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The importance of measuring biotic and abiotic factors in the lower egg pocket to predict coho salmon egg survival

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Based on results from simulated redds of coho salmon *Oncorhynchus kisutch*, the amount of fine sediment <0.5 mm in the lower half of the egg pocket, rather than the entire egg pocket of the redd, was a strong predictor of egg survival to hatching ($r^2 = 0.62$). The relationship was much stronger than observed in other studies, which typically ignore egg pocket structure. Abundance of a fish egg-eating worm, *Haplotaxis ichthyophagous*, an oligochaete that may have been attracted to fine sediment and dead eggs in the egg pocket, was also associated with a decrease in egg survival. The worm, however, accounted for little of the variance in survival compared to fine sediment. Only 10% fine sediment (<0.5 mm) in the lower pocket was required to decrease survival from 100 to 5%. Other abiotic factors had weaker (gravel permeability) or non-existent (dissolved oxygen) correlations with survival.

Key words: dissolved oxygen; egg pocket; fine sediment; permeability; simulated redd; worms

INTRODUCTION

Much research has been conducted and summarized on the effects of fine sediment on salmonid egg survival (Chapman, 1988; Kondolf, 2000). Laboratory and field studies have suggested that infiltration of large amounts of fine sediment into salmonid redds can reduce gravel permeability (McNeil & Ahnell, 1964; Koski, 1966) and delivery of dissolved oxygen (DO) to eggs (Coble, 1961; Rubin & Glimsäter, 1996). The resultant low DO concentrations can kill eggs (Wickett, 1954; Alderice *et al.*, 1958; Sowden & Power, 1985). In addition, fine sediment can occlude interstitial pore spaces and directly interfere with emergence of salmonid fry (Hausle & Coble, 1976; Everest *et al.*, 1987). Although relationships between egg survival and fine sediment or other substratum measures (geometric mean, fredle index) have been strong in the laboratory ($r^2 = 0.6$–0.8; Phillips *et al.*, 1975; Young *et al.*, 1990), they have not been as strong in artificial (Scrivener, 1988; Rubin & Glimsäter, 1996) or natural redds (Koski, 1966; Cederholm *et al.*, 1981; Tagart, 1984; Sowden & Power, 1985) in the field (often $P > 0.05$).

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Correlations with survival in the field may have been weak because fine sediment was measured in the entire gravel column of the redd or egg pocket, rather than in just the lower egg pocket. Though the egg pocket extends from the surface to the floor of the redd, most eggs reside in the bottom half (Hawke, 1978; Chapman *et al.*, 1986). Moreover, gravel conditions in the lower portion of the pocket differ from the overlying gravel (the centrum, located at the bottom, contains larger rocks; Burner, 1951; Jones & Ball, 1954; Vronskiy, 1972), yet most field research has not focused on the lower half (Chapman, 1988).

This oversight is a problem if a seal of sand forms on the surface of the redd. Sand can fill surface interstices and block further infiltration of finer particles into the lower egg pocket, protecting the eggs (Beschta & Jackson, 1979; Chapman, 1988; Lisle, 1989). If the sand seal is not thick enough to trap emerging fry, but thick enough to block other fine sediment, even egg survival to emergence could be high in redds with large amounts of sand in the overlying gravel. No studies have addressed whether fine sediment levels in the lower egg pocket are more predictive of egg survival to hatching than the levels that have traditionally been measured throughout the egg pocket in a redd.

Factors other than sediment can affect egg survival, including abiotic and biotic conditions such as DO concentration, gravel permeability and abundance of egg predators. Such variables should also be measured deep in the egg pocket to evaluate their effects on survival relative to fine sediment. Some field studies have addressed effects of DO and permeability on egg survival (Turnpenny & Williams, 1980; Tagart, 1984; Sowden & Power, 1985; Rubin & Glimsäter, 1996); but, unlike this study, they did not always measure these factors in the same location as the eggs. Also, egg predators have been ignored, even though they may have a substantial effect in some streams. Large masses of a fish egg-eating worm, *Haplotaxis ichthyophagous* (Gates), have been observed to invade salmonid redds or planted egg boxes in a number of streams in northern California (Briggs, 1953; Williams, 1996; R. Barnhardt, pers. comm.). When this worm was present, egg survival decreased (Briggs, 1953; Meyer *et al.*, 1993).

This study had two objectives. The first was to determine which combination of abiotic (percentage of fine sediment, DO concentration, permeability) or biotic (oligochaete abundance) conditions in the lower egg pocket best predicted egg survival to hatching of coho salmon *Oncorhynchus kisutch* (Walbaum) in a sediment-impacted stream. Because of their direct effects on the eggs, a combination of DO and oligochaete abundance was expected to be the best predictor, better than fine sediment or gravel permeability. The second objective was to test the hypothesis that fine sediment in just the lower egg pocket of simulated coho salmon redds is more predictive of egg survival to hatching than fine sediment measured in the entire gravel column of the egg pocket.

