

Effects of Highway-Construction Sediment, Worms, and Peak Streamflow on Salmonid Redds
in an Old-Growth Forest Stream

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Abstract.--During a rainstorm in October 1989, an exposed highway construction alignment delivered fine sediment into a pristine old-growth forest stream. Fine sediment in potential spawning gravels significantly increased following the October storm in both the old-growth stream and in unaffected reference streams that were not pristine. Following the storm, we studied the effect of fine sediment on coho salmon (*Oncorhynchus kisutch*) egg survival in artificial redds during low flow years (1991-92) and a relatively high flow year (1993). Peak streamflow predicted fine sediment infiltration rates within a reach. Egg survival to hatching was lowest during the first low flow year of the study (5% in 1991) and higher during the other years (> 40%), including the high flow year. Oligochaete worms correspondingly proliferated in redds in 1991 but were much less abundant in the next two years. Worms were detrimental to egg survival and, during the low flow years, they were most abundant in redds that contained the most fine sediment. The 1993 high flow year required higher fine sediment (<0.5 mm) loads and streamflows to adversely affect egg survival or increase worm abundance than did the low flow years. The inverse relationships of sediment, worms, and streamflow to egg survival were strongest when scaled up from the redd to the stream reach. We hypothesize that a sand seal protected the redds from extensive silt and worm invasion during the high flow year in 1993. The seal did not protect redds in 1991, when streamflows were high enough to move silt and fine sand into the redds, yet too low to entrain the coarser sand needed to form a protective seal.

Introduction

To protect native fish stocks, land managers must know the magnitude of the effects of stream sedimentation events on survival of fish eggs (Scrivener and Brownlee 1988). Infiltration of large amounts of fine sediment can reduce availability of dissolved oxygen (DO) and kill eggs (Wickett 1954; Alderice et al. 1958; Coble 1961; Sowden and Power 1985). Moreover, fines can occlude interstitial pore spaces, and directly interfere with emergence of salmonid fry (Hausle and Coble 1976; Everest et al. 1987). Some evidence also suggests that fine sediment can increase oligochaete worms (*Haplotaxis ichthyophagous*) that indirectly predate on salmonid eggs (Briggs 1953; Meyer et al. 1993). Notably, peak streamflow during the incubation period influences the amount of fine sediment transported and deposited into a salmonid redd (Beschta and Jackson 1979; Lisle 1989; Sear 1993). However, following a sedimentation event, no field studies have tried to quantify the complex inter-relationships between peak streamflow, suspended sediment discharge, sediment infiltrating into the redd, egg predators, DO concentration, and egg survival during flow years when deep scouring of the redd is not of concern.

An opportunity to study such relationships arose when a rainstorm lasting from October 20 to 27, 1989 delivered fine sediment from 10 km of an unprotected highway construction alignment into Prairie Creek, a relatively pristine old-growth forest stream running parallel to the highway alignment (Figure 1). A layer of light-colored silt (up to 0.5 cm thick) visibly settled on the dark, sandy streambanks, and fine sediment infiltrated into subsurface gravels of Prairie Creek and its tributaries. During the storm, the creek carried over 300 tons of suspended

sediment--30 times the amount carried during later storms of similar magnitude that year (RNP 1991). We initiated two studies following this event. First, using long-term monitoring data, we studied the effect of this new sediment on gravel quality for spawning. Second, we studied the direct and indirect effects on salmonid eggs of streamflow and infiltration of fine sediment into the egg pockets of artificial redds. For the latter study, the results from the first pilot year (1990) indicated that the additional fine sediment had no effect on eyed steelhead egg survival when peak streamflow during the egg incubation period was very low (Meyer et al. 1993). The following two years (1991-1992) also had relatively low streamflows, but indicated that the finest fraction of sediment (<0.5 mm) decreased survival of fertilized coho salmon eggs, although concomitant decreases in DO concentrations were not observed (Meyer and Coey, in review). However, several questions raised during the preliminary studies remained unanswered. We still did not know the effect on egg survival of high stream discharges, which can deposit large amounts of fine sediment into redds; nor did we know if fine sediment in the spawning gravels increased due to the October 1989 storm. Moreover, it was not clear if the presence of sediment increased the density of predators on salmonid eggs. To resolve some of these questions, we had three objectives for the present study. First, we evaluated if the sedimentation event significantly increased fine sediment in the spawning gravels. Second, we determined if the resultant fine sediment stored in the streambed decreased DO concentrations and salmonid egg survival more at high than at low water and low suspended sediment discharges. Third, we determined if increased egg predation was associated with deposition of fine sediment.

Methods

Study Site

Located within Redwood National and State Parks in northwestern California, Prairie Creek supports large runs of anadromous coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), and steelhead trout (*O. mykiss*) (Anderson 1988). We established a 10-km study area on the portion of Prairie Creek affected by the sedimentation event (called the affected stream, Figure 1). This affected portion had an average gradient of <1% and drained 35 km². Lost Man Creek, a large tributary to Prairie Creek of similar size to the upper portion of Prairie Creek, was unaffected by highway sediment inputs and was used as a reference stream for the study. Another stream used as a reference was Tarup Creek, a tributary in the Klamath River watershed located east of the Prairie Creek basin. Both reference streams support the same salmonid species as Prairie Creek. These reference streams were not ideal because they contained sediment from past (Lost Man Creek) and present logging (Tarup Creek) and are geologically dissimilar from Prairie Creek. However, they were the only suitable choices and were useful for comparing annual trends and correlations.

Riffle Gravel Quality at Long-Term Monitoring Sites

In 1985, the affected stream, Prairie Creek, was stratified into four reaches bounded by major tributary confluences (Figure 1). Six long-term monitoring sites, 82 to 156 m in length, were established in the reaches, with at least one in each reach. For the reference streams, one long-term monitoring site was established on each stream. Quality of potential spawning gravels was annually sampled during the summer from 1985 to 1992, a period which bracketed the 1989 storm. At each long-term site, we froze six 40-cm-deep gravel cores at random points along

riffle crests (Lotspeich and Reid 1980), removed them from the streambed, and air-dried samples for four to five months. Gravels were mechanically dry-sieved using the following sieve sizes: 64, 32, 4, 1, and 0.125 mm (Platts et al. 1983). Sediment data from the six cores at each site were averaged to estimate three parameters that quantify spawning gravel quality in each reach: percent fines <1.0 mm in diameter, geometric mean of the gravel size calculated using the method of moments, and the fredle index (Lotspeich and Everest 1981).

Artificial Redds

Egg Survival.—For the artificial redd study, we stratified the affected stream, Prairie Creek into four reaches bounded by major tributaries and included a reach on Lost Man Creek (but not Tarup Creek) as the reference stream (Figure 1). Redd sites were randomly selected within each reach. On the affected stream, we constructed 20 redds in 1991, 12 in 1992, and 4 in 1993. On the reference stream, we constructed five redds in 1992 and one in 1993. Unfortunately, no redds were constructed on the reference stream in 1991, due to our initial misconception that the upstream portion of Prairie Creek could be used as a reference. Later, we discovered this portion also had been subjected to sedimentation from the October storm. To overcome the constraints of the small sample size in 1993, we placed each 1993 redd in the same location as a 1992 redd that had egg survival and fines infiltration representative of its stream reach. The artificial redds were constructed in January, the same time most coho salmon were spawning.

