = 0.019$). Compared with fry produced from eggs of the Saratoga Hatchery stock, fry from eggs of Soda Lake stock were longer and emerged later and over a longer interval.

Substrate composition was significantly correlated with STE. In regressions of STE and substrate composition, I found no significant differences among the regression coefficients for the two stocks or between years, consequently I combined these data for further analyses. Though all measures of substrate composition were related to STE, the geometric mean accounted for the greatest proportion of the variation in STE when all treatments were pooled (Figure 2). When the treatments were divided into skewed, uniform, and geometric groups, the geometric mean performed nearly as well; only for the geometric group of treatments did another measure of substrate composition account for a greater proportion of variation in STE (Table 9).

The relation between substrate composition and the other dependent variables was influenced by the measure of substrate composition and stock used in the analysis. For the stock from the

Table 8. Averages of Untransformed Survival to Emergence, Fry Length at Emergence, Days to First Emergence, Days to 50% Emergence, and Length of the Emergence Interval for Soda Lake (SL) and Saratoga National Fish Hatchery (SNFH) Stocks of Brown Trout in the 1988 Test (S is the Skewed Substrate Distribution, U is the Uniform Distribution, and G is the Geometric Distribution; C is the Non-gravel Control).

	Substrate mixes									
	7.5% < 0.85 mm			15% < 1.70 mm			25% < 3.35 mm			
Variable	S	U	G	S	U	G	S	U	G	C
Survival to emergence (%)										
SL	80.3	74.0	79.3	86.7	55.3	78.3	81.0	40.7	55.7	95.7
SNFH	88.0	87.7	79.0	70.7	58.0	73.7	78.3	40.0	27.7	92.0
Fry length (mm)										
SL	24.5	25.0	24.7	24.9	24.3	24.9	24.0	24.9	23.6	---
SNFH	22.6	22.5	22.8	23.0	22.5	21.8	22.4	22.8	22.9	---
Days to first emergence										
SL	71.7	78.0	73.7	73.0	71.0	76.0	63.0	72.3	66.0	---
SNFH	73.7	73.0	67.7	70.7	72.7	70.0	60.0	72.0	70.0	---
Days to 50% emergence										
SL	87.0	89.7	89.7	89.0	89.7	90.3	90.3	92.3	93.0	---
SNFH	85.0	83.3	81.0	85.0	85.0	84.3	81.7	87.0	84.3	---
Length of emergence interval (days)										
SL	38.7	29.7	34.3	30.7	39.3	33.0	55.3	40.7	46.7	---
SNFH	26.7	28.7	35.0	36.3	30.0	29.0	39.7	25.7	29.7	---

Table 9. Matrix of Coefficients of Determination for Several Measures of Substrate Composition and the Arcsine Transformation of Survival to Emergence for All Substrates and for Substrates Separated into Skewed, Uniform, and Geometric Categories. Data are from Both Stocks in 1987 and 1988 (D_g is the Geometric Mean Particle Size (mm), F_s is the Fredle Index, and F_m is the Modified Fredle Index).

	Substrate measure									
				Percentage of fine sediment						
Substrate	Statistics			less than the diameter (mm) shown:						
category	D_g	F_s	F_m	9.5	6.3	3.35	1.70	0.85	0.43	0.21
All	0.54	0.47	0.49	0.38	0.38	0.38	0.27	0.23	0.24	0.24
Skewed	0.55	0.49	0.45	0.37	0.36	0.37	0.14	0.10	0.15	0.16
Uniform	0.63	0.49	0.62	0.40	0.39	0.39	0.46	0.48	0.59	0.50
Geometric	0.42	0.44	0.36	0.45	0.45	0.45	0.18	0.06	0.04	0.04

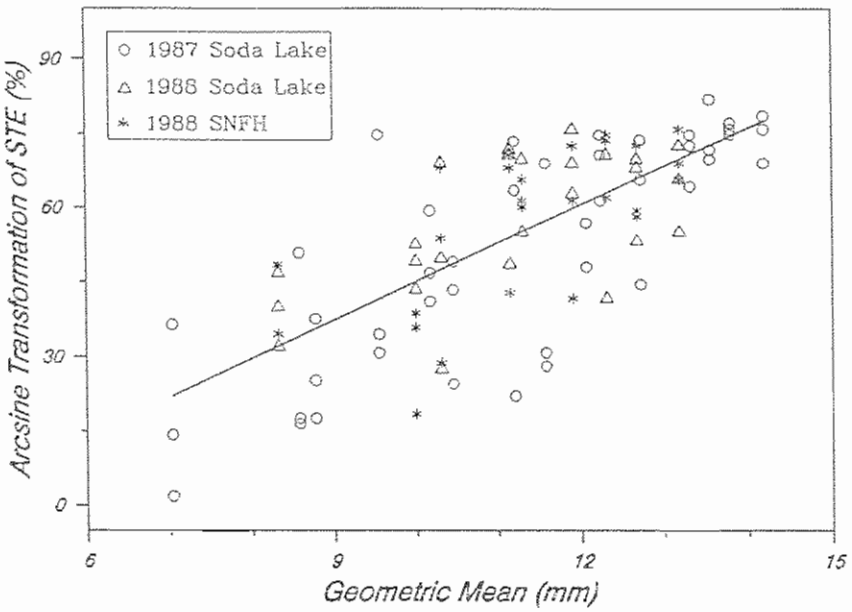

Figure 2. Relation Between Survival to Emergence and the Geometric Mean Particle Size (mm). The Equation is Arcsine(Survival to Emergence) = 7.75(Geometric Mean) - 32.53 ($F = 112.65$, $r^2 = 0.54$, $P < 0.0001$, $N = 99$). Data are from Both Stocks in 1987 and 1988; SNFH is the Saratoga National Fish Hatchery.

Saratoga Hatchery, only the correlation between the percentage of substrate less than 1.70 mm in diameter and days to first emergence was significant ($r = 0.44$, $P = 0.02$). I found no other relation between any measure of substrate composition and alevin length, days to first emergence, days to 50% emergence, or length of the emergence interval. But for the Soda Lake stock, at least three measures of substrate composition were significantly correlated with days to first and 50% emergence and length of the emergence interval (Table 10). Again, no measure of substrate composition was significantly correlated with fry length at emergence.

DISCUSSION

The geometric mean particle size of a substrate consistently accounted for the greatest proportion of the variation in STE. However, the fredle index and modified fredle index often explained nearly as much of this variation. Chapman (1988) favored the fredle index over the geometric mean, but his analyses revealed few substantial differences in the predictive ability of the two measures. Also, Lotspeich and Everest (1981) suggested that a single value of the geometric mean could represent several different values of the fredle index, and therefore concluded that the fredle index was more sensitive to changes in substrate composition. But substrates of differing composition can be represented by a single value of the fredle index and several values of the geometric mean as well. Unless additional research reveals major differences, I prefer the geometric mean as a measure of substrate composition in models of STE due to its predictive ability, computational simplicity, and widespread use by

Table 10. Correlation Coefficients for Measures of Substrate Composition and Days to First Emergence, Days to 50% Emergence, and Length of the Emergence Interval for the Eggs from Soda Lake Stock in 1987 and 1988 (V is the Variable, D_g is the Geometric Mean Particle Size (mm), F_i is the Fredle Index, and F_m is the Modified Fredle Index. An Asterisk Indicates Significance at $P \leq 0.05$).

Substrate measure										
Statistics				Percentage of fine sediment less than the diameter (mm) shown:						
V	D_g	F_i	F_m	9.5	6.3	3.35	1.70	0.85	0.43	0.21
Days to first emergence										
	0.23	0.36*	0.06	-0.45*	-0.45*	-0.45*	-0.11	-0.07	-0.09	-0.09
Days to 50% emergence										
	-0.41*	-0.41*	-0.41*	-0.05	-0.05	-0.05	-0.15	-0.18	-0.17	-0.17
Length of the emergence interval (days)										
	-0.31*	-0.39*	-0.21	0.33*	0.33*	0.33*	-0.14	-0.15	-0.10	-0.10

fluvial geomorphologists (Platts et al. 1979). Finally, I do not recommend that the equation for STE of brown trout be considered a quantitative predictor of STE in the field, because it has not been validated under natural field conditions.

Despite its popularity, the percentage of fine sediment less than a given diameter was the poorest predictor of STE in most tests. Though smaller-sized sediment may reduce STE to a greater extent than larger sediment (Reiser and White 1988), it appears that the overall substrate composition has a greater influence on STE (cf. Chapman 1988). Models of STE based on the percentage of one or more sizes of fine sediment can be informative (e.g., Tappel and Bjornn 1983), but the applicability of these models to substrates containing similar proportions but different distributions of the selected sizes of fine sediment is unknown. Finally, I recognized that my experimental design would rigorously test the influence of 'percent fines' on STE. Consequently, I encourage additional comparisons of measures of substrate composition in laboratory and field experiments.

Surprisingly, I found no significant difference in the STE of eggs from two stocks of brown trout, despite the disparity in egg size and female age. Previous studies have demonstrated greater STE of large (Bagenal 1969) or small (Beacham and Murray 1985) eggs. Furthermore, survival to hatch of eggs of coho salmon from a Lake Erie stock was significantly greater for eggs taken from large females than for those taken from small females (Morrison et al. 1985). I assessed the STE of the eggs from the two stocks over a relatively narrow range of substrate compositions. Additional tests over a greater range of

substrate compositions might reveal differences in the STE of eggs from these two stocks.

A reduction in the geometric mean of substrates significantly accelerated the timing of peak emergence and lengthened the emergence interval. Olsson and Persson (1986) also demonstrated that the time to 50% emergence decreased and the length of the emergence interval increased as the proportion of fine sediment in substrates increased. Witzel and MacCrimmon (1983) reported a decrease in the time to 50% emergence as mean particle size decreased, but noted that the length of the emergence interval also decreased. However, the decreases may be attributed to very low STE in treatments containing large proportions of fine sediment i.e., the emergence interval is likely to be short when few fry emerge. Alternatively, substrates of low mean particle size may induce synchronous premature emergence by restricting delivery of dissolved oxygen. Fry acquire oxygen much more efficiently than eggs, and eggs under stress due to low dissolved oxygen hatch prematurely into fry that assume a free-swimming existence while still carrying a large yolk sac (Bams 1969). Thus synchrony of emergence may exist at two different stages of embryonic development in response to the intragravel environment.

CHAPTER V

SELECTION OF MEASURES OF SUBSTRATE COMPOSITION TO ESTIMATE SURVIVAL TO EMERGENCE OF SALMONIDS AND TO DETECT CHANGES IN SUBSTRATE COMPOSITION

Researchers have demonstrated that fine sediment can reduce survival to emergence (STE) of embryonic salmonids (Tappel and Bjornn 1983) and that certain land management practices can increase the proportion of fine sediment in spawning gravels in streams (Platts et al. 1989). Managers have attempted to link the impacts of land management to STE of salmonids by assessing changes in substrate composition (Stowell et al. 1983), but the inconsistent definition of substrate composition, in addition to other problems (Chapman 1988; Young et al. in press), has obscured this linkage.

Two approaches have been widely used to describe substrate composition. The first quantifies the proportion of substrate (by weight or volume) less than a given size. These sizes have included 6.4 mm (Stowell et al. 1983), 4.0 mm (MacCrimmon and Gots 1986), 3.33 mm (Koski 1975; Ringler and Hall 1988), 3.0 mm (Hall and Lantz 1969; Phillips et al. 1975), 2.0 mm (Hausle and Coble 1976; Witzel and MacCrimmon 1983a), 1.0 mm (Crisp and Carling 1989), 0.84 mm (Reiser and White 1988), 0.83 mm (McNeil and Ahnell 1964), and 0.75 mm (Olsson and Persson 1988). In addition, Tappel and Bjornn (1983) chose two sizes of sediment (9.5 mm and 0.85 mm) to describe substrate

composition (also see Reiser and White 1988).

Substrate composition has also been described using measures related to the central tendency of the entire particle distribution. These measures include the geometric mean particle size (Platts et al. 1979), fredle index (Lotspeich and Everest 1981), modified fredle index (Beschta 1982), arithmetic mean particle size (Crisp and Carling 1989), median particle size (Witzel and MacCrimmon 1983b), sorting coefficient (Sowden 1983), and skewness (Crisp and Carling 1989). Both graphical and mathematical techniques have been used to calculate most of these measures (Shirazi and Seim 1979). However, these techniques produce different estimates of a particular measure, particularly if the distribution of particle sizes in a substrate sample is not lognormal (see Folk and Ward 1957).

I know of no studies that have assessed the relation between several measures of substrate composition and STE. Often, a single measure of substrate composition is arbitrarily selected and related to STE (usually as the percentage of fines less than a given size e.g., Phillips et al. 1975). Occasionally, a measure has been chosen based on theoretical or empirical relations between substrate composition and the intragravel environment (Platts et al. 1979). Though some studies included comparisons of more than one measure of substrate composition (e.g., Tappel and Bjornn 1983), such works frequently compare only similar statistics e.g., the percentages of substrate less than several sizes (Reiser and White 1988).

Failure to standardize measurement of substrate composition has plagued the assessment of land management impacts on stream

substrates. To evaluate the effects of logging and road construction on spawning areas in the South Fork Salmon River, Platts and Megahan (1975) visually estimated the amount of fine sediment less than 4.7 mm. Alternatively, Shirazi and Seim (1981) favored the geometric mean to monitor changes in substrate composition. But Beschta (1982) suggested that not all substrate measures were equally sensitive to changes in substrate composition due to logging.

My objectives were to compare the relation between several different substrate statistics and STE in the laboratory and to examine the sensitivity of a subset of these statistics to known changes in substrate composition in the field.

METHODS

I conducted experiments at the University of Wyoming's Red Buttes Environmental Biology Laboratory, 16 km south of Laramie, Wyoming, in experimental aquaria equipped with a horizontal flow system. Test substrate was placed between porous baffles in glass-walled, plexiglass-bottomed aquaria 50.8 cm long, 25.4 cm wide, and 30.5 cm deep. Baffles, consisting of a plexiglass frame covered with fiberglass screen, were positioned 7.5 cm from each end of an aquarium. Flow splitters (Mount and Brungs 1967) maintained constant flows of 1 L/min of 9°C well water at or near oxygen saturation to each aquarium. An adjustable standpipe inside a venturi standpipe controlled water depth; the venturi standpipe drew water from the lower one-third of the aquarium.