MATERIALS AND METHODS

STUDY AREA

The study was completed in Prairie Creek (41°22′ N; 124°00′ W), a coastal stream in Prairie Creek Redwoods State Park in north-western California. The creek supports runs of anadromous coho salmon, chinook salmon *Oncorhynchus tshawytscha* (Walbaum) and steelhead *Oncorhynchus mykiss* (Walbaum) (Anderson, 1988). Before 1989, the creek was a relatively pristine old-growth redwood forest stream. During a rainstorm in October 1989, Prairie Creek received a large load of silt and fine sediment from 10 km of an unprotected dirt road-construction alignment in its watershed (Meyer *et al.*, 1993). Long-term monitoring of the gravel in riffle crests over 8 years with freeze-cores (beginning in 1985) indicated fine sediment significantly increased and the geometric mean particle diameter and fredle index significantly decreased after the 1989 storm (unpubl. data). To investigate the effects of the fine sediment on survival of salmonid eggs, a 10 km reach was established on the portion of Prairie Creek affected by the sedimentation event. A second stream in an adjacent watershed, Lost Man Creek (41°22′ N; 124°00′ W), was used to obtain independent data to test the adequacy of the regression models. Lost Man Creek had also been subjected to sediment inputs, but from past logging rather than from road construction.

EGG SURVIVAL

Abiotic and biotic factors that can affect salmonid egg survival were studied using simulated redds in Prairie Creek for 3 years (1991–1993). The Prairie Creek study area was stratified into four reaches bounded by major tributaries (Meyer *et al.*, 1993). Within each reach, simulated redd sites were randomly selected within riffle crests that were potential spawning habitat (real redds had been observed in many of these areas in previous years during spawning surveys). Twenty simulated redds were constructed in 1991, 17 in 1992 and four in 1993 during January, the month in which most coho salmon were spawning. Due to budget constraints, only four simulated redds were constructed in 1993, one in each reach. The 1993 redds were placed in a location that had approximately average egg survival for that reach the previous year. Three of the four reaches had gauging stations. Peak stream flow was recorded as the highest water discharge recorded at the nearest gauging station upstream of the simulated redd during its egg-incubation period.

For each simulated redd, a cylindrical basket constructed from 3.2 mm plastic mesh was filled with sieved (<4.75 mm), clean gravel interspersed with 100 freshly fertilized coho salmon eggs. Large cobbles (64–128 mm) were at the bottom of each basket to simulate the egg pocket centrum (Coey, 1998). Each simulated redd had one basket in 1991, but two in 1992 and 1993 to reduce the variance in estimates (variables were averaged for the two baskets). The baskets were buried 30 cm deep in each shovel-sifted simulated redd, and a pot and tail-spill were constructed. Each basket (15 cm tall × 15 cm diameter) represented the lower egg pocket and had 15 cm of gravel above it. After eggs were expected to have hatched (based on stream temperatures), the baskets were retrieved with winches and surviving sac fry counted.

All egg survival rates were adjusted for parental fertility and egg viability rates, determined from eggs incubated in a controlled streamside hatchbox. Handling mortality, estimated from 12 unburied control egg baskets placed in clean stream water, was minimal (0–2%). Variability in estimates of mean egg survival percentages for each parent fish in the controls was relatively low (mean S.E. over all fish = 3% in 1991, 4% in 1992 and 1% in 1993).

DISSOLVED OXYGEN AND PERMEABILITY

Dissolved oxygen and gravel permeability were measured in standpipes in the lower half of the egg pocket. Before the gravel and eggs were added, a perforated, 3.5 cm-diameter standpipe (Terhune, 1958) was placed in the base of each basket between the centrum cobbles. After the addition of gravel and eggs, plastic mesh with a tight-fitting hole for the standpipe was sewn on the tops of the baskets, and the standpipes were capped when not in use.

At the end of the incubation period, DO concentration and gravel permeability were measured in the standpipe at least three times consecutively to obtain a reliable average. Dissolved oxygen concentrations of the intragravel water in the standpipe and adjacent surface water were measured with an air-calibrated YSI Model 54 DO meter and probe. For permeability, the rate of water inflow into a graduated chamber was measured after a vacuum generator established a 2.5 cm head in the pipe (Coey, 1998). Use of a motorized vacuum generator with constant suction improved the ease of permeability monitoring over the hand pumps often used in other studies (Koski, 1966; Turnpenny & Williams, 1980; Young *et al.*, 1989). In the present study, the same individuals measured the conditions in all simulated redds (Young *et al.*, 1989). Water infiltration rates were converted to permeability rates at 10° C with Terhune's (1958) calibration curve. Because the standpipe was not identical with Terhune's (having slits instead of holes), his calibration curve might have been slightly biased for the pipes. Nonetheless, a second calibration curve developed for a larger diameter pipe (4·1 cm; Barnard, 1992) was identical to Terhune's (1958) in the pertinent data range, which suggests differences caused by slight changes in pipe design were minor.

