Michael K. Young,[1] and **Wayne A. Hubert,** U.S. Fish and Wildlife Service, Wyoming
Cooperative Fish and Wildlife Research Unit[2], University of Wyoming, Laramie, Wyoming 82071

and

Thomas A. Wesche, Wyoming Water Research Center, University of Wyoming, Laramie, Wyoming 82071

Effect of Substrate Composition and Stock Origin on the Survival to Emergence of Brown Trout: A Laboratory Study

Abstract

Few researchers investigating the survival to emergence of embryonic salmonids have simultaneously compared the predictive ability of the percentage of fine sediment less than a given diameter, the geometric mean particle size, and the fredle index. We quantified the relation between these different measures of substrate composition and survival to emergence of two stocks of brown trout, *Salmo trutta*, and also examined the effects of substrate composition on the timing of emergence and size of alevins. The geometric mean particle size generally accounted for the greatest proportion of variation in survival to emergence, whereas the percentage of fines less than a given size was usually the poorest predictor. Substrate composition also influenced days to first emergence and 50% emergence and the length of the emergence interval. We found no difference in the survival to emergence of the two stocks. We concluded that the geometric mean particle size was the best predictor of survival to emergence for brown trout and that substrate composition may alter other ecological characteristics of emerging fry.

Introduction

The survival of salmonid eggs and alevins during incubation in a 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), have caused increases in 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, *Oncorhynchus mykiss*, and chinook salmon, *O. tshawytscha* (Stowell *et al.* 1983), but no models have been developed for introduced resident salmonids such as brown trout, *Salmo trutta*.

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 diameter (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, *O. kisutch*, from the Great Lakes, and Beacham and Murray (1987) noted variation in STE among stocks of chum salmon, *O. keta*, 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.

Our study 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

---

[1] Current address: Rocky Mountain Forest and Range Experiment Station, 222 S. 22nd Street, Laramie, Wyoming 82070

[2] The Unit is jointly supported by the University of Wyoming, the Wyoming Game and Fish Department, and the U.S. Fish and Wildlife Service.

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

We 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, 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 1976) 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.

We filled each aquarium with substrate to a depth of 10 cm and constructed a centrum. Each centrum consisted of a particle greater than 50 mm in diameter topped by two or three 25-50 mm particles; this created crevices for the eggs and mimicked the structure of egg pockets (Chapman 1988). Next, we began filling each tank with water; when the water level exceeded the depth of the substrate, we poured 100 eggs into 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.

We monitored the aquaria weekly for fry 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. Three to four weeks after emergence in the experimental treatments began, we counted all the surviving fry in the trays. 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).

We conducted two STE experiments, the first from 20 November 1987 to 6 April 1988 and the

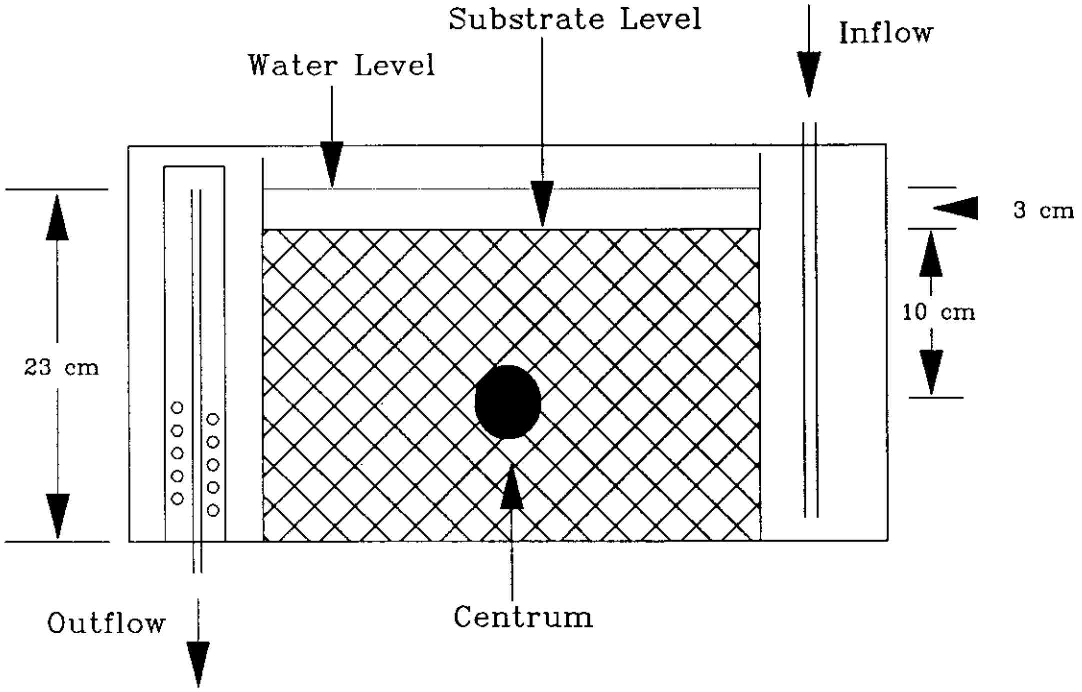

Figure 1. Side view of an experimental aquarium. Water flowed through the substrate from right to left.

