REVIEW / SYNTHÈSE

Riverine salmonid egg burial depths: review of published data and implications for scour studies

Paul DeVries

Abstract: Published data on salmon, trout, and charr egg burial depths are highly variable and inconsistent. Primary sources of variation include elevation datum and portion of the egg pocket referenced to; differences in spawning behavior and the number, thickness, and location of egg pockets; relationships between egg depth, fish species, and corresponding size of female and spawning substrate and velocity characteristics; sampling method; presence of excavation barriers; redd superimposition; and scour and fill by hydraulic and other mechanical processes. Such sources of variability in the reported data have important implications for studies of scouring processes in salmonid spawning areas that require accurate identification of egg burial depths for predicting and preventing potential scour impacts. Cumulative measurement error and unexplained variation may amount to 5–20 cm or more in published values. The most relevant data for scour impact assessments are depths from the original stream bed elevation down to the top of the main egg pocket. Frequency distribution data are needed for determining probabilities and cumulative levels of scour impacts and for managing genetic diversity as well as population size. Preliminary depth threshold criteria are proposed for use now, pending further research.

Résumé : Les données publiées sur les profondeurs d'enfouissement des oeufs de saumon, de truite et d'omble sont hautement variables et manquent d'uniformité. Parmi les principales sources de variation figurent : l'élément de référence d'altitude et la partie de la chambre à oeufs dont on parle; des différences dans le comportement de frai et le nombre, l'épaisseur et l'emplacement des chambres d'oeufs; les relations entre la profondeur des oeufs, l'espèce de poisson et la taille correspondante de la femelle et le substrat du lieu de frai et les caractéristiques de vitesse; la méthode d'échantillonnage; la présence de barrières d'excavation; la superposition des nids de frai; et le creusement et le remblaiement par des moyens mécaniques hydrauliques et autres. Ces sources de variabilité dans les données publiées ont des répercussions importantes sur les études des processus de creusement dans les aires de frai de salmonidés qui nécessitent la détermination précise des profondeurs d'enfouissement des oeufs pour prévoir et prévenir les effets potentiels du creusement. L'erreur de mesures cumulée et la variation d'origine inexpliquée peuvent représenter 5–20 cm ou plus dans les valeurs publiées. Les données les plus pertinentes pour l'évaluation des effets du creusement sont les profondeurs depuis l'altitude initiale du lit du cours d'eau jusqu'à la partie supérieure de la chambre d'oeufs principale. Les données de distribution de fréquences sont nécessaires pour déterminer les probabilités et les degrés cumulés d'effet de creusement, ainsi que pour gérer la diversité génétique et la taille de la population. On propose des critères seuils préliminaires que l'on peut utiliser maintenant en attendant les résultats d'autres travaux de recherche.

[Traduit par la Rédaction]

Introduction

Salmon, trout, and charr spawning behavior is distinct from that of most other riverine fish species because of the manner in which eggs are deposited and incubated, the size of the eggs, and the length of the incubation period (Peterson and Quinn 1996). Male salmonids may participate in egg nest, or redd, construction (Crisp and Carling 1989) but characteristically only the female digs a functional redd in a gravel stream bed. The female releases her eggs into the depression where they are fertilized simultaneously by one or more males. She then covers the eggs with a layer of gravel that is relatively free of fine sediments. Usually, the female deposits the eggs in several pockets, laid in an upstream progression within a single general nest or redd (e.g., Hawke 1978). In contrast, most riverine species broadcast their eggs above the river bed, letting the eggs either settle to the bottom or be carried downstream in the current. Alternatively, they may produce small eggs that incubate over a relatively short time period (Scott and Crossman 1973). Salmonid eggs and embryos remain in the gravel for a relatively long time, ranging between roughly 2 and 8 months. The length of time between egg deposition and emergence depends on species, location, water temperature, dissolved oxygen levels, amount of infiltrated fine sediments, and other features that influence the rate of development or movement

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Paul DeVries. Department of Civil Engineering,
P.O. Box 352700, University of Washington, Seattle,
WA 98195, U.S.A. e-mail: pdevries@u.washington.edu

within the gravel matrix (Bjornn and Reiser 1991; Groot and Margolis 1991).

The relatively long duration of the intragravel life stage implies that the survival of salmonid eggs and embryos is influenced more strongly by deposition and infiltration of fine sediments, changes in water quality, redd superimposition, disturbance by wading mammals, and stream bed scour and fill, than is the early life stage survival of other fish species. The depth to which the eggs are buried can affect the degree to which each of the above factors influences the survival to emergence. In the case of stream bed scour, this specific phase of the life cycle can limit the size of salmonid populations if the substrate is excavated down to, and (or) begins moving at, the elevation of the eggs (McNeil 1966; Seegrist and Gard 1972; Kondolf et al. 1991). The term "scour depth" is used here to refer to the difference in elevation (at a specific location in the channel) between the original stream bed surface at the time of spawning and the bottom of the active bedload transport layer during individual peak runoff events, including possible net excavation of local material.

Montgomery et al. (1996) studied scour depths in a small west-coast stream and determined that stream bed scour depths during frequent, bankfull flows were generally shallower than, or near the smaller values of, depths to the top of chum salmon (*Oncorhynchus keta*) egg pockets. They postulated that egg burial depth could be an evolutionary adaptation to scour events that occur on an episodic basis in coarse-bed channels. This observation may well be true for most other riverine salmonid populations and more work is needed on the subject. A literature search of the data on egg burial depth was conducted to evaluate further the hypothesized relationship between scour depth and the incubation success of different riverine salmonid species. Such data have not been summarized within a consistent, comprehensive source to date. This paper (*i*) summarizes egg burial depth information in a form useful to fisheries and environmental professionals interested in assessing scour-related impacts of land-use activities, (*ii*) identifies potential sources of variation, (*iii*) evaluates the utility of existing data for scour studies, and (*iv*) proposes threshold criteria pending collection of new data.

Egg depth data

Data on egg burial depths for riverine salmon, trout, and charr species vary widely (Table 1). Species for which data were found included chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), chum salmon, pink salmon (*O. gorbuscha*), Atlantic salmon (*Salmo salar*), (non-anadromous) kokanee and (anadromous) sockeye salmon (*O. nerka*), (non-anadromous) rainbow and (anadromous) steelhead trout (*O. mykiss*), resident cutthroat trout (*O. clarki*), (non-anadromous) brown and (anadromous) sea trout (*S. trutta*), and golden trout (*O. aguabonita*). Data were also compiled for charr species including brook trout (*Salvelinus fontinalis*), bull trout (*S. confluentus*), and Dolly Varden trout (*S. malma*). The compilation was intended to be as exhaustive as possible. There undoubtedly are other data available in less accessible, diverse sources such as university and fishery agency project reports that were not identified in the current literature search. However, the collection here represents a significant amount of the best information available in the refereed and nonrefereed literature and may be considered descriptive of individual species' egg-laying behavior.