At a suitable riffle crest, we dug a deep hole and sifted the gravel to remove fine sediment using a rake. About one-third of the gravel was further sieved to remove fines <4.75 mm in diameter. We interspersed the more finely sieved gravel with 100 fertilized coho salmon eggs in

a cylindrical plastic mesh (3.2 mm) basket. Prior to adding the gravel and eggs, we placed large cobbles (64 to 128 mm) and a standpipe (Terhune 1958) at the base of each basket to simulate the egg pocket centrum (Chapman 1988). Mesh tops with a hole for the standpipe were sewn on, and two baskets per redd were buried 30-cm deep, just downstream of the pot of the artificial redd. In 1991, one of the two baskets was short (15-cm tall and 25-cm in diameter) and used to estimate egg survival to hatching. The second basket, used to estimate survival to fry emergence, was taller (30 cm) and positioned so the top was flush with the streambed surface. After an incubation period of over 1100 degree-days, a period determined from continuous recording thermographs placed in the creeks, we slid the short hatching baskets into dishtubs filled with water, and counted alevins and dead eggs. About one month later, fry emerged from the tall basket into a redd cap (Field-Dodgson 1983) that we clamped over the top of the basket just before the emergence period. Because we found most mortality occurred before hatching, the emergence basket was not used in 1992 and 1993. In those years, both baskets just tested survival to hatching, and data from the two baskets were averaged to represent one sample per redd. When we mention “egg survival” in this paper, we are referring to egg survival to hatching unless it is explicitly stated to be survival to emergence.

To control for variation in fertility rates of parent fish, egg survival proportions in artificial redds were divided by survival of control eggs that were incubated in a hatchbox, located alongside an unaffected pristine tributary of Prairie Creek. To assess the effects of handling mortality, 12 baskets filled with gravel and eggs were placed unburied in clean-flowing water in a tributary stream or streamside trough over the three years. Survival rates in these baskets (65 – 98%) were higher or within 2% of the hatchbox control eggs that had the same

parent fish, indicating handling mortality was minimal. Variability of the control egg survival percentages for each parent fish was relatively low (SE averaged over fish = 3% in 1991, 4% in 1992, and 1% in 1993).

Dissolved Oxygen and Fine Sediment in Redds—We measured DO concentration in the water in the perforated standpipe in the egg baskets and in adjacent surface water just before removing the baskets. In 1991 and 1992, we also measured gravel permeability and intragravel water velocity in the standpipes, but found these variables were less predictive of egg survival than was fine sediment (Meyer and Coey, in review). Thus, we discontinued measuring gravel permeability and intragravel velocity, and they are not included in this study. To capture fine sediment that infiltrated the gravel in the artificial redds, we placed collapsed, waterproof infiltration bags beneath each basket. After the egg-incubation period was over in March, we hooked a chain winch on a tripod to the cables of the cylindrical bags, and removed the short baskets and gravel surrounding and on top of the basket. To prevent loss of fine sediment, a 66-cm-tall x 30-cm-diameter core sampler was held vertically on top of the sediment to create slack water as the infiltration bag was winched up through it.

The 1991 tall baskets used to evaluate fry emergence were removed in a similar manner with an infiltration bag after all fry had emerged in April. Prior to removal, we slid a plugged piece of copper tubing into the standpipe to close off the perforations, and injected pressurized carbon dioxide into the tube to freeze a core of gravel in the basket. This enabled us to examine gravel stratigraphy and test if fines were less in the egg pocket centrum than in the above gravel (Chapman 1988). Sediment suspended in the water from the infiltration bags was allowed to settle for 45 minutes in graduated cones. Using mechanically sieved, oven-dried gravel and fine

sediment from the infiltration bags and cones, we calculated percent fines by weight for particles <0.5 , <1.0, and <4.75 mm.

Water Discharge and Suspended Sediment Flux.—Water and suspended sediment discharge were intensively monitored at three gaging stations, located in three of the four reaches on the affected Prairie Creek (Figure 1). No gaging stations were available on the reference streams. Automated samplers collected water at 0.6 stream water depth during storms (Eads and Thomas 1983). Samples were analyzed for concentration of suspended solids using the filtration or evaporation method (APHA et al. 1989). To obtain suspended sediment discharge, concentrations of suspended solids were multiplied by flow at 10-min intervals. Sediment discharge was summed over the egg incubation period to obtain sediment flux (Meyer et al. 1994). Peak streamflow was recorded as the highest water discharge during the incubation period.

Oligochaete worms. —The effect of worms in the egg pocket was difficult to quantify because these worms are very mobile (Gates 1971) and probably had left many of the baskets before we opened them. For this reason, we coded relative worm abundance of the stream reaches as absent, low, medium, and high (0 – 3), based on percentage of baskets infested in that reach. Additionally, we weighed worm masses found in the baskets.

Natural Redds

To determine if natural redds produced results similar to artificial redds, salmonid redds that were observed during regular spawning surveys were capped with emergent-fry traps (Porter 1973; Field-Dodgson 1983) in 1991, the year we lacked artificial redds on a reference stream. We capped 10 redds on the affected Prairie Creek and three redds on the reference stream, Lost

Man Creek. Having not observed the fish creating the redd, we could not calculate fecundity and estimate survival to emergence. To compensate, we simply compared the percentages of capped natural redds that produced some fry between the affected and reference stream.

Data Analysis

We normalized survival percentages with the arcsine square root transformation (Zar 1984). We used analysis of variance or, when parametric assumptions were violated, the Kruskal-Wallis test (indicated by KW) to detect differences among years or groups. When within-redd differences were evaluated, we used the paired t-test or Wilcoxon sign test (WS). Differences in mean gravel quality in riffle crests between the affected and reference stream reaches over time were tested using general linear models with repeated measures on time (Neter et al. 1990). Linear regressions were used to identify relationships among variables by stream reach. The variables were averaged per stream reach to match the scale at which streamflow and suspended sediment flux were measured. Generally, regressions using individual redds were reported only when relationships were stronger than when averaged by stream reach. Fine sediment <0.5 mm was the size fraction reported in the regression results, because it was the fraction most correlated to egg survival to hatching (Meyer and Coey, in review). When regression intercepts and slopes did not differ significantly, data from different years were pooled (Neter et al. 1990). Most 1993 data were not pooled with 1991 and 1992. We conducted all analyses in SPSS (Norusis 1997) with $\alpha = 0.05$.

