

Fines in Redds of Large Salmonids

**Michael K. Young
Thomas A. Wesche**

Wayne A. Hubert

Journal Article

1990

WWRC-90-21

In

Transactions of the American Fisheries Society

Volume 119

**Michael K. Young and Wayne A. Hubert
U. S. Fish and Wildlife Service
Wyoming Cooperative Fish and
Wildlife Research Unit**

**Thomas A. Wesche
Wyoming Water Research Center
and
Department of Range Management
University of Wyoming
Laramie, Wyoming**

Fines in Redds of Large Salmonids

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.

We 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 reduce 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. 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 *Salmo trutta* (Harshbarger and Porter 1979; Witzel and MacCrimmon 1983), bull trout *Salvelinus confluentus* (Shepard et al. 1985), cutthroat trout *Oncorhynchus clarki* (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 nongravel treatments and thus created a laboratory control. Implicit in studies lacking a laboratory control is the assumption that survival equals 100% under ideal conditions, but we contend that this belief is unjustified.

Embryonic survival may vary among 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. Survival to the swim-up stage of 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 from nine 3-year-old rainbow trout (Bruhn and Bowen 1973).

Considering the number of factors that influ-

ence 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 this variation 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. We 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 47–78% of the variation in fecundity. This observation suggests that an equation developed for one stock should not be extrapolated to other stocks. Healey and Heard (1984) found significant changes between years in the size-specific fecundity of four stocks of chinook salmon, and they 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 the data 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 (Wootton 1973), or it can undergo directional change if older fish are selectively removed by exploitation (Ricker 1981).

To demonstrate the potential difficulty of accurately estimating fecundity, we used the length-fecundity data of Tagart (1976), which were also

used by Chapman (1988), to try to demonstrate a precise relation between fecundity and length; however, Chapman's results actually pertain to the estimation of fecundity from a subsample of egg mass. We found a significant relation between fecundity and length ($r^2 = 0.69$, $P = 0.002$). Next, we found that the mean predicted fecundity for a female coho salmon 628 mm long (roughly one standard deviation below the mean size) was 3,019 eggs. However, the 95% prediction interval for fecundity was 2,002–4,036 eggs. We concluded that meaningful estimates of STE based on fecundity-length relations must rely on fish from a small size range, a single stock, and a single year. These restrictions reduce the generality of any relation between intragravel conditions and STE.

Other sources of variability in estimations of 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. 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, personal communication).

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

S. Wolff, EA Engineering, personal communication) and time for installation (up to 4 h/trap: Phillips and Koski 1969) and monitoring may deter fisheries researchers and managers from using this approach.

As an alternative, we 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, we 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 percentages of fine sediment less than 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 who conduct laboratory and field investigations of egg pockets and redds should focus on the fredle index, on the percentages of sediment less than 0.85 mm and 9.5 mm in diameter, and on permeability.

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

TABLE 1.—Relation between survival to emergence of steelhead and chinook salmon and several measures of substrate composition (data from Tappel and Bjornn 1983). Abbreviations: F_i = fredle index; d_g = geometric mean particle size (diameter); N = number of substrate treatments examined. All regressions are significant ($P < 0.05$).

Type of substrate	N	Expression	r^2
Steelhead			
All	15	$21.4 + 68.9(\log_{10}F_i)$	0.79
		$-38.9 + 111.1(\log_{10}d_g)$	0.77
$d_g < 10.0$ mm	7	$-1.5 + 134.0(\log_{10}F_i)$	0.94
		$-133.4 + 233.1(\log_{10}d_g)$	0.96
Chinook salmon			
All	15	$25.4 + 69.3(\log_{10}F_i)$	0.76
		$-33.7 + 110.2(\log_{10}d_g)$	0.71
$d_g < 10.0$ mm	7	$-1.4 + 149.8(\log_{10}F_i)$	0.93
		$-141.0 + 250.3(\log_{10}d_g)$	0.85

dle index because he examined only substrates with a fredle index of less than 4.0.