FINE SEDIMENT

To capture fine sediment that infiltrated the entire gravel column in the simulated egg pocket, collapsed, 25 cm diameter, waterproof infiltration bags (Meyer *et al.*, 1993) were placed beneath each basket. Cables were attached to the infiltration bags to allow removal at a later date. Although the bags may have hindered some upward and downward movement of hyporheic water, the chemistry (total dissolved solids, DO) of the ground and surface water is probably not different enough (Meyer *et al.*, 1993; M. Sparkman, pers. comm.) to warrant concern that the bags were strongly changing the egg pocket environment. After the egg-incubation period ended in March, a chain winch on a tripod was hooked to these cables and pulled up to unfold each infiltration bag. In this way, the egg baskets and all gravels surrounding and on top of each basket were removed from the streambed. The egg baskets were removed from the infiltration bag and immediately placed in a water-filled dishtub to minimize loss of water and fine sediment. Sediment suspended in the water from each basket and infiltration bag was allowed to settle in graduated cones for 45 min.

Gravels (including the suspended sediment) were oven-dried and mechanically sieved through the following sieve sizes: 128, 64, 45, 32, 22, 16, 11, 8, 5·6, 4·7, 2, 1 and 0·5 mm (Coey, 1998). The percentage of fine sediment was calculated by mass for particles <0·5 mm and 0·5–4·75 mm. Percentages were calculated for (1) gravel in baskets and (2) the gravel column of the entire egg pocket, which combined all gravel in the egg basket and infiltration bag. Percentage by dry volume was also calculated with the water displacement method and conversion factors that compensated for water content (Platts *et al.*, 1983).

Despite efforts to duplicate conditions, the gravel composition of the simulated redds was not identical to natural redds exposed to the same stream conditions. Composition of the gravel column in 10 natural redds (after fry emergence) in a separate study on Prairie Creek (Coey, 1998) was compared to the composition of the entire gravel column of the simulated redds after eggs hatched. Although mean percentage of sediment <4·75 mm was similar ($P > 0{\cdot}10$), the finest fraction (<0·5 mm) averaged somewhat higher in the simulated redds (11 *v.* 7% by volume, $P = 0{\cdot}02$).

Scour chains (Leopold *et al.*, 1964) placed adjacent to the simulated redds in 1991 and 1992 supported the assumption that most of the redds were not scoured down to the level of the hatching basket in those years (maximum scour was 5·5 cm). Overall, during the 3 year study period, scour was probably minimal because the baskets remained in place within the constructed redds.

OLIGOCHAETE WORMS

After each egg basket was opened, oligochaete abundance was recorded as absent, low (1–15 g of worms), medium (16–59 g) or high (>60 g). This categorical variable (0–3) was used in the data analyses. It should be noted, however, that these worms are mobile and may have left an egg basket by the time it was opened.

DATA ANALYSIS

All survival and fine-sediment percentages were normalized with the arcsine square root transformation (Neter *et al.*, 1990). The size fraction of fine sediment that best predicted egg survival was determined by separately regressing percentages of particle sizes <0·5 mm and 0·5–4·75 mm on egg survival for each individual year and combination of the 3 years. Because it was unknown whether mass or volume of fine sediment was most predictive, linear regression results were compared for both statistics. Dissolved oxygen concentration, gravel permeability and worm abundance categories were each regressed on survival and then added in various combinations with fine sediment to find the most predictive regression equation. To test for non-linearity and interactions among variables, polynomial and interaction terms were added to check if they improved the best models (Neter *et al.*, 1990). Data were evaluated for each year and all 3 years combined. To select the best models from the family of 15 models tested (all combinations of the four variables), the techniques of Burnham & Anderson (1998) and Franklin *et al.* (2000) were used. An Akaike weight (w_i) was calculated as

$$w_i = e^{-0{\cdot}5\Delta_i}\left[\sum_{r=1}^{R} e^{-0{\cdot}5\Delta_r}\right]^{-1},$$

where $\Delta_i = \mathrm{AIC}_i - \text{minimum AIC}$ (AIC = Akaike's Information Criterion, a measure of model fit) for the *i*th model of *R* compared models (Burnham & Anderson, 1998). The AIC was corrected for sample size ($\mathrm{AIC_c}$ in Burnham & Anderson, 1998). The weights represent the likelihood that one model better approximates the true relationships than the other models. Of the two top models with the highest Akaike weights, the model with significant variables, a high R^2_{adj}, and that was most predictive when applied to an independent dataset was selected as the best model.