Authors have not determined or reported egg burial depths consistently. They have reported depths from two different types of elevation datum: the level of the original undisturbed substrate and the level of the top of the redistributed, overlying gravel (Fig. 1). It is not always clear which datum applies. I present my own best estimate where possible in Table 1 when the respective publication did not specify the datum clearly but implied it in the text. Data have furthermore been reported for either the depth down to the top, center, or bottom of the egg pocket (Fig. 1), or for individual eggs throughout the thickness of the pocket. Like the datum, it was not always reported explicitly and interpretation was occasionally necessary in the preparation of Table 1. Redd excavation depths were assumed to be analogous to the top of the egg pocket: the eggs settle among the crevices of the redd bottom during the spawning act. Redd pit depth data (postspawning) were not included here because they may underestimate egg depths: the female is digging only deep enough to cover her last eggs.

The variable, nonstandard formats used to report egg burial depths made it impossible to analyze the data using exploratory statistics as Kondolf and Wolman (1993) did for evaluating substrate size characteristics selected by spawning salmonids. Many data were reported as ranges only, limiting their usefulness for frequency-based analyses. Instead, I created charts to depict the range of the data and to facilitate development of first-order depth criteria for assessment of scour risks (Fig. 2). The charts were based only on measured data for which the distance down to the top or bottom of the pocket, and the corresponding reference datum, could be determined reasonably. The smaller value of each reported range of depths of discrete eggs in Table 1 was assumed analogous to the top, and the larger value to the bottom of the egg pocket.

Larger species can clearly bury their eggs at greater depths than smaller species (Fig. 2). The listed order of species in Fig. 2 was based on general species size differences, from largest (chinook salmon) to smallest (brook trout and kokanee salmon). Although the trend is less clear for the shallowest depths, the smaller species appear to bury their eggs closer to the stream bed surface than do the larger species. A few species seem to dig less deeply than might be expected on the basis of size considerations alone (e.g., steelhead trout and Atlantic salmon), whereas others appear to dig more deeply (e.g., pink salmon). This may be an artifact of the small size of the data base, a biologic response to hydrologic and geomorphic features, or may be due to several sources of variation that are described in the next section.

Sources of variability, and their implications for scour assessments

The wide range found in egg burial depth values implies that there is presently considerable uncertainty inherent in scour assessments designed to relate anthropogenic changes in sediment inputs and flood hydrology to the survival of the salmonid incubation life stage (e.g., Schuett-Hames et al. 1996). Accurate knowledge of egg burial depths allows identification of the elevation at which scouring impacts can be expected, either because of lowering of the stream bed elevation caused by sediment transport imbalances or as a result of mechanical

Table 1. Summary of reported egg burial depth data, to nearest centimetre.

			Depth (cm)					
Species/authors	Datum[a]	Portion of pocket[a]	Mean	*n*	Range	Location	Method	Comments[b]
Atlantic salmon								
Belding (1934)	Original level	Top			15–30	Canada	Observation	Depth of pit prior to egg deposition
White (1942)	Original level	Top			15–30+	Nova Scotia	Observation	Depth of pit prior to egg deposition
Ottaway et al. (1981)	Overlying gravel	Bottom	18	1		United Kingdom	Freeze	Main egg pocket; RFL = 67 cm
Barlaup et al. (1994)	Overlying gravel	Bottom	27	10		Norway	Excavation	1 SD = 3.9 cm
Heggberget et al. (1988)	Overlying gravel	Center	18	159		Norway	Excavation	1 SD = 6.0 cm
Ottaway et al. (1981)	Overlying gravel	Discrete eggs		1	10–18	United Kingdom	Freeze	RFL = 67 cm
Crisp and Carling (1989)	Overlying gravel	Discrete eggs	17–23	3		United Kingdom	Freeze	Means of redds with >4 eggs; RFL = 51–85 cm
Brook trout								
Needham (1961)	Original level	Top		1	10–15	California	Observation	Depth of pit prior to egg deposition
Reiser and Wesche (1977)	Original level	Top			<9	Wyoming	Excavation	Pit depths; RFL <26 cm
Young et al. (1989)	Overlying gravel	Bottom	8	31	6–12	Wyoming	Freeze	1 Standard Error = 1.7 cm; RFL = 15–30 cm
Witzel and MacCrimmon (1983)	Overlying gravel	Discrete eggs			<15	Ontario	McNeil	Depths noted to rarely exceed this
Brown trout								
Hobbs (1937)	Original level	Bottom			15–25	New Zealand	Excavation	
Hobbs (1940)	Original level	Discrete eggs			20–25	New Zealand		Usual depth
Hobbs (1937)	Original level	Top	20			New Zealand	Excavation	Usual depth
Jones and Ball (1954)	Original level	Top	8			United Kingdom	Observation	"Typical" trout redd
Jones and Ball (1954)	Original level	Top		4	6–10	United Kingdom	Observation	Approximate depths of egg pockets
Reiser and Wesche (1977)	Original level	Top			<17	Wyoming	Excavation	Pit depths; RFL <41 cm
Ottaway et al. (1981)	Overlying gravel	Bottom	9	5	7–14	United Kingdom	Freeze	Main egg pocket; RFL = 26–35 cm
Grost et al. (1991)	Overlying gravel	Bottom	12	75	2–23	Wyoming	Freeze	RFL = 20–50 cm
Heggberget et al. (1988)	Overlying gravel	Center	12	73		Norway	Excavation	1 SD = 12 cm
Reiser and Wesche (1977)	Overlying gravel	Discrete eggs	9–12			Wyoming	Excavation	Normal depths of egg pockets; RFL <41 cm
Ottaway et al. (1981)	Overlying gravel	Discrete eggs		5	0–25	United Kingdom	Freeze	RFL = 26–35 cm
Witzel and MacCrimmon (1983)	Overlying gravel	Discrete eggs			>13	Ontario	McNeil	Specified as general burial depth
Elliott (1984)	Overlying gravel	Discrete eggs	4	16	2–12	United Kingdom	Excavation	Mean is for modal depths; RFL = 18–28 cm
Crisp and Carling (1989)	Overlying gravel	Discrete eggs	7–16	6		United Kingdom	Freeze	Means of redds with >4 eggs; RFL = 24–44 cm
Grost et al. (1991)	Overlying gravel	Discrete eggs	11	75	2–20	Wyoming	Freeze	Discrete samples; mean egg depths; RFL = 20–50 cm
Grost et al. (1991)	Overlying gravel	Discrete eggs	12			Wyoming	Freeze	Samples with >19 eggs; RFL = 20–50 cm
Hardy (1963)	Overlying gravel	Top	16	8	10–20	New Zealand	Excavation	Stranded redds; redd means
Hardy (1963)	Overlying gravel	Top			8–22	New Zealand	Excavation	Stranded redds; all data
Grost et al. (1991)	Overlying gravel	Top	9	75	2–16	Wyoming	Freeze	RFL = 20–50 cm
Bull trout								
McPhail and Murray (1979)	Original level	Top			10–16	B.C.		Redd excavation depth
Leggett (1980)	Original level	Top			10–15	B.C.	Observation	Redd excavation depth; spawning in artificial channel
Block (1955)	Overlying gravel	Top	20	1		Montana		
Leggett (1980)	Overlying gravel	Top			15–20	B.C.	Excavation	Spawning in artificial channel

Table 1 (*continued*).