We reanalyzed these data and came to different conclusions about the relation of the fredle index and geometric mean particle size to STE (Table 1). For chinook salmon, \log_{10} of the fredle index accounted for slightly more of the variation in STE than did \log_{10} of the geometric mean for both the entire range of substrates and the substrates below a geometric mean particle size of 10 mm in diameter (roughly corresponding to a fredle index less than 5). For steelhead, \log_{10} of the geometric mean particle size accounted for slightly more of the variation in STE for the substrates from the restricted range, and for nearly as much from the entire range.

Using data from Phillips et al. (1975), we also examined the relation between these two substrate statistics and the survival of alevins of steelhead and coho salmon to the swim-up stage. Again, we found very little difference in the amount of variation in survival accounted for by the \log_{10} transformations of the fredle index and the geometric mean particle size and the untransformed geometric mean particle size (Table 2). From these results, we concluded that the fredle index and the geometric mean particle size are both adequate descriptors of the effects of substrate composition on STE.

In multiple regression equations used to predict STE, Chapman (1988) included the geometric mean particle size, \log_{10} of the fredle index, and permeability. Equations in which these variables

TABLE 2.—Relation between the arcsine transformation of survival to emergence of steelhead and coho salmon on alevins and several measures of substrate composition (data from Phillips et al. 1975). Abbreviations: F_i = fredle index; d_g = geometric mean particle size. For all equations, $N = 48$ substrate treatments examined. All regressions are significant ($P < 0.05$).

Species	Expression	r^2
Steelhead	$16.4 + 65.4(\log_{10}F_i)$	0.78
	$-34.5 + 92.0(\log_{10}d_g)$	0.76
	$9.4 + 4.3d_g$	0.78
Coho salmon	$2.6 + 70.0(\log_{10}F_i)$	0.83
	$-50.5 + 97.0(\log_{10}d_g)$	0.77
	$-4.5 + 4.6d_g$	0.82

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). An informal technique for detecting multicollinearity is inspection of a correlation matrix of independent variables (Neter et al. 1983). 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 3). 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.

Finally, we 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 our reassessment of the data from Tappel and Bjornn (1983).¹ For comparison, we regressed the arcsine transformation of the proportion of successfully emerging coho salmon alevins against \log_{10} of the fredle index (as in Table 2) 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. We 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 16 egg pockets and the permeability of 15 egg pockets (Chapman 1988). We 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. Because of the sources of variation and error associated with egg viability and deposition in the field, we question the utility

¹ Identical results were obtained from his analyses and ours when we used the means. We contacted Tappel and Bjornn in an attempt to obtain the entire data sets, but these data were unavailable.

TABLE 3.—Correlation matrix between several measures of substrate composition (data from Tappel and Bjornn 1983). Abbreviations: F_i = fredle index; d_g = geometric mean particle size (diameter). All correlations are significant ($P < 0.05$).

Substrate measures	Log F_i	Log d_g	d_g	Percent of substrate with particle diameter less than	
				9.5 mm	0.85 mm
Log F_i	1.000				
Log d_g	0.996	1.000			
d_g	0.959	0.976	1.000		
Percent < 9.5 mm	-0.944	-0.940	-0.943	1.000	
Percent < 0.85 mm	-0.899	-0.904	-0.826	0.760	1.000

of capping redds to accurately estimate STE in the field.

We concur with Chapman that information on the structure of egg pockets should be incorporated in laboratory experiments conducted to evaluate the relation between STE and intragravel conditions. Unlike Chapman, we 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 investigations of egg pockets we have suggested 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.

Acknowledgments

We thank T. C. Bjornn, F. Everest, P. Eschmeyer, K. V. Koski, R. Marston, F. Rahel, and R. Wiley for reviewing the manuscript, and J. Hall for contributing data from Phillips et al. (1975).

MICHAEL K. YOUNG
WAYNE A. HUBERT

*U.S. Fish and Wildlife Service
Wyoming Cooperative Fish and Wildlife
Research Unit²
University of Wyoming
Laramie, Wyoming 82071, USA*

THOMAS A. WESCHE
*Wyoming Water Research Center
University of Wyoming*

The comment by Young, Hubert, and Wesche impels me to offer a short response. First, and least, in their tenth paragraph the commenters indicate that I tried to demonstrate a precise relation between fecundity and length; I did not.