To validate and test whether the top models were applicable to an independent dataset on a nearby stream, the regressions developed for Prairie Creek were applied to a dataset obtained from simulated coho salmon redds constructed on Lost Man Creek during 1992 ($n = 5$) and 1993 ($n = 1$). Mean square prediction errors from the observed and predicted values for these six redds were calculated and compared between the models (Neter *et al.*, 1990). All the above statistical analyses were conducted in SAS (SAS Institute, 1990). Results were considered highly significant at $\alpha = 0{\cdot}05$ and moderately significant at $\alpha = 0{\cdot}10$.

Because autocorrelation can inflate the significance of regression coefficients, spatial and temporal autocorrelation of the residuals of the best regression were addressed using Moran's *I*-test in S+ (Mathsoft, version 1.5) and by adding year as a variable. The inverse of the distance between the simulated redds was used as the spatial weighting statistic.

RESULTS

ANNUAL VARIATION

Based on data from a long-term rain gauge near Prairie Creek, rainfall was 80, 60 and 125% of normal in 1991, 1992 and 1993, respectively. Correspondingly, peak stream discharge during the incubation period was moderate in 1991, low in 1992 and relatively high in 1993 [Fig. 1(a)]. The high flows in 1993 delivered the most sediment <4·75 mm into the entire gravel column of the egg pocket of the simulated redd (24% in 1993 *v.* 13% in 1991 and 10% in 1992, ANOVA, $P \leq 0{\cdot}01$). When percentages of sediment <4·75 mm were determined for just the lower egg pocket, however, more fine sediment was observed in 1991 [Fig. 1(a)]. More of the fine sediment <4·75 mm that infiltrated the simulated redd reached the lower egg pocket that year [11·2% in 1991 *v.* <4·5% in the other years, Fig. 1(a)]. Worms were also more abundant in 1991, infesting 75% of the simulated redds (often in very large masses of >400 worms and up to 121 g wet mass in a basket), whereas they only infested one or two of the simulated redds in the other years [Fig. 1(b)]. In conjunction with the high sediment loads in the lower egg pocket that year, redd gravel permeability was lowest in 1991 [Fig. 1(b)].

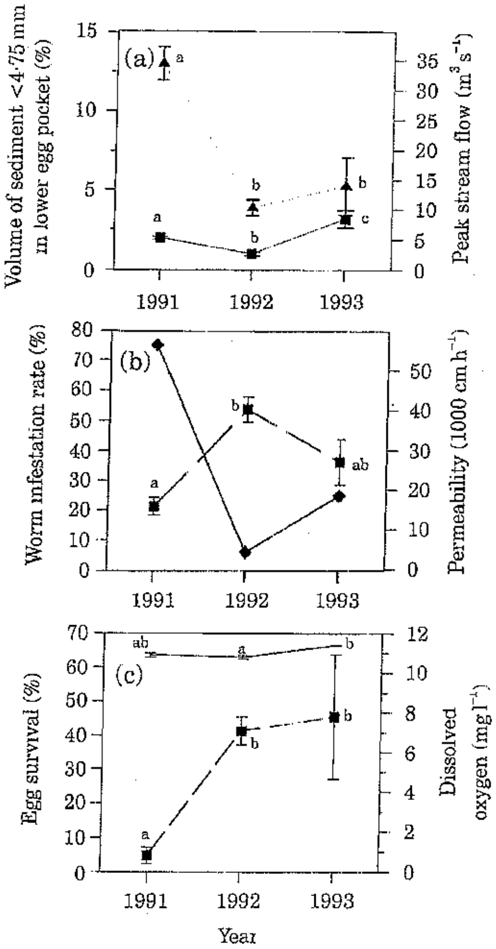

FIG. 1. Annual variation (1991, $n = 10$; 1992, $n = 12$; 1993, $n = 4$) in mean ± S.E. of (a) streamflow (■) and fine sediment (▲) (b) worm infestation (◆) and permeability (■), and (c) egg survival to hatching (■) and dissolved oxygen (—) in the lower egg pocket of simulated coho salmon redds. For each variable, means with similar letters are not significantly different ($P < 0{\cdot}05$; Tukey's HSD *post-hoc* comparisons, except survival and stream flow for which the Mann–Whitney *U*-test was conducted).

