

Quantitative linkages among sediment supply, streambed fine sediment, and benthic macroinvertebrates in northern California streams

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Abstract. The absence of quantified relationships among sediment supply, stream channel conditions, and biological responses limits our ability to predict the cumulative watershed effects of management activities in forested mountainous watersheds. We addressed this uncertainty by testing whether increased sediment supply resulted in elevated levels of streambed fine sediment stored in pools and riffles and whether fine bed material was correlated with spawning-gravel quality and altered benthic macroinvertebrate assemblages in 6 streams of the Klamath Mountains, northern California. Sediment supply was estimated using 2 models: 1) an empirical model of landslide volumes based on terrain types present in a basin, and 2) a surface erosion model using a locally calibrated version of the universal soil loss equation. Riffle-surface fine sediment and the fractional volume of pools filled with fine sediment (V^*) were both positively correlated with estimated sediment supply, whereas subsurface spawning-gravel permeability was inversely correlated with estimated sediment supply. Fine sediment levels were relatively low compared to published values. Reach-average values of riffle-surface fine sediment ranged from 4 to 16% and V^* values ranged from 0.05 to 0.20. Based on established relationships between subsurface flow rates and salmonid egg survival, median predicted egg survival was quite low and ranged from 15 to 38%. Riffle-surface fine sediment and common benthic macroinvertebrate biological metrics were not correlated, but several taxa showed responses to riffle-surface fine sediment. Taxa that showed negative responses to fine sediment are hypothesized to be more available as prey for salmonids than taxa that showed positive responses. This relationship suggests that fine sediments might cause an overall reduction in prey availability for salmonids. Monitoring the effects of increased sediment supply in steep, forested streams should focus on fine sediment in pools and riffles, salmonid spawning-gravel quality, and specific macroinvertebrate taxa that are especially responsive to fine sediment. The linkages described in our paper can be used to make quantitative predictions of the cumulative watershed effects of management activities on stream conditions, salmonid habitat, and benthic macroinvertebrates.

Key words: cumulative watershed effects, fine sediment, sediment supply, V^* , benthic macroinvertebrates, spawning gravel, egg survival, Klamath.

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Accelerated rates of erosion and sediment delivery to streams after timber harvest and road construction are common occurrences in mountainous, forested watersheds that are prone to landslides (e.g., Sidle et al. 1985, Montgomery et al. 2000). Increased supply of

sediment to streams can cause dramatic changes to channels. These changes can include increased streambed fine sediment, aggradation (sediment deposition), channel widening, and pool filling, especially in lower gradient reaches (e.g., Kelsey 1980, Lisle 1982, Coats et al. 1985, Roberts and Church 1986, Knighton 1991). Fine sediment deposition is one of the most pervasive pollutants affecting water quality in US streams (USEPA 2002) and is an important factor in the decline of anadromous salmonid populations in the Pacific Northwest (Platts et al. 1989, Nehlsen et al. 1991).

Deposited fine sediment that fills interstitial pore spaces in the streambed can change the abundance and composition of benthic invertebrate assemblages (Waters 1995, Angradi 1999, Zweig and Rabeni 2001, Bond and Downes 2003, Kaller and Hartman 2004, Suttle et al. 2004, Rabeni et al. 2005, Matthaei et al. 2006). For example, experimental manipulations of fine sediment in a northern California stream caused a shift in the invertebrate assemblage from epibenthic grazers and predators to burrowing taxa as embeddedness increased (Suttle et al. 2004). Increased fine sediment in experimental substratum mixtures in a West Virginia stream produced decreased macroinvertebrate density, biomass, and taxon richness (Angradi 1999). Increased supply of fine sediment also can affect habitat for salmon by decreasing spawning-gravel quality, reducing food availability and foraging efficiency, and degrading rearing habitat (Platts et al. 1989). Fine sediment is especially detrimental to the eggs and embryos of salmon and trout, and reduced subsurface flow rates in spawning gravels can cause high levels of mortality (Koski 1966, Chapman 1988, Bjornn and Reiser 1991, Curry and MacNeill 2004).

The biological effects of increased levels of fine sediment in streams have been well documented (reviewed by Waters 1995), but few studies have addressed the linkages among increased sediment supply to stream channels from hillslope erosion, consequent changes in streambed conditions, and effects on stream biota. These linkages are examples of cumulative watershed effects: hydrologic, geomorphic, and biological responses to multiple landuse activities that result in altered watershed function (Reid 1993). Currently, various landuse regulations, such as the National Environmental Policy Act and the California Environmental Quality Act, require that public agencies and private landowners assess the potential cumulative watershed effects of proposed land management activities. In California, timber harvest plans must explicitly consider the cumulative watershed effects of harvesting operations, including any potential effects on hillslope erosion and sediment supply to streams. Our ability to predict the cumula-

tive watershed effects of forest management activities is limited by the absence of studies that have quantified relationships among sediment supply to streams, channel conditions, and biological responses (Dunne et al. 2001).

Our research was initiated because of concerns about the cumulative watershed effects of past and present forest management activities in steep mountainous terrain. Timber harvest, road construction, and livestock grazing are common practices in the Klamath Mountains of northwestern California and in many publicly and privately managed forests in the western US. Populations of anadromous fish, including steelhead trout (*Oncorhynchus mykiss*) and autumn-run and spring-run Chinook salmon (*Oncorhynchus tshawytscha*), have declined significantly in the Klamath River watershed during the past century (Moyle 2002). We asked whether these declines might have been caused by the effects of increased sediment supply to stream systems resulting from forest management practices. We sought to identify the direct linkages between sediment supply and channel conditions that might be limiting for salmonid fishes in the Klamath Mountains. We focused on infilling of pools by fine sediment, surficial fine sediment in riffles, permeability of spawning gravels, and the prey base of benthic invertebrates. The objectives of our study were to quantify the linkages between: 1) hillslope sediment supply and fine sediment on streambeds, and 2) streambed fine sediment and benthic macroinvertebrate assemblages. We determined whether increased sediment supply, as estimated from models of landslides and surface erosion, resulted in elevated levels of streambed fine sediment in pools, riffles, and potential spawning gravels, and whether streambed fine sediment was correlated with altered benthic macroinvertebrate assemblages.