second from 16 November 1988 to 31 March 1989. We devised 24 test substrates of various compositions; Young (1989; p. 55) provides the proportions of each substrate size comprising these test substrates. We used three replicates of each of 15 different test substrates in 1987, and six replicates of each of nine additional substrate mixtures in 1988. Each stock in each year was tested in three replicates of the mixtures used in those years.

In 1987 we 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 we 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, we created skewed, uniform, and geometric distributions of sediment less than 3.35 mm in diameter in each test substrate (Young 1989). 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, we 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 substrate size for each treatment using the formula:

$$D_g = D_a^{Pa} * D_b^{Pb} * \ldots D_i^{Pi}$$

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, we 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 could be improved 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. We used the notation F_m to indicate the geometric mean divided by its standard deviation.

We 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, we 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, we conducted two-way analysis of variance using the GANOVA-4 program (Courtesy of D. G. Bonett, Department of Statistics, University of Wyoming, Laramie, Wyoming). We performed regression analyses using SPSS^x (SPSS Inc. 1986) to assess the relation between STE and substrate composition for all substrate treatments. In addition, we evaluated this relation for skewed, uniform, and geometric treatments separately. We 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. We decided from the start to pool the data from both stocks and both years if we failed to reject the null hypothesis of no difference in the regression coefficients between stocks or years or both. Using only data from 1988, we 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. An alpha of ≤ 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 1). 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, we found no significant differences among the regression coefficients for the two stocks or between years, consequently we 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 2).

The relation between substrate composition and the other dependent variables was determined by the measure of substrate composition and stock used in the analysis. For the stock from the Saratoga Hatchery, only the correlation between the percentage of substrate less than 1.70 mm in diameter and days to first emergence was significant ($r = 0.44$, $P = 0.02$). We found no other relation between any measure of substrate

TABLE 1. Averages of 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			15% < 1.70			25% < 3.35			
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	—

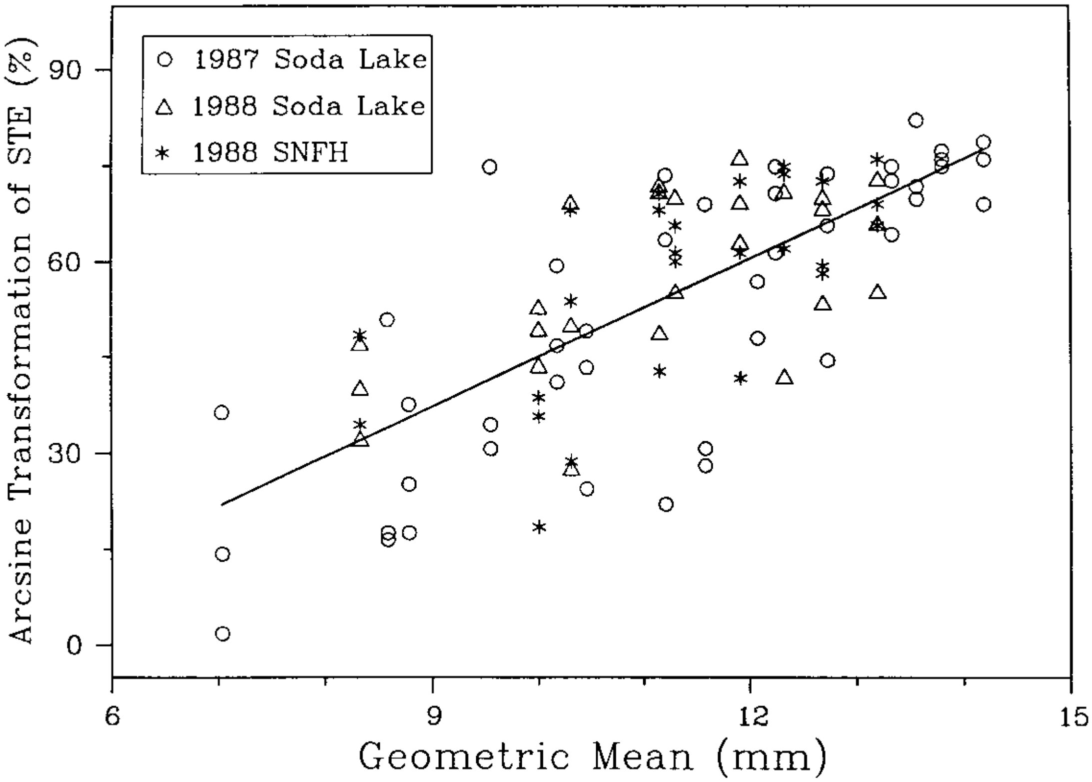

Figure 2. Relation between survival to emergence and the geometric mean particle size. The equation is arcsine (survival to emergence) = 7.75 (geometric mean) − 32.53 ($F = 112.65$, $r^2 = 0.54$, $P < 0.0001$, $N = 99$). Data are from both stocks in 1987 and 1988; SNFH is the Saratoga National Fish Hatchery.