Corresponding to the poor conditions (high amounts of fine sediment, abundant worms and low permeability in the lower egg pocket), egg survival was extremely low in 1991 (5%) compared to the other two years [>40%; Fig. 1(c)]. Dissolved oxygen concentration, however, was not correspondingly low that year [Fig. 1(c)]. In all 3 years, DO concentrations in the egg pocket of all simulated redds remained high, and only slightly lower than the surface water ($\bar{x} = 10{\cdot}9$ v. $11{\cdot}5$ mg l^{-1}).

EGG SURVIVAL CORRELATIONS IN THE EGG POCKET

When regressions were examined separately for individual years, all relationships of fine sediment to survival except one were not highly significant. The only

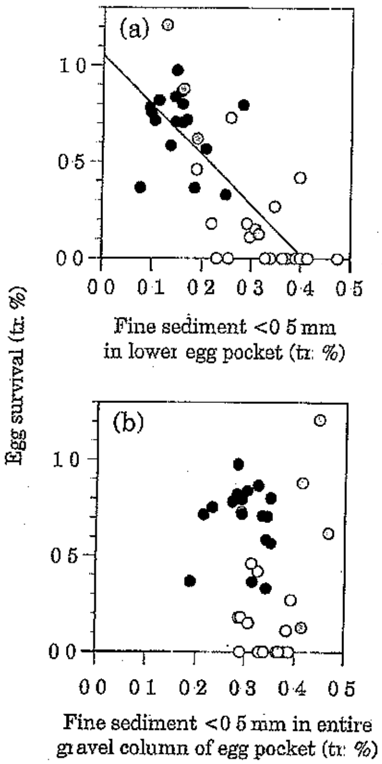

FIG. 2. Relationship between egg survival and volume of fine sediment in the (a) lower egg pocket ($r^2 = 0{\cdot}62$) and (b) entire gravel column of the pocket in simulated redds ($r^2 = 0{\cdot}07$) in 1991 (○), 1992 (●) and 1993 (⊙). The regression was significant when measured in the lower egg pocket ($P < 0{\cdot}0001$, $n = 41$), but not in the entire gravel column ($P = 0{\cdot}293$). tr. %, arcsin square-root transformed percentage.

highly significant relationship ($P < 0{\cdot}05$) for an individual year was in 1993, the year in which sample size was small ($n = 4$). Volume of fine sediment <0·5 mm was negatively correlated with survival that year ($R^2_{adj} = 0{\cdot}91$, $P = 0{\cdot}03$). Some other regressions on survival, however, were moderately significant ($0{\cdot}05 < P < 0{\cdot}10$) within individual years. The predictors for those regressions were: (1) 1991: volume of fine sediment <0·5 mm ($R^2_{adj} = 0{\cdot}15$, $P = 0{\cdot}051$, $n = 20$); (2) 1992: mass of fine sediment <0·5 mm ($R^2_{adj} = 0{\cdot}12$, $P = 0{\cdot}095$, $n = 17$); (3) 1993: mass of fine sediment <0·5 mm ($R^2_{adj} = 0{\cdot}75$, $P = 0{\cdot}087$, $n = 4$). Fine sediment <0·5 mm always had a negative correlation with survival. The lack of strong significant relationships within the individual years of 1991 and 1992 was not surprising because each year covered only part of the full range of fine sediment conditions found in the lower egg pocket of the simulated redds over the 3 years [Fig. 2(a)]. The finding that the data in 1993 (which also did not cover the full range) had a strong significant relationship may have been fortuitous, given the small sample size that year.

All 3 years of data were combined to capture the full range of sediment amounts found in the simulated redds and to obtain a larger sample size. When the data

TABLE I. Results for particle sizes (by mass and volume) regressed on egg survival. Data from 1991 to 1993 are combined ($n = 41$). (−), Negative coefficient

	P	R^2_{adj}*	Akaike weight†
Lower egg pocket sediment (% by mass)			
<0·5 mm (−)	<0·0001	0·54	0·439
0·5–4·75 mm (−)	0·0695	0·06	$4·8 \times 10^{-10}$
Lower egg pocket sediment (% by volume)			
<0·5 mm (−)	<0·0001	0·61	0·561
0·5–4·75 mm (−)	0·1895	0·02	$2·1 \times 10^{-10}$

*R^2_{adj} is the coefficient of determination adjusted for number of parameters in the regression.

†An Akaike weight sums to one for the family of compared models (Burnham & Anderson, 1998). The model with the highest weight has the highest likelihood of approximating the 'true' relationship.

were combined, volume of fine sediment <0·5 mm produced highly significant relationships with survival that explained 62% of the variance [Table I and Fig. 2(a)]. In contrast, relationships with coarse sands (0·5–4·75 mm) were not significant. Volume of fine sediment <0·5 mm had higher Akaike weights and explained more variance than mass of fine sediment (Table I). Thus, volume of fine sediment <0·5 mm in the lower egg pocket was the fraction used to relate fine sediment to egg survival in all other analyses.