Methods

Study area

The Klamath Mountains of northwestern California encompass the central portion of the Klamath River watershed, which has its headwaters in south-central Oregon and empties into the Pacific Ocean near Crescent City, California (Fig. 1). The Klamath Mountains are extremely rugged. The total relief is 2400 m, and hillslopes steeper than 65% are common. Annual precipitation ranges from <800 mm in inland valleys to >2000 mm in the high mountains, where much of it falls as snow. The Klamath Mountains are recognized as an ecoregion of high conservation value (Olson and Dinerstein 1998), and the area supports one of the most floristically diverse temperate coniferous forests in the

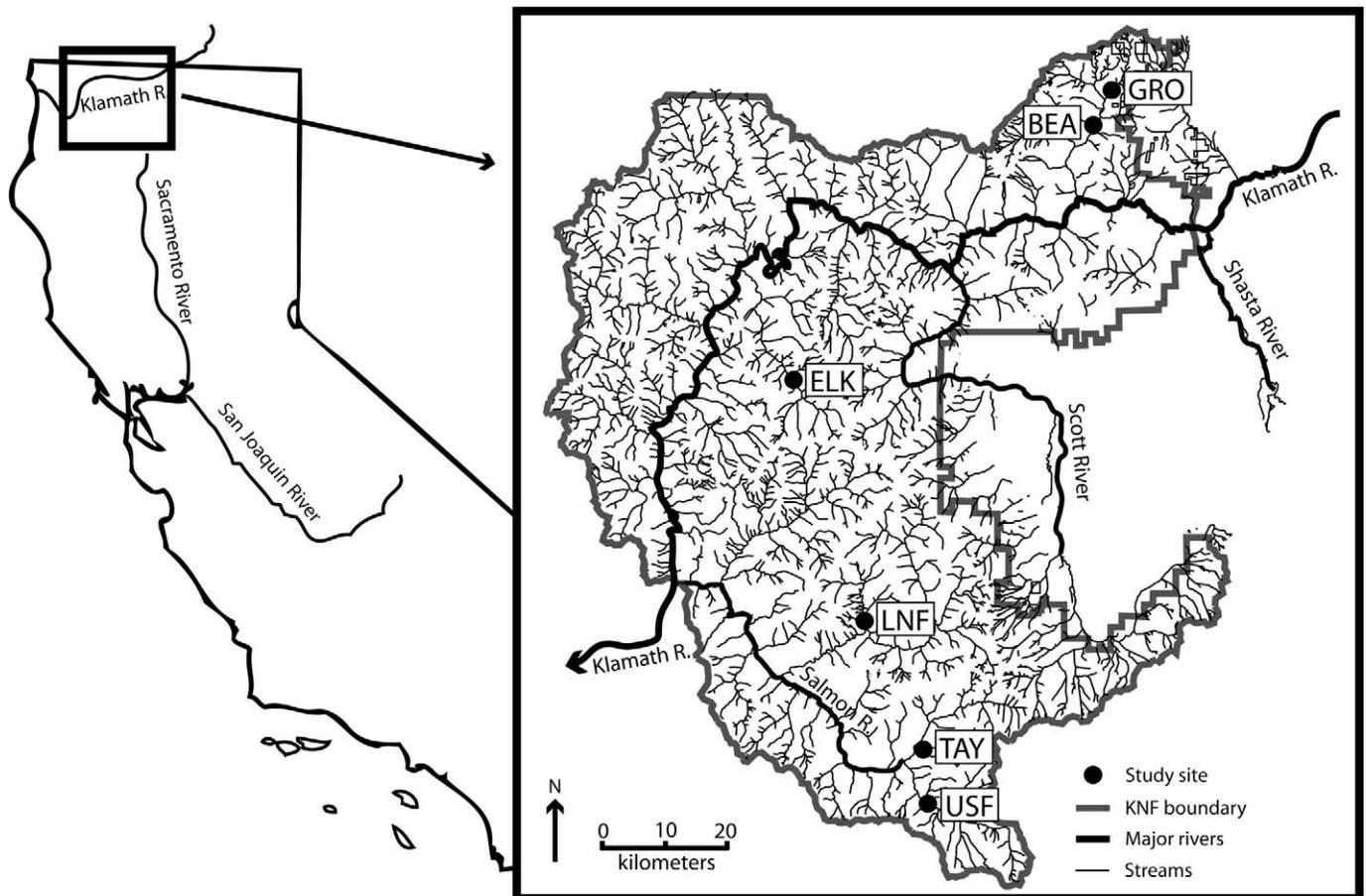


FIG. 1. Location of study reaches in the Klamath National Forest (KNF), northern California. R = River, GRO = Grouse Creek, BEA = Beaver Creek, ELK = Elk Creek, LNF = Little North Fork Salmon River, TAY = Taylor Creek, USF = Upper South Fork Salmon River.

world. Most of the area is managed by the Klamath National Forest (KNF), with some private landholdings in the eastern mountains and low-elevation valleys. The human population in the Klamath Mountains is quite small, and population density is <1 person/km². Extensive road building and timber harvest occurred in the KNF in the 20th century, and the most intense activity occurred between 1960 and 1990. Present-day harvest levels are very low relative to historic levels.

Six watersheds (Fig. 1) were selected for our study of the effects of increased supply of sediment to stream channels resulting from forest management activities and natural processes (wildfires and floods). One study reach in each of the 6 watersheds was sampled during autumn 2003. Watersheds and study reaches met the following criteria: 1) stream channel gradient between 1.5 and 4%, 2) gravel and cobble substrate, 3) bedrock lithology that produces abundant fine sediment (predominantly sand-sized particles from highly

weathered granitic plutons), 4) no recent channel-scouring debris flows that directly affected the sampling reach, 5) known use by anadromous fishes, and 6) minimal human land use other than forest management activities (i.e., timber harvest, roads, recreation, and grazing). The supply of sediment to stream channels in the watersheds was estimated from 2 models, and 3 watersheds with high sediment supply and 3 with low sediment supply were selected for study (Table 1).

Estimates of sediment supply

Two models developed by KNF staff to predict the cumulative watershed effects of forestry activities were used to estimate sediment delivery to stream channels (sediment supply) in the study watersheds (de la Fuente and Haessig 1994). The *landslide model* uses empirical studies of landslide occurrence in various geomorphic terrain types and disturbance classes (i.e., timber harvest, roads, and fire) to predict sediment

TABLE 1. Watershed characteristics, channel characteristics, and sediment supply model estimates for the 6 study reaches. The 3 basins with lower sediment supply are listed first, followed by the 3 basins with higher sediment supply. The surface erosion model is based on the universal soil loss equation (Wischmeier 1976).

| Characteristic | Elk Creek | Little North Fork Salmon River | Upper South Fork Salmon River | Beaver Creek | Grouse Creek | Taylor Creek |
|--|-----------|--------------------------------|-------------------------------|--------------|--------------|--------------|
| Drainage area (km ²) | 83 | 84 | 156 | 93 | 26 | 48 |
| Granitic pluton bedrock (% of basin) | 65 | 57 | 49 | 52 | 99 | 50 |
| Reach length (km) | 1.6 | 0.9 | 1.9 | 1.7 | 1.0 | 0.6 |
| Channel slope (%) | 4.3 | 2.5 | 1.6 | 2.3 | 2.8 | 3.4 |
| Stream order | 4 | 4 | 4 | 4 | 3 | 4 |
| Stream power index | 3.56 | 2.11 | 2.50 | 2.14 | 0.74 | 1.61 |
| Bankfull width (m) | 18.6 | 14.5 | 19.0 | 10.4 | 5.5 | 7.5 |
| Bankfull depth (m) | 0.67 | 0.81 | 0.60 | 0.47 | 0.44 | 0.65 |
| Median grain size (mm) | 288 | 284 | 169 | 121 | 54 | 135 |
| Landslide model | | | | | | |
| Sediment supply (m ³ km ⁻² y ⁻¹) | 69 | 98 | 61 | 151 | 156 | 72 |
| Increase over undisturbed (%) | 44 | 109 | 14 | 248 | 397 | 79 |
| Surface erosion model | | | | | | |
| Sediment supply (m ³ km ⁻² y ⁻¹) | 5.0 | 9.1 | 5.0 | 14.0 | 13.5 | 11.3 |
| Increase over undisturbed (%) | 0 | 148 | 24 | 811 | 800 | 310 |
| Road-related erosion (% of total) | 0 | 30 | 19 | 88 | 88 | 73 |