Species/authors	Datum[a]	Portion of pocket[a]	Depth (cm)			Location	Method	Comments[b]
			Mean	*n*	Range			
Shepard et al. (1984*a*)	Overlying gravel	Top			>14	Montana	McNeil	
Shepard et al. (1984*b*)	Overlying gravel	Top			10–20	Montana		
Heimer (1965)					8–15	Idaho		Cited in Shepard et al. 1984*b*
Allan (1980)					3–18	Alberta		Cited in Shepard et al. 1984*b*
Chinook salmon								
Miller (1985)	Original level	Bottom	30			Washington		General criterion based in part on own data
Hobbs (1937)	Original level	Discrete eggs			30–41	New Zealand	Excavation	Considered 99% of eggs to be within this layer
Vronskii and Leman (1991)	Original level	Discrete eggs			21–50	USSR		Depths at which eggs reportedly found most frequently
Hobbs (1937)	Original level	Top			15–46	New Zealand	Observation	Redd excavation depths
Hobbs (1937)	Original level	Top			>20	New Zealand	Excavation	Eggs usually expected below this depth
Burner (1951)	Original level	Top	22–27		5–51	Washington	Observation	Deepest part of redd measured at different time intervals
Briggs (1953)	Original level	Top		2	28–36	California	Observation	Depth of pit prior to egg deposition
Scott and Crossman (1973)	Original level	Top			<31	Canada		Redd excavation depth; general criterion
Miller (1985)	Original level	Top	15			Washington		General criterion based in part on own data
Vronskiy (1972)	Overlying gravel	Bottom	53	10	40–80	USSR	Excavation	Maximum depths in 10 mounds
Chapman et al. (1986)	Overlying gravel	Bottom	29	54	19–37	Columbia River	Probing	May be underestimates according to authors
Hawke (1978)	Overlying gravel	Center	36	7	32–41	New Zealand	Excavation	Stranded redds; redd means
Hawke (1978)	Overlying gravel	Center			18–43	New Zealand	Excavation	Stranded redds; all data
Briggs (1953)	Overlying gravel	Top	28	8	20–36	California	Excavation	
Vronskiy (1972)	Overlying gravel	Top	21	10	10–46	USSR	Excavation	Minimum depths in 10 mounds
Chapman et al. (1986)	Overlying gravel	Top	19	116	10–33	Columbia River	Excavation	Depth to first embryos encountered
Chum salmon								
Bruya (1981)	Original level	Bottom		4	20–40	Washington	Freeze	Gravel disturbance by spawners (control); RFL = 65–74 cm
Burner (1951)	Original level	Top	22		8–43	Washington	Observation	Deepest part of redd measured at different time intervals
Scott and Crossman (1973)	Original level	Top			<41	Washington		Redd excavation depth; general criterion
Salo (1991)	Original level	Top			20–40	North America		General criterion for redd pit depth prior to egg deposition
Montgomery et al. (1996)	Original level	Top	23	40	10–49	Washington	Excavation	
Bruya (1981)	Overlying gravel	Discrete eggs		4	10–30	Washington	Freeze	93% of eggs recovered (control); RFL = 65–74 cm
Tripp and Poulin (1986)	Overlying gravel	Discrete eggs		34	0–45	B.C.	Probing	
Tripp and Poulin (1986)	Overlying gravel	Discrete eggs			10–35	B.C.	Probing	Majority of eggs (>90%)
L. Powell (in Scrivener and Brownlee 1989)	Overlying gravel	Discrete eggs			5–20	B.C.	Freeze	Cited personal communication
K.V. Koski (in Scrivener and Brownlee 1989)		Discrete eggs			10–50	Washington		Cited personal communication
K.V. Koski (in Scrivener and Brownlee 1989)		Discrete eggs	22			Alaska		Cited personal communication
Bazarkin (1990)		Discrete eggs			30–40	USSR		
Meehan and Bjornn (1991)		Discrete eggs			15–30	North America		General criterion

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Table 1 (*continued*).