As expected, fine sediment measured in the entire gravel column of the egg pocket, instead of only the lower egg pocket, did not predict egg survival well [Fig. 2(b)]. The regressions were not significant in any individual year or for all 3 years combined ($P > 0·10$). For example, during the high-flow year (1993), fine sediment loads in the entire gravel column of the simulated redds were very high, yet survival was highly variable and not correlated with the sediment load [Fig. 2(b)]. Only when the upper layer of gravel was removed from the analysis, did correlations in each year become significant.

Egg survival was regressed individually on each of the four factors measured in the egg pocket (DO, permeability, fine sediment and worms). Fine sediment, permeability and worm abundance each produced highly significant models (Table II), but DO was not significantly correlated to survival ($r^2 = 0·018$, $P = 0·9102$). No non-linear trends were evident for any of these variables.

When the variables were entered into multiple regressions in various combinations and then compared to one another and to the models with individual variables (15 models compared), the top two models based on Akaike weights were fine sediment alone and fine sediment with worms (Table II). These also had a high R^2_{adj}. The coefficient for worm abundance was moderately significant in the latter regression ($P = 0·090$). The interaction term between worms and fine sediment was also moderately significant ($P = 0·089$). None of the multiple regressions had significant coefficients for DO or permeability.

The top two regression models (worms plus fines and fines alone) and the worms plus fines regression with the interaction term were applied to independent data

TABLE II. Regression model variables and measures of model fit. All models combined data from 1991 to 1993 ($n = 41$). All 15 models compared are not shown, but the top two based on Akaike weights were fines-worms and fines (shown)

Model	P	R^2_{adj}*	Akaike weight*
Fines† (–), Worms (–)	<0·0001	0·630	0·304
Fines (–)	<0·0001	0·612	0·224
Worms (–)	<0·0001	0·381	$1·6 \times 10^{-5}$
Permeability (+)	0·0030	0·174	$4·1 \times 10^{-8}$

*See Table I for definition of R^2_{adj} and Akaike weight.
†(+) or (–) indicates a positive or negative coefficient for the variable in the regression model. All fine sediment percentages (<0·5 mm) were calculated for the lower egg pocket (basket) by volume.

collected from six simulated redds on Lost Man Creek in 1992 and 1993. The regression equations were:

$$\text{survival} = 1·053 - 2·587\,(\text{fines}), \tag{1}$$
$$\text{survival} = 0·996 - 2·138\,(\text{fines}) - 0·0789\,(\text{worms}) \text{ and} \tag{2}$$
$$\text{survival} = 1·081 - 2·539\,(\text{fines}) - 0·329\,(\text{worms}) + 0·783\,(\text{worm} \times \text{fines}), \tag{3}$$

where percentages of survival and fine sediment (fines) were arcsine square root transformed. For equations (1), (2) and (3), the mean prediction square error (MPSE) of the independent data was 0·073, 0·057 and 0·075, respectively. These values are a good fit if they are close to the mean square error (MSE) of the original models. The differences between the MPSE and MSE for equations (1), (2) and (3) were 0·022, 0·008 and 0·029, respectively. Thus, equation (2) (worms–fines with no interaction term) had the lowest difference and best fit. When data were entered into equation (2), the predicted mean survival for the six independent redds was 21% (S.E. = 4·9%), which was relatively close to an observed mean of 27% (S.E. = 5·1%). When worms were excluded, the predicted mean (19%) differed more from the observed mean. Therefore, the combination of fine sediment <0·5 mm and worm abundance, both negatively correlated to egg survival, provided a moderately predictive model for incubation success in simulated redds in a nearby sediment-impacted stream.

Fine sediment explained far more variance than worm abundance. When added to a model with just worm abundance, fine sediment explained an additional 25% of the variance. When worm abundance was added to a model with just fine sediment, worms explained only an additional 3% of the variance. Unfortunately, fine sediment and worm abundance were moderately and positively correlated ($r = 0·63$), making the interpretation of the relative effects of the two difficult (Neter *et al.*, 1990).

Spatial autocorrelation was not significant ($P \geq 0·95$); thus, no adjustments to the final regression equations were required. The year in which the simulated redd was created was a significant variable when added to the regression with worm abundance and percentage of fine sediment, indicating the data were temporally autocorrelated. The equation was:

$$\text{survival} = 0·462 - 1·273\,(\text{fines}) - 0·088\,(\text{worms}) + 0·203\,(\text{year}). \tag{4}$$

ach of the four coefficients in equation (4) were highly significant ($P < 0.04$) and he regression had a high r^2 (0·73) Year was negatively correlated with fine sediient ($r = -0.66$) Thus, even after accounting for sediment and worms, later years the study had conditions more conducive to high egg survival.