volumes delivered to the stream channel network by shallow landslides. The *surface erosion model* uses the universal soil loss equation (Wischmeier 1976), empirically calibrated with erosion plot data from the KNF, to predict surface erosion. Both models predict background levels of sediment supply from natural sources and adjust rates based on the type and amount of forest management activities (i.e., roads and timber harvest). The landslide model estimates sediment delivery during relatively infrequent, episodic storms (return interval ≈ 10 y), whereas the surface erosion model predicts sediment delivery from chronic sources during more frequent storm events (return interval ≈ 2 y). Sediment supply estimates from the models were not combined because the models predict sediment supply over different time scales. Information on model development and testing is available in an unpublished report (de la Fuente and Haessig 1994) and at <http://nature.berkeley.edu/~mcover/sedmodels>.

Stream power is a measure of the energy available to transport sediment and is a function of the product of channel slope and stream flow (Bagnold 1966). In our study, streams with higher sediment supply (standardized by watershed area) were smaller and had lower stream power than streams with lower sediment supply (Table 1). It is unclear whether this relationship is an artifact of site selection and small sample size or unit-area sediment supply is greater in small watersheds (perhaps because smaller watersheds are more prone to increased sediment supply caused by more intense management practices). Streams with low stream power have lower transport capacity and are more likely to accumulate fine sediment in response to

increased sediment supply. To examine the relationship between sediment supply and streambed fine sediment while controlling for differences in transport capacity among study reaches, estimates of sediment supply from both models were scaled by stream power by dividing the sediment supply estimate by the stream power index (SPI) for each reach. SPI is calculated as the product of reach-scale slope and watershed area (a proxy for stream discharge) and represents the transport capacity of the channel (e.g., Mosley 1978, Moore et al. 1993).

Bed surface fine sediment

In each reach, the fractional volume of each pool filled with fine sediment (V^* ; Lisle and Hilton 1992, 1999, Hilton and Lisle 1993) was measured in every pool that met a minimum size criterion (depth $>2\times$ the average riffle crest depth) and contained most of the flow (following the methods described by Hilton and Lisle 1993). V^* is determined by measuring water depth and the depth of fine sediment deposited at multiple locations on the bottom of a pool (Lisle and Hilton 1999). For V^* determinations, fine sediment was defined as sand and gravel deposits with a median grain size (D_{50}) <11 mm, following the suggestions of Hilton and Lisle (1993). Bed material of this size forms the matrix between the framework of bed material and is commonly winnowed from riffles and deposited in pools (Hilton and Lisle 1993). Eleven to 20 (mean = 17) pools were surveyed in each study reach. V^* values from all pools in a reach were weighted by the residual

pool volumes and averaged to obtain a reach-wide V^* value.

In each reach, the steepest and shallowest riffles and 2 riffles representing the 25th and 75th percentiles of slope of all riffles in the reach were selected for intensive sampling of surficial fine sediment, grain size, benthic macroinvertebrates, and bankfull width and depth measurements. The proportion of fine sediment on the surface of the streambed was measured in each riffle by placing a large sampling grid on the streambed (2.8 m × 1.25 m with 13-cm grid spacing and 220 grid intersections). A point count was taken at each grid intersection by placing the point of a steel pin on the bed and noting the presence or absence of fine sediment at the tip of the pin. For riffle-surface fine sediment surveys, fine sediment was defined as particles with an intermediate diameter <4 mm. Definitions of fine sediment in the literature range from particles <0.25 mm (Kaller and Hartman 2004) to ~10 mm. We chose 4 mm as the definition of fine sediment in riffles because fine gravel (2–6 mm) has a significant effect on the emergence success of salmonids (Kondolf 2000), and distinguishing among neighboring grains of fine gravel (2–4 mm) is difficult when using a visual sampling method (Bunte and Abt 2001). Fine sediment measurements were made along 3 equally spaced transects that spanned the full width of the channel in each riffle. Point counts of fine sediment ranged from 5330 to 16,850 per reach, depending on channel width. Most of the fine sediment in riffles is found in interstitial spaces between gravel and cobble grains. Larger particles become more embedded in fine sediment as the proportion of the bed surface covered with fines increases. Thus, data collected using this surface-based sampling approach should be correlated with embeddedness and volumetric measures of fine sediment. However, these relationships were not examined, and the correlations might not be linear.

Subsurface gravel permeability

Spawning-gravel quality was assessed by direct measurements of subsurface gravel permeability during the summer of 2004 (methods modified from Barnard and McBain 1994). Reach-average subsurface gravel permeability was calculated from measurements made in each of the 4 sample riffles per study stream. Permeability sample sites were located at the upstream end of each riffle, near the pool tailout, in patches of gravel that ranged from 40 to 80 mm in median particle size. At each site, a perforated standpipe was driven into the streambed to a depth of 36 cm, a sampling depth 14 to 22 cm below the bed

elevation. This grain size and depth were chosen because they reflect the average egg-pocket depth and substrate size used for spawning by several species of anadromous salmonids (Kondolf and Wolman 1993). Water was pumped from the standpipe with a battery-powered vacuum pump into a measurement chamber. The rate at which interstitial water refilled the void was measured, and 5 replicate samples were drawn for each standpipe location. Permeability was calculated from the inflow rate using methods described by Barnard and McBain (1994).

Quantifying subsurface gravel permeability in preferred spawning sites is one of the most effective ways of assessing spawning-gravel quality because permeability directly affects egg survival. Egg survival rates were inferred from our direct measurements of subsurface gravel permeability from the equation:

$$\% \text{ egg survival} = 14.615 \ln(P) - 81.132,$$

where P is gravel permeability (cm/h). This regression is based on data compiled from studies of survival to emergence of salmonid embryos (Tagart 1976, McCuddin 1977, Chapman 1988, Stillwater Sciences 2000), and explains a large portion of observed variation in survival to emergence of coho and Chinook salmon ($r^2 = 0.85$).

Benthic macroinvertebrates

Benthic macroinvertebrates were sampled along 3 transects in each riffle. Transects were positioned where fine sediment had been measured with the sampling grid. A timed 4-min sample was made at each transect by disturbing the substrate upstream of a 500- μm -mesh D-frame kick net. The 3 transect samples were composited into 1 sample per riffle. Samples were elutriated in the field, the inorganic portion of the sample was carefully examined for benthic organisms, and the organic portion of the sample was preserved in 95% ethyl alcohol.

Laboratory sorting and identifications were done at the National Aquatic Monitoring Center (Utah State University, Logan, Utah), following their established laboratory methods (described in Vinson and Hawkins 1996). Benthic macroinvertebrates were removed from the sample under a dissecting microscope at 10× magnification. Individual riffle samples were quantitatively subsampled until ≥ 500 organisms were identified (range: 541–1443). Organisms were identified to the lowest practical taxonomic level, usually genus or species, except for Chironomidae (subfamily), Collembola (order), Trombidiformes (order), Oligochaeta (class), Ostracoda (class), Turbellaria (class), and Nematoda (phylum).

Each invertebrate taxon was classified as burrowing, armored, or vulnerable (Suttle et al. 2004), based on life-history information (e.g., from Merritt and Cummins 1996). In addition, prey availability scores of invertebrates (Rader 1997) were used to predict the effects of changes in taxon abundances on prey availability for salmonids. Prey availability scores were developed from 12 biological traits (e.g., drifting frequency, size, habit) that are thought to make taxa more available for consumption by drift-feeding fish (Rader 1997).

Other channel characteristics

A continuous longitudinal profile of water-surface slope at low flow was measured along the full length of each study reach. The slope of each channel unit (e.g., pool or riffle) was measured using a hand level, stadia rod, and reel tape. Data from the profile were used to calculate reach-scale slope and to assess the slope of each individual riffle.

Grain size was measured in each riffle with transect-based pebble counts (Wolman 1954). Particles were measured every 0.3 m along transects with a gravel template (gravelometer) or cloth measuring tape (for particles with intermediate axes >180 mm; Bunte and Abt 2001). The number and spacing of transects needed to obtain ≥ 200 equally spaced grain measurements was determined at each riffle. Riffles were not observed to be organized into textural patches (Buffington and Montgomery 1999).

Data analysis

The hypotheses that reach-average ($n = 6$) measures of streambed fine sediment (V^* , riffle-surface fine sediment, and subsurface gravel permeability) were positively correlated with quantitative predictions of sediment supply (from the surface erosion and landslide models) was tested with linear regression analyses. V^* varies with sediment yield (Lisle and Hilton 1999), so linear regression also was used to examine whether V^* was positively correlated with reach-average riffle-surface fine sediment.

The first step of examining the relationships between benthic macroinvertebrates and fine sediment was a review of the literature for taxa and metrics that have been reported as being especially responsive to increased levels of fine sediment. The review was focused on studies done in steep, forested streams (Hawkins 1984, Waters 1995, Angradi 1999, Relyea et al. 2000, Suttle et al. 2004, Braccia and Voshell 2006). From the literature, 27 macroinvertebrate taxa (that are common in our study area) and 10 biological metrics were identified as response variables to be tested in

this study (Table 2). Linear regression was used to examine whether reach-average taxon abundances and metric values were correlated with reach-average riffle-surface fine sediment levels for the 6 study reaches (*interreach* analysis).

Separate samples of benthic invertebrates and fine sediment were collected from each of 4 riffles in the 6 study reaches ($n = 24$), but these samples were potentially spatially autocorrelated (i.e., invertebrate assemblages or environmental variables from riffles within the same reach might be more similar than expected for randomly associated observations) and could not be treated as independent samples in a linear regression. Spatial autocorrelation is common in ecological studies, and it impairs our ability to use standard statistical hypothesis testing because computed test statistics are too often declared significant (Legendre 1993). Correlograms (Legendre and Fortin 1989) of our data showed significant spatial structure. Riffles from the same reach had much more similar assemblages and environmental characteristics than riffles from different streams. Therefore, sediment-biota relationships were examined among the 4 riffle samples within single reaches. Riffle samples represented the full range of riffle slopes (usually 1–8%) present in each reach, and therefore, should have represented a wide range of fine sediment levels. In reaches where variation in fine sediment levels was high between the 4 riffles, linear regression was used to examine relationships between fine sediment and benthic invertebrate assemblages within each reach (*intrareach* analysis).

Statistical significance was judged at a false-positive rate of $\alpha = 0.05$, and 1-tailed tests were made on all a priori hypotheses. The experiment-wise false-positive rate (α_e) was not adjusted using the sequential Bonferroni adjustment because individual a priori hypotheses were made for each metric and taxon and because a lower α value would have increased the risk of Type II errors. Others have argued that use of Bonferroni p -value adjustments is impractical when a priori hypotheses have been made and the universal (study-wide) null hypothesis is not of primary interest (e.g., Moran 2003). We did apply the Bonferroni adjustment when testing metrics and taxa without a priori hypotheses.

SPI-adjusted sediment supply estimates and median gravel permeability values were $\log_{10}(x)$ -transformed for the statistical analyses to approximate linear relationships and to satisfy criteria for normality and homoscedasticity of residuals. Raw taxonomic abundance data were $\log_{10}(x + 1)$ -transformed to prevent undefined values and for the reasons listed above.

TABLE 2. Predicted responses of biological metrics and benthic macroinvertebrate taxa to increased levels of fine sediment as reported in other studies. EPT = Ephemeroptera, Plecoptera, Trichoptera.

| Metrics and taxa | Predicted response | Source of prediction | Study location |
|-----------------------------------|--------------------|----------------------------------|-----------------------------|
| Taxon richness | – | Waters 1995 | Widespread |
| Total abundance | – | Angradi 1999 | Appalachians, West Virginia |
| EPT richness | – | Angradi 1999 | Appalachians, West Virginia |
| EPT abundance | – | Waters 1995 | Widespread |
| % burrowers | + | Suttle et al. 2004 | Coast Range, California |
| % vulnerable | – | Suttle et al. 2004 | Coast Range, California |
| % Coleoptera | – | Braccia and Voshell 2006 | Appalachians, Virginia |
| % crawlers | – | Braccia and Voshell 2006 | Appalachians, Virginia |
| Chironominae/Chironomidae | – | Angradi 1999 | Appalachians, West Virginia |
| Orthocladiinae/Chironomidae | + | Angradi 1999 | Appalachians, West Virginia |
| <i>Antocha</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Arctopsyche</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Attenella delantala</i> | + | Hawkins 1984 | Cascades, Oregon |
| <i>Caudatella</i> spp. | – | Hawkins 1984, Relyea et al. 2000 | Pacific Northwest |
| Chironomidae | + | Waters 1995 | Widespread |
| Chironominae | – | Angradi 1999 | Appalachians, West Virginia |
| <i>Cinygmula</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Dicranota</i> spp. | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Drunella doddsi</i> | – | Hawkins 1984, Relyea et al. 2000 | Pacific Northwest |
| <i>Drunella spinifera</i> | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Ecclisomyia</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Epeorus</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Glossosoma</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Hesperoperla pacifica</i> | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Hexatoma</i> spp. | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Isoperla</i> spp. | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Lepidostoma</i> spp. | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Malenka</i> spp. | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Neophylax</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| Oligochaeta | + | Waters 1995 | Widespread |
| <i>Optioservus</i> spp. | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Rhithrogena</i> spp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Rhyacophila</i> Betteni grp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Rhyacophila</i> Hyalinata grp. | – | Relyea et al. 2000 | Pacific Northwest |
| <i>Simulium</i> spp. | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Zapada cinctipes</i> | + | Relyea et al. 2000 | Pacific Northwest |
| <i>Zapada columbiana</i> | + | Relyea et al. 2000 | Pacific Northwest |

Results

Sediment supply models

Sediment supply estimates from the landslide model ranged from 61 to 156 m³ km⁻² y⁻¹ for the 6 watersheds (Table 1). The landslide model predicted that sediment supply was, on average, 149% greater than if no disturbances had occurred in the watersheds. This result indicates that most of the erosion was associated with roads, timber harvest, and fires (Table 1).

Sediment supply estimates from the surface erosion model ranged from 5 to 14 m³ km⁻² y⁻¹ (Table 1). The surface erosion model predicted that sediment supply increased an average of 349% over predisturbance conditions, primarily as a result of much higher

postdisturbance surface erosion rates attributed to roads (Table 1).

Estimates of watershed-area-adjusted sediment supply (Table 1) from the landslide and surface erosion models were strongly and positively related (linear regression, $p = 0.01$, $r^2 = 0.72$; Fig. 2). The sediment supply estimates from the surface erosion model were slightly better correlated with streambed fine sediment than were estimates from the landslide model. Thus, graphs showing sediment supply estimates include results from only the surface erosion model.

Linkages between sediment supply and streambed fine sediment

Reach-average V* ranged from 0.05 to ~0.20 (Table 3). V* values were strongly and positively

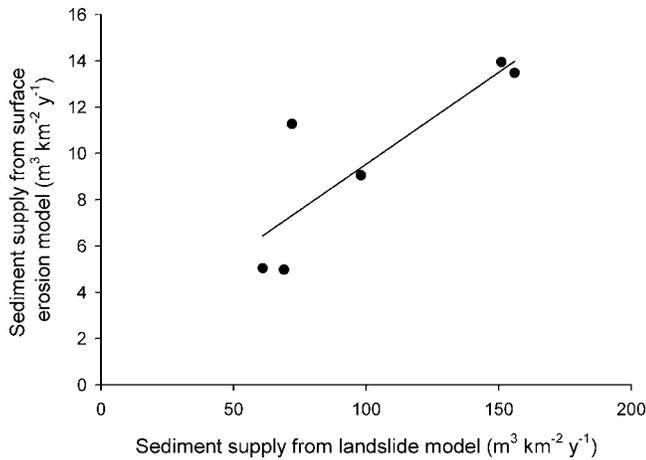


FIG. 2. Linear relationship between estimated sediment supply from the landslide model and estimated sediment supply from the surface erosion model.

correlated with $\log_{10}(x)$ -transformed fine sediment supply estimates from the surface erosion model adjusted by the reach-averaged SPI (linear regression, $p = 0.006$, $r^2 = 0.83$; Fig. 3A). V^* also was strongly correlated with $\log_{10}(x)$ -transformed sediment supply estimates from the landslide model adjusted by the reach-averaged SPI (linear regression, $p = 0.006$, $r^2 = 0.83$).

Individual values of riffle-surface fine sediment ranged from 2.0 to 23.3% of the riffle surface area, whereas reach-average values ranged from 3.7 to 16.2% (Table 3). Reach-average riffle-surface fine sediment was significantly and positively related to fine sediment supply predicted from the surface erosion model adjusted by the SPI (logarithmic regression, $p = 0.01$, $r^2 = 0.79$; Fig. 3B). Riffle-surface fine sediment was significantly and positively related to fine sediment supply predicted from the landslide model adjusted by the SPI, but the relationship was slightly weaker (logarithmic regression, $p = 0.04$, $r^2 = 0.56$) than the relationship with the surface erosion model predictions. Three of the 6 study streams contained riffles with a wide range of riffle-surface

fine sediment levels. The standard deviation of riffle-surface fine sediment levels in Beaver Creek, Grouse Creek, and Little North Fork Salmon River ranged from 3.6 to 7.8%, whereas the standard deviation at the other 3 reaches was $<2.0\%$ (Table 3). The 3 reaches with high variation in riffle-surface fine sediment were considered in the intrareach analyses of benthic macroinvertebrate taxa.

Values of subsurface gravel permeability were highly variable within and among stream reaches, reflecting the heterogeneous nature of spawning-gravel quality in the study area (Table 3). Subsurface gravel permeability measured in potential salmonid spawning gravels was significantly and negatively related to fine sediment supply predicted from the surface erosion model (linear regression, $p = 0.04$, $r^2 = 0.58$; Fig. 3C). Subsurface gravel permeability also was significantly and negatively related to sediment supply estimates from the landslide model (linear regression, $p = 0.04$, $r^2 = 0.59$). The range of observed median subsurface flow rates corresponded to a predicted range of 15 to 39% in salmonid egg survival (based on experimental data from Tagart 1976, McCuddin 1977, Chapman 1988, Stillwater Sciences 2000) (Table 3).

Reach-average V^* values were significantly related to riffle-surface fine sediment (linear regression, $p = 0.02$, $r^2 = 0.70$; Fig. 4). The linear regression model predicted roughly a 1:1 positive relationship (slope = 76.5 ± 23.8) between V^* and riffle-surface fine sediment.

Linkages between streambed fine sediment and benthic macroinvertebrates

Benthic macroinvertebrate metrics.—In the interreach analysis, none of the 10 metrics expected to be related to fine sediment were significantly related to reach-average riffle-surface fine sediment levels. Moreover, the strongest relationships between these metrics and riffle-surface fine sediment levels either disagreed with a priori hypotheses or seemed spurious, e.g., positive relationships between taxon richness and reach-average riffle-surface fine sediment levels. In the intrareach

TABLE 3. Reach-average values (SD) of fractional volume of pools filled with fine sediment (V^*) and riffle-surface fine sediment, and reach median values (SD) of subsurface gravel permeability with corresponding predicted egg survival.

| Watershed | V^* | Riffle-surface fine sediment (%) | Permeability (cm/h) | Predicted egg survival (%) |
|--------------------------------|---------------|----------------------------------|---------------------|----------------------------|
| Elk Creek | 0.050 (0.027) | 3.7 (1.5) | 3563 (1503) | 38 |
| Little North Fork Salmon River | 0.066 (0.040) | 10.2 (5.5) | 2802 (1244) | 35 |
| Upper South Fork Salmon River | 0.076 (0.038) | 8.5 (2.0) | 3675 (4734) | 39 |
| Beaver Creek | 0.102 (0.054) | 9.7 (3.6) | 731 (1127) | 15 |
| Grouse Creek | 0.197 (0.116) | 16.2 (7.8) | 1177 (2543) | 22 |
| Taylor Creek | 0.123 (0.065) | 16.1 (1.3) | 1954 (1284) | 30 |

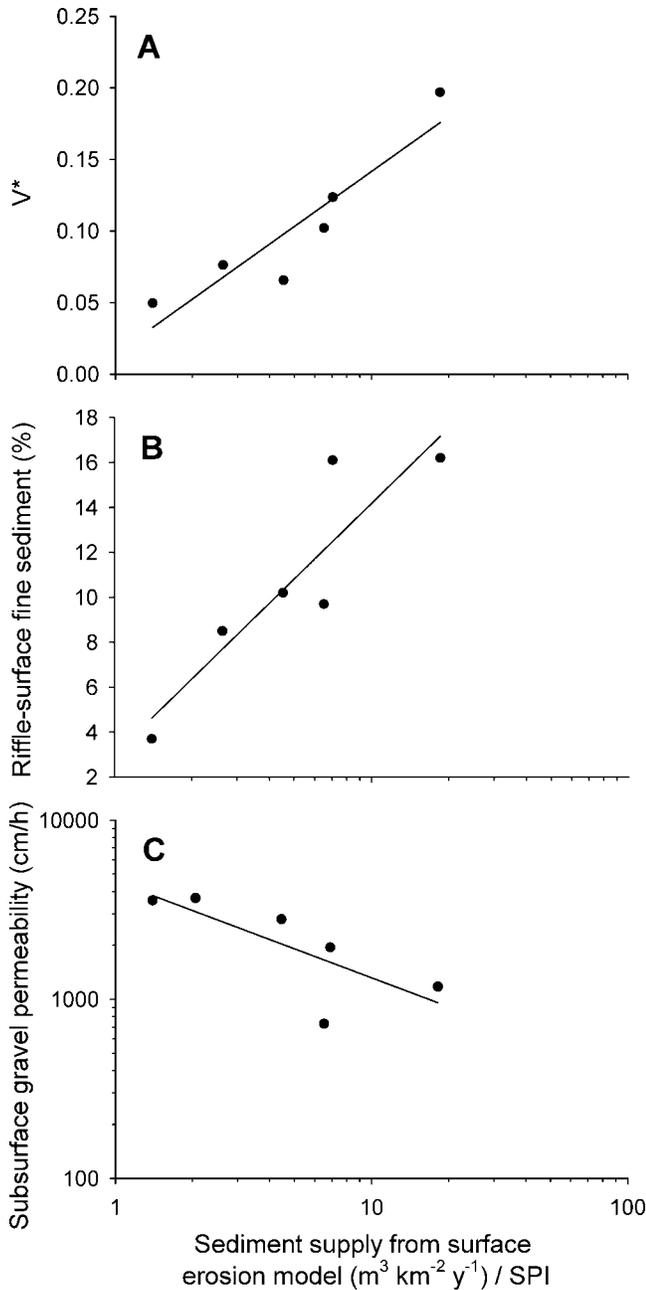


FIG. 3. Relationships between sediment supply estimated from the surface erosion model (scaled by stream power index [SPI]) and 3 measures of streambed fine sediment. A.—Logarithmic relationship between estimated sediment supply and reach-average volumetric fraction of fine sediment stored in pools (V^*). B.—Logarithmic relationship between estimated sediment supply and reach-average riffle-surface fine sediment. C.—Inverse power-law relationship between sediment supply and subsurface gravel permeability.

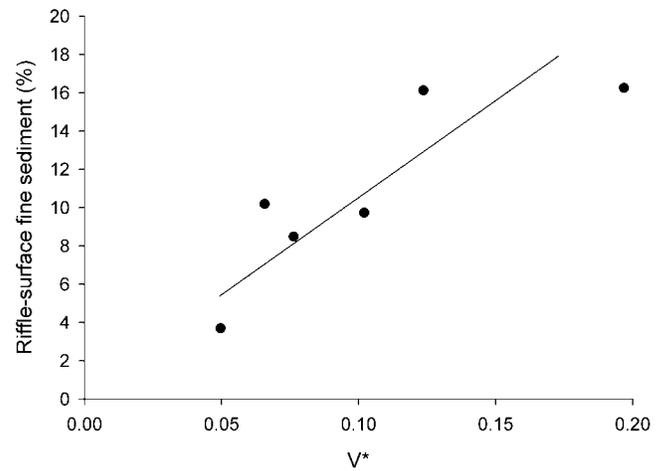


FIG. 4. Linear relationship between reach-average volumetric fraction of fine sediment stored in pools (V^*) and the reach-average riffle-surface fine sediment.

analysis, % burrowers (+) and % vulnerable (-) were significantly related to riffle-surface fine sediment levels in the Little North Fork Salmon River (Table 4). None of the metrics without a priori hypotheses were significantly related to riffle-surface fine sediment levels after applying the sequential Bonferroni adjustment.

Benthic macroinvertebrate taxa.—In the interreach analysis, only 5 of 27 taxa with a priori hypotheses were significantly related to reach-average riffle-surface fine sediment levels (Table 4). Abundances of the tipulid *Antocha*, the midge subfamily Chironomi-

TABLE 4. Observed responses of metrics and taxa that were expected to respond to fine sediment deposition based on other studies (see Table 2). Only those metrics or taxa that were significantly related to riffle-surface fine sediments in the interreach or intrareach analyses are shown. * = $p < 0.05$, ** = $p < 0.01$.

| Metrics and taxa | Direction of relationship with fine sediment | Direction of relationship with fine sediment | |
|----------------------------|--|--|------------|
| | | Interreach | Intrareach |
| % burrowers | + | | * |
| % vulnerable | - | | * |
| <i>Antocha</i> spp. | - | * | |
| <i>Attenella delantala</i> | + | * | * |
| Chironominae | - | ** | |
| <i>Dicranota</i> spp. | - | | * |
| <i>Drunella doddsi</i> | - | | * |
| <i>Drunella spinifera</i> | - | | * |
| <i>Ecclisomyia</i> spp. | - | * | |
| <i>Epeorus</i> spp. | - | | * |
| Oligochaeta | + | | * |
| <i>Zapada columbiana</i> | + | * | |

nae, and the limnephilid caddisfly *Ecclisomyia* were negatively related to reach-average riffle-surface fine sediment levels, whereas abundances of the ephemereid mayfly *Attenella delantala* and the nemourid stonefly *Zapada columbiana* were positively related to reach-average riffle-surface fine sediment levels. Only 1 taxon, *A. delantala*, had a significant relationship with riffle-surface fine sediment in both the interreach and intrareach analyses.

In the intrareach analysis in Grouse Creek, abundances of the tipulid *Dicranota*, the ephemereid mayfly *Drunella doddsi*, and the heptageniid mayfly *Epeorus* were negatively related to riffle-surface fine sediment levels, whereas *A. delantala* and *Oligochaeta* were positively related to riffle-surface fine sediment levels. In the North Fork Salmon River, abundances of the ephemereid mayfly *Drunella spinifera* were negatively related to riffle-surface fine sediment. No significant relationships were observed in Beaver Creek. No taxon or metric had a significant relationship with riffle-surface fine sediment in >1 stream.

None of the taxa without a priori predictions were significantly related to riffle-surface fine sediment levels after applying the sequential Bonferroni adjustment. Turbellaria were strongly positively related to riffle-surface fine sediment levels in the interreach analysis and in the intrareach analysis of Grouse Creek, but these relationships were not significant at the Bonferroni-adjusted α value.

Discussion

Sediment supply and streambed fine sediment

Sediment supply estimates from the landslide and surface erosion models were strongly correlated, despite vast differences between the 2 modeling approaches. Both models were developed from empirical relationships between erosion volumes and various landscape attributes. However, the landslide model was developed specifically for the study area, whereas the surface erosion model generally has been applied to shallow-gradient, agricultural landscapes. The 2 models predict sediment supply from different processes (landsliding vs soil erosion) that occur over different temporal scales (return intervals of ~ 10 y vs ~ 2 y). The strong correlation between sediment supply estimates from these 2 models is probably a result of the sensitivity of both models to changes in forest management levels. For example, the surface erosion model predicted that erosion from roads was the primary source of fine sediment associated with management activities (Table 1), and empirical observations show that roads greatly increase both surface erosion and landslide volumes and rates (Reid and

Dunne 1984, Sidle et al. 1985, May 2002). The same disturbances that increase the frequency of landsliding during infrequent storms also can increase surface erosion during more frequent storms.

We identified several important linkages between sediment supply and instream habitat. Fine sediment was strongly correlated with increased sediment supply in both riffles and pools. Doubling SPI-adjusted sediment supply (from the surface erosion model) from a moderately low value of $3 \text{ m}^3 \text{ km}^{-2} \text{ y}^{-1}$ to a moderately high value of $6 \text{ m}^3 \text{ km}^{-2} \text{ y}^{-1}$ implies a 27% increase in V^* (from 0.078 to 0.099) and a 40% increase in riffle-surface fine sediment (from 8.1% to 11.3%). As the volumetric fraction of sand in the bed increases to between 10 and 30%, pore spaces between coarser sediments can become completely filled, creating localized patches of fine-grained sediment (Wilcock and Kenworthy 2002). However, our observations of streams in the study area indicate that sand tends to be flushed through these steep, mountain streams and generally is deposited only in the wakes of boulders and in interstitial spaces between coarse grains. Thus, riffle-surface fine sediment is expected to increase as sediment supply increases, but should plateau near 20% as interstitial spaces are filled with sand. Excess fine sediment that is transported out of riffles is expected to be stored temporarily in pools (Lisle 1989).

V^* varied greatly among the study sites (e.g., 0.05–0.20), but values were on the low end of V^* values reported elsewhere (Lisle and Hilton 1999). V^* values in our Klamath Mountain sites were generally lower than values from comparable watersheds with fines-rich parent material in the Northern California Coast Ranges (Lisle and Hilton 1999). This difference in V^* might be a result of the higher transport capacity of steeper stream channels because streams in a given watershed area in the Klamath Mountains are generally much steeper than streams in watersheds of the same drainage area in the nearby Coast Ranges of California and Oregon (May 2007).

Lisle and Hilton (1999) found that V^* was strongly correlated with annual sediment yield in watersheds that have a bedrock lithology that produces abundant sand-sized sediment (e.g., extremely weathered granite, weak sandstones, and schist). Based on the logarithmic relationship between V^* and sediment yield developed by Lisle and Hilton (1999), the range of V^* values in our study implies approximately an order-of-magnitude difference in sediment yield between the sites with the highest (Grouse Creek) and lowest (Elk Creek) V^* values. However, the landslide and surface erosion models predicted only $\sim 3\times$ greater sediment supply in the watersheds with the highest sediment supply than in the watersheds with

the lowest sediment supply. Predicted sediment supply was $\sim 10\times$ greater in the watershed with the highest sediment supply than in the watershed with the lowest sediment supply after sediment supply estimates were adjusted by the SPI. This result suggests that the transport capacity of streams (i.e., stream power) should be considered when comparing relationships between fine sediment levels and sediment supply.

Biological effects of increased fine sediment

Salmonid habitat.—The results of our study provide important empirical evidence that increased sediment supply associated with forest management activities is biologically significant for salmonids. V^* has been widely used as a monitoring tool because it is linked to sediment yield (Lisle and Hilton 1999) and because pools are important rearing habitat for various life stages and species of salmonids (e.g., Lonzarich and Quinn 1995). However, very few studies have quantified the links between V^* and biological responses. Our study shows that V^* is positively related to riffle-surface fine sediment, which in turn is related to salmonid spawning-gravel quality and abundances of several taxa of benthic invertebrates.

Most experimental studies have assessed the effects of much higher concentrations of fine sediment (e.g., Crouse et al. 1981, Suttle et al. 2004) than were measured in our study (2–23%). Fine sediment levels measured in streams are often reported in units of volume instead of surface area (e.g., studies reviewed in Chapman 1988). Thus, biological consequences, in terms of effects on salmonid and invertebrate populations, of the range of riffle-surface fine sediment levels in our study are difficult to infer. In addition, particle-size distribution of fine sediment affects the type and magnitude of biological response. For example, fine sand reduces the emergence success of salmonid eggs more strongly than coarse sand (Peterson and Metcalfe 1981). Nevertheless, most past studies have documented dramatic reductions in salmonid egg and embryo survival when the percentage of fine sediment in spawning gravels exceeds 10 to 20% (Chapman 1988).

Predicted survival of salmonid eggs based on median subsurface gravel permeability measurements ranged from 15 to 39%, implying that egg survival might be an important limiting factor for salmonid populations, especially in watersheds with high sediment supply. Fairly low rates of subsurface gravel permeability were measured in the study streams, even when fine sediment levels were relatively low (<10%). Predicted egg survival rates were fairly low, but riffle-surface fine sediment levels and V^* were

relatively low compared to literature values, and few benthic macroinvertebrate taxa showed significant responses to fine sediment levels. This combination of results suggests that the relationship between surficial fine sediment and subsurface gravel permeability might be different in our study area than in other regions. The high transport capacity of streams in the Klamath Mountains prevents accumulation of fine sediment on the surface of riffles, but abundant sand and silt can accumulate in the subsurface and reduce gravel permeability.

Benthic macroinvertebrates.—The effects of increased sediment supply on benthic macroinvertebrate assemblages observed in our study were fairly subtle, perhaps because of the relatively low levels of fine sediment deposition. Streams in the Klamath Mountains are steep and coarse grained, with generally low levels of fine sediment stored on the streambed. The streams we sampled had the highest potential for fine sediment levels among the streams in our study area, based on sediment supply model predictions and the predominance of rock types that produce abundant sand (i.e., deeply weathered granitic plutons). However, the highest levels of fine sediment measured in our study were low relative to levels in most other studies. Other investigators also have noted relatively minor effects on benthic invertebrates of increased sediment delivery to mountain streams associated with forestry activities (e.g., Murphy et al. 1981). On the other hand, lowland streams with lower stream power might be more susceptible than mountain streams to extensive deposition of fine sediment with increased sediment supply.

Taxonomic richness, especially in the insect orders Ephemeroptera, Plecoptera, and Trichoptera, sometimes decreases in response to large increases in deposited sand (Angradi 1999, Kaller and Hartman 2004). However, many taxa that responded to manipulation of fine sediment levels in experimental studies showed no relationship to fine sediment levels in our study. This discrepancy might be because many experimental studies used a wider range of fine sediment levels (e.g., 0–100%) than occurs in our study sites (2–23%). Some macroinvertebrate taxa did respond as expected to levels of fine sediment, including several ephemeropteran mayflies, several tipulids, Chironominae, and Oligochaeta. These taxa offer potential for improved monitoring of fine sediment in steep, forested streams, but the mechanisms behind these relationships are unclear and should be tested in experimental studies.

Chironomid midges might be particularly useful indicators of fine sediment. Our results are in partial agreement with the findings of Angradi (1999), who

observed differential responses among the Chironomidae to fine sediment additions in a West Virginia stream. Chironominae, often common in organic-matter-rich silt (Pinder 1986), responded negatively to fine sediment in our study. In our study area, organic-matter-rich silt can be found in interstitial spaces beneath stones, but large deposits of sand can smother the organic-matter-rich silt, possibly reducing habitat availability for Chironominae.

Most oligochaetes are obligate burrowers in fine sediment and often are reported to increase in abundance with fine sediment additions (Waters 1995, Zweig and Rabeni 2001). However, one group of oligochaetes, the Lumbricina, is considered moderately intolerant of fine sediment (Relyea et al. 2000).

The ephemereid mayfly *A. delantala* was positively related to fine sediment levels in the Klamath Mountains. In a large-scale analysis of bioassessment data, Relyea et al. (2000) identified *Attenella* as moderately intolerant of fine sediment (occurring in streams with <50% fines), but this result might have been because *Attenella* generally is found only in steep headwater streams where transport capacity can be very high. In the McKenzie River, Oregon, *A. delantala* was confined to patches of sand and fine gravel (<20-mm diameter) in headwater streams (Hawkins 1984).

Overall, changes in the macroinvertebrate assemblage that could be attributed to fine sediment were fairly subtle. Assemblage-based diversity, abundance, feeding group, and tolerance metrics that are commonly used for detecting the effects of water pollution and habitat degradation were not useful for assessing the ecological impacts of increased sediment supply in our study region, despite the fact that sediment supply in several watersheds is estimated to have increased several times over background levels. However, several taxa showed strong responses to fine sediment levels. Further research on the ecology of these taxa will help elucidate the biological mechanisms behind the empirical responses observed in our study. We suggest that, for the purposes of biological monitoring of increased sediment supply in steep, forested streams, it might be necessary to focus on taxa that show direct responses to fine sediment levels to detect and quantify altered streambed conditions reliably.

Prey availability for salmonids.—Changes in the benthic macroinvertebrate assemblage caused by increased levels of fine sediment can affect food availability and survival of insectivorous fish, such as salmonids. A scarcity of invertebrate prey can result in increased competition for available food resources and can cause salmon to forage more often during the day, thereby increasing their risk of predation (Metcalfe et al. 1999). In one stream, the relative abundance of

burrowing taxa that are thought to be unavailable to salmonids increased and the relative abundance of taxa that are vulnerable to predation by salmonids decreased as levels of fine sediment increased. Suttle et al. (2004) observed similar changes in the availability of macroinvertebrates in relation to increasing embeddedness and linked these changes to reduced growth rates of juvenile steelhead trout in nearby northern California streams.

Our results suggest that increased fine sediment levels might reduce abundances of several macroinvertebrate taxa that are important and common food resources for salmonids (Table 4). Rader (1997) developed a trait-based approach for ranking the availability of benthic invertebrates to drift-feeding salmonids. Taxa that responded negatively to fine sediment in our study (e.g., the mayflies *D. doddsi*, *D. spinifera*, and *Epeorus*, and the tipulids *Antocha* and *Dicranota*) are large, soft-bodied organisms that commonly live on or beneath rocks in riffles and have availability scores >50 (more available prey items). Chironominae also were negatively related to fine sediment in our study and are among the taxa most commonly consumed by insectivorous fish (availability score = 70.5). In contrast, 2 taxa that responded positively to fine sediment in our study, *A. delantala* and Oligochaeta, have low availability scores (25.5 and 10, respectively). Thus, increased abundances of these taxa associated with fine sediment deposition will not increase food resources for salmonids (Rader 1997). A 3rd taxon that responded positively to fine sediment, *Z. columbiana*, might be relatively available to salmonids (availability score = 57.6). Overall, we conclude that higher levels of fine sediment in our study streams are likely to result in reduced quantity and quality of prey available to salmonids. However, the importance of this effect on salmonid growth is unknown.

Management applications

Results of small-scale empirical studies can be strongly dependent on the contextual setting of the research. Inferences drawn in our study about the relationships between sediment supply, channel conditions, and the biological responses are limited to moderate-gradient (1.5–4.5%), cobble-bed streams in watersheds that are underlain predominantly by highly weathered granite (>50% watershed area). Lisle and Hilton (1992) found that relevant comparisons of V^* values could be made only for midorder streams of moderate gradient in basins that produce abundant sand-sized particles (Lisle and Hilton 1992). An ongoing study of spawning-gravel quality in the Klamath Mountains indicates that the relationship

between sediment supply and substrate permeability observed in our study does not extend to smaller, steeper streams or to larger streams that drain more resistant rock types (CLM, unpublished data).

In summary, our study documented linkages among sediment supply, streambed fine sediment, and biological responses that affect invertebrate assemblages and salmonid fishes. These results suggest that V^* and riffle-surface fine sediment are potentially useful indicators for linking hillslope sediment supply and aquatic biota. V^* and riffle-surface fine sediment respond predictably to increased sediment supply and have direct biological consequences in watersheds that drain highly weathered granitic terrain. Managers can use this information in broad-scale topography-based analyses to explore the spatial distribution of stream reaches affected by elevated levels of fine sediment. Several benthic macroinvertebrate taxa are potentially useful indicators of fine sediment levels and could be the focus of future biological monitoring efforts. Our analysis demonstrates that sediment supply, estimated from calibrated erosion potential models, is correlated with fine sediment abundance in streams and with biotic responses. This model-based approach can be used quantitatively to predict the cumulative watershed effects of landuse changes on sediment supply, fine sediment levels, benthic macroinvertebrate assemblages, and habitat variables affecting salmonid populations.

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