I filled each aquarium with substrate to a depth of 10 cm and constructed a centrum of 3 or 4 25-mm gravel particles (Chapman

1988). Next, I began filling each tank with water; when the water level exceeded the depth of the substrate, I poured 100 eyed eggs onto the centrum and gently added the remaining substrate and continued filling each tank with water. The rear standpipe was adjusted to maintain a water depth of 3 cm over the substrate.

I monitored the aquaria weekly until emergence began, then collected emerging fry with a suction device every 1 to 3 days until emergence ended. To estimate STE in a non-gravel control, 300 eggs were placed in incubation trays for each test.

From 1987 to 1989, I conducted four STE experiments, two with brown trout and two with Colorado River cutthroat trout. I devised 55 treatment substrates of various compositions (Table 11) and tested at least three replicates of each substrate.

To assess the relation of the various measures of substrate composition to STE, I created skewed, uniform, and geometric distributions of sediment less than 3.35 mm in diameter in each test substrate (Table 11). For example, the test substrates consisting of 30% sediment less than 3.35 mm in diameter contained essentially no sediment less than 1.7 mm in diameter (skewed), roughly equal proportions of sediment from 1.7 mm to less than 0.212 mm (uniform), or increasing proportions of sediment from less than 0.212 mm to 1.7 mm (geometric). Due to changes in my method of designing substrate composition, substrates with the same name (e.g., 30% less than 3.35 mm in a skewed distribution) that were used in experiments with both species had slightly different compositions.

To obtain substrates of different size classes, I sorted

material on a mechanical shaker through sieves of 10 mesh sizes (mm): 50, 25, 12.5, 9.5, 6.3, 3.35, 1.70, 0.85, 0.425, and 0.212; smaller particles were collected on a pan attached to the last sieve. For the brown trout tests, particles larger than 6.3 mm consisted largely of alluvial material and those less than 6.3 mm largely of angular silica. In the Colorado River cutthroat trout tests, all substrate consisted of alluvial material collected from a stream containing a naturally reproducing population of this species.

For each substrate, I calculated several different statistics representing measures of the central tendency. To calculate the geometric mean, I used the formula (Lotspeich and Everest 1981):

$$D_g = D_a^{P_a} * D_b^{P_b} * \ldots D_i^{P_i}$$

where

D_g = the geometric mean, in mm;

D_i = the mean diameter, in mm, of material retained on sieve i, and

P_i = the proportion of the entire sample made up of material retained on sieve i.

Platts et al. (1979) graphed substrate composition on log-probability paper to calculate the graphic geometric mean:

$$D_{gg} = (D_{84} * D_{16})^{0.5}$$

where

D_{84}, D_{16} = the substrate diameter below which 84% and 16% of the sample lies.

The sample median, D_{50}, was also determined from graphs. In addition, Shirazi and Seim (1979) demonstrated a least-squares regression

Table 11. Percentages of Each Substrate Size Class in the Treatment Substrates. Type is the General Description of Each Treatment Substrate; the First and Second Numbers Define the Approximate Percentage of Substrate Less Than a Given Size (mm) and the Letter Defines the Distribution of this Fine Substrate as Skewed (s), Uniform (u), or Geometric (g). The First 24 Treatment Substrates Were Used in the Brown Trout Tests, the Next 15 in the 1988 Cutthroat Trout Test, and the Final 16 in the 1989 Cutthroat Trout Test.

	Sieve size (mm)										
Type	50	25	12.5	9.5	6.3	3.35	1.70	0.85	0.42	0.21	0.0
1987 and 1988 brown trout tests											
7.5-0.85-s	1.8	26.5	34.8	7.7	11.0	4.0	5.2	6.0	2.7	0.2	0.0
7.5-0.85-u	1.8	26.5	34.8	7.7	11.0	4.0	5.1	3.0	1.8	2.6	1.7
7.5-0.85-g	1.8	26.5	34.8	7.7	11.0	4.0	5.1	4.2	2.4	1.5	1.0
15-1.70-s	1.8	24.9	32.7	7.1	10.4	3.7	7.6	11.3	0.4	0.0	0.0
15-1.70-u	1.8	24.9	32.7	7.1	10.4	3.7	5.2	5.0	2.6	3.7	2.4
15-1.70-g	1.8	24.9	32.7	7.1	10.4	3.7	6.1	8.5	2.3	1.5	0.9
25-3.35-s	1.6	22.7	30.0	6.7	9.5	3.6	26.0	0.1	0.0	0.0	0.0
25-3.35-u	1.6	22.7	30.0	6.7	9.5	3.5	7.2	6.8	3.5	5.0	3.3
25-3.35-g	1.6	22.7	30.0	6.7	9.5	3.5	15.5	6.9	1.8	1.3	0.8
5-0.85-s	2.0	27.2	35.8	7.8	11.2	4.2	5.2	4.6	1.8	0.2	0.0
5-0.85-u	2.0	27.2	35.8	7.8	11.2	4.2	5.2	2.6	1.2	1.7	1.1
5-0.85-g	2.0	27.2	35.8	7.8	11.2	4.2	5.2	3.2	1.5	1.1	0.7
10-0.85-s	1.8	25.7	34.0	7.3	10.7	3.9	5.0	7.5	3.6	0.3	0.0
10-0.85-u	1.8	25.7	34.0	7.3	10.7	3.9	5.0	3.4	2.3	3.4	2.2
10-0.85-g	1.8	25.7	34.0	7.3	10.7	3.9	5.0	4.9	3.0	2.2	1.4
10-1.70-s	1.8	26.2	34.7	7.5	10.8	4.0	6.9	7.6	0.3	0.0	0.0
10-1.70-u	1.8	26.2	34.7	7.5	10.8	4.0	5.3	3.5	1.8	2.6	1.7
10-1.70-g	1.8	26.2	34.7	7.5	10.8	4.0	5.9	5.7	1.5	1.0	0.6
20-1.70-s	1.7	23.3	30.8	6.7	9.7	3.5	8.4	15.1	0.5	0.0	0.0
20-1.70-u	1.7	23.3	30.8	6.7	9.7	3.5	5.1	6.9	3.6	5.1	3.3
20-1.70-g	1.7	23.3	30.8	6.7	9.7	3.5	6.4	11.4	3.1	2.0	1.3
30-3.35-s	1.5	21.2	28.0	6.2	8.8	3.3	30.9	0.1	0.0	0.0	0.0
30-3.35-u	1.5	21.2	28.0	6.2	8.8	3.2	8.4	8.3	4.3	6.1	4.0
30-3.35-g	1.5	21.2	28.0	6.2	8.8	3.2	18.2	8.2	2.2	1.5	1.0

Table 11, continued.

Type	Sieve size (mm) 50	25	12.5	9.5	6.3	3.35	1.70	0.85	0.4	0.2	0.0
1988 Colorado River cutthroat trout test											
5-0.85-s	2.0	27.2	35.8	7.8	11.2	5.7	3.3	2.0	5.0	0.0	0.0
5-0.85-u	2.0	27.2	35.8	7.8	11.2	5.7	3.3	2.0	1.7	1.7	1.7
5-0.85-g	2.0	27.2	35.8	7.8	11.2	5.7	3.3	2.0	2.8	1.5	0.7
10-0.85-s	1.8	25.7	34.0	7.3	10.7	5.3	3.2	1.8	10.0	0.0	0.0
10-0.85-u	1.8	25.7	34.0	7.3	10.7	5.3	3.2	1.8	3.3	3.3	3.3
10-0.85-g	1.8	25.7	34.0	7.3	10.7	5.3	3.2	1.8	5.7	2.8	1.5
10-1.70-s	1.8	26.2	34.7	7.5	10.8	5.5	3.3	10.0	0.0	0.0	0.0
10-1.70-u	1.8	26.2	34.7	7.5	10.8	5.5	3.3	2.5	2.5	2.5	2.5
10-1.70-g	1.8	26.2	34.7	7.5	10.8	5.5	3.3	5.3	2.7	1.3	0.7
20-1.70-s	1.7	23.3	30.8	6.7	9.7	4.8	2.8	20.0	0.0	0.0	0.0
20-1.70-u	1.7	23.3	30.8	6.7	9.7	4.8	2.8	5.0	5.0	5.0	5.0
20-1.70-g	1.7	23.3	30.8	6.7	9.7	4.8	2.8	10.7	5.3	2.7	1.3
30-3.35-s	1.5	21.2	28.0	6.2	8.8	4.3	30.0	0.0	0.0	0.0	0.0
30-3.35-u	1.5	21.2	28.0	6.2	8.8	4.3	6.0	6.0	6.0	6.0	6.0
30-3.35-g	1.5	21.2	28.0	6.2	8.8	4.3	15.5	7.7	3.8	2.0	1.0
1989 Colorado River cutthroat trout test											
0-1.7-s	2.1	29.2	38.5	8.4	12.1	6.1	3.6	0.0	0.0	0.0	0.0
7.5-0.85-s	1.8	26.5	34.8	7.7	11.0	5.5	3.3	1.8	7.5	0.0	0.0
7.5-0.85-u	1.8	26.5	34.8	7.7	11.0	5.5	3.3	1.8	2.5	2.5	2.5
7.5-0.85-g	1.8	26.5	34.8	7.7	11.0	5.5	3.3	1.8	4.3	2.1	1.1
15-1.70-s	1.8	24.9	32.7	7.1	10.3	5.1	3.1	15.0	0.0	0.0	0.0
15-1.70-u	1.8	24.9	32.7	7.1	10.3	5.1	3.1	3.8	3.8	3.8	3.8
15-1.70-g	1.8	24.9	32.7	7.1	10.3	5.1	3.1	8.0	4.0	2.0	1.0
20-3.35-s	1.7	24.2	32.0	7.0	10.1	5.0	20.0	0.0	0.0	0.0	0.0
20-3.35-u	1.7	24.2	32.0	7.0	10.1	5.0	4.0	4.0	4.0	4.0	4.0
20-3.35-g	1.7	24.2	32.0	7.0	10.1	5.0	10.3	5.2	2.6	1.3	0.6
25-3.35-s	1.6	22.7	30.0	6.7	9.4	4.7	25.0	0.0	0.0	0.0	0.0
25-3.35-u	1.6	22.7	30.0	6.7	9.4	4.7	5.0	5.0	5.0	5.0	5.0
25-3.35-g	1.6	22.7	30.0	6.7	9.4	4.7	12.9	6.4	3.2	1.6	0.8
40-3.35-s	1.3	18.1	24.0	5.3	7.6	3.7	40.0	0.0	0.0	0.0	0.0
40-3.35-u	1.3	18.1	24.0	5.3	7.6	3.7	8.0	8.0	8.0	8.0	8.0
40-3.35-g	1.3	18.1	24.0	5.3	7.6	3.7	20.6	10.3	5.2	2.6	1.3

technique to determine the geometric mean. I refer to this statistic as D_{gx}.

To calculate the fredle index of each substrate, I used the formula:

$$F_i = D_g/S_o$$

where

S_o = a sorting coefficient, $(D_{75}/D_{25})^{0.5}$, and

D_{75}, D_{25} = the substrate diameter below which 75% and 25% of the sample lies.

Beschta (1982) suggested that the fredle index could be improved by using the standard deviation of the geometric mean rather than a sorting coefficient. Shirazi and Seim (1979) provided a method of moments formula for determining the geometric standard deviation. I referred to the the geometric mean divided by its standard deviation as the modified fredle index (F_m).

I performed regression analyses using SPSS* (SPSS Inc. 1986) to assess the relation between STE and substrate composition. For each substrate treatment, I calculated the aforementioned measures of central tendency as well as the percentages of fine sediment less than 6.3 mm, 3.35 mm, 1.70 mm, 0.85 mm, 0.425 mm, and 0.212 mm. Prior to any analyses, I applied the arcsine transformation (Zar 1984; p. 286) to normalize STE. For all analyses, $p \leq 0.05$ was accepted as indicating significance.

I used indicator variables in regression analyses (Neter et al. 1983; p. 343) of STE and substrate composition to determine whether data from different years could be combined. I chose to pool the data

if I failed to reject the null hypothesis of no difference in the regression coefficients between species or years. Based on these analyses, I combined the data from both brown trout tests but separately analyzed the two experiments involving Colorado River cutthroat trout.

Tests of the sensitivity of substrate measures to known changes in stream substrates relied on data from two sources. First, I reexamined the data on the modification of substrate composition by spawning brook trout (Young et al. 1989). To assess that modification, I collected freeze-core samples of substrate from egg pockets, from locations in the redd (excluding egg pockets) and from locations immediately adjacent to brook trout redds. After stratifying the samples into upper and lower layers (representing substrates altered and unaltered by spawning fish), these substrates were dried, sieved, and weighed as described above. Due to possible biases associated with the sampling technique (Adams and Beschta 1980; Chapman et al. 1986), I excluded the substrate retained on the 50-mm and 25-mm sieves. I then compared the ability of D_g, F_m, and the percentage of fine sediment less than 0.85 mm to detect the anticipated differences in substrate composition among upper strata samples and among unstratified (recombined) samples. Based on my previous work, I expected to find differences among all three locations using the upper strata samples, and between egg pockets and outside redds using unstratified samples. I used the Wilcoxon signed-rank test to compare locations (Sokal and Rohlf 1981). I considered the level of significance an indicator of sensitivity to changes in

substrate composition.

The second source of field data consisted of substrate samples collected with shovels from new and former redds of Colorado River cutthroat trout. I obtained these samples from two second-order streams, Green Timber Creek and Harrison Creek, in south-central Wyoming that contain naturally reproducing populations of this species. In July 1987, all samples represented egg pockets. I measured the distance from each sample location to a marker on the nearest stream bank. During May 1988, over 1500 m^2 of fine sediment were deposited in Green Timber Creek due to the failure of a trans-basin water pipeline (R. N. Schmal, U. S. Forest Service, Laramie, Wyoming, personal communication). In July 1988 and 1989, I resampled most of these former redds (some were not sampled due to the loss of markers). Again, all samples were dried, sieved, and weighed, and particles larger than 25 mm were excluded from further analyses. After calculating the D_g, F_m, and percentage of fine sediment less than 0.85 mm from each sample, I compared the substrates between years and streams using these statistics. I expected to find no differences between streams in 1987 (only egg pockets were sampled), but, due to the sediment spill, I anticipated that 1987 samples from Green Timber Creek would differ from those collected in 1988 and 1989 and that Harrison Creek samples would differ from Green Timber Creek samples in 1988 and 1989. I used the Wilcoxon signed-rank test to compare between years for each stream and the Mann-Whitney U-test to compare between streams for each year (Sokal and Rohlf 1981). Again, the level of significance was considered an indicator of sensitivity to

change.