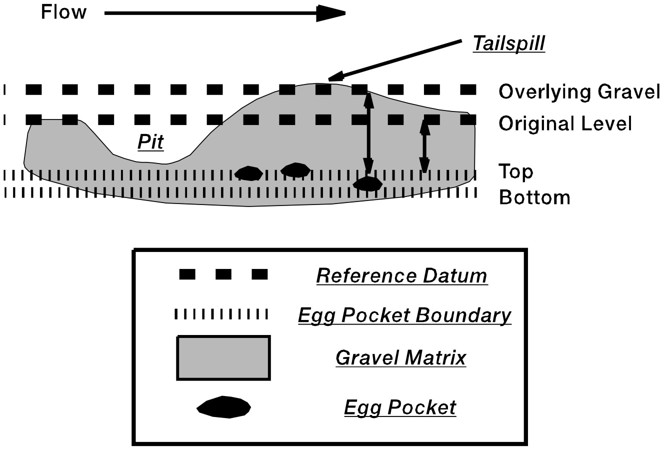
Species/authors	Datum[a]	Portion of pocket[a]	Depth (cm)			Location	Method	Comments[b]
			Mean	n	Range			
Coho salmon								
Gribanov (1962)	Original level	Discrete eggs		4	10–15	USSR	Excavation	Opened 2m × 2m of level stream bed in mass spawning area
Burner (1951)	Original level	Top	20		8–51	Washington	Observation	Deepest part of redd measured at different time intervals
Briggs (1953)	Original level	Top		2	20–25	California	Observation	Depth of pit prior to egg deposition
van den Berghe and Gross (1984)	Original level	Top	15	13	9–27	Washington	Observation	Redd excavation depths; RFL = 47–74 cm
Zorbidi (1988)	Overlying gravel	Bottom	33	10	16–55	USSR	Excavation	
Briggs (1953)	Overlying gravel	Top	25	16	18–38	California	Excavation	
Gribanov (1962)	Overlying gravel	Top	22	15	15–27	USSR	Excavation	Examined during spawning season
Gribanov (1962)	Overlying gravel	Top	21	9	16–30	USSR	Excavation	Examined 2 months after spawning
Zorbidi (1988)	Overlying gravel	Top	12	10	6–20	USSR	Excavation	
Koski (1966)	Overlying gravel	Discrete eggs			18–28	Oregon	Excavation	Embryos prior to emergence in two redds
Tripp and Poulin (1986)	Overlying gravel	Discrete eggs		30	0–45	B.C.	Probing	
Tripp and Poulin (1986)	Overlying gravel	Discrete eggs			20–35	B.C.	Probing	Majority of eggs (>90%)
Cutthroat trout								
Smith (1941)	Original level	Top			10–13	California	Observation	Depth of pit prior to egg deposition
Smith (1941)	Overlying gravel	Top			15–20	California	Observation	Apparent depth of refilled gravel
Wydoski and Whitney (1979)	Overlying gravel	Top			13–18	Washington		General criterion
Kiefling (1978)	Overlying gravel	Top			15–20	Wyoming	Excavation	
Dolly Varden trout								
Blackett (1968)	Original level	Top			15–20	Alaska	Observation	Redd excavation depth
Scott and Crossman (1973)	Original level	Top			<31	Canada		Redd excavation depth; general criterion
Golden trout								
Knapp and Vredenburg (1996)	Original level	Bottom	5	65	4–6	California	Excavation	Sampled 29 redds
Kokanee salmon								
Scott and Crossman (1973)	Original level	Top			5–10	Canada		Redd excavation depth; general criterion
Pink salmon								
Scott and Crossman (1973)	Original level	Top			<46	Canada		Redd excavation depth; general criterion
Dvinin (1957, 1959)	Overlying gravel	Discrete eggs	15–25		7–45	USSR	Excavation	Eggs rarely found deeper than 30–35 cm; cited in Raleigh and Nelson 1985
Vasilenko-Lukina (1962)	Overlying gravel	Discrete eggs	25–30	29		USSR	Excavation	
Enyutina (1974)	Overlying gravel	Discrete eggs	20–30		18–50	USSR		
Rukhlov (1969)			32–23			USSR		Mean deposition depth changes over time due to scouring
Rainbow trout								
Hobbs (1937)	Original level	Top	20	4		New Zealand	Excavation	Approximate depth of egg pockets
Hooper (1973)	Original level	Top	15			California	Observation	Most excavation depths (out of 10 redds); RFL = 30–36 cm

Table 1 (*concluded*).

Species/authors	Datum[a]	Portion of pocket[a]	Depth (cm)			Location	Method	Comments[b]
			Mean	*n*	Range			
Sea (brown) trout								
Ottaway et al. (1981)	Overlying gravel	Bottom	21	2	20–22	United Kingdom	Freeze	Main egg pocket; RFL = 55–57 cm
Barlaup et al. (1994)	Overlying gravel	Bottom	17	10		Norway	Excavation	1 SD = 5.2 cm
Ottaway et al. (1981)	Overlying gravel	Discrete eggs		2	3–22	United Kingdom	Freeze	RFL = 55–57 cm
Elliott (1984)	Overlying gravel	Discrete eggs	17	22	5–24	United Kingdom	Excavation	Mean is for modal depths; RFL = 25–45 cm
Crisp and Carling (1989)	Overlying gravel	Discrete eggs	8–26	24		United Kingdom	Freeze	Means of redds with >4 eggs; RFL = 31–74 cm
Sockeye salmon								
Mathisen (1962)	Original level	Center		22	8–13	Alaska	Excavation	
Mathisen (1962)	Original level	Center		149	15–23	Alaska	Excavation	
Mathisen (1962)	Original level	Center		27	25–30	Alaska	Excavation	
Burner (1951)	Original level	Top	11–14		5–28	Washington	Observation	Deepest part of redd measured at different time intervals
Kuznetsov (1928)	Overlying gravel	Discrete eggs			9–29	USSR	Excavation?	Majority of eggs deeper than 17 cm; cited in Foerster 1968
Mathisen (1955)	Overlying gravel	Discrete eggs	19	130		Alaska	Excavation	Pockets with <11% of eggs dead (unfertilized)
Mathisen (1955)	Overlying gravel	Discrete eggs	18	28		Alaska	Excavation	Pockets with >89% of eggs dead (unfertilized)
Mathisen (1955)	Overlying gravel	Top			18–28	Alaska	Excavation	Pocket depths within single redd; RFL = 59 cm
Mathisen (1955)	Overlying gravel	Top	12	1		Alaska	Excavation	Diagram of pocket within single redd
Steelhead trout								
Miller (1985)	Original level	Bottom	30			Washington		General criterion based in part on own data
Needham and Taft (1934)	Original level	Top		1	10–13	California	Observation	Depth of pit prior to egg deposition
Briggs (1953)	Original level	Top	20	1		California	Observation	Depth of pit prior to egg deposition
Shapovolov and Taft (1954)	Original level	Top			10–30	California	Observation	Depth of pit prior to egg deposition
Miller (1985)	Original level	Top	15			Washington		General criterion based in part on own data
Briggs (1953)	Overlying gravel	Top	21	13	15–28	California	Excavation	
Wydoski and Whitney (1979)	Overlying gravel	Top			<31	Washington		General criterion

[a] See Fig. 1 for a depiction of relevant geometry.
[b] RFL = Range of female lengths.

Fig. 1. Schematic of a generic salmonid redd depicting geometries applicable to scour studies. Depths to the top of an egg pocket are indicated for each reference datum. An egg pocket is considered to consist of a cluster of five or more eggs; individual eggs may be scattered outside of the main pocket(s) as well.



crushing and washing out of eggs and embryos during episodes of bedload transport. Predicted scour depths can then be related to egg burial depths to determine potential influences on salmonid populations. However, the magnitude of error in the reported data appears to be much larger than the resolution needed. Data collected by Montgomery et al. (1996) suggest that small increases in scour depth (on the order of several centimetres) may seriously reduce incubation survival. It is therefore important to identify and account for the potential sources of variability in reported egg depth data before evaluating measured or predicted scour depth increases.

I divided sources of variability into two general categories: variation linked more directly to (*i*) sampling considerations or (*ii*) fish excavation capability and spawning behavior. Each potential form of variation is identified and discussed below in the context of determining scour impacts to the incubation life-history stage. I subsequently estimated the maximum error magnitude that each source may contribute to a study of egg burial depths.