TABLE 2. 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, F_i is the fredle index, and F_m is the modified fredle index).

	Substrate measure									
	Statistics			Percentage of fine sediment less than the diameter (mm) shown:						
Substrate category	D_g	F_i	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

TABLE 3. 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 (D_g is the geometric mean, F_i is the fredle index, and F_m is the modified fredle index). Asterisk indicates significance at alpha ≤ 0.05).

	Substrate measure									
	Statistics			Percentage of fine sediment less than the diameter (mm) shown:						
Variable	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 intervals (days)	−0.31*	−0.39*	−0.21	0.33*	0.33*	0.33*	−0.14	−0.15	−0.10	−0.10

composition and alevin length, days to first emergence, days to 50% emergence, or length of the emergence interval. But at least three measures of substrate composition were significantly correlated with days to first and 50% emergence and length of the emergence interval for the Soda Lake stock (Table 3). Again, no measure of substrate composition was significantly correlated with fry length at emergence.

Discussion

The geometric mean diameter of the 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, we prefer to geometric mean as a measure of substrate composition in models of STE due to its predictive ability, computational simplicity, and widespread use by fluvial geomorphologists (Platts *et al.* 1979). However, we do not recommend that the equation for STE of brown trout be considered a quantitative predictor of STE in the field, due to the artificiality of the substrate treatments, the control of other variables important to STE (such as intragravel water velocity and dissolved oxygen), and the lack of model validation 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, the percentage of fine sediment less than 3.35 mm did account for a marginally greater proportion (3%) of the variation in STE than did the geometric mean particle size for the geometric group of substrate treatments. That group of substrate treatments has a bimodal particle distribution that may be poorly represented by the geometric mean. Consequently, we encourage additional comparisons of measures of substrate composition in laboratory and field experiments.

Surprisingly, we 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). We 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 geometric mean particle size 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 increased and the length of the emergence interval decreased as the proportion of fine sediment in substrates decreased. Witzel and MacCrimmon (1983) reported an increase in the time to 50% emergence as mean particle size increased, but noted that the length of the emergence interval also increased. However, the increases 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.

Acknowledgments

We thank J. Bobbitt for monitoring portions of the tests, D. Lanning and P. Guenther for assisting with the initiation of the 1988 test, the Wyoming Game and Fish Department and the U.S. Fish and Wildlife Service for providing eggs, and P. Eschmeyer for reviewing the manuscript.

Literature Cited

Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. J. Fish Biol. 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.

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. Can. J. Fish. Aquat. Sci. 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. Can. J. Fish Aquat. Sci. 44:244-261.

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 Resour. Res. 18:1292-1295.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Trans. Amer. Fish. Soc. 117:1-21.

Lotspeich, F. B., and F. H. Everest. 1981. A new method for reporting and interpreting textural composition of spawning gravel. USDA, For. Serv., Pac. Northw. For. Range Exp. Stn., Portland, Oregon. Res. Note PNW-369.

McNeil, J. W., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. USDI, Fish Wildl. Serv. Spec. Sci. Rep.—Fisheries 469.

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

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. Can. J. Zool. 63:1096-1100.

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

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

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.

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

Reiser, D. W., and R. G. White. 1988. Effects of two sediment size-classes on survival of steelhead and chinook salmon eggs. N. Amer. J. Fish. Manage. 8:432-437.

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. Amer. Inst. Fish. Res. Biol., Juneau, AK. Available from J. W. Reintjes, Rt. 4, Box 85, Morehead City, NC 28557.

Shirazi, M. A., and W. K. Seim. 1979. A stream systems evaluation: an emphasis on spawning habitat for salmonids. USEPA, Corvallis, OR. EPA-600/3-79-109.

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. Trans. Amer. Fish. Soc. 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. Trans. Amer. Fish. Soc. 92:327-343.

Received 11 October 1989
Accepted for publication 3 May 1990

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^x user's guide. Second edition. SPSS Inc., 444 N. Michigan Avenue, Chicago, IL.

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. USDA, For. Serv., Northern and Intermountain Reg., Ogden, UT.

Tappel, P. D., and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. N. Amer. J. Fish. Manage. 3:123-135.

Young, M. K. 1989. Effect of substrate composition on the survival to emergence of Colorado River cutthroat trout and brown trout. Ph.D. diss., Univ. Wyoming, Laramie.

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