RESULTS

The geometric mean accounted for the greatest proportion of variation in STE for two of the three cases (Table 12). In the 1988 test with Colorado River cutthroat trout, the graphic geometric mean had a slightly greater coefficient of determination. Generally, the percentage of substrate less than any given size did not perform as well as the measures of central tendency.

I found significant differences among the STE equations for the combined brown trout tests, the 1988 Colorado River cutthroat trout test, and the 1989 Colorado River cutthroat trout test (Figure 3). In addition, the mean STE in incubator trays varied from 94% ($\pm$ 5%) for brown trout, to 93% ($\pm$ 0%) for Colorado River cutthroat trout in 1988, and to 71% ($\pm$ 17%) for Colorado River cutthroat trout in 1989.

The percentage of fine sediment less than 0.85 mm was the most sensitive indicator of the alteration of substrates by spawning brook trout, especially in unstratified substrates (Table 13). Furthermore, the modified fredle index was a better indicator of change than was the geometric mean for both upper strata samples.

Similarly, the percentage of fine sediment less than 0.85 mm was the most sensitive indicator of change in substrate composition due to the sediment spill in Green Timber Creek (Tables 14 and 15). When using either the modified fredle index or the geometric mean I failed to detect all of the anticipated differences between streams and years.

Table 12. Coefficients of Determination Between the Arcsine Transformation of Survival to Emergence and Various Measures of Substrate Composition for Three Sets of Data. BNT is for the 1987 and 1988 Brown Trout Data (N = 99), CRCT88 is for the 1988 Colorado River Cutthroat Trout Data (N = 45), and CRCT89 is for the 1989 Colorado River Cutthroat Trout Data (N = 57). D_g is the Geometric Mean Particle Size (mm), D_{gr} is the Least-squares Geometric Mean (mm), D_{gg} is the Graphic Geometric Mean (mm), D_{50} is the Median (mm), F_1 is the Fredle Index, F_m is the Modified Fredle Index, and % Fines < is the Percentage of Fine Sediment Less Than a Given Size (mm).

Independent variable	Survival to emergence data		
	BNT	CRCT88	CRCT89
Dg	0.54	0.65	0.58
Dgr	0.46	0.56	0.53
Dgg	0.43	0.67	0.45
D50	0.39	0.51	0.42
F_1	0.47	0.63	0.54
F_m	0.49	0.60	0.47
Log(Dg)	0.54	0.64	0.57
Log(F_1)	0.48	0.58	0.53
Log(F_m)	0.49	0.58	0.54
% Fines <:			
6.3	0.38	0.52	0.46
3.35	0.38	0.52	0.46
1.70	0.27	0.48	0.33
0.85	0.23	0.14	0.33
0.425	0.24	0.25	0.26
0.212	0.24	0.22	0.22

DISCUSSION

Overall, my laboratory studies indicated that the geometric meanwas the best predictor of STE. Furthermore, measures of central tendency that were based on the entire particle distribution e.g., D_g, F_s, and F_m, typically performed better than did other measures that relied on only a portion of the distribution. Based on the reanalysis of other data, Chapman (1988) preferred the log transformation of the fredle index to the geometric mean, but my analyses of the same data indicated that the two measures accounted for almost equal proportions of the variation in STE for several species (Young et al. in press). Sowden and Power (1985) found that the modified fredle index was significantly correlated with survival of embryonic rainbow trout to shortly after hatching, whereas the geometric mean was not. However, the authors relied on a small sample of redds (N = 5) and only estimated survival during a portion of the intragravel phase.

Predicting STE from the percentage of substrate less than a given size proved unsatisfactory, apparently because different distributions of fine sediment less than a single size produced different proportions of STE. For example, in the 1989 test with Colorado River cutthroat trout, the treatments consisting of 25% substrate less than 3.35 mm produced mean STE of 39%, 25%, and 11% from the skewed, geometric, and uniform distributions of that substrate. Consequently, I question the application of models estimating STE from the percentage of fine sediment in a substrate (e.g., Stowell et al. 1983).

Chapman (1988) noted that evaluations of measures of substrate

Table 13. Levels of Significance from the Wilcoxon Signed-rank Test on Substrate Samples from in or near Brook Trout Redds Using Three Different Measures of Substrate Composition. Comparisons Are of Upper Strata Samples or Unstratified Samples from Inside and Outside Redds (IR/OR; N = 12), Egg Pockets and Inside Redds (EP/IR; N = 13), and Egg Pockets and Outside Redds (EP/OR; N = 28). D_g is the Geometric Mean Particle Size (mm), F_m is the Modified Fredle Index, and % Fines is the Percentage of Sediment Less Than 0.85 mm.

Sample	Substrate measure	Comparisons		
		IR/OR	EP/IR	EP/OR
Upper Strata				
	D_g	0.023	0.055	0.001
	F_m	0.008	0.039	<0.001
	% Fines	0.005	0.007	<0.001
Unstratified				
	D_g	0.117	0.075	0.002
	F_m	0.071	0.055	<0.001
	% Fines	0.071	0.033	<0.001

Table 14. Levels of Significance from the Wilcoxon Signed-rank Test Using Three Different Measures of Substrate Composition. I Used Substrate Samples from New or Former Egg Pockets of Colorado River Cutthroat Trout Collected from Two Streams in Three Years. For Green Timber Creek, Comparisons Are of Samples from 1987 and 1988 (87/88; $N = 7$), 1988 and 1989 (88/89; $N = 5$), and 1987 and 1989 (87/89; $N = 5$). For Harrison Creek, Comparisons Are of Samples from 1987 and 1988 (87/88; $N = 12$), 1988 and 1989 (88/89; $N = 11$), and 1987 and 1989 (87/89; $N = 12$). D_g is the Geometric Mean Particle Size (mm), F_m is the Modified Fredle Index, and % Fines is the Percentage of Sediment Less Than 0.85 mm.

Stream	Substrate measure	Comparisons 87/88	88/89	87/89
Green Timber				
	D_g	0.128	0.345	0.043
	F_m	0.028	0.225	0.043
	% Fines	0.018	0.500	0.043
Harrison				
	D_g	0.480	0.155	0.239
	F_m	0.689	0.131	0.182
	% Fines	0.845	0.168	0.038

Table 15. Levels of Significance from the Mann-Whitney U-test Using Three Different Measures of Substrate Composition. I Used Substrate Samples from New or Former Egg Pockets of Colorado River Cutthroat Trout Collected from Two Streams in Three Years. Between-stream Comparisons are of Samples from 1987 (N = 20), 1988 (N = 19), and 1989 (N = 17). D_g is the Geometric Mean Particle Size (mm), F_m is the Modified Fredle Index, and % Fines is the Percentage of Sediment Less Than 0.85 mm.

Substrate	Comparisons		
measure	87/88	88/89	87/89
D_g	0.438	0.385	0.009
F_m	0.438	0.083	0.006
% Fines	0.275	0.001	0.009

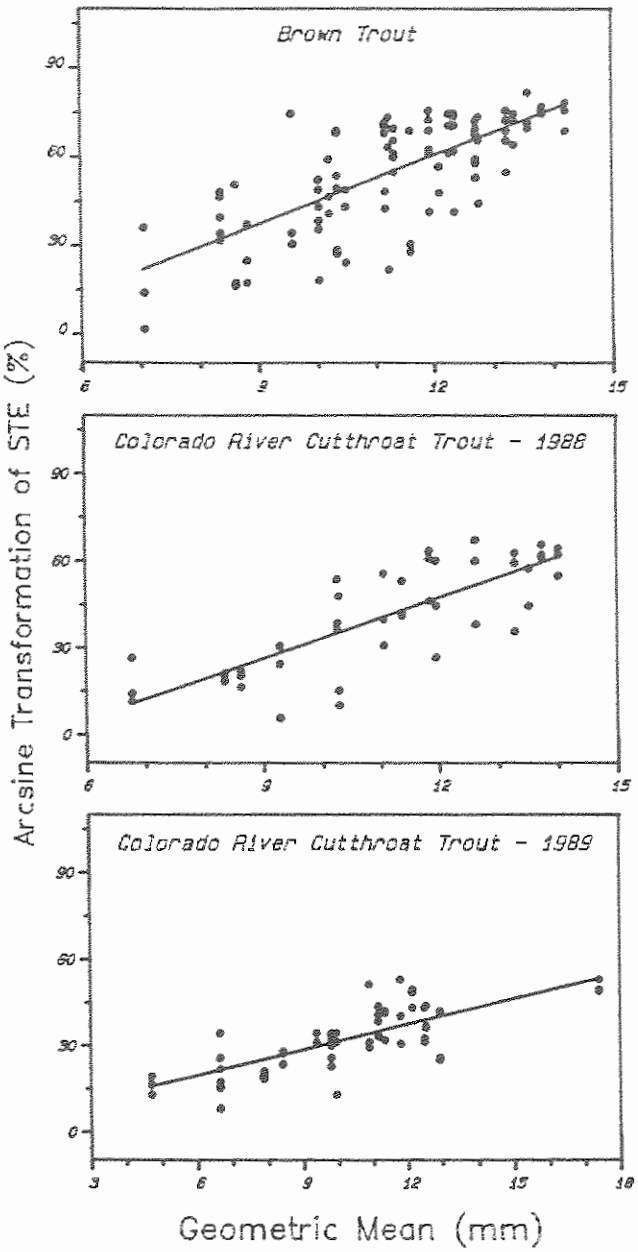

Figure 3. Relation Between Survival to Emergence and the Geometric Mean Particle Size (mm) in Three Laboratory Tests. For Brown Trout, the Equation is Arcsine(Survival to Emergence) = 7.75(Geometric Mean) - 32.53 ($F = 112.65$, $r^2 = 0.54$, $P < 0.0001$, $N = 99$). For Cutthroat Trout in 1988, the Equation is Arcsine(Survival to Emergence) = 7.01(Geometric Mean) - 36.89 ($F = 81.39$, $r^2 = 0.65$, $P < 0.0001$, $N = 45$). For Cutthroat Trout in 1989, the Equation is Arcsine(Survival to Emergence) = 2.98(Geometric Mean) + 1.67 ($F = 75.09$, $r^2 = 0.58$, $P < 0.0001$, $N = 57$).

composition "have produced results that are quantitatively inconsistent among and usually within fish species." He contended that this was largely due to a lack of understanding of the structure of egg pockets. However, I suggested that these inconsistencies may also be created by variation in the inherent viability of eggs from different stocks in different years (Young et al. in press). I believe that the significant differences between regression coefficients from the data for STE of Colorado River cutthroat trout in 1988 and 1989, as well as the differences in STE in the non-gravel control in those two years, support this conclusion.

In the field, the percentage of substrate less than 0.85 mm revealed the expected changes in substrate composition more frequently than the geometric mean or the modified fredle index. Beschta (1982) also noted that the percentage of fine sediment was a better indicator of the intensity of land use than was the geometric mean. However, he speculated that the modified fredle index might be the best statistic for describing the composition of spawning gravels i.e., he implied that the modified fredle index might be the best predictor of STE and the most sensitive to changes in substrate composition. But my results suggested that the modified fredle index was outperformed in both contexts by other statistics.

I believe that the percentage of substrate less than a given size was the best indicator of changes in substrate composition because it measured the portion of the particle size distribution that was modified. Thus, the nature of an impact on stream substrates may dictate the most appropriate measure of substrate composition. For

example, debris torrents produce deep scouring of stream channels and alter the proportion of many sizes of substrate; these changes might best be detected by using a measure of central tendency (R. Marston, Department of Geography and Recreation, University of Wyoming, Laramie, WY, personal communication). Alternatively, bank erosion of floodplain alluvium would primarily introduce fine sediment; such changes might best be detected using the percentage of substrate less than a given size.

Sheridan et al. (1984) made a plea for the standardization of measures of substrate composition in western North America, in hopes that a single measure would be selected. However, I have demonstrated that a single measure would be inadequate to describe both the potential STE in a substrate and to detect the alteration of that substrate by land management or fish behavior.

CHAPTER VI

BIASES ASSOCIATED WITH FOUR STREAM SUBSTRATE SAMPLERS

Fisheries biologists frequently sample substrate composition in streams to assess substrate quality for spawning by salmonids (Stowell et al. 1983) or to detect changes in substrate composition caused by land management (Scrivener and Brownlee 1989). To obtain substrate samples, biologists generally have used one of three sampling devices: single-probe freeze-core samplers (Walkotten 1976), triple-probe freeze-core samplers (Everest et al. 1980), or McNeil samplers (McNeil and Ahnell 1960). Variations of all these samplers have been developed (Koski 1966, Ringler and Hall 1988, this paper). In addition, shovels have been used to collect substrate samples (P. Carling, Freshwater Biological Association, Far Sawrey, Ambleside, Cumbria, United Kingdom, personal communication).

Each technique samples the substrate in a different way, but these differences have been assumed to have little effect on the composition of the sample (Shirazi and Seim 1979). The freeze-core sampler freezes interstitial water and nearby substrate to probes that have been driven into the stream bottom. After some interval, the probes are extracted with the sample attached. McNeil samplers are forced into the substrate, then the material is collected by scooping it behind a rim inside the sampler. Shovels simply skim through the

upper layers of the stream bottom. The insertion of all these devices disturbs the substrate before the sample is extracted.

I questioned the assumption that samples of identical composition were collected by these techniques. My objectives were to: 1) determine whether samples that were collected from identical substrates by different techniques would have identical compositions; 2) determine whether samples that were collected from test substrates would duplicate the composition of those substrates; 3) assess the variation in substrate composition associated with samples taken using each technique; and 4) identify the particle sizes that were under or oversampled by each technique.

METHODS

All tests were conducted at the Sediment Laboratory in the University of Wyoming Department of Range Management from 22 March to 18 April 1989. I compared samples collected by four devices: a single-probe freeze-core sampler, a triple-probe freeze-core sampler, a McNeil sampler, and a shovel.

I designed ten test substrates for these experiments (Table 16). Substrates A-G were devised to rigorously test any biases associated with the samplers. Alternatively, substrates H-J represented samples collected from redds of brook trout (M. K. Young, unpublished data), Colorado River cutthroat trout (Appendix C), and coho salmon (K V. Koski, National Marine Fisheries Service, Auke Bay, Alaska, unpublished data), respectively. I created eight replicates of the first four substrates and 16 replicates of the last six substrates. I took a single sample from each replicate; consequently, I obtained 128

Table 16. Percentages of Each Substrate Size Class in the Test Substrates. Type is the Label for Each Test Substrate.