Results

Change in Gravel Quality at Long-Term Monitoring Sites

The geometric mean of gravel size and fredle index, parameters which increase as gravel quality improves for salmonids (Lotspeich and Everest 1981), significantly decreased in the riffle crests of the affected Prairie Creek after the October 1989 storm (Table 1). Fine sediment (<1.0 mm) tended to correspondingly increase, but the increase was not quite significant. The means for the reference reaches showed the same increasing trend. Interactions between time and treatment were not significant, indicating the effects of sedimentation on the affected creek did not decrease gravel quality more than the reference streams. Evaluation of each individual stream reach showed that, after the storm, percent fines increased in all four reaches on the affected Prairie Creek (Figure 2). However, for the reference streams, changes were not as consistent. Fines decreased on Lost Man Creek, but increased on Tarup Creek. In contrast, the geometric mean and fredle index decreased on every reach, whether it was affected by the October storm or not.

Artificial Redds

Egg Survival—Artificial redds were exposed to much higher peak streamflows, suspended sediment flux, and fine sediment infiltration in 1993 than in 1991 and 1992 ($P \leq 0.0001$), yet salmon egg survival was not correspondingly lower in 1993 on the affected Prairie Creek (Figures 3a and 3b). Rather, mean salmon egg survival to hatching in the affected stream was very low in 1991 compared to 1992 and 1993 ($P < 0.0001$). Survival from egg to hatching was the same as survival from egg to emergence (5%) in redds subjected to the same stream

conditions in 1991.

Fine Sediment in Redds—Fine sediment and egg survival to hatching were inversely correlated only when 1993 results were separated from the other two years (Figures 4a and 4b). Much higher accumulations of fine sediment were required to adversely affect survival in 1993. Of note, proportionally more of the fine sediment in the redds was of the coarser fraction (1-4.75 mm) in 1993 than in other years (Figure 5). Although we successfully extracted 12 freeze cores intact from the 20 tall emergence baskets, only seven froze from top to bottom and could be used to examine stratigraphy in the redd. On average, 68% of the fine sediment was distributed in the lower 20 to 30 cm (the egg pocket centrum), 19% was in the middle 10 to 20 cm, and 13% was in the top 0 to 10 cm stratum ($P < 0.001$, KW). Fines (< 1.0 mm) in the egg pocket centrum were not significantly greater than in the overall basket (3.4% versus 3.1%, respectively, $n = 12$, $P = 0.1823$, WS). Averaged over reaches, they explained slightly less variability in egg survival to emergence than total basket fines in 1991 ($r^2 = 0.96$ versus 0.97). For individual baskets, centrum fines explained more variance in survival than did total basket fines ($r^2 = 0.36$ versus 0.45)

Dissolved Oxygen—In all three years, DO concentrations in the egg pocket remained high (≥ 10 ppm, $\bar{x} = 11.0$ ppm, Figure 3c) and were only slightly lower than surface water values ($\bar{x} = 11.5$ ppm, $P < 0.0001$). Dissolved oxygen concentration was not significantly correlated to egg survival ($P = 0.8417$). Unexpectedly, fine sediment was positively correlated with DO concentrations in the redd when averaged by reach ($r^2 = 0.65$, $P = 0.0005$), but accounted for little of the variance in DO concentration for individual redds ($r^2 = 0.17$, $P = 0.0040$).

Streamflow and Suspended Sediment Flux—Over the three years, increases in peak

streamflow and suspended sediment flux were associated with increases in fine sediment infiltration into redds (Figure 3b). Although suspended sediment flux was positively correlated to peak streamflow ($r^2 = 0.70$, $P < 0.0001$), peak streamflow was much more predictive of fine sediment in the redds than sediment flux ($r^2 = 0.85$ versus 0.45 , $P < 0.0001$, Figure 4f). Similar to fine sediment, peak streamflow accounted for a high percentage of variation in egg survival in 1991-92 (Figure 4e). In contrast, suspended sediment flux was not quite significantly correlated to survival ($P = 0.064$).

Worms—Relative density of oligochaete worms was strongly related to egg survival (Figure 4c). Worms were often found in the baskets in wet masses of up to 132 g. They were especially abundant in 1991, infesting 75% of the redds in Prairie Creek (Figure 3c). Worm abundance by reach was also positively correlated with fine sediment infiltration rates, although higher percentages of fines were required to increase worms in 1993 and the relationship was not quite significant that year (Figure 4d). Fine sediment explained much less variance in worm abundance when analyzed by individual redd ($r^2 = 0.26$, $P = 0.0014$) than by reach ($r^2 = 0.64$, Figure 4d). The variable most predictive of worm abundance was peak streamflow, accounting for 87% of the variance in its positive relationship with worm abundance ($P = 0.0007$) in the 1991-92 period, and 88% in 1993 (not quite significant at $P = 0.0609$). Sediment flux accounted for 93% of the variance in worm abundance in 1993 ($P = 0.0058$), but only 44% in 1991-92 (not quite significant, $P = 0.073$). When the influence of worms was removed (i.e., excluding all redds with worms and reaches with less than two redds without worms), fine sediment had a stronger relationship to survival than worms had to survival (Figures 4b and 4c).

No multiple regressions provided stronger relationships to egg survival than did the

simple regressions. Although fine sediment <0.5 mm alone (without worms) was the variable most correlated with egg survival, coarser fine sediment (1 - 4.75 mm) did not significantly contribute to relationships with egg survival ($P = 0.238$, and the relationship tended to be positive rather than negative).

Reference Stream.—Although the reference redds were included in the regression relationships, they tended to weaken the fit of the data to the line for 1991-92 (Figures 4a-4d). In general, fine sediment infiltration was higher and egg survival lower in the reference stream than in the affected stream (Figures 3a and 3b, $P < 0.0001$). Correspondingly, proportionally fewer artificial redds were infested with worms on the affected stream (10%, $n = 21$) than in the reference stream (17%, $n = 6$) in the two years combined that both streams had artificial redds (1992 and 1993, Figure 3c). However, the reference stream never had the large masses of worms that were found in the affected Prairie Creek redds in 1992-93. The affected redds averaged over four times the amount of worms per redd (affected $\bar{x} = 7.3$ g, maximum = 132 g; reference $\bar{x} = 1.8$ g, maximum = 11 g). Although fine sediment increased by approximately the same percent on both the reference and affected stream from 1992 to 1993 (Figure 3b, $P \leq 0.0005$), egg survival did not significantly change during that period (Figure 3a, $P > 0.3004$).

Natural Redds

Although sample size was low, all three natural redds in the reference stream in 1991 produced over 200 fry, whereas only one of 10 natural redds produced >25 fry on the affected Prairie Creek (Table 2).

Discussion

Effects of the October 1989 Storm

Our results suggest that fine sediment increased and quality for spawning decreased in riffle crest gravels in the formerly pristine Prairie Creek following the October storm. Unfortunately, large, pristine reference creeks, which would provide the best comparison to Prairie Creek, do not exist in the study region. In general, our reference streams, which were subjected to sedimentation from past and current logging, showed the same trends of increasing sediment as Prairie Creek. Only in one case did gravel quality improve on a reference stream following the storm (on Lost Man Creek, Figure 2). Because trends did not significantly differ between the treatment stream and the reference streams, it is not clear whether the sediment increase on Prairie Creek was due to the highway construction or to climate-related factors. The study occurred during a relatively dry period (annual rainfall averaged 76% of normal for 7 of the 8 years, based on a Prairie Creek raingage). Our main conclusion from the long-term sediment monitoring study is that the 1989 sedimentation event did not affect Prairie Creek spawning gravels more than logging has affected gravels of the reference streams. The artificial redd results in 1992 and 1993 led to the same conclusion. The reference stream shared similar annual trends in fines infiltration as the affected Prairie Creek, and egg survival was not significantly lower in Prairie Creek than in the reference stream in 1992 and 1993.