Young et al. noted that in high-density spawning areas, redd superimposition may occur. In spawning areas of fall chinook salmon *Oncorhynchus tshawytscha* on the Columbia River, a very high density of spawners caused some overlap of the periphery of early and late redds. However, overlap does not necessarily disturb egg pockets

(Chapman et al. 1986). Where it does, I agree with Young et al. that the structure of disturbed egg pockets has little definable relationship to STE. However, instances of excessive escapements have become rarer with time, and discrete redds remain the norm in most areas outside some in Alaska.

I see other criticisms by Young et al. as far more important than those related to superimposition. I do not agree that we should drop redd capping in favor of constructing artificial egg pockets and redds. We need both research avenues. Neither the problems associated with fecundity and viability nor the costs quoted by Young et al. of \$300 for a redd cap and the labor to install and service it alter my conviction. (Young et al. may be heartened to know that W. Platts, in the office next to mine, agrees with them, not with me!) I remain convinced that selective application of redd capping is a productive exercise.

I think Young et al. did a better job of examining regressions of survival on substrate statistics than I did. However, their analyses in Tables 1 and 2 would only lead me to continue to prefer the fredle index. Furthermore, readers should note that the data used by the commenters in their Tables 1-3, and in some of my analyses of substrate statistics for laboratory data, were derived from homogeneous mixes of incubation media in laboratory cells, not from egg pockets (Phillips et al. 1975; Tappel and Bjornn 1983). Survival to emergence in Phillips et al. (1975), as used in Young et al.'s Table 2, covered the very late part of the incubation period only, from the late sac-fry stage to emergence.

Finally, the commenters felt that much of the current information on STE derived from laboratory studies could be applied to the field when STE and intragravel conditions in laboratory tests match those in the field. I do not see how, unless we find in the future that egg pocket structure makes no difference. More likely, we will find that only future STE information from accurate analogs of egg pockets will prove useful for field application.

I hope that the thoughtful comments offered by Young et al. on my review, together with the review itself, will provide impetus for further research on the effects of fines in salmonid redds. The problems offered should drive graduate students mad for at least one generation.

D. W. CHAPMAN

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.

*Don Chapman Consultants, Inc.
3180 Airport Way
Boise, Idaho 83705, USA*

References

- 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.
- Bianchi, D. R. 1963. The effects of sedimentation on egg survival of rainbow trout and cutthroat trout. Master's thesis. Montana State College, Bozeman.
- Bruhn, D. S., and J. T. Bowen. 1973. Selection of rainbow trout broodstock, 1968. *Progressive Fish-Culturist* 35:119-120.
- 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., D. E. Weitkamp, T. L. Welsh, M. B. Dell, and T. H. Schadt. 1986. Effects of river flow on the distribution of chinook salmon redds. *Transactions of the American Fisheries Society* 115:537-547.
- 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.
- 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.
- 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, Technical Report 84-6, University of Idaho, Moscow.
- Leitritz, E., and R. C. Lewis. 1976. Trout and salmon culture (hatchery methods). California Department of Fish and Game. 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 Research Note PNW-369.
- 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.
- 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 Research Paper PNW-220.
- 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.
- 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, Technical Bulletin 429, New York.
- Neter, J., W. Wasserman, and M. H. Kutner. 1983. Applied linear regression models. Irwin, Homewood, Illinois.
- 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., 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, EPA-600/3-79-043, Corvallis, Oregon.
- 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.
- 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.
- Shepard, B. B., S. A. Leathe, T. M. Weaver, and M. D. Enk. 1985. 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. Wild trout III. Federation of Fly Fishers and Trout Unlimited, West Yellowstone, Montana.
- 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.
- 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.
- 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.
- 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.
- 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. 1983. 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.
- Wootton, 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.
- Zar, J. H. 1984. *Biostatistical analysis*, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.