	Sieve size (mm)										
Type	50	25	12.5	9.5	6.3	3.35	1.70	0.85	0.42	0.21	0.0
A	9.1	9.1	9.1	9.1	9.1	9.1	9.1	9.1	9.1	9.1	9.1
B	9.1	9.1	9.1	6.1	12.2	6.7	13.4	12.5	6.6	9.3	6.0
C	16.7	15.2	13.6	12.1	10.6	9.1	7.6	6.1	4.5	3.0	1.5
D	16.7	15.2	13.6	8.1	14.7	6.7	11.2	7.4	2.7	2.2	1.4
E	1.5	3.0	4.5	4.1	9.7	6.7	15.5	17.6	10.3	16.4	10.7
F	9.1	9.1	9.1	6.1	12.2	6.7	20.0	14.8	5.6	4.5	2.9
G	3.0	6.1	9.1	8.1	19.2	6.7	13.4	12.5	6.6	9.3	6.0
H	0.0	0.0	27.7	5.3	11.8	12.2	22.9	14.6	3.3	1.4	0.8
I	10.8	24.8	19.7	4.5	10.3	8.0	12.6	6.1	1.6	1.0	0.6
J	5.2	24.6	19.9	3.3	9.6	5.9	8.4	5.1	3.1	9.0	5.8

samples. From test substrates A and C I collected four samples each with the single-probe and triple-probe freeze-core samplers, and from substrates B and D I collected four samples each with the McNeil sampler and shovel. I collected four samples with each device from the remaining six test substrates.

To obtain substrate particles of different sizes, I sorted material on a mechanical shaker through sieves of 10 mesh sizes (mm): 50, 25, 12.5, 9.5, 6.3, 3.35, 1.70, 0.85, 0.425, and 0.212; smaller particles were collected on a pan attached to the last sieve. To create each substrate replicate, I mixed the specified amounts (by weight) of each size class in a large rotating bin. After mixing for 15 sec, I poured each substrate into a sampling container. Finally, I filled the sampling container with water until the top of each test substrate was submerged at least 3 cm. Water temperature remained constant at 18.5°C.

Because each device collects substrate differently, I devised separate sampling techniques that allowed all particle sizes to be available to each device. Substrates for both freeze-core samplers and the McNeil sampler were placed in 20 cm by 20 cm by 35 cm plastic buckets. However, test substrates for the McNeil sampler weighed 12.7 kg and for the freeze-core samplers weighed 20.0 kg. This should have accommodated the tendency of freeze-core samplers to collect long, relatively narrow samples (Carling and Reader 1981) and the tendency of McNeil samplers to collect shorter samples (especially if insertion of this device is hampered by large substrate particles).

To obtain freeze-core samples, I drove either one or three steel

probes, 50 cm long and 2 cm in diameter, to the bottom of the plastic bucket containing a test substrate. For the triple-probe freeze-core sampler, a steel template held the probes in an equilateral triangle with 5 cm sides (Everest et al. 1980). I froze the sample to the probe(s) by injecting liquid carbon dioxide for 2 min into each probe. Next I lifted the probe(s) from the sampling container and thawed each sample in a separate plastic bucket.

The McNeil sampler had a tube diameter and tube length of 15 cm. It was twisted into the substrate 15 cm and all material within the tube was scooped by hand onto a retaining rim. Afterwards, the sampler was lifted from the substrate, and the material on the rim was washed into a separate plastic bucket.

Test substrates for shovels weighed 10 kg and were placed in 25 cm by 38 cm by 13 cm plastic trays. I inserted a pointed 21 cm by 28 cm shovel at a 90° angle into the substrate, then lifted the sample from the tray. After allowing it to drain for 5 sec, the sample was placed into a plastic bucket.

I dried all samples in an electric drier at 60°C for at least 72 hours. Next, I sieved the samples as described above and weighed the amount retained on each sieve on an electronic balance. I described the composition of the samples by calculating the proportion of material retained on each sieve and by calculating the geometric mean particle size (by the method of moments; Lotspeich and Everest 1981).

Adams and Beschta (1980), Lotspeich and Reid (1980) and Chapman et al. (1986) noted that some devices do not accurately sample large particles. Before comparing samples, I regressed the frequency of

particles greater than 50 mm in samples with that frequency in test substrates. I concluded that if this particle size was consistently absent from certain samples, I would eliminate it from further analyses and recalculate the proportions of the other particle sizes in the samples and test substrates. Furthermore, I would test for differences in the presence of these particles among samples collected by different samplers using the G test (Zar 1984).

To determine if there were differences in substrate composition among samples and between samples and test substrates, I compared the proportions of each particle size using the Wilcoxon signed-rank test (Sokal and Rohlf 1981). Because these proportions were not independent, I applied the Bonferroni procedure to produce an experiment-wide alpha of 0.1 (alpha for individual comparisons = 0.01) for all nonparametric tests (Neter et al. 1985). For all other tests, I considered $P \leq 0.05$ as indicating significance.

I further assessed differences in substrate composition between samples and test substrates by comparing their geometric means. I calculated means and standard errors before conducting planned comparisons using t-tests (Sokal and Rohlf 1981). In contrast to my analysis of separate particle sizes, this analysis should have been much less affected by the presence or absence of particles larger than 50 mm in diameter. Therefore, I retained all particle sizes for the calculation of the geometric mean.

RESULTS

The frequency of substrate particles greater than 50 mm in diameter in samples was positively correlated with the frequency of

such particles in the test substrates (N = 10, P = 0.001, r^2 = 0.81). However, I failed to reject the null hypothesis of no differences in the presence of those particles in samples collected by the four devices (N = 35, P > 0.5). For my analysis of proportions of individual particle sizes, I excluded particles larger than 50 mm in diameter and recalculated the proportions for the other sizes.

I found significant differences between test substrates and samples collected by the four methods for several particle sizes (Table 17). Of these, single-probe freeze-core samples differed most often and McNeil and shovel samples differed least often from the test substrates. All devices undersampled particles 6.3-9.5 mm and less than 0.212 mm in diameter. Both freeze-core samplers oversampled particles 25-50 mm in diameter.

Similarly, the samples collected by most of the devices significantly differed for at least one particle size (Table 18). But there were no differences between samples collected by the freeze-core samplers, and only one difference between samples collected by McNeil samplers and shovels. Freeze-core samples contained greater proportions of substrate 25-50 mm and less than 0.212 mm in diameter than did McNeil and shovel samples, which contained greater proportions of intermediate sizes.

Finally, means of geometric means of samples significantly differed from the geometric means of several of the test substrates (Table 19). Also, 28 of the 32 sample geometric means exceeded those of the test substrates. Of the samples collected by the four devices, the geometric means of single-probe freeze-core samples were generally

Table 17. Comparisons of Proportions of Substrate Retained on Sieves of Different Sizes Between the Test Substrates and Substrate Samples Collected by Four Devices. Single-probe Freeze-core Samples Are Represented by FC1, Triple-probe Freeze-core Samples by FC3, McNeil Samples by McN, and Shovel Samples by Shv. An Inequality Sign Indicates a Significant Difference Between Samples Collected by a Device and the Test Substrates.

Sieve size (mm)	Device			
	FC1	FC3	McN	Shv
25.0	>	>		
12.5				
9.5				
6.3	<	<	<	<
3.35	<		>	>
1.70	<	<		
0.85	<			
0.425				
0.212		>		
<0.212	<	<	<	<

Table 18. Comparisons of Proportions of Substrate Retained on Sieves of Different Sizes Among Substrate Samples Collected by Four Devices. Single-probe Freeze-core samples Are Represented by FC1, Triple-probe Freeze-core Samples by FC3, McNeil Samples by McN, and Shovel Samples by Shv. An Inequality Sign Indicates the Significant Difference of the Upper Sample from the Lower Sample.

	Devices					
Sieve size (mm)	FC1: FC3	FC1: McN	FC1: Shv	FC3: McN	FC3: Shv	McN: Shv
25.0		>	>	>		
12.5				>		<
9.5						
6.3				<	<	
3.35		<	<	<	<	
1.70		<	<	<	<	
0.85		<				
0.425						
0.212				>		
<0.212		>	>	>	>	

Table 19. Arithmetic Means (and Standard Errors) of Geometric Mean Particle Sizes (mm) of Samples Collected by Four Devices from Ten Substrates of Varying Composition. Substrate is the Test Substrate Label and its Geometric Mean. Single-probe Freeze-core Samples Are Represented by FC1, Triple-probe Freeze-core Samples by FC3, McNeil Samples by McN, and Shovel Samples by Shv. An asterisk indicates significance at $P \leq 0.05$.

Substrate	Device			
	FC1	FC3	McN	Shv
A 3.6	14.1 (8.1)	6.8 (2.8)	----	----
B 3.9	----	----	5.9 (2.3)	7.0 (2.1)
C 9.9	23.7 (10.2)	20.9* (4.3)	----	----
D 9.9	----	----	8.9 (1.5)	14.7* (1.3)
E 1.5	2.7 (0.9)	2.6* (0.4)	2.3* (0.3)	2.3* (0.5)
F 4.7	15.3* (6.2)	7.8 (2.3)	4.3 (1.6)	6.5 (2.0)
G 3.3	6.2 (5.0)	4.6* (0.5)	3.1 (0.6)	4.0 (0.5)
H 4.8	4.7 (0.8)	5.0 (0.7)	5.0 (0.2)	5.3 (0.5)
I 11.8	17.4 (8.2)	17.2 (4.7)	13.6 (3.4)	15.2 (4.5)
J 6.7	13.3* (3.9)	11.6* (1.9)	8.9 (1.9)	7.1 (1.8)

the largest and varied the most. Alternatively, geometric means ofMcNeil samples usually varied the least and frequently were close to the geometric mean of the test substrates.

DISCUSSION

Substrate composition of samples collected by all devices often differed from the composition of test substrates, both for individual particular sizes and for the geometric means. These differences indicate biases associated with the samplers, especially for the larger particles, but may also suggest problems with the sampling techniques. For example, the insertion of all samplers disturbed the substrate. Such disturbance could cause fine sediment to displaced deeper into the substrate or downstream by the current and lead to undersampling of this size. Field studies (Everest et al. 1982, Young et al. 1989) have reported that fine sediment increases with depth in the substrate, but they may actually be detecting infiltration associated with sampling. This problem requires further investigation.

Both freeze-core samplers, particularly the single-probe sampler, tended to oversample large particles. Consider that only for the test substrate lacking particles 25-50 mm and larger than 50 mm in diameter did the mean of the single-probe samples underestimate the geometric mean of that substrate. Adams and Beschta (1980) also reported that the single-probe freeze-core sampler was biased in favor of large particles; they hypothesized that only a small portion of a large particle needed to be frozen to the probe to be sampled. Lotspeich and Reid (1980) suggested that the triple-probe freeze-core

sampler would overcome this problem, but I found that it also oversampled large particles.

Interestingly, I found virtually no differences in the substrate composition of samples collected by similar samplers i.e., between both freeze-core samplers and between the McNeil sampler and shovel. Again, this conflicted with the suggestion that the triple-probe freeze-core sampler should collect less biased samples than the single-probe device (Everest et al. 1980). And my finding of differences in the samples collected by dissimilar samplers contrasted with the suggestion that freeze-core and McNeil samples are similar (Everest et al. 1980, Lotspeich and Reid 1980, Shirazi and Seim 1981). However, Ringler (1970) also reported differences between freeze-core and McNeil samples.

The variation in substrate composition of samples taken by the triple-probe freeze-core sampler, McNeil sampler, and shovel was moderate. But the extreme variation of single-probe freeze-core samples reduces the value of this technique for field surveys. Adams and Beschta (1980) reported large spatial and temporal variation in the composition of stream substrates, but they did not quantify the proportion of that variation that was caused by their use of a single-probe freeze-core sampler. Crisp and Carling (1989), using this device, failed to detect significant differences in substrate composition at sites before and after spawning by brown trout. Yet Young et al. (1989) noted a significant reduction in fine sediment in stream substrates after spawning by brook trout, based on samples collected with the same technique. These contrasting results may

reflect initial differences between study areas in the composition of substrates that increased the the variability of single-probe freeze-core samples. Young et al. (1989) excluded particles larger than 25 mm in diameter from their analyses, which probably improved the precision of their samples. Nonetheless, Shirazi and Seim (1981) suggested that sampling with a single-probe freeze-core sampler in coarse substrates was unreliable. And I noted the tendency for the variance of these samples to increase as the geometric mean of the test substrate increased.

Based on the relatively low variances associated with McNeil samples, and on their frequent proximity of their geometric mean to the mean of the test substrates, I consider the McNeil sampler to be the most accurate device for assessing overall substrate composition. Furthermore, this accuracy might be enhanced by including a suction mechanism inside the sampling tube to improve the retention of fine sediment (Koski 1966). Interestingly, shovel samples were quite similar to McNeil samples. Because sampling with a shovel is faster and easier, I recommend further laboratory and field comparisons of these two sampling techniques.

Freeze-core samplers remain useful, because only this technique allows the stratification of a sample and an assessment of changes in substrate composition with depth (Everest et al. 1980). But neither freeze-core sampler accurately sampled the known substrate composition. Perhaps further refinements of these devices, such as a greater spread between probes, additional probes, or longer freezing

intervals, could reduce the imprecision and biases associated with their samples.

CHAPTER VII

SUMMARY AND MANAGEMENT GUIDELINES

As stated in Chapter 1, the goals of my research were to develop a field-validated model of survival to emergence for Colorado River cutthroat trout and a laboratory model of survival to emergence for brown trout. To achieve these goals, I conducted field and laboratory experiments on substrate permeability, substrate measurement, and substrate sampling, as well as developing laboratory models of survival to emergence for both species (Chapters 2-6). In support of these experiments, I also obtained information on the alteration of substrate composition by spawning brook trout, on the measurement of permeability with a new technique, on the substrate composition of egg pockets in redds of Colorado River cutthroat trout, and on the survival to emergence of Colorado River cutthroat trout in the field (Appendices A-D).

I demonstrated that permeability measurements collected by one person at a single site often significantly differed from the those collected by a different person at that same site (Young et al. 1989a). Furthermore, the variation associated with the standard technique (Terhune 1958) prevented the meaningful estimation of permeability from a single measurement. By replacing the hand-powered suction device with an electric vacuum pump, I substantially reduced

the variation of permeability measurements (Appendix B). But comparisons of substrate composition and permeability to survival to emergence in the 1988 brown trout test indicated that substrate composition alone was a better predictor of survival to emergence than was permeability.