Sampling variability

Greatest sampling-related variability is introduced by the form of elevation datum used and referenced portion of the egg pocket. Choice of datum causes differences on the order of 0–5 cm. Differences of 5–10 cm may occur depending on which boundary of the egg pocket is referenced (Fig. 2). Differences in elevation between the first eggs encountered and the top of the main egg cluster likely introduce variation on the order of 1–2 cm.

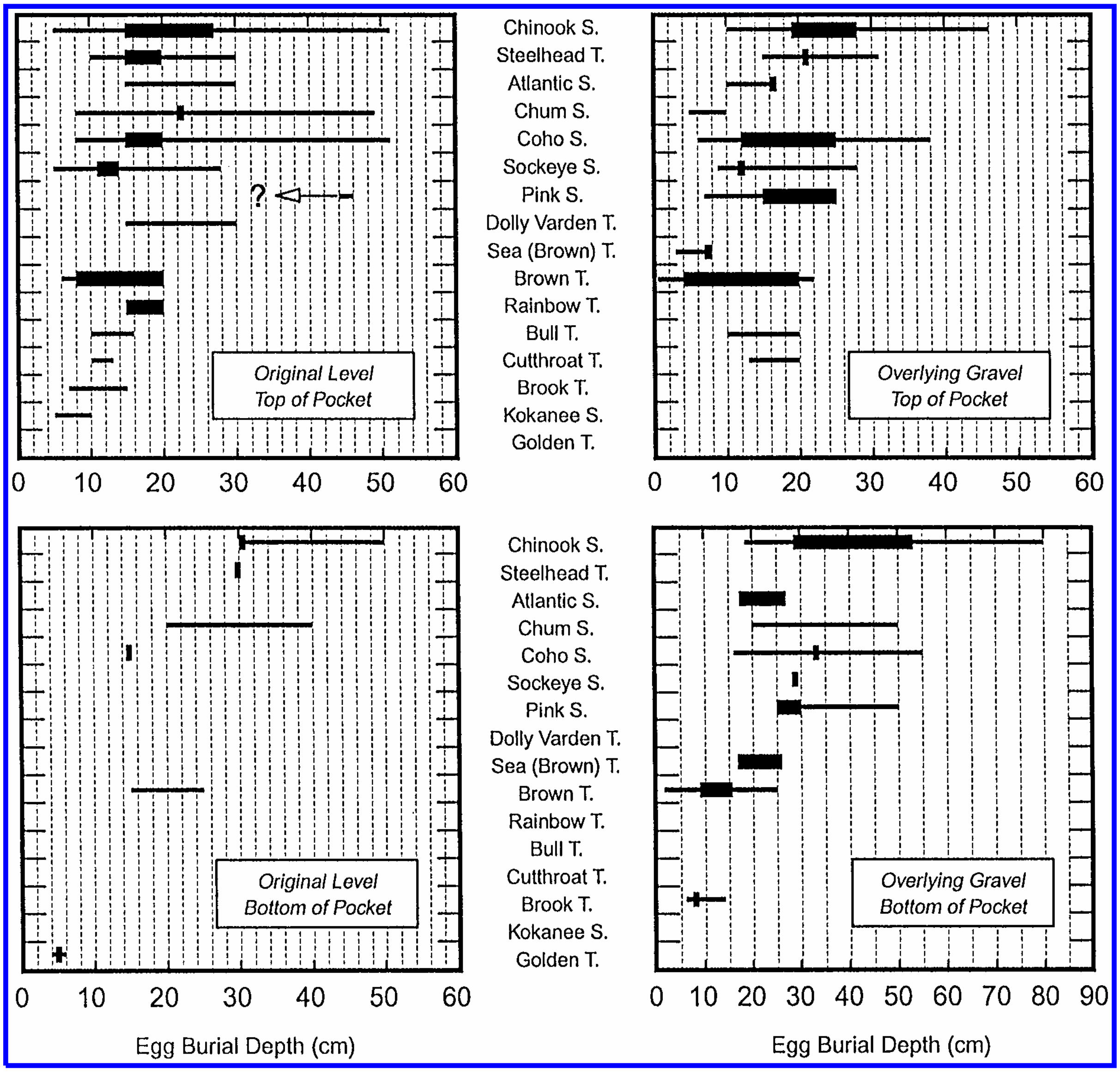
The depth below the overlying gravel may not be a sufficiently consistent measure for scour studies because the difference between the tailspill mound and surrounding stream bed elevations varies with position on the redd. Also, the burial depth of egg pockets under the hump of the tailspill may become shallower over the course of the incubation period if the redd is leveled gradually by the stream flow. Stuart (1953) noted such a decrease in brown trout egg burial depths relative to the overlying gravel surface, on the order of half the original value. Crisp and Carling (1989) and others have also noted that redds will generally level out with sufficient flow. Scour depth predictions for spawning areas can be linked more accurately to the original elevation of the surrounding, undisturbed gravel surface than to the elevation of specific portions of the tailspill (Fig. 1) because most of the stream bed will move once bedload transport rates are sufficient to wash out or crush eggs. Within a relatively narrow band on the cross section, corresponding to the width of the portion of the redd in which eggs lie, it may be reasonable to assume that the active bedload transport layer has a uniform thickness that can be referenced more accurately to the mean elevation of the surrounding stream bed surface. Hence, the most useful datum in scour studies appears to be the elevation of the original undisturbed stream bed.

A related source of variability is the horizontal location of the egg pocket within the redd. Egg pockets are generally found in the upstream third of the tailspill, but they may be found in the pit of the redd or farther downstream along the tailspill of long redds with multiple pockets (Hardy 1963; Hawke 1978; Young et al. 1989; Grost et al. 1991). The depth of the egg pocket, relative to either the original gravel surface elevation or to the overlying gravel, can thus vary with position within the redd. Grost et al. (1991) observed that brown trout egg depth increased from the redd pit downstream to the tailspill end. Hawke (1978) noted the same for chinook salmon and postulated that egg burial depth decreased over time as the female expended her energy. Hardy (1963) noted conversely that the first egg pocket was not buried as deep as subsequent pockets. Crisp and Carling (1989) noted that in two redds examined intensively, all egg pockets within a redd were at approximately the same burial depth relative to the overlying gravel surface. Hawke (1978) noted that the number of chinook salmon eggs tended to decrease as successive pockets were created, i.e., were generally greatest in the slightly deeper, downstream pockets of the redd. The data of Hardy (1963) and Hawke (1978) suggest that this form of variability can be on the order of as much as 11 cm for trout and 22 cm for salmon redds.