Unfortunately, because no artificial redds were established on the reference stream in 1991, we do not know if the reference stream had the extremely low egg survival rates (5%) and proliferation of worms in 1991 that we saw in Prairie Creek. Fortunately, three natural redds

were capped in the reference stream that year, and those results suggest that egg survival on the reference stream might not have decreased to the low levels observed on Prairie Creek in 1991. All the natural redds on the reference stream produced over 200 fry, but only one of ten natural redds produced that many fry on Prairie Creek (similar to the 15% of artificial redds producing more than 10 fry of 100 eggs on Prairie Creek that year).

Worm masses in artificial redds were much more substantial in Prairie Creek than in the reference stream in 1990 (Meyer et al. 1993), 1992, and 1993, and possibly the same was true in 1991. Thus, one hypothesis is that the additional sediment from the October storm increased worm abundance on Prairie Creek to unnaturally high levels and reduced egg survival in 1991. Alternatively, the high worm incidence seen in 1991 was within the range of natural variability of worm population fluctuations on Prairie Creek.

Effects of Fine Sediment in Redds at Different Streamflows

Whether the source of the fine sediment was from the highway construction or from changes in climate-related factors, the sediment increase on the once pristine stream is of concern because our artificial redd results demonstrate that the increase is associated with a severe decrease in egg survival. However, the magnitude of the effect on egg survival depended on the peak streamflow during the incubation period. To decrease egg survival to <10%, fine sediment that infiltrated into artificial redds had to exceed 2% in the first two low flow years (1991 and 1992, when seasonal rainfall was 80% and 66% of normal, respectively) and 4% during the high flow year (1993, when seasonal rainfall was 125% of normal). Contrary to our expectations, the year with high flows did not have lower egg survival than the years with low flows. Although flows were not high enough to scour out the egg baskets in 1993, over four times as much fine

sediment was deposited in the redds during 1993 compared to the low flow years, and fine sediment infiltration was strongly related to peak streamflow.

The different thresholds for the effects of fine sediment on egg survival may be due to formation of a sand seal over the egg pocket in 1993, a seal which might not have formed in the previous years. In 1993, stream flows were large enough to move more of the coarser fine sediment in the streambed and possibly fill redd interstices on the surface. Such a seal on the top layer could have prevented further infiltration of fine sediment. In the laboratory, Beschta and Jackson (1979) found that sand ≥ 0.5 mm formed a seal in the upper 5 to 10 cm of a clean gravel bed, but sand < 0.5 mm did not form a seal. Lisle (1989) detected similar results in Prairie Creek with fine sediment > 0.25 mm forming a seal. His results suggested fine material ≤ 0.25 mm (fine sand, silt, and clay) is mostly deposited in the egg pocket of redds when flows are too low to entrain the armored surface layer and allow formation of a sand seal.

If a sand seal formed, additional fine sediment < 0.5 mm could have accumulated on top of the redd, thus increasing the amount of fine sediment in our infiltration bags (as was seen in 1993), without much fine sediment reaching the egg pocket. However, sand seals can be patchy (Carling 1984), allowing some of the finer sediment through. When suspended sediment and bedloads become very large and heavy, the sand seal can thicken and eventually reach the egg pocket, or finer sediment can be forced through the patchy seal. Such an increase in egg-pocket sediment might have happened in the most downstream artificial redd in 1993 on the affected reach. That redd had the highest fine sediment infiltration and very low egg survival (Figure 4a). In contrast, even the small sediment loads seen on Prairie Creek in 1991 and 1992 could have affected egg survival if no seal formed (Carling 1984), thus allowing the redd to fill from the

bottom up as was observed in 1991.

Unfortunately, we did not evaluate the stratigraphy of fine sediment fractions in the redds in 1993, which would have enabled us to look for a sand seal. The lack of a significant relationship of survival with coarse fines (1 – 4.75 mm) supports that coarser sands are not detrimental, and may even be beneficial up to a certain peak streamflow. We propose a model in which peak streamflow increases the finest fraction of fine sediment in the egg pocket at low flows, decreases that fraction at medium flows when a sand seal forms, and increases the coarser fraction at higher flows (Figure 6). At higher flows, accumulation of fine sediment in the redd should eventually reach a maximum (Lisle 1989), when a thick seal has developed. The model only applies to streamflows that do not deeply scour the redd.

One might expect sediment flux, which includes fine sand, silt and clay particles accumulated over many storms, to have a stronger relationship with fine sediment infiltration and egg survival than does peak streamflow (Carling 1984). Yet it did not in our study, possibly because in low flow years most fine sand and silt are deposited in redds during the rising and not the descending limb of the hydrograph (Lisle 1989; Sear 1993). Our estimation of suspended sediment flux is cumulative over the entire hydrograph, not just the rising limb.

In redds without worms and an apparent sand seal, 1.2% by weight of fines <0.5 mm (about 10% by volume based on volumetric data we collected) was required to reduce hatching success to 30% in our study (Figure 4d). In comparison, a 7% volume of fines <0.85 mm decreased chinook egg survival to 30% in a gravel experiment with no sand seal or worms (Reiser and White 1988). A sand seal can decrease survival by entrapping emerging fry (Witzel and MacCrimmon 1983). In 1991, we did not observe this problem, supporting our hypothesis

that sand seals did not form in that year. We did not test survival to emergence in 1993, when entrapment might have been more of a problem. Notably, most egg survival relationships were substantially strengthened (r^2 increase of ≥ 0.2) when data for each redd were averaged by stream reach, suggesting egg survival is affected by the high variability in the site conditions at individual redds.

Effects of Dissolved Oxygen in Redds

Although fine sediment appeared to adversely affect egg survival, DO concentrations were never low enough to cause egg mortality. Dissolved oxygen concentration usually must decrease to between 5 and 8 ppm to reduce egg survival to hatching (Wickett 1954; Alderice et al. 1958; Turnpenny and Williams 1980; Sowden and Power 1985), although Rubin and Glimsäter (1996) found high egg mortality at ≤ 9.8 ppm for sea trout (*Salmo trutta*). No redd in our study had a DO concentration lower than 9.6 ppm. Meyer and Coey (in review) suggested that abundant silt during the low flow years of 1991 and 1992 might have coated and suffocated the eggs without affecting oxygen in the adjacent intragravel water. If a sand seal formed in 1993, the oxygen would be expected to also remain high in that year and have little effect on survival during high streamflows, which was what we observed.