No model of survival to emergence has been successfully validated in the field. Furthermore, Chapman (1988) believed that no laboratory experiments adequately mimicked the natural intragravel environment; consequently, he concluded that no laboratory model would accurately predict survival to emergence in the field. He proposed field and laboratory experiments (based on a review of the literature and reanalysis of data therein) designed to improve our understanding of redd structure, to determine which variables should be measured to estimate survival to emergence, and to estimate survival to emergence in natural redds.

Though I agreed with Chapman that we need to better understand the structure and function of egg pockets in redds, I disagreed with his proposed experiments (Young et al. in press). He suggested capping natural redds to estimate survival to emergence, but the variation in egg deposition and viability, coupled with the difficulty in obtaining enough redds to sample, may preclude widespread use of this technique. I also questioned the statistical reliability of his analyses, and presented additional analyses of the same data which led me to reach different conclusions about variable selection for estimating survival to emergence. Finally, I stated that existing laboratory data on survival to emergence could be successfully applied

to the field, but that field conditions must meet those used in the laboratory.

I successfully developed a laboratory model of survival to emergence for brown trout (Young et al. in review). Of the variables tested, the geometric mean particle size accounted for the greatest proportion of the variation in survival to emergence. The percentage of fine sediment less than a given size was a poorer predictor of survival to emergence. These relations also held for Colorado River cutthroat trout (Chapter 5). However, the percentage of fine sediment less than a given size was more sensitive to changes in stream substrate composition caused by spawning brook trout and by a sediment spill than was the geometric mean. Thus the selection of a measure of substrate composition relies on the objectives of the sampling program.

Additionally, one must consider the effects of the device selected for substrate sampling. In my laboratory experiments, the samples collected by different devices often significantly differed, because each device is biased with respect to different particle sizes (Chapter 6). These biases led to significant differences in substrate composition between samples and the test substrates from which they were drawn. I concluded that the McNeil sampler was the most accurate and precise device for sampling stream substrates. Nonetheless, freeze-core samplers preserve the vertical stratification of substrates, which may be important in studies of egg pockets (Young et al. 1989b), and further improvements of this device could reduce its biases.

Based on the results of this research, I have developed a general strategy for monitoring substrate composition and for estimating its effects on survival to emergence. First, I emphasize that the models of survival to emergence for brown trout and Colorado River cutthroat trout should be used as indexes of the potential effect of substrate alteration by land management on the survival to emergence of these species. Because neither model has been successfully validated in the field (Appendix D), the accurate prediction of survival to emergence in the field is not possible unless the laboratory conditions present in the development of these models match those found in the field. Those conditions include dissolved oxygen concentration, intragravel water velocity, and substrate composition. Sampling of the latter variable has been described; sampling of the first two variables is also difficult, but techniques have been developed (Scrivener 1988; Orchard 1988).

The recommended strategy for sample location is simple but strict; substrate samples designed to estimate survival to emergence must be collected from the egg pocket (Chapman 1988, Young et al. 1989b). For the detection of changes in substrate composition due to land management, I suggest establishing fixed sampling locations. The number of locations needed will be determined by the proportion of change in substrate composition that one wishes to detect. In unstable stream channels, samples should be collected from specific locations in similar habitat types (Bisson et al. 1982) e.g., from the tails of pools, etc.

The timing of sampling to assess survival to emergence is

dependent on the dynamics of sediment transport (Young et al. 1989b). If bedload and suspended load transport are largely absent during incubation of the eggs and alevins, then sampling can occur anytime after spawning but before emergence has ended. This might be appropriate for spring-spawning species such as the Colorado River cutthroat trout (but note that a particularly severe thunderstorm may be sufficient to induce sediment transport; M. Bozek, Department of Zoology and Physiology, University of Wyoming, personal communication). The effect of sediment intrusion during incubation is unknown, but Everest et al. (1987) suggested sampling during the midpoint of emergence under these circumstances. Grost (1989) demonstrated that sediment transport occurred during the incubation of embryos of fall-spawning brown trout in a Wyoming stream. He attributed this transport to channel changes caused by surface ice formation. In streams lacking surface ice during winter, sediment transport may be minor, and samples could be taken anytime during incubation. For simply detecting changes in substrate composition caused by land management, one should sample at the same time each year. This could be modified if short-term changes are important i.e., one could sample immediately before and after a specific land management activity.

Finally, the preferred measure and sampler of substrate composition depends on the objectives of the sampling scheme. To estimate survival to emergence, one should measure the geometric mean. To detect changes in substrate composition caused by land management, one should select the measure most likely to change due to a specific

activity. Furthermore, the most accurate device for sampling stream substrates is the McNeil sampler, but shovel samples are almost as good and can be collected much more quickly and easily. Alternatively, freeze-core samplers provide fairly exact information on the vertical composition of substrates, but they are labor- and cost-intensive.

APPENDIX A

SUBSTRATE ALTERATION BY SPAWNING BROOK TROUT IN A SOUTHEASTERN WYOMING STREAM

Fine sediment often affects the survival of embryonic trout and salmon (Cordone and Kelly 1961; Iwamoto et al. 1978; Everest et al. 1987). Survival to emergence of salmonid embryos decreases as the quantity of fine sediment in the incubation substrate increases (Phillips et al. 1975; Witzel and MacCrimmon 1983a). To determine the consequences of human-induced sediment introduction into spawning streams, researchers have linked models that predict sediment delivery (e.g., Cline et al. 1981) with sediment-related predictions of survival to emergence (e.g., Tappel and Bjornn 1983). Stowell et al. (1983), who used this approach, suggested that predictions of survival to emergence might be based on substrates collected before the spawning season. This implies that increases in fine sediment deposition before spawning will be reflected in the substrate composition of redds--i.e., that there is a direct relation between pre-spawning and post-spawning substrates.

Everest et al. (1987) stated that salmonids are not passive users of substrates, but that they distinctively modify substrate composition during redd construction. For example, McNeil and Ahnell (1964) suggested that pink salmon removed 3600 kg of sediment less than 0.1 mm in diameter from a single spawning riffle. Helle (1970)

reported a 3.6% decrease in sediment less than 0.8 mm in diameter after the spawning of pink salmon. Compared to 1-year-old redds, new redds of coho salmon contained 25% less sediment less than 3.33 mm (Ringler and Hall 1988). Thus, predicting the survival to emergence of embryos based on the sediment content of undisturbed pre-spawning substrates may be unrealistic.

Most research on substrate modification has focused on large, anadromous salmonids in the Pacific Northwest (Everest et al. 1987). To determine if relatively small resident salmonids could measurably alter substrate composition during spawning in small, high-elevation streams, and if a correlation existed between undisturbed pre-spawning substrates and disturbed post-spawning substrates, I examined substrate modification by brook trout in a second-order mountain stream.

Besides identifying substrate changes caused by spawning, I hoped to collect information on the substrate composition of redds and egg pockets. Salmonid redds usually have a depression in the anterior portion (the pit or pot) and a mound of substrate (the tailspill) that has been excavated from in and upstream of the egg pocket(s) (Ottaway et al. 1981). Though much research has focused on measuring the responses of incubating salmonid embryos to various intragravel environments (e.g., Irving and Bjornn 1984), less work has concentrated on defining the natural environment of embryos (e.g., Tagart 1976). Frequently, survival has been evaluated in laboratory studies of "redds" with artificial structure or substrate composition (Hamor and Garside 1976; MacCrimmon and Gots 1986); yet Chapman (1988)

noted that conditions in the egg pocket, rather than in the entire redd, probably determine embryo survival.

I also studied the depth and location of egg pockets. Some researchers (e.g., Hausle and Coble 1976) appeared to assign a variety of depths to egg pockets of brook trout arbitrarily. From unstratified redd samples, Witzel and MacCrimmon (1983b) estimated that the maximum depth of brook trout egg pockets was 14 cm. Also, Chapman et al. (1986) suggested that the tailspill of a redd may not cover the majority of egg pockets in a redd, but others have found most egg pockets under the anterior portion of the tailspill (Ottaway et al. 1981).

METHODS

I obtained samples from a low-gradient (<1.5%) reach of Telephone Creek, a high-elevation (about 2900 m above mean sea level), second-order stream in the Snowy Range of southeastern Wyoming. Chisholm (1985) reported that its standing stock of brook trout averaged 318 kg/hectare, and that most fish were less than 25 cm long. Mean daily flow in Telephone Creek in September is 0.02 $m^3 s^{-1}$ (Wyoming Water Research Center, unpublished data). I sampled that stream because many brook trout redds had been found there by Reiser and Wesche (1977).

To determine substrate composition before the brook trout spawned, I established 27 transects in riffles, known to be used for spawning, on 28 August 1987 and used a freeze-coring technique (Walkotten 1976) to collect three substrate samples per transect between 29 August and 11 September. After spawning began, I stopped

sampling transects and began sampling redds. I identified redds by the presence of cleaned gravel and characteristic redd morphology. Typically, I removed samples from the pit, the leading third of the tailspill, and from one to four sites outside but within 10 cm of the redd. Occasionally, I took only a single sample from small redds, because one sample disturbed the entire redd.

A variety of substrate sampling techniques have been used to collect samples from redds (Sheridan et al. 1984), and several researchers have noted that fine sediment tends to increase with depth (Adams and Beschta 1980; Everest et al. 1982). Because the freeze-core technique enables one to stratify substrate samples vertically (Everest et al. 1982), one can determine whether either the upper portions of redd samples or the entire sample yields the most information about substrate modification. This also provides an indirect evaluation of the potential efficiency of sampling techniques that do not allow vertical stratification of samples.

I measured water depths at each site, then obtained freeze-core samples by use of a single-probe apparatus similar to that described by Walkotten (1976) along transects and in or near redds. Freeze-core probes were driven 20 cm deep, injected with liquid CO_2 for at least 2 min, and extracted. I collected samples at the downstream end of each redd and progressed upstream.

I collected 81 freeze cores from transects between 2 and 11 September 1987. I first observed redds on 12 September and discontinued transect sampling on that date. By 4 October I had obtained 106 cores from or near 31 redds. Surface area of redds

averaged 1900 cm^2 and weight of the substrate samples averaged 1100 g.

I described three kinds of redd-associated samples. When I found eggs in a core or in the depression created by removal of the core, I defined that core as an egg pocket sample. I considered other cores from disturbed sites but without eggs to be inside-redd samples and defined cores from immediately outside the disturbed area as outside-redd samples. Multiple samples from inside or outside of a single redd were pooled to form an average for each location near that redd. Of the 106 cores, I had 12 pairs of inside-redd and outside-redd samples, 13 pairs of egg pocket and inside-redd samples, and 28 pairs of egg pocket and outside-redd samples.

The three kinds of samples were divided into upper and lower strata. The lower boundary of the upper stratum was defined by the bottom of the egg pocket, the bottom of the area that appeared to have been disturbed by fish, or at the core midpoint if no difference could be detected visually between the lower and upper portions. Transect samples were not stratified. I thawed samples with a propane torch and placed them in plastic bags for transport to the laboratory.

After drying a sample for 72 h at 60°C, I weighed it, sieved it for 8 min on a mechanical shaker, and weighed separately the material retained on sieves with meshes (mm) of 50, 25, 12.5, 9.5, 6.3, 3.35, 1.70, 0.85, 0.425, 0.212, and less than 0.212. Adams and Beschta (1980) excluded large particle sizes from their analysis; they stated that freeze-core samplers may be biased in favor of large particles. Alternatively, Chapman et al. (1986) noted that large particles tended to be lost from frozen cores during extraction of the sample. To

avoid bias in either direction, I excluded particles retained on the 50-mm and 25-mm sieves. However, these large particles appeared more frequently in egg pocket samples (39 and 100%, respectively) than in inside-redd samples (9 and 82%) or outside-redd samples (26 and 84%).

To determine if the substrate composition from the three kinds of samples differed, I compared the proportions of each substrate size from the upper stratum of cores from these locations. After combining upper and lower strata, I again compared redd-associated samples and also compared these to a set of 27 unstratified transect samples that had been collected from the reach that eventually contained the majority of sampled redds. I also examined the differences in substrate composition between upper and lower strata at all three locations by use of a sign test (Sokal and Rohlf 1981). To test for differences among redd-associated samples I used the Wilcoxon signed-rank test, and to compare redd-associated samples with transect samples I used the Mann-Whitney U-test (Sokal and Rohlf 1981).

To evaluate the relation between pre-spawning and post-spawning substrates, I used rank correlation (Mosteller and Rourke 1973) on upper stratum samples to compare the proportion of each substrate size in the three kinds of samples. I assumed that unstratified outside-redd samples were equivalent to samples collected before spawning, and combined the upper and lower strata of the three kinds of redd-associated cores to assess their relation to samples from nearby transects.

I expected spawning brook trout to reduce the proportion of substrate less than 1.7 mm in diameter and correspondingly increase

the proportion of substrate greater than 3.35 mm in diameter inside redds and in egg pockets; thus I used one-tailed tests of significance for those substrate sizes. For substrate from 1.70-3.35 mm (the central size in my set of sieves), I used a two-tailed test. I used the Bonferroni procedure to produce an experiment-wide alpha = 0.09 (alpha for individual comparisons = 0.01) that used to determine significance in all nonparametric tests (Neter et al. 1985).

I calculated both water depth over egg pockets and egg pocket depth in the substrate, and determined whether the pit or the tailspill was more likely to contain an egg pocket based on binomial probabilities (Sokal and Rohlf 1981). For these tests, $P \leq 0.05$ was accepted as indicating significance.

RESULTS

Brook trout altered substrate during spawning; comparisons of substrate sizes 0.85-1.70, 0.425-0.85, 0.212-0.425, and less than 0.212 mm in diameter from upper strata revealed significant differences among egg pocket, inside-redd, and outside-redd samples (Table 20). The number of significant differences in substrate composition among these three kinds of samples decreased when I performed the same tests on samples in which the upper and lower strata were combined. I found no significant differences between inside-redd samples and either outside-redd or egg pocket samples (Table 20).