Such “primary” pockets would certainly be of greatest interest in scour studies should it be determined that loss of shallower, secondary pockets would not lead to excessive loss of eggs and embryos (what is considered excessive still needs to be defined and should factor in the loss of embryos of the adaptive components of a population). The uppermost developing embryos may emerge prematurely or be impacted by fine sediment deposition (Everest et al. 1987; Crisp and Carling 1989). Loss of the uppermost eggs to scour could thus have a negligible influence on production in many instances. However, given the declining status of a large number of salmonid stocks (Nehlsen et al. 1991), it is reasonable to assume that the shallowest pockets may still need to be protected (if possible) to maximize embryonic survival to emergence. It is thus important to know the range of egg pocket depths within the redd and where they are located if the depth datum used is with respect to the overlying gravel. For data reported according to that datum, it is difficult to recalculate the egg pocket elevation with respect to the level of the original stream bed surface.

The reported mean depth of the egg pocket may not always represent actual digging ability because excavation barriers during spawning can limit it. Clay layers can restrict burial

Fig. 2. Summary of egg burial depth data. Species were ordered according to general female size differences and differences in expected egg burial depths assumed a priori. The thin bar depicts the range of data, including depths of discrete eggs; the thick bar the range of different study means, or single observations where no range was available.



depths in completed redds (Barlaup et al. 1994) or induce the female to move elsewhere (Mathisen 1955). Large, flat rocks beneath the stream bed surface can also limit burial depth (Crisp and Carling 1989). The spawning instinct may be so strong that in streams with relatively limited spawning gravel quantities, the female constructs a shallower redd than one in which she might normally spawn (Stuart 1953). Some of the shallower egg depths reported in the literature for a given fish size may have resulted from such limitations, thereby contributing to the overall variance in the data. This is a difficult factor to assess and characterize quantitatively within an equation that could be used to predict egg burial depth. Available data suggest that eggs buried shallower than about 5 cm are likely the result of excavation barriers, excepting the eggs of females smaller than about 150–160 mm in length (cf. Knapp and Vredenburg 1996).

The field method used to determine egg depth can also lead to differences in reported egg depths. Data based on observation of the spawning act can be influenced by parallax, refraction, and observer calibration errors. Crisp and Carling (1989) felt that the freeze-core method gave more accurate and complete estimates of egg depth than manual excavation of in-channel redds. Manual excavation probably does yield less accurate estimates of depth to the uppermost eggs because stream flow may wash away the first few eggs before they are detected. The flow field around the excavation may cause the edges of the excavated pit to cave in, making it more difficult to both see the eggs and estimate the depth relative to the original gravel surface elevation. Nonetheless, excavation-based depth estimates of pockets containing the majority of eggs are likely to be reasonably accurate because there are more eggs to be detected. Use of a McNeil sampler (McNeil and Ahnell 1964) or other device that shields the excavation from the flow field probably gives results similar to the freeze-core method. A drawback to the use of freeze corers or McNeil samplers for deriving scour criteria is that the measured datum is typically the overlying gravel and thus varies depending on sampling location on a redd (Fig. 1). However, both are still reasonable approaches if the top of the core sample is indexed against the original, level stream bed elevation. Excavation is practical for sampling stranded redds. Without specific experimental data, the variability introduced by measurement technique is estimated here to be on the order of less than 3–5 cm (possibly more if the tailspill is extremely pronounced), with greatest error inherent in visual observations of excavated redd depths.

Some of the data in Table 1 may have been subjected to varying episodes of scour and (or) aggradation between the times of redd construction and sampling. Scrivener and Brownlee (1989) posited that scour may leave eggs at shallower incubation depths during most of the incubation period than at the time of spawning. Peterson and Quinn (1996) noted scouring of some redds where measured mean depths of egg pocket ceilings decreased from 22 to 19 cm between the fall spawning period and the following spring. Rukhlov (1969) observed a gradual decrease in mean deposition depth of pink salmon eggs over several months after a storm but noted that the event was not a normal flood. Aggradation was also noted, where egg depths were as much as 65 cm (cf. Fig. 2). However, much of the data in Table 1 were collected during or shortly after spawning activity, well before significant stream bed elevation changes could have occurred. Grost et al. (1991) found no significant difference in brown trout egg depths between fall and winter sampling. Furthermore, researchers would likely have known of severe scouring events such as large floods, ice breakups, and significant flood transport of large woody debris and qualified the data accordingly. This source of variability thus was probably not a significant problem for most of the data in Table 1 and Fig. 2.

Mass spawning and repeated, heavy spawning use over many years at the same location may lead to formation of persistent bedforms with maximum dune heights as much as 0.75–1.5 m (Tutty 1986; Everest et al. 1987; Salo 1991). A hole nearly 1 m deep was noted in association with mass spawning of cutthroat trout (Kiefling 1978). Egg burial depths may be much deeper or shallower than in areas with low concentrations of redds, making identification of a consistent egg burial depth difficult. The magnitude relative to the original stream bed elevation could thus be on the order of as much as a meter, but the data in Table 1 suggest that such an occurrence would be relatively infrequent. The hydraulics over such bedforms can be quite complicated, and it is difficult to identify a consistent scour depth within them as well. However, mass spawning activity could reduce bed mobility because of surface coarsening and creation of bedform roughness (Montgomery et al. 1996). Hence it is possible that scour down to egg depths is less of a concern for spawning areas with bedforms than in areas without, but this needs to be confirmed.

Species and microhabitat influences on egg burial depth

The tendency for certain species to bury their eggs deeper than others has been noted frequently since the first published observations of salmonid spawning activity. Greeley (1932) wrote that brown and rainbow trout redd pits were, on average, larger than brook trout pits. Inter- and intra-species variation in egg burial depth may have important survival implications. Variation in spatial and temporal distributions of scour may influence which species can best reproduce and survive in a specific stream (e.g., Kondolf et al. 1991). Tripp and Poulin (1986) collected egg depth data in recently spawned coho and chum salmon redds that suggested the former species buried its eggs deeper than the latter; estimated scour-related loss rates were consequently greater for chum salmon. Reduction in average fish size over time through selective fisheries may lead to reduction or possibly eradication of a stock in streams where the prevailing scour depths favor larger individuals that are able to bury their eggs deeper (van den Berghe and Gross 1984; Montgomery et al. 1996).