Effects of Worms

Although fine sediment alone appeared to be detrimental to egg survival, worm abundance appeared to increase the effect (steeper slope of the regression line, Figures 4a and 4b). Worms increased with increasing fine sediment in the egg pocket, particularly in low flow years, when a sand seal could not prevent mixing of silt and eggs. We suspect that a combination of silt and eggs is very attractive to these oligochaetes. Instead of eating live fish eggs, these

worms are known to spread their copious mucus on the eggs. The mucus appears to kill them by asphyxia or allowing toxic wastes to accumulate, and the worms consume the eggs post-death (Briggs 1953). The baskets with low survival often had a copious mixture of mucus and silt. When placed in a fish tank filled with creek gravel, we observed that worms sought the substrate portion where thick silt deposits had settled, supporting our hypothesis that silt attracts worms to the redds. Moreover, worm abundance was more correlated to the finest fraction of sediment, which would contain the most silt ($r^2 = 0.64$ for <0.5 mm, 0.57 for $0.5-1.0$ mm, and 0.50 for $1.0-4.75$ mm). In general, more work is needed to evaluate the effects of silt, which we did not specifically measure, on egg survival and the abundance of oligochaete worms. Some silt and finer particles remained in suspension even after 45 minutes in our settling cones (Guy 1969), and hence, were not fully included in our estimates of fine sediment <0.5 mm. If all the silt had been included, the fine sediment relationships might have been even stronger. It is not clear why peak streamflow was more correlated to worm abundance than was fine sediment in the redds.

Oligochaete worms have been a natural part of the Prairie Creek fauna since the 1940s, but egg survival has never before been documented to be reduced to 5% by such worms, as was seen in 1991. Briggs (1953) reported that the same species of worm infested 27% of natural coho salmon redds in 1948 and 1951 and reduced egg survival from 85 to 44%. In our study, worms reduced egg survival from 37 to 7% (uninfested versus infested). The increased fine sediment after the October 1989 storm might have perturbed the invertebrate community and increased the abundance of this worm by 1991. In April 1990, not long after the storm, masses of worms were abundant only in artificial redds placed in the most downstream reach of Prairie Creek (Meyer et al. 1993). The downstream reach (reach 5, Figure 1) might have been the source

of worms throughout Prairie Creek the following year.

Oligochaete worms have been observed on other streams in northern California including tributaries of the Sacramento River (Gangmark and Bakkala 1960). For streams that have such worms, an increase in fine sediment in the streambed should be of concern not only because of its direct effects on egg survival, but because it may also increase worm densities. The combination of high infiltration rates of fine sediment <0.5 mm and worm migration into egg pockets of redds appears to be very deadly for salmonid eggs. However, high fine sediment infiltration during high flow years does not necessarily increase egg mortality if worms and fine sediment are blocked from infiltrating the egg pocket by a barrier such as a sand seal.

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Table 1. Mean percent fines by weight, geometric mean of gravel size, and fredle index in potential spawning sites within summer riffle crests in Prairie Creek and reference reaches before (1985-1989) and after (1990-1992) the October 1989 sedimentation event. Means were compared using general linear models with repeated measures on time.

	Fines <1.0 mm			Geometric mean			Fredle index		
	Before	After	<i>P</i>	Before	After	<i>P</i>	Before	After	<i>P</i>
Time			0.084			0.009			0.004
Affected Prairie Creek (n = 4) ^a	8.5	9.9		23.3	18.5		11.2	7.3	
Reference Creeks (n = 2) ^b	8.1	9.1		24.1	20.1		11.4	7.5	
Treatment			0.667			0.777			0.931
Interaction (Time x Treatment)			0.769			0.646			0.982

^aTwo reaches had one monitoring site and two reaches had two sites (results for latter were averaged). At each site, results were averaged from six freeze-core samples across several riffles.

^bEach creek had one site. At each monitoring site, results were averaged for six freeze-core samples across several riffles.

Table 2. Number of fry that emerged from natural redds on Prairie Creek (affected) and Lost Man Creek (reference).

Stream		Number of emerging fry									
Affected	0	0	0	2	3,671 ^a	37	0	0	0	0	0
Reference	804 ^a	219	208								

^aAnother redd was superimposed onto the redd and subjected to lower infiltration of fine sediment than was the original redd.

Figure 1. Location of the sediment-affected Prairie Creek watershed in California, showing locations of highway construction alignment, study reaches, gaging stations, and the reference stream, Lost Man Creek. Tarup Creek, a second reference stream added in the long-term sediment-monitoring study, is located to the northeast in the adjacent watershed (not shown). On Prairie Creek, reaches 1, 3, 4, and 5 were used in the long-term study, and 1-4 were used in the artificial and natural redd studies.

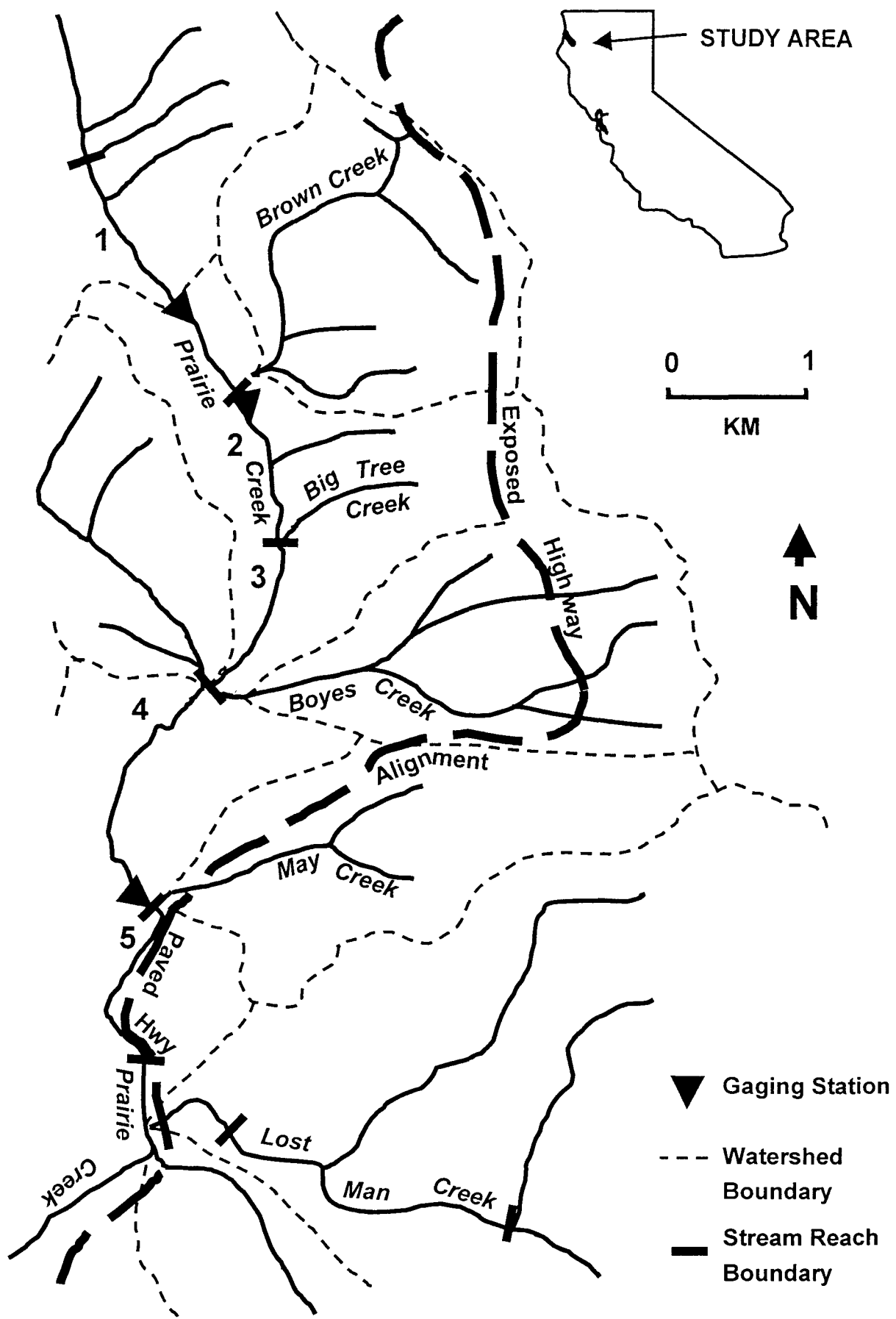
Figure 2. Comparison of fine-sediment content (<1.0 mm) of spawning gravels in riffle crests averaged over the years before and after the October 1989 storm that delivered sediment into Prairie Creek, the affected stream. The change in fine-sediment content is shown for two reference streams for comparison.

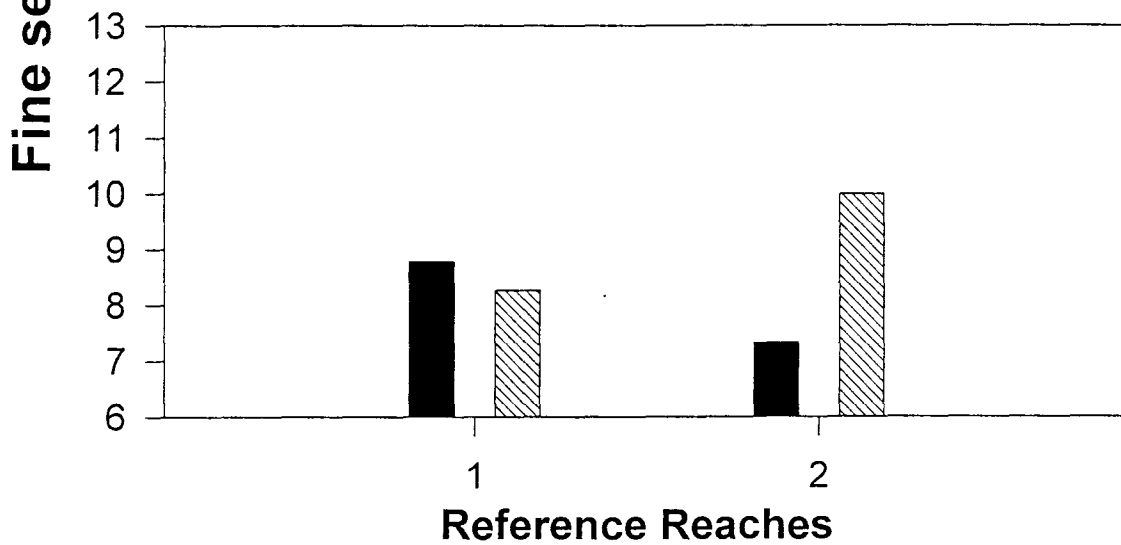
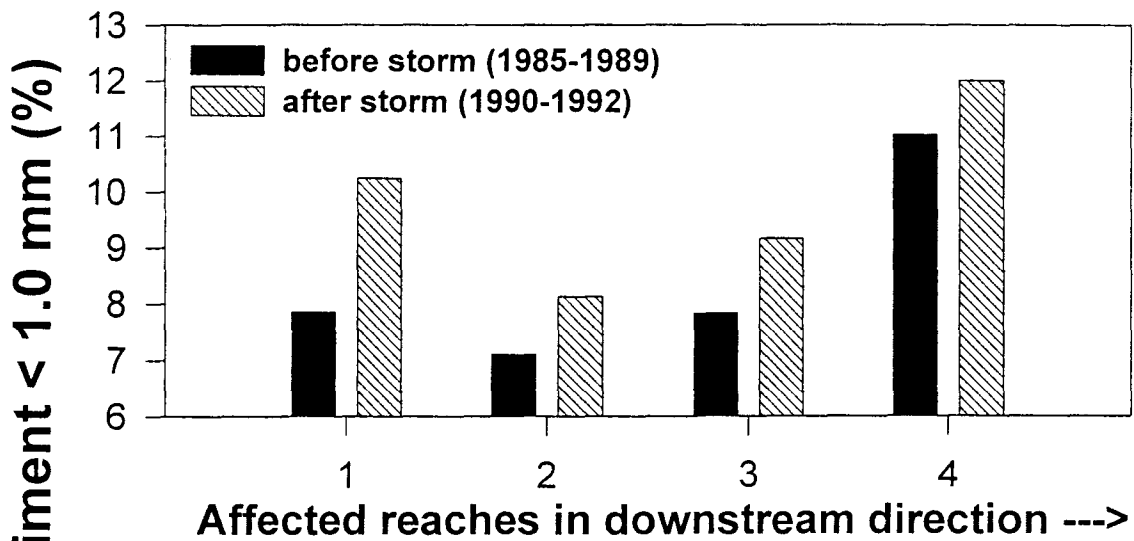
Figure 3. Change over time in means (± 1 SE) of survival of coho salmon eggs to hatching, fine sediment content, and dissolved oxygen concentration in artificial redds relative to means of water and sediment discharge in stream reaches (± 1 SE) and percentage of redds infested with worms during the incubation period. Streams affected by the October 1989 sedimentation event (affected) and unaffected (reference) are compared.

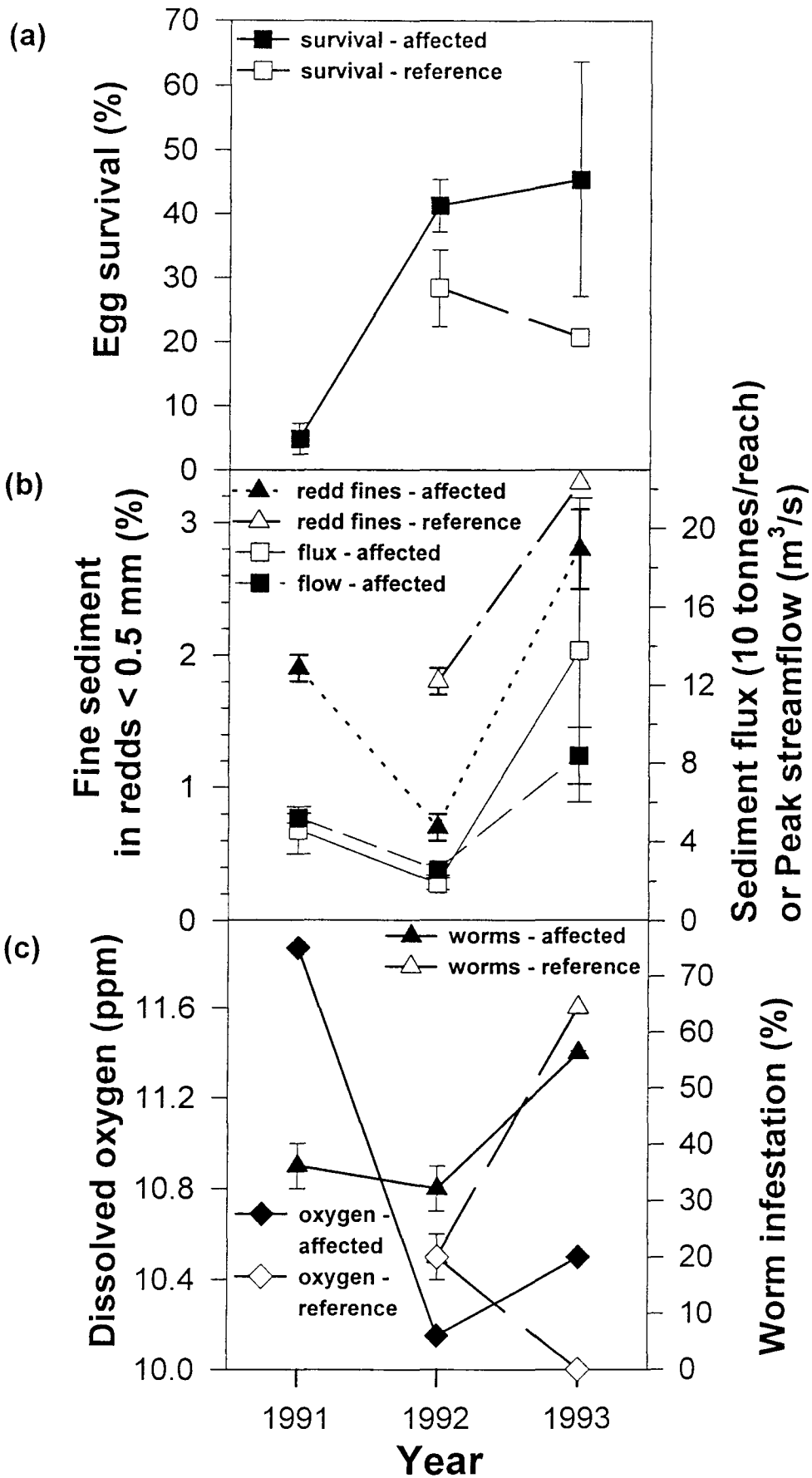
Figure 4. Relationships between survival of coho salmon eggs, fine sediment, and oligochaete worm abundance in artificial redds averaged per stream reach in northwestern California. Worm abundance was coded from none to high (0-3). The r^2 of 1991-92 regressions improved to 0.68, 0.91, 0.87, and 0.71, respectively, when the reference stream was excluded in (a) - (d). This r^2 set should be compared to the r^2 for (e) and (f), regressions which also excluded the reference stream because no stream gage was available.

Figure 5. Distribution of fine sediment by size class in coho salmon artificial redds over the three years of the study in the affected Prairie Creek. Proportion of coarse fines (between 0.5 and 4.75 mm) was higher in 1993 than in 1991 and 1992 (ANOVA, $P = 0.036$). Sample size is shown above each bar.

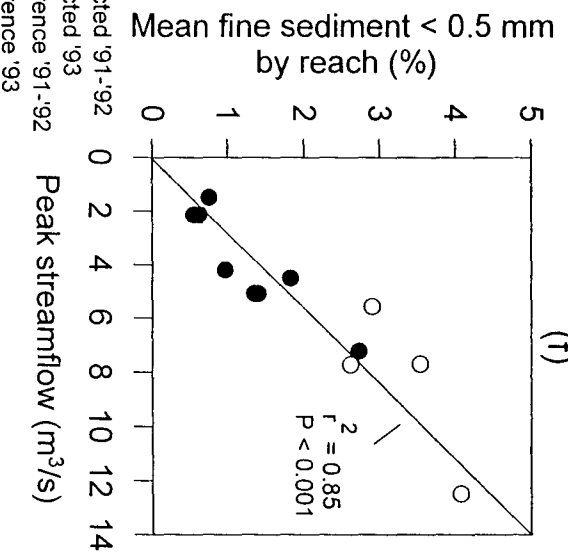
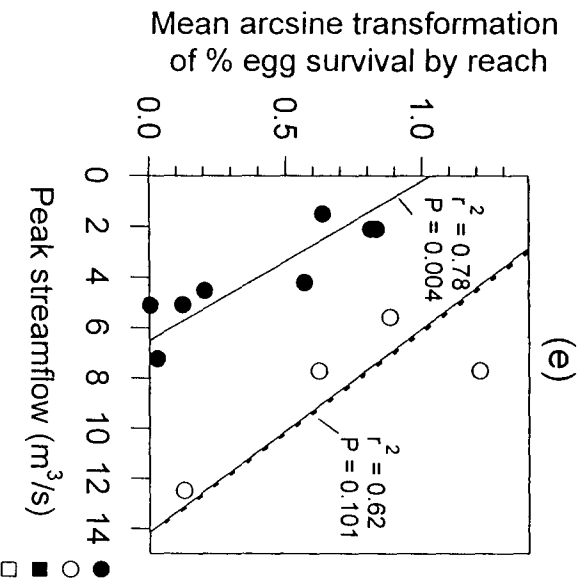
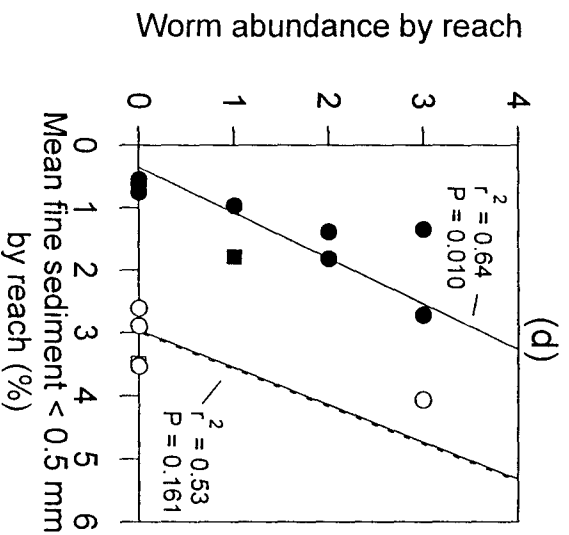
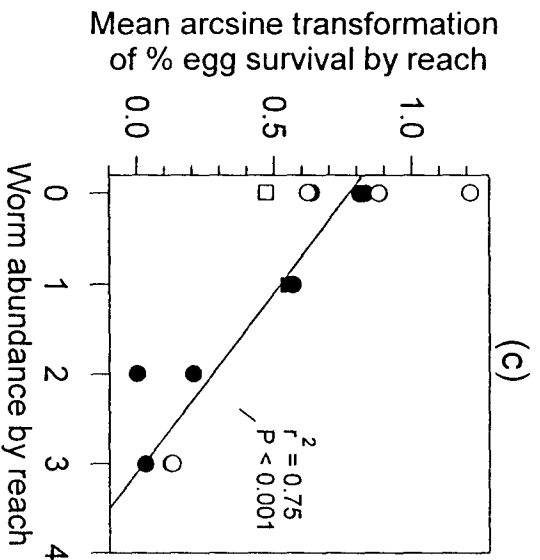
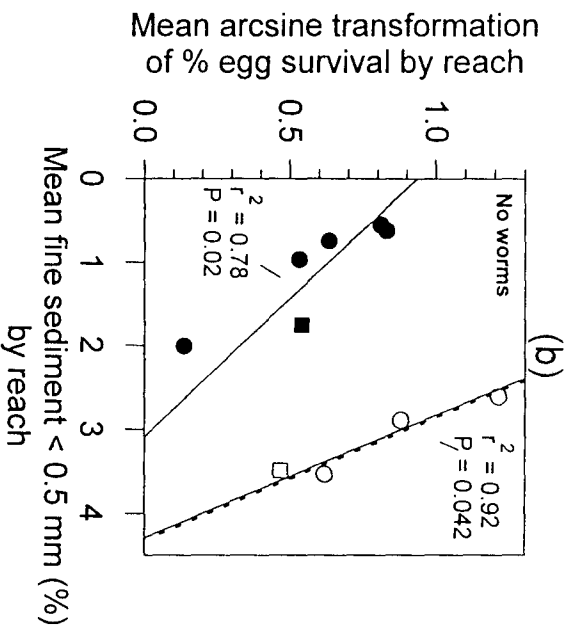
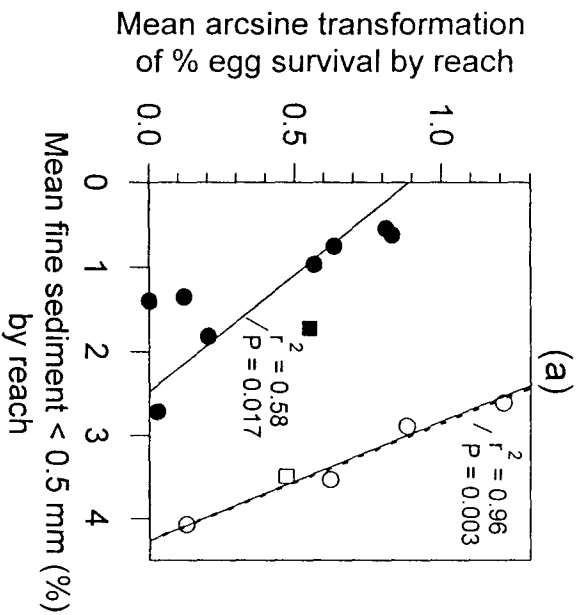
Figure 6. Hypothesized relationship between peak stream discharge and fine sediment infiltrating a redd. Fines <0.25 mm accumulate as flow increases until the entrainment streamflow is reached (Q_s). Flows $\geq Q_s$ entrain coarser sands and pea gravel into the stream current and deposit them downstream. A sand seal forms and thickens in redds at flows $\geq Q_s$ until the gravel becomes fully saturated with the coarser sediment at the highest flows.



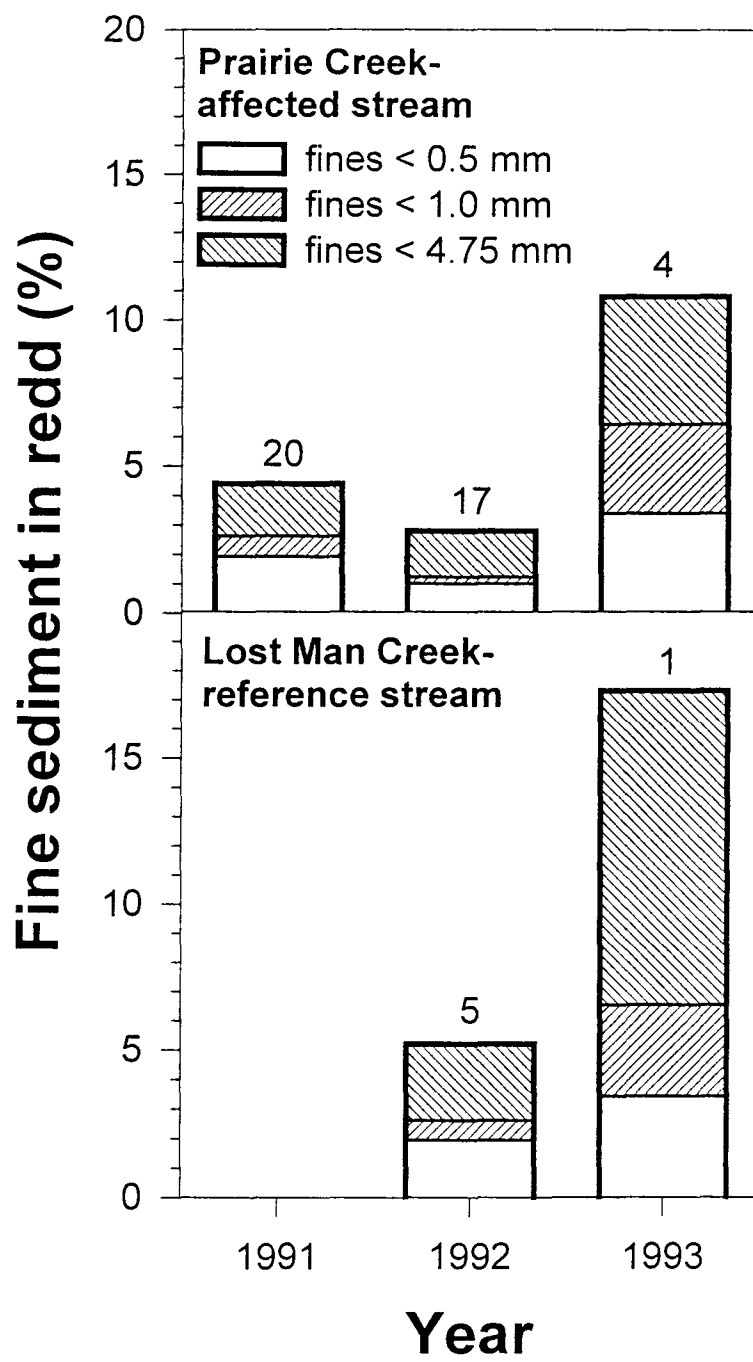




Affected redds	n = 10	12	4
Reference redds	n =	5	1
Affected reaches	n = 4	4	4
Reference reaches	n =	1	1



● affected '91-'92
○ affected '93
■ reference '91-'92
□ reference '93



Fine sediment in redd