The relation in substrate composition among the redd-associated locations was inconsistent. Using upper strata, I found no significant correlations in substrate composition among the three kinds of

Table 20. Mean Proportions (Ranges in Parentheses) of Substrate Retained on Sieves from Both Upper Strata Samples and Unstratified Samples Collected Outside Redds (OR; N = 28), Inside Redds (IR; N = 13), in Egg Pockets (EP; N = 31), and from Unstratified Samples Along Transects (TR; N = 27). Significant Differences Between Redd-Associated Samples for a Given Substrate Size Are Based on a Wilcoxon Signed-rank Test, and Between Transects and Other Locations Based on Mann-Whitney U-tests (Alpha for Individual Comparisons = 0.01). Within Each Row for Upper Strata Samples and for Unstratified Samples (Separately), Values with a Letter in Common Are not Significantly Different.

Sieve size (mm)	Sampling Location		
	OR	IR	EP
		Upper strata samples	
12.5	35.4 z (11.9-63.5)	38.7 z (14.1-80.6)	40.8 z (24.8-61.5)
9.5	11.2 z (4.0-17.5)	10.7 z (4.0-20.3)	14.1 z (5.3-40.0)
6.3	11.7 z (5.8-20.8)	11.2 z (3.6-15.8)	12.1 z (4.9-17.5)
3.35	12.0 z (5.1-18.2)	12.7 z (3.6-19.7)	12.2 z (8.8-16.9)
1.70	10.3 z (1.1-18.2)	10.3 z (2.5-17.7)	9.0 z (5.4-15.7)
0.85	8.6 z (0.7-17.5)	8.1 zy (2.0-13.1)	6.4 y (2.4-13.7)
0.425	5.9 z (0.8-11.4)	5.1 y (1.4-8.7)	3.6 x (0.8-7.6)
0.212	2.6 z (0.5-7.6)	1.9 y (0.4-3.0)	1.0 x (0.2-2.0)
<0.212	2.3 z (0.6-9.2)	1.5 y (0.2-2.8)	0.7 x (0.2-1.3)

Table 20, continued.

Sieve size (mm)	Sampling Location			
	OR	IR	EP	TR
	Unstratified Samples			
12.5	29.8 zy (6.4-58.6)	28.8 zy (5.5-50.0)	34.1 z (21.1-61.4)	28.0 y (18.3-37.6)
9.5	9.9 z (3.8-14.4)	8.8 z (2.6-14.6)	11.3 z (6.1-25.6)	9.7 z (6.8-13.8)
6.3	10.5 z (5.0-14.8)	10.0 z (4.1-14.0)	11.1 z (6.1-14.8)	11.5 z (8.0-15.3)
3.35	12.2 z (5.9-15.6)	11.6 z (6.0-14.7)	12.5 z (9.9-15.5)	13.5 y (9.6-15.9)
1.70	11.1 z (3.4-15.6)	11.1 z (7.1-14.0)	10.8 z (6.5-15.1)	11.9 z (8.2-13.6)
0.85	10.1 zy (3.1-15.0)	10.7 zy (7.0-15.7)	9.1 z (3.7-12.8)	10.6 y (7.8-13.4)
0.425	7.5 z (2.5-15.7)	8.7 zy (4.9-20.2)	5.9 y (2.0-8.9)	7.5 z (5.2-10.4)
0.212	4.3 z (1.1-13.8)	5.2 zy (1.4-19.8)	2.4 y (0.8-5.4)	3.4 z (2.0-4.9)
<0.212	4.6 z (1.4-22.4)	5.1 zy (1.3-15.0)	2.7 y (0.8-6.9)	4.0 z (2.5-7.9)

samples. In samples in which the upper and lower strata were combined, I found significant correlations between certain pairs of the three locations for substrates 0.425-0.85, 0.212-0.425, and less than 0.212 mm in diameter (Table 21).

Samples collected before redds were built appeared to be similar to unstratified outside-redd samples. The proportion of sediment retained on the 3.35-mm sieve was the only significant difference between transect samples and both unstratified outside-redd and inside-redd samples. However, unstratified egg pocket samples differed significantly from transect samples at five additional substrate sizes (Table 20).

With regard to vertical substrate properties, upper and lower strata from egg pocket, inside-redd, and outside-redd samples differed significantly at seven, five, and five of the nine substrate sizes, respectively. Lower strata consistently contained a greater proportion of substrate particles 0.85-1.70, 0.425-0.85, 0.212-0.425, and less than 0.212 mm in diameter and a lesser proportion of substrate 12.5-25.0 mm in diameter than did upper strata.

Egg pockets tended to be in shallow water and buried close to the substrate surface in the tailspill of the redd. Mean depth of the water over egg pockets was 8.1 cm (N = 31; SE = 3.7 cm; range, 3.0 to 15.0 cm). The base of egg pockets was 8.4 cm (N = 31; SE = 1.7 cm; range, 5.5 to 12.0 cm) below the streambed surface. Egg pockets were more likely to be found in the leading third of the tailspill than in the pit (28 of 31 egg pockets; $P < 0.002$).

Table 21. Spearman's Rank Correlation Coefficients (Probability in Parentheses) for Substrates Retained on the 0.425, 0.212, and Less Than 0.212 mm Sieves. Comparisons Are of Unstratified Samples from Inside and Outside Redds (IR/OR; N = 12), Egg Pockets and Inside Redds (EP/IR; N = 13), and Egg Pockets and Outside Redds (EP/OR; N = 28). For Individual Comparisons, $P \leq 0.01$ Was Accepted as Indicating Significance. All Comparisons of Larger Sizes Were Nonsignificant.

Sieve size (mm)	Comparisons		
	IR/OR	EP/IR	EP/OR
0.425	0.37 (0.12)	0.03 (0.46)	0.66 (<0.01)
0.212	0.54 (0.03)	0.67 (<0.01)	0.43 (0.01)
<0.212	0.87 (<0.01)	0.74 (<0.01)	0.55 (<0.01)

DISCUSSION

Despite the small size of brook trout in Telephone Creek, their excavation of the substrate during spawning removed sediment less than 1.70 mm in diameter. These reductions in fine sediment parallel those observed for much larger steelhead and Pacific salmon in the Pacific Northwest, though these species also removed larger particles (Everest et al. 1987).

Chapman (1988) contended that egg pockets should be the focus of sampling in evaluations of the intragravel environment of embryonic salmonids. In my study, the differences in substrate composition between upper strata samples from the egg pocket and from inside the redd were striking, and confirmed the unique substrate composition of the egg pocket. My results suggested that researchers should sample the upstream third of the tailspill to locate egg pockets in brook trout redds, but I recognize the difficulty in locating egg pockets consistently. Ideally, researchers would like to characterize intragravel water velocity, dissolved oxygen concentration, and substrate composition to predict survival to emergence of embryonic salmonids, but most techniques for determining intragravel conditions (e.g., Terhune 1958) alter the structure of egg pockets and preclude collection of accurate data on all three variables.

Because I was unable to detect differences between inside-redd and egg pocket locations based on unstratified samples, I concluded that sampling techniques incapable of preserving the vertical stratification of substrates (e.g., sampling with a shovel or McNeil device) may be less informative than the freeze-core technique. This

may be partially due to the increase in fine sediment with depth. Everest et al. (1982) also noted that McNeil samples cannot reveal differences between the upper modified substrate and the undisturbed deeper layers. However, I inferred from my data that one might still differentiate between egg pockets and undisturbed locations by use of unstratified samples. Please note that sampling with either a shovel or McNeil device is much faster than freeze coring, requires less equipment, and is less costly.

Fisheries biologists often assume that increases in fine sediment delivery to a stream will be reflected in the substrate composition of egg pockets, but my failure to find strong correlations between the proportions of fine sediment in upper strata samples from egg pockets and outside redds implies otherwise. Such correlations could develop later during incubation, because fine sediment can rapidly infiltrate egg pockets if streams are transporting such material (Beschta and Jackson 1979). This may happen during the winter incubation of eggs and alevins of fall-spawning salmonids in the Pacific Northwest. Yet, due to high flows in winter that apparently disturbed the upper layer of substrate, gravel quality increased throughout the incubation period in a British Columbia stream (Scrivener 1988). In the central Rocky Mountains, streams may carry little sediment during incubation of embryos of fall-spawning or spring-spawning species because flows (and hence sediment transport) are low or declining during these intervals. Consequently, substrates collected before spawning may not reflect the actual substrate conditions that affect survival to emergence.

Perhaps the lack of a relation between outside-redd (and presumably undisturbed substrates before spawning) and egg pocket substrates is due to brook trout reducing the amount of fine sediment to a given "standard," regardless of the pre-spawning conditions. This interpretation centers on the narrow range in the proportions of substrate 0.212-0.425 and less than 0.212 mm in diameter in the upper strata from egg pocket samples and the broader range of those two sizes in upper strata from outside-redd samples. However, Telephone Creek is relatively undisturbed, and I do not know how brook trout would modify substrates that contain a greater proportion of fine sediment.

I suggest that substrate samples used to predict survival to emergence should be collected after spawning but before the complete emergence of alevins. Additionally, samples from egg pockets should yield the most information about the immediate environment of eggs and alevins of salmonids. My data on egg pocket depth, structure, and location should be useful for designing laboratory tests of survival to emergence of embryonic brook trout; for example, researchers can construct more realistic substrates than those devised in previous studies (Hausle and Coble 1976; Witzel and MacCrimmon 1983a). And these data can be compared to field samples of brook trout spawning sites before redd construction (Witzel and MacCrimmon 1983b) and after spawning (Reiser and Wesche 1977) to help describe the natural variation in substrate composition produced by spawning.

APPENDIX B

EVALUATION OF PERMEABILITY MEASUREMENTS TAKEN USING AN ELECTRIC VACUUM PUMP

The variability of permeability readings taken using a bicycle pump (Young et al. 1989) prompted a search for alternative techniques. An electric vacuum pump allows one to fix vacuum at a constant pressure. I hypothesized that constant vacuum pressure would reduce the variance associated with permeability measurements.

I measured permeability in 41 of the 45 substrates from the Fall 1987 test of survival to emergence of brown trout. Other than replacing the bicycle pump with an electric vacuum pump, the measuring technique remained unchanged (Terhune 1958). In each tank, I drove the MARK VI standpipe to the floor of the tank. After setting pressure at 350 mm, water was drawn from the standpipe for 10 s. I took five measurements to estimate mean permeability in each tank.

The technique was far less variable than that using the bicycle pump. The mean coefficient of variation across all substrates was 2.4% (range 0.6% to 5.7%) (Chapter 2). Turnpenny and Williams (1982) reported greater coefficients of variation for permeability measurements from laboratory tests, but they combined measurements collected by hand-powered and electric vacuum pumps.

Mean permeability was significantly related to both the arcsine transformation of survival to emergence of brown trout ($r^2 = 0.45$; $F =$

31.97; $P < 0.0001$) and the geometric mean particle size of substrates ($r^2 = 0.66$; $F = 74.39$; $P < 0.0001$). However, measures of substrate composition accounted for greater proportions of the variation in survival to emergence (Chapter 4) and combinations of permeability and measures of substrate composition in multiple regressions would violate the assumption of independence of variables (Young et al. in press).

The technique did enable me to identify possible sources of error that caused variation when using the bicycle pump. Leaks in the tubing connections frequently appeared. Because pressure was monitored, these leaks could be detected and corrected. Kinks in the tubing occasionally reduced suction. Even slight non-vertical insertion of the standpipe altered the head depth for suction and caused estimates to differ from those taken in the same substrate after returning the standpipe to vertical.

Potentially, this technique could provide a precise method for measuring the permeability of stream substrates. However, measurements of substrate composition have been better predictors of survival to emergence, so I do not recommend measuring permeability to estimate survival to emergence.

APPENDIX C

SUBSTRATE COMPOSITION OF 41 SAMPLES FROM EGG POCKETS OF REDDS OF COLORADO RIVER CUTTHROAT TROUT

Table 22. Substrate Composition of 41 Samples from Egg Pockets of Redds of Colorado River Cutthroat Trout. Samples Were Collected from 1986-1988 in the Sierra Madre of South-central Wyoming. I Used a Shovel to Collect All Samples Except TC-1, Which Is a McNeil Sample. I Obtained Samples from Third Creek (TC), North Fork Little Snake River (NFLS), West Branch of the North Fork Little Snake River (WB), Green Timber Creek (GTC), Harrison Creek (HC), and Deep Creek (DC).