Differences between species appear linked to a combination of physical and behavioral factors. Possible sources of variation in egg burial depth include the size of female (e.g., van den Berghe and Gross 1984; Heggberget et al. 1988; Crisp and Carling 1989); her excavation behavior (e.g., Burner 1951; Scott and Crossman 1973; Groot and Margolis 1991; Meehan and Bjornn 1991); and her selection of particular substrate size distributions, velocities, and depths (e.g., Bovee 1978; Kondolf and Wolman 1993). It has also been suggested that differential egg burial depths may reflect differences in egg size and energy reserves between stocks of the same species (Scrivener and Brownlee 1989). Furthermore, egg burial depth appears to be controlled by the character and availability of spawning habitat within a given stream. Streams with substrates that are smaller and less armored, overlapping, or cemented may facilitate deeper redds than streams with contrasting substrate characteristics (e.g., Burner 1951). Egg burial depth may be inversely related to the amount of fine sediments present (Everest et al. 1987), a behavioral response that might improve survival to emergence in some instances.

Most empirical evidence points to a set of specific factors that are best correlated with egg burial depth: fish size (Fig. 2), and local substrate and hydraulic characteristics. Of these, fish size appears to be the most important determinant of maximum egg burial depth. Larger females have greater strength and mechanical advantage over smaller ones (van den Berghe and Gross 1984). Observations and analyses supporting a relationship between fish size and egg burial depth are numerous. Early researchers implied a length-dependent relation by noting that female salmon and trout excavate redds that are longer and deeper than their bodies (e.g., Greeley 1932; White 1942; Scott and Crossman 1973). Others have noted that a proportionality exists between fish size and redd size (e.g., Burner 1951; Shapovalov and Taft 1954). Crisp and Carling (1989) considered the proportionality to be a reflection more of fish size than of species.

Several quantitative relationships have been developed. Ottaway et al. (1981) found a significant semilogarithmic relationship between female fork length and depth to base of main egg pocket for brown trout and Atlantic salmon. Van den Berghe and Gross (1984) also found a significant linear relationship between female fork length and depth to the egg nest bottom for coho salmon. Crisp and Carling (1989) found a linear relation between female length and egg burial depth for anadromous and resident brown trout and Atlantic salmon in some streams but not others; scatter was sufficiently large that regression slopes did not significantly differ from zero, however. Ranges in predicted egg depths, for the range of all fish sizes measured, were on the order of 13–15 cm in all three studies.

A smaller number of researchers have found little to no relationship between fish size and egg burial depth. Elliott (1984) studied two streams and found no such relation within a specific stream: all egg burial data fell consistently about a mean depth that appeared to be invariant with fish size. However, the anadromous brown trout in one stream were generally larger than the resident brown trout in the other, and the substrates in the former stream appeared to be generally smaller (Elliott 1973, 1984). Average egg burial depth was substantially deeper for the anadromous trout stock, indicating that the trends observed in Elliott's (1984) data could have been linked to differences between not only stocks (which was reflected in fish size) but also substrate and hydraulic characteristics within the two streams.

Any correlation between egg depth and fish size is thus likely to be influenced by variability in local spawning microhabitat parameters. Larger fish or species can use deeper and faster water and larger gravel than smaller individuals (Arnold 1974; Bovee 1978), although larger gravel used by larger fish may counteract the tendency to dig deeper, and a positive correlation between egg size (which in turn is correlated with fish size) and spawning gravel size (Quinn et al. 1995) may partially offset differences in egg settling depth. Of the potential hydraulic and geomorphic features influencing spawning habitat, substrate characteristics appear most influential, followed by velocity. Many researchers have suggested that gravel size characteristics are very important in determining egg burial depth (e.g., Burner 1951; Vasilenko-Lukina 1962; Tautz and Groot 1975; Grost et al. 1991). Heggberget et al. (1988) found that gravel sizes used by Atlantic salmon and brown trout differed significantly. However, there was considerable overlap in the ranges of gravel sizes used, and it is possible that other studies that did not find a relationship did not have sufficiently large sample sizes to detect a statistically significant difference (e.g., Ottaway et al. 1981; Crisp and Carling 1989). Characterizations of the surface layer (e.g., Heggberget et al. 1988) neglect the effects of armoring and variable layer composition (e.g., coarser surface and finer subsurface) on the final redd depth and thus may add variability to results. Given such problems, I was unable to estimate potential magnitudes of variation in egg depths owing to substrate influences from the data.

Experimental evidence for the influence of velocity on egg depth is less conclusive than for substrate. Researchers have made visual correlations between egg depth and velocity (e.g., Vasilenko-Lukina 1962), but the exact relationship remains to be determined. Egg burial depth in faster water may be shallower than in slower water (Vronskii 1972; Neilson and Banford 1983). However, Burner (1951) noted the opposite trend. Combinations of velocity with energy slope and substrate characteristics likely act in concert to determine the depth of the redd. Tautz and Groot (1975) commented that velocity may have a greater influence on redd depth in the initial stages of redd building rather than later. As the redd takes shape, the dominant influence was thought to be the hydraulic force exerted by the female's tail. However, since the female uses her tail to redirect and accelerate higher momentum fluid from the main flow field down into the redd, it is likely that the velocity field is important throughout redd construction.

More data are needed on fish size, substrate characteristics, and the velocity field at the time of redd construction. A large set of consistent data with the same datum and reference frame for the egg pocket boundary would facilitate multiple regressions or more advanced multivariate techniques. An organized approach is recommended in which data on egg burial depth are collected systematically in several streams that characterize a range of substrate and hydraulic conditions. Each stream should ideally contain a range of naturally reproducing salmonid species such that species and fish size differences can be investigated more fully. Fish size appears to be the most important influence on egg burial depth and should be evaluated first, followed by other variables. The power available to the fish in digging a redd clearly must contribute to redd depth, but more studies are needed with larger numbers of females across all size ranges to develop relationships that are more definitive than existing ones. Although the results of investigations into the importance of microhabitat characteristics are to date inconclusive, the substrate grain size distribution of the surface and subsurface layers and the degree of overlap must be important in view of armoring effects and the critical shear and normal stresses needed to dislodge and transport material. Hydraulic principles suggest that the near-bed velocity field in the water column just upstream of the redd is also likely to be important. Water depth and energy gradient influence the shear stress acting at the stream bed at the time redd excavation is begun. However, flow separation at the upstream edge of the pit once the redd is more developed implies that tractive force due to the main flow field is not necessarily a determinant for the eventual egg burial depth, and water depth at the time of redd construction would therefore not be expected to correlate strongly with redd depth (as has indeed been the case to date). Relationships between egg burial depth and fish species and size therefore need to be developed that include adjustments for substrate (primarily) and velocity (secondarily) characteristics but not necessarily water column depth.