DISCUSSION

OST PREDICTIVE VARIABLES IN THE LOWER EGG OCKET

If it is assumed that simulated redds represent natural redds, the results suggest hat fine sediment <0·5 mm measured in the lower egg pocket may be one of the nost reliable predictors of salmonid embryo survival in some coastal streams. lthough the most parsimonious model (Burnham & Anderson, 1998) that still it the data well was the fine-sediment model without the worms, the negative corelation of oligochaete worm abundance with survival should not be completely gnored Adding worm abundance to fine sediment in a multiple regression mproved predictions on the independent dataset

The results refute the hypotheses that DO concentration and worm abundance vould be the most predictive variables Dissolved oxygen was more important han sediment in a stream that had strong upwelling of groundwater with low DO Sowden & Power, 1985), but in Prairie Creek, where DO concentrations were lways high, DO was a poor predictor. Dissolved oxygen concentrations were ever low enough (≥ 9.9 mg l^{-1}) to cause egg mortality (Wickett, 1954; Alderice *et al.*, 958; Turnpenny & Williams, 1980; Sowden & Power, 1985; Rubin & Glimsäter, 1996). erhaps pores in the large gravel framework (average median diameter = 50 mm) haracteristic of Prairie Creek were permeable enough to allow water with high O concentrations to flow into the egg pocket, even though silt and worm nucus covered and eventually suffocated the eggs. The relationship between fine ediment and DO should not be accepted uncritically because it is often weak Shapley & Bishop, 1965; Scrivener & Brownlee, 1989; Peterson & Quinn, 1996) ermeability was also not as predictive as fine sediment or worm abundance, posibly because the Terhune (1958) method commonly used to measure permeability s not as accurate or consistent as the methods used for measuring fine sediment

Unexpectedly, year was an important predictor of egg survival It is unknown vhat conditions changed that favoured egg survival as the study progressed from 991 to 1993 Possibly, fine silt, which is difficult to fully measure in the egg pocket ecause it does not completely settle in measuring cones even after 45 min (Guy, 969), became less abundant in the creek and thus in the simulated redds over ime Over the course of the study, stream flows may have flushed out some of the etrimental silt that was delivered to the creek and coated the streambanks in 1989

The reason worms did not appear to be a major mortality factor once the fine ediment was taken into account may be because worms are attracted to redds hat already have silty conditions and dead eggs (Williams, 1996). These oligohaetes, however, can easily destroy eggs without any silt present Worms added to lean laboratory gravel increased salmonid egg mortality from 21 to 98% by coverng eggs with copious mucus, asphyxiating them before consuming them (Briggs, 953). The worms might be initially attracted to redds with some egg mortality and then kill additional live eggs. The correlation between worms and survival, independent of sediment, might have been stronger if a technique could be developed that detected whether worms were ever present (*e.g.* identify traces of mucus), as some worms certainly left egg baskets before they were opened (Williams, 1996; M. Sparkman, pers. comm.). Field experiments designed to fully separate the effects of worms and sediment <0·5 mm are needed before it can be concluded with certainty that worms are relatively unimportant to egg survival in northern California streams.

With or without worms, the sediment increase in the formerly pristine old-growth stream is of concern. The results from the simulated redds demonstrate that an increase of fine sediment in the lower egg pocket is associated with a severe decrease in survival of coho salmon eggs, as was seen in 1991. For all simulated redds in the study, a 10% volume of sediment <0·5 mm reduced hatching success from 100% (fertility-adjusted value in control baskets) to an average of <5%. In simulated redds without worms ($n = 24$), it dropped less steeply to 10%. Reiser & White (1988) similarly found a 10% volume of sediment <0·85 mm in gravel surrounding the eggs reduced hatching success of chinook salmon to 10% in the laboratory. The results suggest not much sediment is required in the egg pocket to create deleterious effects.

IMPORTANCE OF MEASURING FINE SEDIMENT IN THE LOWER EGG POCKET

In contrast to the results for the lower egg pocket, fine sediment in the entire gravel column of the simulated redd was not predictive of egg survival to hatching. As an illustration of the importance of measuring conditions in the lower egg pocket, at least a 30% volume of fine sediment (<0·85 mm) in the entire gravel column of natural redds was needed to reduce coho salmon egg survival to emergence to *c.* 10% in Washington streams (Cederholm *et al.*, 1981). That volume is much higher than the level of sediment (5–10%) found for this study when just the lower egg pocket was included. Based on a summary of egg-survival studies that mostly did not consider redd and egg pocket structure, Kondolf (2000) recommended sediment <0·8 mm be <12–14% of stream gravels for successful incubation (>50% success). Such a level may be appropriate for potential spawning beds (levels were much higher than 14% in the riffle crests of Prairie Creek), but the results from simulated redds in Prairie Creek suggest the threshold is lower for the actual location of the eggs.