Sample	50	25	12.5	9.5	6.3	3.35	1.7	0.85	0.42	0.21	pan
TC-1	52.0	15.5	17.4	4.4	3.2	3.8	2.1	0.9	0.4	0.3	0.2
TC-1-89	0.0	0.0	26.9	0.0	21.0	9.2	17.7	14.9	7.6	1.9	0.7
NFLS-1	0.0	17.2	21.4	8.6	10.4	12.9	13.7	9.9	4.5	1.3	0.2
NFLS-2	0.0	30.8	16.6	6.3	9.3	12.4	13.1	7.5	3.0	0.9	0.2
NFLS-3	0.0	37.3	29.6	10.4	7.5	6.4	3.6	2.6	1.8	0.7	0.1
NFLS-4	0.0	7.1	37.9	11.5	10.9	11.0	7.8	6.4	5.4	1.8	0.2
NFLS-5	0.0	33.0	31.0	7.8	8.0	6.0	4.2	4.1	3.9	1.6	0.2
WB-1	0.0	9.6	25.1	11.8	13.2	13.3	13.6	9.4	2.9	0.8	0.4
WB-2	0.0	12.0	37.7	9.8	10.5	11.1	9.2	6.2	2.5	0.7	0.3
WB-3	0.0	27.5	22.9	9.2	9.8	11.1	9.3	6.1	2.8	1.0	0.4
WB-4	0.0	47.1	22.0	7.0	5.7	5.8	6.1	4.4	1.5	0.2	0.2
WB-5	33.7	26.9	15.2	4.2	3.8	4.7	5.0	4.1	1.7	0.5	0.4
GTC-1	0.0	0.0	7.2	6.3	13.5	29.0	25.2	12.2	4.6	1.4	0.6
GTC-2	14.5	18.5	28.3	8.7	9.9	11.6	6.0	1.4	0.7	0.3	0.1
GTC-3	0.0	35.8	21.4	7.6	8.5	12.3	8.7	3.2	1.3	0.7	0.5
GTC-4	0.0	35.4	32.5	4.0	6.5	8.8	7.2	3.6	1.3	0.6	0.2
GTC-5	0.0	5.6	40.9	7.5	5.8	8.7	10.3	8.2	3.3	1.2	0.4
GTC-6	0.0	37.3	23.4	3.6	4.5	8.4	8.4	7.6	4.6	1.7	0.6
GTC-7	0.0	25.8	27.9	8.2	8.6	12.1	8.4	4.7	2.8	1.1	0.4
HC-1	7.7	31.7	17.4	4.3	6.6	9.4	10.0	6.7	2.8	1.4	2.1
HC-2	0.0	8.4	28.1	12.9	16.8	15.3	8.9	5.9	2.8	0.6	0.4
HC-3	0.0	25.8	22.5	6.8	7.0	10.8	12.0	8.2	4.0	1.7	1.2
HC-4	0.0	36.5	24.3	6.8	7.4	9.0	7.0	4.7	2.7	1.1	0.5
HC-5	16.4	54.5	14.3	3.1	3.8	3.9	2.3	1.2	0.4	0.2	0.2
HC-6	0.0	18.4	34.3	8.0	9.2	11.2	9.4	5.7	2.3	0.8	0.7
HC-7	24.3	26.6	6.5	8.2	1.4	10.6	9.2	6.9	3.9	1.5	1.0
HC-8	18.9	24.2	14.1	5.0	6.8	10.6	8.4	6.7	3.6	1.2	0.7
HC-9	0.0	7.1	20.7	10.7	14.6	20.8	14.2	7.3	3.2	0.9	0.4
HC-10	33.2	13.3	12.7	4.3	6.5	10.1	9.1	6.1	3.3	1.0	0.4
HC-11	10.6	27.3	26.8	6.0	6.2	7.7	6.2	4.9	2.6	1.0	0.7
HC-12	0.0	12.4	18.2	8.2	13.2	18.5	12.5	7.2	4.7	2.7	2.3
HC-13	29.3	35.0	16.6	3.1	4.2	4.2	3.2	2.4	1.2	0.4	0.3
HC-14	0.0	0.0	28.5	14.5	22.6	21.2	7.0	2.2	1.7	1.3	1.0
DC-1	0.0	50.3	21.5	4.1	6.5	6.3	4.8	3.0	2.0	0.8	0.5
DC-2	0.0	34.2	28.5	10.5	7.9	6.9	4.9	3.8	2.2	0.6	0.6
DC-3	0.0	15.7	28.4	10.1	10.7	11.7	9.7	7.4	4.0	1.4	1.0
DC-4	0.0	15.3	29.4	6.8	9.1	9.5	9.8	7.7	6.2	3.8	2.5
DC-5	0.0	10.9	16.7	11.7	10.9	13.4	12.1	11.3	8.1	3.0	1.9
DC-6	0.0	13.2	25.2	13.2	10.2	10.6	10.0	7.5	5.5	2.6	2.0
DC-7	0.0	30.0	35.8	10.9	8.4	8.9	3.5	1.3	0.6	0.3	0.3
DC-8	0.0	24.6	23.7	9.7	10.4	9.3	6.2	5.4	6.5	2.8	1.4

APPENDIX D

FIELD TEST OF A SURVIVAL TO EMERGENCE MODEL FOR COLORADO RIVER CUTTHROAT TROUT

I have argued that a major shortcoming of most survival to emergence models has been the lack of field validation (Chapter 1). In 1988 and 1989, I attempted to estimate the survival to emergence of Colorado River cutthroat trout in field experiments. The objective was to compare the laboratory and field relations between survival to emergence and substrate composition.

In 1988, I established 24 artificial redds in Telephone Creek in the Snowy Range of southeastern Wyoming. In 1989, I constructed 27 artificial redds three streams in the Snowy Range: South Brush Creek, Medicine Bow River, and Telephone Creek. Each redd consisted of a 3-mm-mesh nylon sack filled with substrate. A capture bottle at the downstream end of the sack held emerged fry.

To install a redd, I first excavated a small depression in the stream bottom. The nylon sack was placed in the depression and held there by inserting a 1-m long PVC tube 2.5 mm in diameter. Next I placed several substrate particle larger than 25 mm in diameter in the nylon sack (to simulate the centrum; Chapman 1988). I mixed 50 eyed eggs with water, then poured them into the tube. I filled the sack with substrate, then slowly removed the tube by twisting it; this prevented eggs from being washed out of the substrate. Lastly, I

fastened a capture bottle to the neck of the sack to prevent escape of the emerged fry. I removed emerged fry from each sack at least twice each week.

In 1988, I used substrate gathered from Telephone Creek during redd construction. I tried to vary substrate composition in each sack by subjectively adding different particle sizes. For the 1989 tests, I created nine 10-kg test substrates (Table 23). Each test substrate consisted of material obtained from the North Fork Little Snake River that had been sieved on a mechanical shaker (Chapter 5). I used three replicates of each test substrate in each stream.

After emergence ended in the sacks in 1988, I removed them from the stream. In 1988, six sacks became dewatered as stream flow declined during emergence; these sacks were excluded from further analyses. The substrate in each was dried, sieved, and weighed (Chapter 5). I calculated several measures of substrate composition for each substrate and regressed survival to emergence on these measures using SPSS* (SPSS Inc. 1986). I performed the same analyses with the data from 1989. But rather than dry and sieve those substrates, I used measures of composition of the substrate placed in the sacks at the beginning of the test.

I found no significant relation between survival to emergence and geometric mean particle size using the 1988 data ($r^2 = 0.02$; $P = 0.583$), nor did I find significant relations between survival to emergence and the fredle index or sample weight. In 1989, virtually no fry emerged from sacks in North Brush Creek and the Medicine Bow River, thus no analyses were performed of these data. However, fry

Table 23. Particle Size Distribution of Substrates Used in the Summer 1989 Field Test of Survival to Emergence of Colorado River Cutthroat Trout.

	Sieve size (mm)										
Label	50	25	12.5	9.5	6.3	3.35	1.7	0.85	0.42	0.21	pan
A	1.8	26.5	34.8	7.7	11.0	5.5	3.3	1.8	4.3	2.1	1.1
B	1.6	22.7	30.0	6.7	9.4	4.7	12.9	6.4	3.2	1.6	0.8
C	2.0	27.2	35.8	7.8	11.2	5.7	3.3	2.0	5.0	0.0	0.0
D	1.8	25.7	34.0	7.3	10.7	5.3	3.2	1.8	10.0	0.0	0.0
E	1.8	25.7	34.0	7.3	10.7	5.3	3.2	1.8	5.7	2.8	1.5
F	1.8	26.2	34.7	7.5	10.8	5.5	3.3	10.0	0.0	0.0	0.0
G	1.7	23.3	30.8	6.7	9.7	4.8	2.8	20.0	0.0	0.0	0.0
H	1.7	23.3	30.8	6.7	9.7	4.8	2.8	5.0	5.0	5.0	5.0
I	1.5	21.2	28.0	6.2	8.8	4.3	6.0	6.0	6.0	6.0	6.0

emerged from 19 of the 27 sacks in Telephone Creek.

If the sacks without emerging fry were included, there was no significant relation between survival to emergence and the geometric mean ($r^2 = 0.14$; $P = 0.0562$). If the sacks without emerging fry were excluded, a significant relation resulted ($r^2 = 0.33$; $P = 0.0095$). Using indicator variables in regression analysis, I concluded that the field relation between survival to emergence and the geometric mean significantly differed from the laboratory relation between these variables.

The analysis of survival to emergence only in sacks producing emerging fry seemed questionable. However, for an analysis of survival to the eyed egg stage in redds, Sowden and Power (1985) excluded redds if mean dissolved oxygen in the redd was less than 5.3 mg/L. Coincidentally, this excluded all redds with an estimated survival to emergence less than 1.0%, and produced a significant relation between survival to emergence and substrate composition.

I believe that this was not a meaningful validation of my laboratory model of survival to emergence. Further refinement of the egg planting technique may improve the relation. More critical is the monitoring of other variables, such as dissolved oxygen concentration and intragravel water velocity, that affect survival to emergence.

BIBLIOGRAPHY

Adams, J. N., and R. L. Beschta. 1980. Gravel bed composition in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 37: 1514-1521.

Alderdice, D. F., And F. P. J. Nelson. 1978. Relation between temperature and incubation time for eggs of chinook salmon (Oncorhynchus tshawytscha). Journal of the Fisheries Research Board of Canada 35: 69-75.

Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout Salmo trutta L. Journal of Fish Biology 1: 349-353.

Bams, R. A. 1969. Adaptations of sockeye salmon associated with incubation in stream gravels. Pages 71-87 in T. G. Northcote, editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, British Columbia.

Beacham, T. D., and C. B. Murray. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (Oncorhynchus keta) from the Nitinat River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 42: 1755-1765.

Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (Oncorhynchus keta) in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44: 244-261.

Behnke, R. J., and M. Zarn. 1976. Biology and management of threatened and endangered western trouts. U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. General Technical Report RM-28.

Beschta, R. L. 1982. Comment on 'Stream system evaluation with emphasis on spawning habitat for salmonids' by M. A. Shirazi and W. K. Seim. Water Resources Research 18: 1292-1295.

Beschta, R. L., and W. L. Jackson. 1979. The intrusion of fine sediments into a stable gravel bed. Journal of the Fisheries Research Board of Canada 36: 204-210.

Bianchi, D. R. 1963. The effects of sedimentation on egg survival of rainbow trout and cutthroat trout. Master's thesis, Montana State College, Bozeman, Montana.

Binns, N. A. 1977. Present status of indigenous populations of cutthroat trout, (Salmo clarki), in southwest Wyoming. Wyoming Game and Fish Department, Cheyenne, Wyoming. Fisheries Technical Bulletin 2.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73 in N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. Western Division, American Fisheries Society, Bethesda, Maryland.

Bjornn, T. C. 1968. Survival and emergence of trout and salmon in various gravel-sand mixtures. Pages 80-88 in R. F. Myren, editor. Proceedings: forum on the relation between logging and salmon. American Institute of Fisheries Research Biologists and Alaska Department of Fish and Game, Juneau, Alaska.

Bjornn, T. C. 1969. Embryo survival and emergence studies. Salmon and steelhead investigations. Job Completion Report. Idaho Project F-49-R-7. Job 5 and 6.

Bruhn, D. S., and J. T. Bowen. 1973. Selection of rainbow trout broodstock, 1968. Progressive Fish-Culturist 35: 119-120.

Carling, P. A., and N. A. Reader. 1981. A freeze-sampling technique suitable for coarse river bed-material. Sedimentary Geology 29: 233-239.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society 117: 1-21.

Chapman, D. W., and K. P. McLeod. 1987. Development of criteria for sediment in the northern Rockies ecoregion. U.S. Environmental Protection Agency, Region 10, Seattle, Washington. EPA 910/9-87-162.

Chapman, D. W., D. E. Weitkamp, T. L. Welsh, M. B. Dell, and T. H. Schadt. 1986. Effects of fiver flow on the distribution of chinook salmon redds. Transactions of the American Fisheries Society 115: 537-547.

Chisholm, I. M. 1985. Winter stream conditions and brook trout habitat use on the Snowy Range, Wyoming. Master's thesis, University of Wyoming, Laramie.

Cline, R., G. Cole, W. Megahan, R. Patten, and J. Potyondy. 1981. Guide for predicting sediment yields from forested watersheds. U. S. Forest Service, Northern and Intermountain Regions, Ogden, Utah.

Coble, D. W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Transactions of the American Fisheries Society 90: 469-474.

Cooper, A. C. 1965. The effect of transported stream sediments on the survival of sockeye and pink salmon eggs and alevins. International Pacific Salmon Fisheries Commission Bulletin 18.

Cordone, A. J., and D. W. Kelly. 1961. The influences of inorganic sediment on the aquatic life of streams. California Fish and Game 47: 189-228.

Crisp, D. T., and P. A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology 34: 119-134.

Daykin, P. N. 1965. Application of mass transfer theory to the problem of respiration of fish eggs. Journal of the Fisheries Research Board of Canada 22: 159-171.

Everest, F. H., R. L. Beschta, J. C. Scrivener, K V. Koski, J. R. Sedell, and C. J. Cederholm. 1987. Fine sediment and salmonid production: a paradox. Pages 98-142 in E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. College of Forest Resources, University of Washington, Seattle, Washington. Contribution 57.

Everest, F. H., F. B. Lotspeich, and W. R. Meehan. 1982. New perspectives on sampling, analysis, and interpretation of spawning gravel quality. Pages 325-333 in N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. Western Division, American Fisheries Society, Portland, Oregon.

Everest, F. H., C. E. McLemore, and J. F. Ward. 1980. An improved tri-tube cryogenic gravel sampler. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. Research Note PNW-350.

Folk, R. L., and W. C. Ward. 1957. Brazos River bar: a study in the significance of grain size parameters. Journal of Sedimentary Petrology 27: 3-26.

Fowler, L. G. 1972. Growth and mortality of fingerling chinook salmon as affected by egg size. Progressive Fish-Culturist 34: 66-69.

Freund, R. J. 1971. Some observations on regressions with grouped data. American Statistician 25(3): 29-30.

Gangmark, H. A., and R. G. Bakkala. 1958. Plastic standpipe for sampling the streambed environment of salmon spawn. U. S. Fish and Wildlife Service Special Scientific Report Fisheries 261.

Grost, R. T. 1989. A description of brown trout redds in Douglas Creek, Wyoming. Master's thesis, University of Wyoming, Laramie, Wyoming.

Grost, R. T., T. A. Wesche, M. K. Young, W. A. Hubert, and V. R. Hasfurther. 1988. Evaluation of procedures to measure intragravel water velocity in streambeds. United States Geological Survey and Wyoming Water Research Center, University of Wyoming, Laramie, Wyoming. Job Completion Report, Projects 5-33863 and 5-38704.

Hall, J. D., and R. L. Lantz. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams. Pages 355-375 in T.G. Northcote, editor. Symposium on salmon and trout in streams. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, British Columbia.

Hamor, T., and E. T. Garside. 1976. Developmental rates of embryos of Atlantic salmon, Salmo salar L., in response to various levels of temperature, dissolved oxygen, and water exchange. Canadian Journal of Zoology 54: 1912-1917.

Hansen, E. A. 1975. Some effects of groundwater on brown trout redds. Transactions of the American Fisheries Society 104: 100-110.

Harrison, C. W. 1923. Planting eyed salmon and trout eggs. Transactions of the American Fisheries Society 52: 191-200.

Harshbarger, T. J., and P. E. Porter. 1979. Survival of brown trout eggs: two planting techniques compared. Progressive Fish-Culturist 41: 206-209.

Hausle, D. A., and D. W. Coble. 1976. Influence of sand in redds on survival and emergence of brook trout (Salvelinus fontinalis). Transactions of the American Fisheries Society 104: 57-63.