A final source of variability is related to the egg pocket thickness, which is likely scaled to the size of the larger substrate particles present. Mathisen (1955) noted that egg pockets of Alaskan sockeye salmon were approximately 10 cm thick, while F. Everest (personal communication cited in Chapman (1988)) observed that the majority of eggs in chinook salmon redds in Oregon lay in a stratum 2–3 cm thick just above the undisturbed surface of the stream bed. Peterson and Quinn (1997; N.P. Peterson, Simpson Timber Co., Shelton, WA 98584, U.S.A., personal communication) observed that chum salmon egg pockets were usually about 10 cm thick. Crisp and Carling (1989) found that the majority (85–90%) of eggs in 40 Atlantic salmon and brown trout redds were aggregated within ±2–3 cm of the mean burial depth. Barlaup et al. (1994) found that Atlantic salmon and sea (brown) trout egg pockets were 6.4 and 8.0 cm thick on average, respectively. The data suggest that the larger, anadromous salmonids tend to bury their eggs in a pocket that is approximately 8–10 cm thick and smaller trout in a pocket that is approximately 6–8 cm thick, but more work is needed in this area. The thickness of the pocket has implications to the vertical distribution of eggs (Holtby and Healey 1986) and the total mortality to scour. For the same pocket bottom depth, eggs buried in a narrower vertical distribution could suffer lower total egg loss than eggs buried in a thicker layer as long as the maximum scour depth was still above the bottom of the egg pocket.

Egg depth criteria for scour evaluations

Egg burial depth data evidently must be interpreted with care. Data presented by Montgomery et al. (1996) suggest that measurement errors in pocket depths of a few centimetres could influence survival predictions significantly for a particular depth of substrate disturbance. Individual sources of variation can contribute to differences in egg depths up to 15 cm or more. Cumulative variation, due to measurement error and unexplained sources, could easily be on the order of 5–20 cm in most studies, depending on species and the other factors discussed above.

A different source of variation not included in this analysis that may influence scour mortality predictions stems from downward movement of alevins through the substrate after hatching (Bams 1969; Dill 1969; Fast et al. 1981). However, alevin movement generally may not happen until more than halfway through the intragravel life-history phase (e.g., see individual species reviews in Groot and Margolis 1991). Scour down to the egg burial depth will impact developing embryos until then. Scour depth criteria developed from egg depth data are expected to provide a conservative level of protection for alevins in consideration of their mobility.

Pending additional research, I offer suggested preliminary threshold criteria for scour studies in Table 2. The criteria were developed in consideration of the data compiled in Table 1 and summarized in Fig. 2 and of expected size differences between species. They were based primarily on the range of reported mean values, which was assumed to approximate the depth at which the majority of eggs may be found. The criteria are biased towards smaller females because insufficient data exist for developing consistent size-dependent criteria. The reader is referred to the studies of Ottaway et al. (1981), van den Berghe and Gross (1984), Holtby and Healey (1986), and Crisp and Carling (1989) for preliminary quantitative relationships of egg depth and fish size; I recommend drawing conditional conclusions concerning scour impacts from those relationships. The criteria that are proposed here are in many cases based on limited data and should change as better data become available. In the meantime, the values in Table 2 for the top of the egg pocket are appropriate for estimating the onset of scour impacts, while the criteria for the bottom of the pocket can be considered as conservative estimates of the point at which the population will become decimated because of scour. Such information should prove useful for modeling studies that link hydrology and sediment inputs to scour and incubation survival, although assumptions would still need to be made concerning the distribution of eggs between the two limits (e.g., Holtby and Healey 1986; Scrivener and Brownlee 1989).

For improved threshold criteria, a more consistent approach is needed wherein depths are measured to both the top and the bottom of each egg pocket, relative to the original stream bed surface elevation. Regression analyses may be more useful in scour studies if based on the lower envelope of egg depth data rather than the mean of the data. Such threshold-type relationships could be used to predict the onset of scour-related mortality of incubating embryos. It should be possible to develop functional relationships for the minimum or maximum depths of the egg pocket that would be expected for a given fish size (or, say, 10 or 90 percent regression quantile; cf. Terrell et al. 1996). Because a few loose eggs are often deposited close to the surface, a less variable relationship may be determined for the distance down to the top of distinct egg pockets rather than the first few eggs encountered. An egg pocket could be defined as containing five or more eggs (cf. Crisp and Carling 1989; Tripp and Poulin 1986, Fig. 6) separated in space by no more than a few egg diameters. A drawback to threshold criteria is that they indicate only when impacts may occur rather than how much.

Table 2. Preliminary egg burial depth criteria proposed for use in scour studies.

	Depth (cm) below original stream bed level	
Species	Top of pocket	Bottom of pocket
Atlantic salmon	15	30
Brook trout	5	15
Brown trout	8	25
Bull trout	10	20
Chinook salmon	15	50
Chum salmon	15	35
Coho salmon	15	35
Cutthroat trout	10	20
Dolly Varden trout	15	30
Golden trout	3	6
Kokanee salmon	5	15
Pink salmon	15	35
Rainbow trout	10	25
Sea (brown) trout	10	25
Sockeye salmon	10	25
Steelhead trout	15	35

Note: Criteria are proposed as maximum allowable depths of scour before initial (“top”) and total (“bottom”) egg loss.

Frequency distribution data for both egg pocket depths and for discrete eggs within the pocket are more useful for estimating scour-related loss rates (e.g., Mathisen 1962; Tripp and Poulin 1986; Montgomery et al. 1996). Data for chum salmon in Kennedy Creek in western Washington State indicated that egg pocket ceiling depths were distributed lognormally (Montgomery et al. 1996), where the median depth was smaller than the mean value by approximately 2 cm (i.e., skewed right; Peterson and Quinn 1996). However, data for discrete coho and chum salmon eggs collected by Tripp and Poulin (1986) indicated a skewed-left lognormal distribution. The two results suggest that interpretations of scour impacts will vary depending on the form in which egg depth data are presented. The frequency data for depths down to the top of egg pockets suggest that scour depths approximating the mean value would result in impacts to more than half of the total number of redds created. Conversely, the frequency data of Tripp and Poulin (1986) suggest that scour depths approximating the mean depth of discrete egg burial would result in the loss of less than half the eggs. Both views are important because they provide information on impacts to genetic variability and total production, respectively.

More comprehensive relationships should be developed that describe the frequency characteristics of egg burial depth. Ideally, egg depth distributions should be developed for different size-classes of females, for each species. Frequency data need to be established for both the top of the egg pocket and for discrete eggs. Such data would facilitate comparisons of predicted egg burial depths with spatial and temporal frequency distributions of scour depth for spawning runs composed of different-sized individuals and species. Management decisions regarding land-use practices influencing sediment supply and flood hydrology, fish size and species or stock harvest restrictions, hatchery brood stock characteristics, and escapement goals could all benefit. Decisions that consider egg depth frequency characteristics may ultimately prove to be more effective for preserving specific salmonid stocks than decisions based on threshold conditions, because they would be based on the goals of protecting both genetic variability and population size from scour impacts.

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