Factors such as formation of sand bridges or sand seals in the gravel overlying the egg pocket that are protective, rather than detrimental, might be causing the poor correlations for the entire gravel column (Chapman, 1988). Correlations of similar substratum measures with salmonid egg survival to either hatching or emergence have been relatively weak in other field studies. Compared to the Prairie Creek study ($r^2 = 0{\cdot}62$, $P < 0{\cdot}0001$), most field studies (*e.g.* natural redd studies Cederholm *et al.*, 1981; Tagart, 1984; Sowden & Power, 1985; buried egg boxes: Scrivener, 1988; Rubin & Glimsäter, 1996) had a low r^2 (<0·20 and insignificant at $P > 0{\cdot}05$), possibly because effects of sand seals near the redd surface were not removed in these studies. The two exceptions are Koski's (1966) study of survival to emergence in natural coho salmon redds ($r^2 = 0{\cdot}47$, $P = 0{\cdot}0005$) and Weaver & Fraley's (1993) study in artificial redds of cutthroat trout *Oncorhynchus clarki* (Richardson) ($r^2 = 0{\cdot}73$, $P < 0{\cdot}005$). The latter study, however, missed the critical early incubation stages because it only addressed survival to emergence from the eyed egg stage.

Thick sand seals may not always be beneficial, however, because they might entrap fry (Phillips *et al.*, 1975). In streams where fry entrapment is the major problem rather than incubation success [possibly true of Koski (1966) and Weaver & Fraley (1993) studies], correlations with emergence might improve by including the entire gravel column (Phillips *et al.*, 1975; Witzel & MacCrimmon, 1983). Entrapment did not appear to be a problem in Prairie Creek in 1991, the year of low survival. Based on simulated coho salmon redds that were capped in the creek that year (Coey, 1998), survival to emergence was generally the same or higher than survival to hatching in adjacent egg pockets.

APPLICABILITY TO NATURAL REDDS

To evaluate whether simulated redds represent natural redds, results were compared to a study of coho salmon egg survival to emergence in natural redds in Prairie Creek (Coey, 1998; unpubl. data). If the two types of redds are similar, survival from egg deposition to hatching in simulated redds should be higher than survival from egg deposition to emergence in natural redds, which appeared to be the case. In 1991, 10 natural redds were capped with fry traps and exposed to the same peak stream discharges as the 20 simulated redds. Only 30% of the simulated redds had ≥2% egg survival that year. Similarly, natural redd production was low, with only three of the 10 natural redds producing any fry; and two of those produced <40 fry (the third had very high success with 3671 fry). In 1992, the natural redds were exposed to a much higher peak discharge than the simulated redds, making the results less comparable. Notably, as might be expected with late high flows during the emergence period, none of the 10 natural redds produced >41 fry; and five redds produced no fry, possibly due to entrapment. The simulated redds, subjected to lower flows, had moderate incubation success that year (41%). In 1993, four natural redds were capped and exposed to stream conditions similar to those in simulated redds, but only one redd produced fry (399). The latter result is lower than the relatively high survival found in simulated redds that year (mean = 45%), which could mean conditions were better for incubating eggs in simulated redds or that the many high flows of that year deposited sand that entrapped emerging fry (or traps unnaturally clogged the redd with sand).

The foregoing comparisons neither confirm nor refute that the experimental simulated redds approximate natural conditions. The best way to determine if they apply to natural conditions is to develop techniques to study factors that affect egg survival during incubation and then emergence in the lower egg pocket in natural redds. The natural redd results reported above suggest that fry entrapment may have been more of a problem than incubation success in 1992 and 1993, information not available from the more limited scope of the simulated redd study.

Overall, this study presents field evidence that abundant fine sediment surrounding coho salmon eggs is detrimental, and volume of sediment <0.5 mm in the lower egg pocket can be one of the best variables to measure to predict incubation success. By contrast, fine sediment in the upper egg pocket and variables such as DO concentration may have no relationship to egg survival in some streams. Any equations developed to predict survival to hatching should be based on fine sediment amounts expected to reach the lower egg pocket. Additional geomorphic research might help elucidate the factors (*e.g.* stream discharge and spawning bed morphology and composition) that affect how much reaches the lower pocket. The effects of predaceous oligochaetes on egg survival are less clear. Because oligochaete abundance and sediment levels were positively correlated in this study, more work is needed to separate the two to determine if worms cause much egg mortality beyond the mortality caused by fine sediment.

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