Hawke, S. P. 1978. Stranded redds of quinnat salmon in the Mathias River, South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 12: 167-171.

Healey, M. C., and W. R. Heard. 1984. Inter- and intra-population variation in the fecundity of chinook salmon (Oncorhynchus tshawytscha) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 41: 476-483.

Helle, J. H. 1970. Biological characteristics of intertidal and fresh-water spawning pink salmon at Olsen Creek, Prince William Sound, Alaska, 1962-63. U. S. Fish and Wildlife Service Special Scientific Report Fisheries 602.

Irving, J. S., and T. C. Bjornn. 1984. Effects of substrate size composition on survival of kokanee salmon and cutthroat and rainbow trout embryos. Idaho Cooperative Fisheries Research Unit, University of Idaho, Moscow, Idaho. Technical Report 84-6.

Iwamoto, R. N., E. O. Salo, M. A. Madej, and R. L. McComas. 1978. Sediment and water quality: a review of the literature, including a suggested approach for water quality criterion. U. S. Environmental Protection Agency, Region 10, Seattle, Washington. EPA 910/9-78-048.

Jespersen, D. M. 1981. A study of the effects of water diversion on the Colorado River cutthroat trout (Salmo clarki pleuriticus) in the drainage of the North Fork of the Little Snake River in Wyoming. Master's thesis, University of Wyoming, Laramie, Wyoming.

Koski, K V. 1966. The survival of coho salmon (Oncorhynchus kisutch) from egg deposition to emergence in three Oregon coastal streams. Master's thesis, Oregon State University, Corvallis, Oregon.

Koski, K V. 1975. The survival and fitness of two stocks of chum salmon (Oncorhynchus keta) from egg deposition to emergence in a controlled-stream environment at Big Beef Creek. Doctoral dissertation, University of Washington, Seattle, Washington.

Leitritz, E., and R. C. Lewis. 1976. Trout and salmon culture (hatchery methods). California Department of Fish and Game, Sacramento, California. Fish Bulletin 164.

Lotspeich, F. B., and F. H. Everest. 1981. A new method for reporting and interpreting textural composition of spawning gravel. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. Research Note PNW-369.

Lotspeich, F. B., and B. H. Reid. 1980. Tri-tube freeze-core procedure for sampling stream gravels. Progressive Fish-Culturist 42: 96-99.

MacCrimmon, H. R., and B. L. Gots. 1986. Laboratory observations on emergent patterns of juvenile Atlantic salmon, Salmo salar, relative to sediment loadings of test substrate. Canadian Journal of Zoology 64: 1331-1336.

MacKenzie, C., and J. R. Moring. 1988. Estimating survival of Atlantic salmon during the intragravel period. North American Journal of Fisheries Management 8: 45-49.

McNeil, W. J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. Fisheries Bulletin 65: 495-523.

McNeil, W. J., and W. H. Ahnell. 1960. Measurement of gravel composition of salmon stream beds. Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, Washington. Circular 120.

McNeil, J. W. and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U. S. Fish and Wildlife Service Special Scientific Report Fisheries 469.

Meehan, W. R., and D. N. Swanston. 1977. Effects of gravel morphology on fine sediment accumulation and survival of incubating salmon eggs. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. Research Paper PNW-220.

Megahan, W. F., and W. J. Kidd. 1972. Effects of logging and logging roads on erosion and sediment deposition from steep terrain. Journal of Forestry 70: 136-141.

Moring, J. R. 1982. Decrease in stream gravel permeability after clear-cut logging: an indication of intragravel conditions for developing salmonid eggs and alevins. Hydrobiologia 88: 295-298.

Morrison, P. F., J. F. Leatherland, and R. A. Sonstegard. 1985. Comparative fecundity and egg survival of coho salmon (Oncorhynchus kisutch Walbaum) from lakes Ontario, Erie, and Michigan. Canadian Journal of Zoology 63: 1096-1100.

Mosteller, F., and R. E. K. Rourke. 1973. Sturdy statistics: nonparametrics and order statistics. Addison-Wesley Publishing Company, Reading, Massachusetts.

Mount, D. I., and W. A. Brungs. 1967. A simplified dosing apparatus for fish toxicology studies. Water Research 1: 21-29.

NCASI (National Council of the Paper Industry for Air and Stream Improvement, Inc.). 1984. A laboratory study of the effects of sediments of two different size characteristics on survival of rainbow trout (Salmo gairdneri) embryos to fry emergence. NCASI, New York. Technical Bulletin 429.

Neter, J., W. Wasserman, and M. H. Kutner. 1983. Applied linear regression models. Irwin, Homewood, Illinois.

Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models, second edition. Irwin, Homewood, Illinois.

Olsson, T. I., and B.-G. Persson. 1986. Effects of gravel size and peat material concentrations on embryo survival and alevin emergence of brown trout, Salmo trutta L. Hydrobiologia 135: 9-14.

Olsson, T. I., and B.-G. Persson. 1988. Effects of deposited sand on ova survival and alevin emergence in brown trout (Salmo trutta L.). Archiv fèr Hydrobiologie 11: 621-627.

Orchard, R. D. 1988. New method for measuring water seepage through salmon spawning gravel. U. S. Forest Service, Pacific Northwest Research Station, Portland, Oregon. Research Note RN-483.

Ottaway, E. M., P. A. Carling, A. Clarke, and N. A. Reader. 1981. Observations on the structure of brown trout, Salmo trutta Linnaeus, redds. Journal of Fish Biology 19: 593-607.

Phillips, R. W. 1971. Effects of sediment on the gravel environment and fish production. Pages 64-74 in J. T. Krygier and J. D. Hall, editors. Forest land uses and the stream environment. Oregon State University, Corvallis, Oregon.

Phillips, R. W., and K V. Koski. 1969. A fry trap method for estimating salmonid survival from egg deposition to fry emergence. Journal of the Fisheries Research Board of Canada 26: 133-141.

Phillips, R. W., R. L. Lantz, E. W. Claire, and J. R. Moring. 1975. Some effects of gravel mixtures on emergence of coho salmon and steelhead trout fry. Transactions of the American Fisheries Society 104: 461-466.

Platts, W. S., and W. F. Megahan. 1975. Time trends in riverbed sediment composition in salmon and steelhead spawning areas: South Fork Salmon River, Idaho. Transactions of the North American Wildlife and Natural Resources Conference 40: 229-239.

Platts, W. S., M. A. Shirazi, and D. H. Lewis. 1979. Sediment particle sizes used by salmon for spawning with methods for evaluation. U. S. Environmental Protection Agency, Corvallis, Oregon. EPA-600/3-79-043.

Platts, W. S., R. J. Torquemada, M. L. McHenry, and C. K. Graham. 1989. Changes in salmon spawning and rearing habitat from increased delivery of fine sediment to the South Fork Salmon River, Idaho. Transactions of the American Fisheries Society 118: 274-283.

Pollard, R. A. 1955. Measuring seepage through salmon spawning gravel. Journal of the Fisheries Research Board of Canada 12: 706-746.

Reiser, D. W., and T. C. Bjornn. 1979. Influence of forest and rangeland management on anadromous fish habitat in western North America. 1. Habitat requirements of anadromous salmonids. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. General Technical Report PNW-96.

Reiser, D. W., and T. A. Wesche. 1977. Determination of physical and hydraulic preferences of brown and brook trout in the selection of spawning locations. Water Resources Research Institute, University of Wyoming, Laramie, Wyoming. Water Resources Series 64.

Reiser, D. W., and R. G. White. 1981. Influence of streamflow reductions on salmonid embryo development and fry quality. Idaho Water and Energy Resources Research Institute, University of Idaho, Moscow, Idaho. Research Technical Completion Report Proj. A-058-IDA.

Reiser, D. W., and R. G. White. 1988. Effects of two sediment size-classes on survival of steelhead and chinook salmon eggs. North American Journal of Fisheries Management 8: 432-437.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 38: 1636-1656.

Ringler, N. H. 1970. Effects of logging on the spawning bed environment in two Oregon coastal streams. Master's thesis, Oregon State University, Corvallis, Oregon.

Ringler, N. H., and J. D. Hall. 1988. Vertical distribution of sediment and organic debris in coho salmon (Oncorhynchus kisutch) redds in three small Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 45: 742-747.

Rounsefell, G. A. 1957. Fecundity of North American Salmonidae. U. S. Fish and Wildlife Service Fishery Bulletin 57: 451-468.

Scrivener, J. C. 1988. Two devices to assess incubation survival and emergence of salmonid fry in an estuary streambed. North American Journal of Fisheries Management 8: 248-258.

Scrivener, J. C., and M. J. Brownlee. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (Oncorhynchus keta) and coho salmon (O. kisutch) in Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46: 681-696.

Shepard, B. B., S. A. Leathe, T. M. Weaver, and M. D. Enk. 1984. Monitoring levels of fine sediment within tributaries to Flathead Lake, and impacts of fine sediment on bull trout recruitment. Pages 146-156 in F. Richardson and R. H. Hamre, editors. Proceedings of the Wild Trout III Symposium. Mammoth Hot Springs, Yellowstone National Park, Wyoming.

Sheridan, W. L., M. P. Perensovich, T. Faris, and K V. Koski. 1984. Sediment content of streambed gravels in some pink salmon spawning streams. Pages 153-165 in W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley, editors. Fish and wildlife relationships in old-growth forests. American Institute of Fisheries Research Biologists, Juneau, Alaska. Available from J. W. Reintjes, Rt. 4, Box 85, Morehead City, North Carolina 28557.

Shirazi, M. A., and W. K. Seim. 1979. A stream systems evaluation: an emphasis on spawning habitat for salmonids. U. S. Environmental Protection Agency, Corvallis, Oregon. EPA-600/3-79-109.

Shirazi, M. A., and W. K. Seim. 1981. Stream system evaluation with emphasis on spawning habitat for salmonids. Water Resources Research 17: 592-594.

Shirazi, M. A., W. K. Seim, and D. H. Lewis. 1981. Characterization of spawning gravel and stream system evaluation. Pages 227-278 in Proceedings of the conference on salmon spawning gravel: a renewable resource in the Pacific Northwest? Washington Water Research Center, Washington State University, Pullman, Washington. Report 39.

Shumway, D. L., C. E. Warren, and P. Doudoroff. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. Transactions of the American Fisheries Society 93: 342-356.

Silver, S. J., C. E. Warren, and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society 92: 327-343.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman and Company, San Francisco, California.

Sowden, T. K. 1983. The influence of groundwater and spawning-gravel composition on the reproductive success of rainbow trout in an eastern Lake Erie tributary. Master's thesis, University of Waterloo, Waterloo, Ontario.

Sowden, T. K., and G. Power. 1985. Prediction of rainbow trout embryo survival in relation to groundwater seepage and particle size of spawning substrates. Transactions of the American Fisheries Society 114: 804-812.

Springate, J. R. C., and N. R. Bromage. 1985. Effects of egg size on early growth and survival in rainbow trout (Salmo gairdneri Richardson). Aquaculture 47: 163-172.

SPSS Inc. 1986. SPSS* user's guide. Second edition. SPSS Inc, 444 N. Michigan Avenue, Chicago, Illinois.

Stowell, R., A. Espinosa, T. C. Bjornn, W. S. Platts, D. C. Burns, and J. S. Irving. 1983. Guide for predicting salmonid response to sediment yields in Idaho batholith watersheds. U. S. Forest Service Northern and Intermountain Regions, Ogden, Utah.

Tagart, J. V. 1976. The survival from egg deposition to emergence of coho salmon in the Clearwater River, Jefferson County, Washington. Master's thesis, University of Washington, Seattle, Washington.

Tappel, P. D. 1981. A new method of relating spawning gravel size composition to salmonid embryo survival. Master's thesis, University of Idaho, Moscow, Idaho.

Tappel, P. D., and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3: 123-135.

Terhune, L. D. B. 1958. The MARK VI groundwater standpipe for measuring seepage through salmon spawning gravel. Journal of the Fisheries Research Board of Canada 15: 1027-1063.

Turnpenny, A. W. H., and R. Williams. 1980. Effects of sedimentation on the gravels of an industrial river system. Journal of Fish Biology 17: 681-693.

Turnpenny, A. W. H., and R. Williams. 1982. A conductiometric technique for measuring the water velocity in salmonid spawning beds. Water Research 16: 1383-1390.

Vaux, W. G. 1968. Intragravel flow and interchange of water in a streambed. U. S. Fish and Wildlife Service Fisheries Bulletin 66: 479-489.

Walkotten, W. J. 1976. An improved technique for sampling streambed sediments. U. S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. Research Note PNW-281.

Wallace, J. C., and D. Aasjord. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, Salvelinus alpinus (L.). Journal of Fish Biology 24: 427-435.

Wickett, W. P. 1954. The oxygen supply to salmon eggs in spawning beds. Journal of the Fisheries Research Board of Canada 11: 933-953.

Wickett, W. P. 1958. Review of certain environmental factors affecting the production of pink and chum salmon. Journal of the Fisheries Research Board of Canada 15: 1103-1126.

Witzel, L. D., and H. R. MacCrimmon. 1981. Role of gravel substrate on ova survival and alevin emergence of rainbow trout, Salmo gairdneri. Canadian Journal of Zoology 59: 629-636.

Witzel, L. D., and H. R. MacCrimmon. 1983a. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112: 760-771.

Witzel, L. D., and H. R. MacCrimmon. 1983b. Embryo survival and alevin emergence of brook charr, Salvelinus fontinalis, and brown trout, Salmo trutta, relative to redd gravel composition. Canadian Journal of Zoology 61: 1783-1792.

Wooton, R. J. 1973. The effect of size of food ration on egg production in female three-spined stickleback, Gasterosteus aculeatus L. Journal of Fish Biology 5: 89-96.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1989a. Evaluation of variation in permeability measurements when using the MARK VI standpipe. Canadian Journal of Fisheries and Aquatic Sciences 46: 447-450.

Young, M. K., W. A. Hubert, and T. A. Wesche. 1989b. Substrate modification by spawning brook trout in a southeastern Wyoming stream. Transactions of the American Fisheries Society 118: 379-385.

Young, M. K., W. A. Hubert, and T. A. Wesche. In press. Comment on "Critical review of variables used of define effects of fines in redds of large salmonids" by D. W. Chapman. Transactions of the American Fisheries Society.

Young, M. K., W. A. Hubert, and T. A. Wesche. In review. Effect of substrate composition and stock origin on the survival to emergence of brown trout. Submitted to Northwest Science.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey.