

The Effect of Deposited Fine Sediment on Summer Survival and Growth of Rainbow Trout in Riffles of a Small Stream

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Abstract.—Elevated fine-sediment inputs to streams can alter a variety of conditions and processes, including the amount of fine sediment stored in riffles. We sought to measure the influence of deposited fine sediment on the survival and growth of juvenile rainbow trout *Oncorhynchus mykiss* (106–130 mm fork length) using a field experiment that included 18 enclosures in riffles of a small northwestern California stream. The experiment included six replicates of three levels of deposited fine sediment (low, background, and high) that embedded riffle cobbles at 0, 50, and 100%, respectively. Only 1 of 12 fish survived in high-sediment enclosures, while survival of fish in low- and background-sediment treatments equaled or exceeded 50%. Low- and background-sediment treatments could be distinguished from each other by a difference in fish growth: fish in the low-sediment treatment gained mass, on average, while all surviving fish in the background-sediment treatment lost mass. In addition to providing relatively high survival and growth benefits for juvenile rainbow trout, low-sediment experimental units were colonized at significantly higher rates by other vertebrates, particularly coastal giant salamanders *Dicamptodon tenebrosus*. The amount of stored fine sediment in small streams may substantially influence the total amount of habitat available to vertebrates at the watershed scale.

Human activities such as road building, agriculture, and timber harvest can elevate the input of fine sediment into stream channels. This sediment may be periodically transported as suspended load or bed load, or stored in the channel. All three of these outcomes may have important consequences for stream biota. For example, elevated suspended load increases turbidity, which reduces capture success for drift feeding fish (Sweka and Hartman 2001), while higher bed load transport may affect the density of benthic invertebrates (Culp et al. 1986) and the reproductive success of some fishes (Montgomery et al. 1996). During periods of low to moderate streamflow when the capacity for sediment transport is low, stream biota may be most affected by fine sediment stored in the channel.

Stored fine sediment can affect fish in several ways. Channel aggradation can reduce surface streamflow by increasing flow through the streambed, thereby reducing fish survival (May and Lee 2004) and growth (Harvey et al. 2006). Deposited sediment can also reduce the availability of benthic invertebrates vulnerable to fish predators due to species-specific substratum preferences and increase agonistic interactions among fish due to reduced visual isolation. Suttle et al. (2004) linked both of these mechanisms to a negative relationship between the growth of age-0 steelhead

(anadromous rainbow trout *Oncorhynchus mykiss*) and the embeddedness of the substratum in artificial channels placed in pools. The composition of the substratum can also influence predation risk for fish, with consequences for both growth and survival. Fischer (2000) measured 30% higher respiration rates for burbot *Lota lota* on pebble substratum compared with cobble substratum, even in the absence of predators. Fish may forego feeding opportunities if feeding requires substantial exposure to predators. Coarse substratum is more likely to provide microhabitats offering profitable feeding opportunities with relatively low predation risk.

Substrate-dependent predation risk can also directly influence survival (e.g., White and Harvey 2001). The potential value of coarse substratum in reducing predation risk by providing cover is indicated by its increased use by fish when predators are present (Vehanen and Hamari 2004). Relatively coarse, unembedded substratum may be particularly important in shallow habitats in small streams because predation risk can be depth-dependent (Harvey and Stewart 1991), and low streamflows may provide little surface turbulence to conceal fish. In this study, our objective was to measure the effect of deposited fine sediment on the survival and growth of juvenile rainbow trout in shallow habitat in a small stream during summer, using a field experiment that incorporated the potential effects of deposited fine sediment on both energetics and predation risk.

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Study Site

Jacoby Creek drains a 42-km² watershed into Humboldt Bay in the Coast Range of northwestern California. The study area lies within the Arcata City Forest in the upper drainage (watershed area = 15 km²) at an elevation of approximately 250 m. The active stream channel in the reach averages about 4 m wide and alternates between shallow riffles and moderately deep pools (maximum depth ~ 1.5 m) over gravel and cobble substrate. Except for one 50-m-long bedrock-confined section, gradient in the reach rarely exceeds 1–2%. The region experiences dry summers and wet winters. Because of the moderating effect of coastal fog, air temperature at our study site rarely exceeds 25°C in the summer or drops below 4°C in the winter, while water temperature ranges from 9°C to 16°C in summer and from 4°C to 12°C in winter. Mean annual rainfall exceeds 120 cm, more than 90% of which falls between November and March. Streamflow in the study reach averages less than 0.05 m³/s in the summer (mean = 0.022 m³/s; range = 0.017–0.029 m³/s during this study) and approximately 0.75 m³/s in the winter with peak flows greater than 100 m³/s. The combination of a steep, highly erosive watershed, intensive land management (principally logging), and high rainfall delivers substantial sediment to Jacoby Creek. Consequently, extensive bed load movement and channel changes result from high flows in most winters. While the stream remains clear (<5 nephelometric turbidity units [NTU]) in the summer, turbidity averages over 30 NTU in the winter, with peaks in excess of 1000 NTU. Coastal redwood *Sequoia sempervirens* and Douglas-fir *Pseudotsuga menziesii* constitute the majority of the forest cover in the watershed, although red alder *Alnus rubra* and bigleaf maple *Acer macrophyllum* dominate much of the riparian zone. The study reach lies upstream of barriers to fish passage. The fish assemblage in the study reach consists solely of a resident population of rainbow trout. Coastal giant salamander *Dicamptodon tenebrosus*, tailed frogs *Ascaphus truei*, and red-legged frogs *Rana aurora* complete the aquatic vertebrate assemblage. Piscivorous vertebrates observed in the study area include river otter *Lutra canadensis*, raccoon *Procyon lotor*, great blue heron *Ardea herodias*, green heron *Butorides virescens*, belted kingfisher *Ceryle alcyon*, American dipper *Cinclus mexicanus*, and garter snakes *Thamnophis* spp.

Methods

In early July 2002, we selected 18 riffles in a 1.6-km study reach as experimental units. The units spanned the channel, varied in length from 2.25 to 3.75 m, and

enclosed areas of 7–7.75 m². We randomly assigned six replicates of three fine-sediment treatments (high, background, or low) to the 18 units. Prior to any substrate manipulation, we determined the background percentage of fine sediment in the bed material to a depth of 10 cm in each riffle unit by sieving through a 13-mm-square mesh a 0.025-m³ sample of the native substrate that had been collected with a shovel. This step revealed that background fine sediment averaged 40% by volume with low variability. In unmanipulated riffles, surface cobbles were embedded in finer material to a depth of about 50% of their height, on average, with some cobbles in each unmanipulated experimental unit 0–25% embedded. We set the high-sediment treatment at twice the percentage of fine sediment in unmanipulated riffles. We added sand and gravel from nearby exposed bars to increase the fine sediment concentration in high-sediment treatments. This almost completely embedded all cobbles within the enclosures, although each high-sediment enclosure retained a small number of cobbles embedded about 50%. For the low-sediment treatment, we removed all the native substrate within units to a depth of 10 cm with shovels, sieved out the fine sediment using 13-mm-square mesh, and then returned the larger fraction to the unit. This procedure yielded a completely unembedded surface layer of cobbles and coarse gravel. To increase the similarity of disturbance to the substratum among treatments, we brushed the surface of the substrate in the background-sediment treatment with a coarse-bristle push broom and removed and replaced cobbles. All sediment manipulations were completed on 2–3 July 2002.

After waiting 27–28 d to allow recolonization of disturbed substratum by periphyton and benthic invertebrates, we enclosed each unit at the upstream and downstream boundaries with plastic fencing (6-mm mesh) which was buried at least 10 cm below the stream bottom in fine gravel, extended at least 30 cm into the streambank, and was supported by metal stakes. We also made two passes with a backpack electroshocker and removed captured vertebrates from each experimental unit. On 31 July and 1 August 2002, we completed an additional two or three electrofishing passes to ensure removal of all rainbow trout older than age 0 and stocked enclosures with fish collected from outside the experimental units by electrofishing. We stocked each unit with two juvenile rainbow trout that differed in length by a minimum of 10 mm fork length (FL; larger fish: mean FL = 124 mm, range = 116–130; smaller fish: mean FL = 111 mm, range = 105–116) and in mass by at least 3 g (larger fish: mean mass = 21.3 g, range = 17.8–24.4 g; smaller fish: mean mass = 15.1 g, range = 12.0–18.2 g). We selected fish of

different sizes to avoid persistent agonistic interactions between fish within enclosures. Before releasing fish into the experimental units, we measured their FL to the nearest millimeter and their wet weight to the nearest 0.01 g with an electronic balance, and inserted a passive integrated transponder (PIT) tag to allow identification of individuals. Enclosure fences were cleaned once or twice each week over the 6-week experiment. We did not include age-0 fish in experimental manipulations because they were too small to be contained by enclosure fences at the beginning of the experiment. The fences also allowed passage of small larval coastal giant salamanders.

To compare physical conditions among treatments, we measured depth, water velocity, and substrate at 15 points within each experimental unit after installing the enclosure fences. Measurements were made at five equally spaced points along three cross-stream transects that approximately quartered each experimental unit. We measured average water column velocity with a Marsh–McBirney flowmeter equipped with a top-set rod. We classified the substratum by identifying the size-class covering the most area in a 25-cm-diameter circle centered on each point, using a simplification of the Udden–Wentworth particle size scale: cobble (64–256 mm), coarse gravel (16–64 mm), fine gravel (2–16 mm), and sand (0.06–2 mm).

To monitor water temperature during the experiment, we continuously deployed temperature loggers in 4 of the 18 experimental units and shuffled five additional temperature loggers among the remaining units to provide data for developing equations relating temperatures in the temporarily gauged units to temperatures in the continuously gauged units. The loggers recorded stream temperature at 0.5-h intervals. Strong relationships (all $R^2 > 0.93$) in water temperature between units provided estimates of temperature within units that lacked temperature loggers.

At the conclusion of the experiment on 11–12 September 2002, we first collected two Surber samples (0.09 m², 363- μ m mesh) of benthic invertebrates at two randomly selected locations within each unit, then we used multiple-pass electrofishing to collect surviving experimental fish and other vertebrates in the units. In an attempt to estimate the quantity of benthos immediately available to fish, we dislodged invertebrates from substrate surfaces during Surber sampling but did not extensively disturb particles below this level. For each stocked fish collected, we recorded FL, wet mass, and PIT tag number, and collected stomach contents using gastric lavage. The length and mass of all other vertebrates were also recorded. We preserved

both diet and benthic samples in a 70% solution of ethanol.

We processed benthic and diet samples in the laboratory, identifying invertebrates to genus (if possible) using a stereomicroscope with an ocular micrometer (maximum 70X magnification). We recorded body lengths to the nearest 0.1 mm for up to 50 individuals of every taxon in each sample. If a sample held more than 50 individuals for any one taxon, we measured a sample of 50 and counted the rest. We converted individual prey lengths to estimates of dry mass using taxon-specific relationships provided by K. W. Cummins and M. A. Wilzbach (USGS California Cooperative Fishery Research Unit). Gut fullness was expressed as the ratio of invertebrate dry mass (mg) to the wet mass (g) of fish. We also computed the percentage of overlap (Schoener 1970) in taxonomic composition between the benthic samples and fish diets within experimental units.

Analyses followed a one-way analysis of variance (ANOVA) design with three treatments, but with two exceptions: First, the limited number of outcomes for fish survival in each enclosure (zero, one, or two fish) suggested a categorical approach to data analysis; therefore, we used Fisher's Exact Test to analyze the 3×3 table of treatment \times survival outcome. Second, the lack of replicate observations on fish for one treatment dictated the use of *t*-tests to compare fish growth and gut fullness in the other two treatments. We used Ryan's *Q* to make pairwise comparisons among treatments in ANOVAs with significant overall results (Day and Quinn 1989).

Results

Physical conditions other than the composition of the substratum were similar among treatments. The means and variances of depth and water velocity within enclosures did not differ significantly among treatments (Figure 1; *P*-values: 0.35–0.81 for one-way ANOVAs with 2, 15 df). Mean water temperature ranged only 12.0–12.4°C during the experiment among all enclosures. Predictably, different substratum size-classes predominated in the three treatments: cobble (69%) in the low-sediment treatment, coarse gravel (64%) in the background-sediment treatment, and fine gravel (54%) in the high-sediment treatment.

Rainbow trout survival and growth differed among treatments. Survival was poor overall, but lower in the high-sediment treatment than in the other two treatments (Fisher's Exact Test: $P < 0.01$). We recovered only 1 of 12 fish stocked in high-sediment enclosures, while survival reached 6 of 12 fish in the background-sediment enclosures and 7 of 12 fish in the low-sediment enclosures (Figure 2). We did not observe

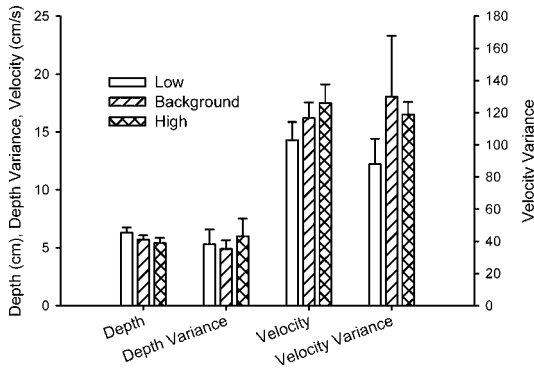


FIGURE 1.—Depth and velocity in enclosed riffles in Jacoby Creek, California, that differed in the amount of deposited fine sediment and cobble embeddedness. (Cobble embeddedness in the three treatments: low, 0%; background, 50%; high, 100%.) Vertical bars indicate 1 SE; $n = 6$ replicates per treatment.

any dead or injured individuals within enclosures, and all enclosure fences remained intact throughout the experiment. While low- and background-sediment treatments yielded similar survival rates, they could be distinguished by differences in growth (Figure 3; $P < 0.05$ for t -test with 8 df). All fish in background-sediment enclosures lost mass while, on average, those in low-sediment treatments gained mass.

Aside from the fish we stocked, the total mass of vertebrates captured at the end of the experiment varied among treatments (Figure 4; $P < 0.01$ for the one-way ANOVA with 2, 15 df). The mean final combined mass of coastal giant salamander larvae, age-0 rainbow trout, and tailed frog adults in the low-sediment treatment exceeded the comparable mean mass in high-sediment treatments by about seven times; Ryan's Q (with $P <$

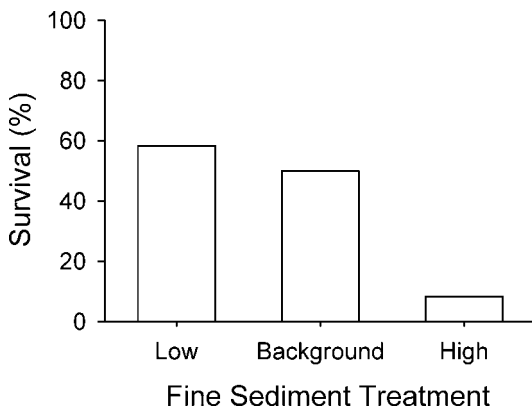


FIGURE 2.—Survival of rainbow trout in enclosed riffles in Jacoby Creek, California, that differed in the amount of deposited fine sediment and cobble embeddedness.

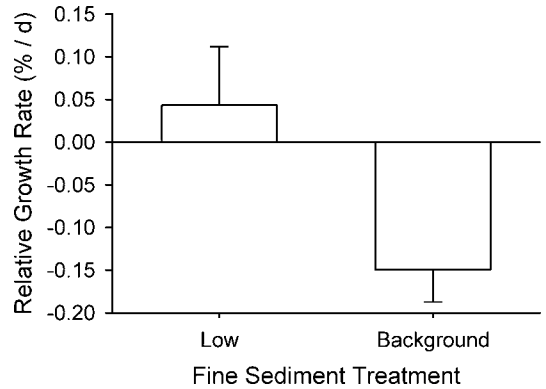


FIGURE 3.—Growth of rainbow trout in enclosed riffles of Jacoby Creek, California, that differed in the amount of deposited fine sediment and cobble embeddedness. Vertical bars indicate 1 SE; $n = 5$ per treatment, because no fish were recovered from one of the six enclosures in each of the background-sediment and low-sediment treatments.

0.05) distinguished the low-sediment treatment from the other two. Coastal giant salamanders contributed 83% of the total mass of other vertebrates, ranging from an average of 67% in the high-sediment treatment to 89% in the low-sediment treatment. We probably failed to remove all coastal giant salamanders from the enclosures at the start of the experiment. Thus, immigration both before and after installation of the enclosure fences probably influenced the number of coastal giant salamanders collected at the end of the experiment, but in both cases the animals were responding to the sediment conditions produced by experimental manipulation.

The pattern in benthic invertebrate biomass among

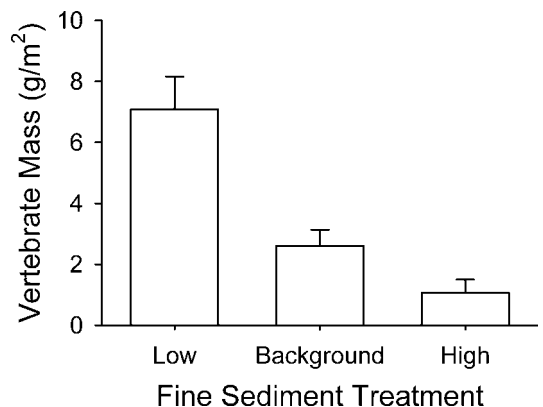


FIGURE 4.—Biomass of vertebrates other than stocked rainbow trout in Jacoby Creek riffle enclosures with three levels of deposited fine sediment, at the end of a 6-week experiment. Vertical bars indicate 1 SE.

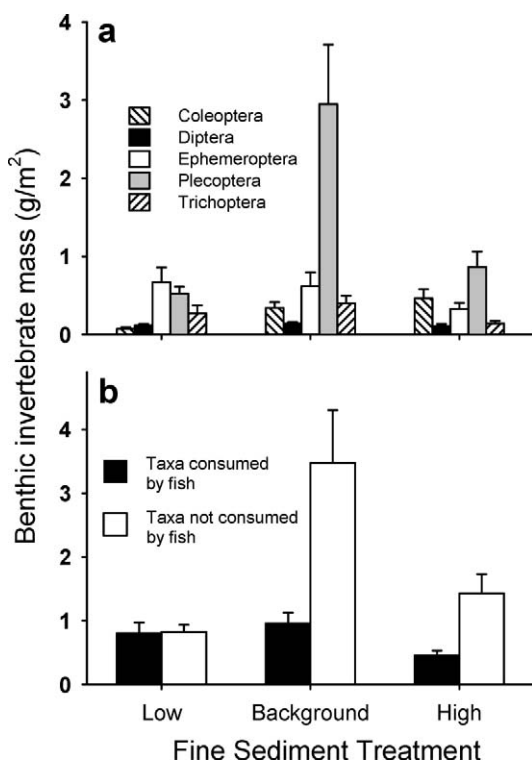


FIGURE 5.—Estimated dry mass of benthic invertebrates on the surface of the substratum of riffle enclosures with different levels of deposited fine sediment and cobble embeddedness in Jacoby Creek, California, categorized by (a) taxonomic order and (b) taxa found in concurrent rainbow trout diet samples versus other taxa. Vertical bars indicate 1 SE.

sediment treatments differed from the pattern for vertebrates (Figure 5a). The background-sediment treatment yielded the highest biomass of benthic invertebrates, due mainly to the relative abundance of perlid and perlotid stoneflies. The other two treatments yielded samples with similar total biomass, although they differed in taxonomic composition. Because these samples were collected by disturbing only the surface of the substratum, samples from the low-sediment treatment consisted almost entirely of invertebrates collected from unembedded cobbles, while samples from the other treatments included animals collected from both cobble and finer bed material.

Diet samples from the 12 fish collected at the end of the experiment varied in total mass and in taxonomic composition. Mean dry mass of stomach contents/wet mass of fish was about six times higher in the low-sediment treatment than in the background-sediment treatment, but results for the low-sediment treatment were highly variable (t -test with 11 df and unequal variance, $P = 0.09$). The taxonomic composition of the

stomach samples did not overlap strongly with benthic samples in background-sediment or low-sediment treatments ($<20\%$ for both). Considering only those taxa found in the diet samples, low- and background-sediment treatments contained similar biomasses of benthic invertebrates, while the biomass of these taxa was lower in the high-sediment treatment (Figure 5b). Perlid and perlotid stoneflies, which were relatively abundant in the benthic samples from the background-sediment treatment, were not found in the diet samples.

Discussion

One key result from this study was that abundant fine sediment in shallow riffles significantly reduced survival for rainbow trout that are more than 100 mm FL, apparently through greater predation risk as a result of reduced habitat complexity. We hypothesize that stocked fish we did not recover at the end of the experiment were removed by predators, because enclosure fences remained intact, with 10 cm or more of fence buried in fine gravel. Also, prior uses of the same fencing materials and techniques have provided no evidence that fish can escape from the enclosures; one previous experiment of similar length in Jacoby Creek yielded more than 90% recovery of tagged fish within fenced enclosures (Harvey et al. 2006). Other studies have documented low survival for similar-sized fish in shallow stream habitats that lack cover. Harvey and Stewart (1991) observed low survival of cyprinids (80–110 mm total length) in enclosures in a Tennessee stream with habitat similar to the high-sediment treatment in this study. Although this study focused on riffles and the Harvey and Stewart (1991) study on pools, the difference in water velocity probably had little influence on the detectability of fish because high-sediment enclosures in this study had little or no disturbance of the water's surface.

Survival results for the background-sediment treatment in this study (50% over 6 weeks) differ somewhat from those of previous studies that have focused on salmonids in shallow stream habitat, but differences in fish density among studies may account for some of the variation. For example, Rosenfeld and Boss (2001) recovered all cutthroat trout *O. clarkii* (120–160 mm total length) enclosed in riffles during a month-long summer experiment in a British Columbia stream similar in size to Jacoby Creek. However, this study used a higher starting density, and the densities of surviving fish in this experiment and in Rosenfeld and Boss (2001) were very similar (0.15–0.17 fish/m²). In a 9-week study in Jacoby Creek (Harvey et al. 2005), survival of rainbow trout (mean FL = 118 mm) averaged 70% in 22 enclosures with mean depth less than 10 cm, but that study used natural fish density,

which was lower than the starting densities in the present experiment. In addition to the possible influence of variation in fish density, survival estimates from experiments like these are likely to vary because of low resolution due to small numbers of fish, limited replication, and variability in survival due to spatio-temporal variation in predator density (Boss and Richardson 2002).

This study's background-sediment results for fish growth parallel results from Rosenfeld and Boss (2001) which indicated that gravel and sand riffles in small streams do not provide energetically favorable habitat for salmonids older than age 0. The negative growth rates of rainbow trout (105–130 mm FL) in the background-sediment enclosures in Jacoby Creek closely paralleled growth rates of slightly larger cutthroat trout at the same final density in Hudson Creek, British Columbia, in enclosures offering similar physical conditions (Rosenfeld and Boss 2001).

In contrast to background riffle conditions, the low-sediment riffles in this experiment provided opportunities for weight gain by rainbow trout over 100 mm at a density (about 0.16 fish/m²) similar to that found in Jacoby Creek pools. Bolliet et al. (2005) hypothesized that the availability of microhabitat providing relatively efficient drift feeding contributed to their finding of lower growth by young of the year brown trout *Salmo trutta* in embedded versus unembedded sections of an artificial stream. While our physical measurements suggested similarity among treatments in mean depth and velocity, low-sediment riffles may have offered a few microhabitats among unembedded cobbles that provided both feeding opportunities and cover exceeding those of any microhabitats available in background- and high-sediment enclosures. This possibility may link to the similarity in survival for fish in the low- and background-sediment treatments in this study: survival in the background-sediment treatments may have come at the cost of growth as fish spent time in refuges that did not provide feeding opportunities. Fish in either the low-sediment or background-sediment enclosures were rarely detected by streamside observers.

One related mechanism that might have contributed to mass gain by fish in low-sediment enclosures is the influence of substrate-mediated stress on metabolic rates (Fischer 2000). While Fischer (2000) measured this effect in a benthic species (burbot), similar effects might be expected in any species for which substrate strongly influences the risk of predation and predator activity is not easily assessed. Millidine et al. (2006) recently documented a relationship between metabolic rate and habitat features for a salmonid: a 30% reduction in the metabolic rate of juvenile Atlantic salmon *S. salar* provided with overhead hiding cover.

Previous research by Suttle et al. (2004) has linked salmonid growth rates to the effects of deposited sediment on food availability. That study demonstrated lower growth for young of the year steelhead and lower densities of benthic invertebrates classified as vulnerable to fish predation as deposited sediment increased in experimental channels placed in stream pools. In contrast to that experimental setting, the enclosures in this study spanned the wetted stream channel in areas of high water velocity. Therefore, we assume immigration strongly influenced prey densities in both the drift and the benthos. Considering the influence of immigration and the potential for movements by benthic invertebrates between lower levels of the substratum and the level we sampled, we do not consider the results of our benthic collections a clear indication of greater availability or production of benthic invertebrates in the background-sediment treatment compared with the low-sediment treatment. More information on the effects of elevated fine-sediment transport and storage regimes on overall food availability for fish at the whole-stream scale would clearly be valuable. Much of the work on links between stream invertebrates and fine sediment has focused on response variables such as species richness, which are not readily translated to food availability for fish.

Suttle et al. (2004) also documented higher rates of aggressive interactions for young of the year steelhead when embeddedness increases into the range of 60–100%. This mechanism probably did not strongly influence our results, because we used large fish at relatively high densities in treatments that provided few high-quality microhabitats: interactions between individuals would be expected in all three treatments. In fact, the experiment provides evidence of density-dependent growth in the low-sediment treatment that might be attributable in part to aggressive interactions, because all three fish in low-sediment enclosures with one remaining fish gained weight while those in the two low-sediment enclosures with two remaining fish lost mass.

This study adds to existing experimental evidence of the detrimental effects of deposited fine sediment on juvenile salmonid growth in streams (Suttle et al. 2004; Bolliet et al. 2005) and also suggests that deposited fine sediment can lower survival by enhancing predation risk. The low-sediment treatments in this experiment appeared to offer relatively large juvenile trout energetically favorable microhabitats that also provided relatively low risk of predation. Evaluation of the potential effects of deposited fine sediment on salmonid population dynamics must also incorporate mechanisms that operate on other life stages and in other seasons. A complete analysis of how elevated

input of fine sediment affects population dynamics must also include the effects of suspended sediment and bed load transport, such as the effect of suspended sediment on reactive distance to drifting prey and on predation risk, and the effect of bed load transport on incubation success and production of benthic invertebrates. Combined with observations linking unembedded substrates in streams to higher densities of various other vertebrates, such as salamanders observed in this and other studies (Parker 1991; Welsh and Ollivier 1998) and benthic fish (Jowett and Boustead 2001; White and Harvey 2001), these results indicate that elevated fine-sediment inputs will often deserve consideration by resource managers. In some watersheds, reducing the levels of stored fine sediment in small stream channels may substantially increase the watershed-scale total of productive habitat available to both fish and other vertebrates.

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