Technical Report on Quantitative Linkages Between Sediment Supply, Streambed Fine Sediment, and Benthic Macroinvertebrates in Streams of the Klamath National Forest

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Abstract

A major gap that currently limits accurate prediction of cumulative watershed effects is the lack of quantifiable relationships between sediment supply, channel conditions, and the magnitude of a biological response. We addressed this uncertainty by testing in six streams of the Klamath National Forest whether increased sediment supply resulted in elevated levels of streambed fine sediment stored in pools and riffles, and whether fine bed material in turn was correlated with spawning gravel quality and altered benthic assemblages. Results of this study indicate that there are significant, measurable differences in streambed fine sediment levels between basins in the Klamath National Forest with high and low sediment supply as estimated by two models: (1) a fine sediment model based on a locally-calibrated version of the universal soil loss equation and (2) an empirical mass-wasting-based landslide model. Increased sediment supply was directly correlated with fine sediment stored in pools and riffles, and with an overall fining of the median grain size. Model estimates of sediment supply were inversely correlated with subsurface flow rates, which have been directly correlated with salmonid egg survival in laboratory studies. Increased fine sediment was also associated with minor changes in the benthic invertebrate assemblage. There was no correlation between fine sediment and common biological metrics used to describe the benthic invertebrate assemblage such as taxa richness, EPT richness, and total abundance. There were, however, detectable changes in the abundance of several taxa (e.g. Chironominae, Oligochaeta, *Attenella delantala)*, and an overall reduction in presumed prey availability for salmonid fishes. These empirical relationships advance our present-day abilities to monitor and predict cumulative effects by quantifying linkages between landuse effects on hillslope sediment supply, channel conditions, and biologically significant habitat characteristics.

1. Introduction

Cumulative watershed effects can be defined as significant influences on water quality and biological resources that arise from the way watersheds function, and particularly from the ways that disturbances within a watershed can be transmitted and magnified within channels and riparian habitats downstream of disturbed areas (Dunne et al. 2001). Effects related to accelerated rates of erosion and sediment delivery to streams are of particular importance in forested watersheds. Concomitantly, one of the major knowledge gaps that currently restrict our ability to predict cumulative watershed effects is the lack of quantifiable relationships among sediment supply, channel conditions, and the magnitude of a biological response.

This report describes the results of a small-scale study conducted in August-November 2003. The study plan was developed during the summer of 2003 in meetings between the Klamath National Forest (KNF; represented by Al Olson, Juan de la Fuente, and Don Elder), U.S. Forest Service Region 5 (Brian Staab and Joseph Furnish), U.C. Berkeley (Vincent Resh, William Dietrich, Christine May and Matthew Cover), the U.S. Forest Service Pacific Southwest Research Station (Tom Lisle and Sue Hilton), and Lassen National Forest (Ken Roby). Field work was conducted under contract by Resource Management. Their crew was led by Sue Maurer and included Jeremy Warner, John Bowman and Wind Beaver. Don Elder served as a liaison for the Klamath National Forest and conducted GIS analysis and modeling. KNF staff developed the two erosion models used in this work. Juan de al Fuente, Polly Haessig, Don Elder, and Bill Snavely developed the landslide model and Tom Laurent, Don Elder, and Mark Reichert calibrated the surface erosion model.

The objective of this study was to quantify empirical linkages between fine sediment supply, channel conditions, and the magnitude of biological response. Specifically, we tested whether estimated increases in sediment supply resulted in elevated levels of streambed fine sediment stored in pools and riffles, and whether streambed fine sediment in turn was correlated with spawning gravel quality and altered benthic macroinvertebrate assemblages (**Figure 1**). Benthic macroinvertebrates are an important component of aquatic food webs. As such, they reflect one of the primary beneficial uses to be protected and restored in forested mountain streams.

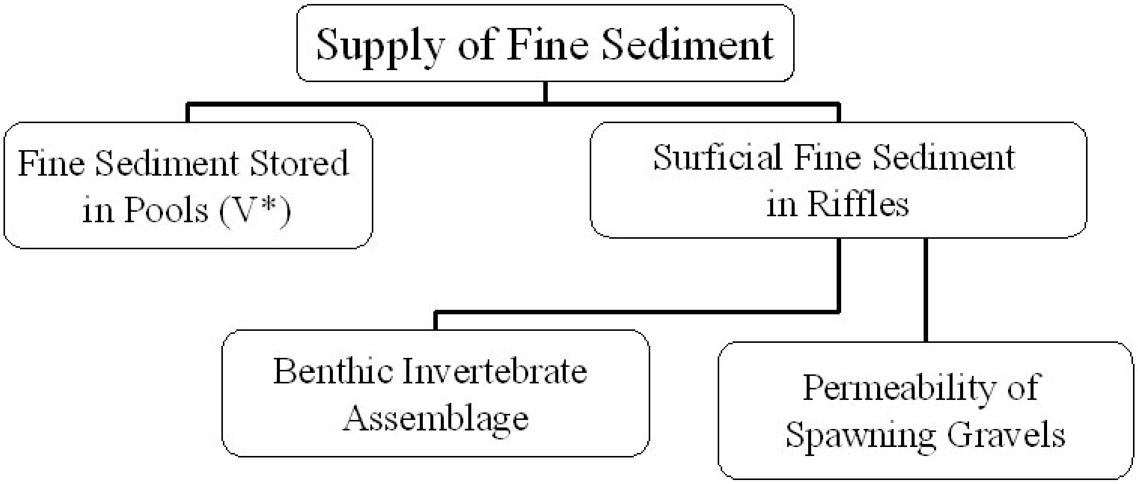

Figure 1. Conceptual diagram of linkages between fine sediment supply, channel conditions, and biological responses investigated in the Klamath National Forest.

2. Methods

Study Area

Sampling of channel conditions and benthic macroinvertebrates was performed in six streams in the Klamath National Forest (KNF) during the fall of 2003 (**Table 1**; **Figure 2**). Streams were selected based on the following criteria: (1) moderate gradient (1.5-4%); (2) gravel and cobble substrate; (3) bedrock lithology that produced 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 sites were selected to represent endpoints of sediment supply, based on qualitative assessments of fine sediment production by KNF personnel (Al Olson, Don Elder, and Juan de la Fuente) and sediment supply models developed by KNF staff (see below, **Table 2**). Four of the six study reaches were selected because previous monitoring studies of fine bed material had been conducted at the sites by the KNF. Specific reach locations for the remaining two basins (Beaver and Grouse) were located between major tributary junctions in order to avoid large changes in drainage area and sediment supply within the reach. Study reaches ranged in length from 0.5 – 2.0 km, and contained a minimum of 15 pools.

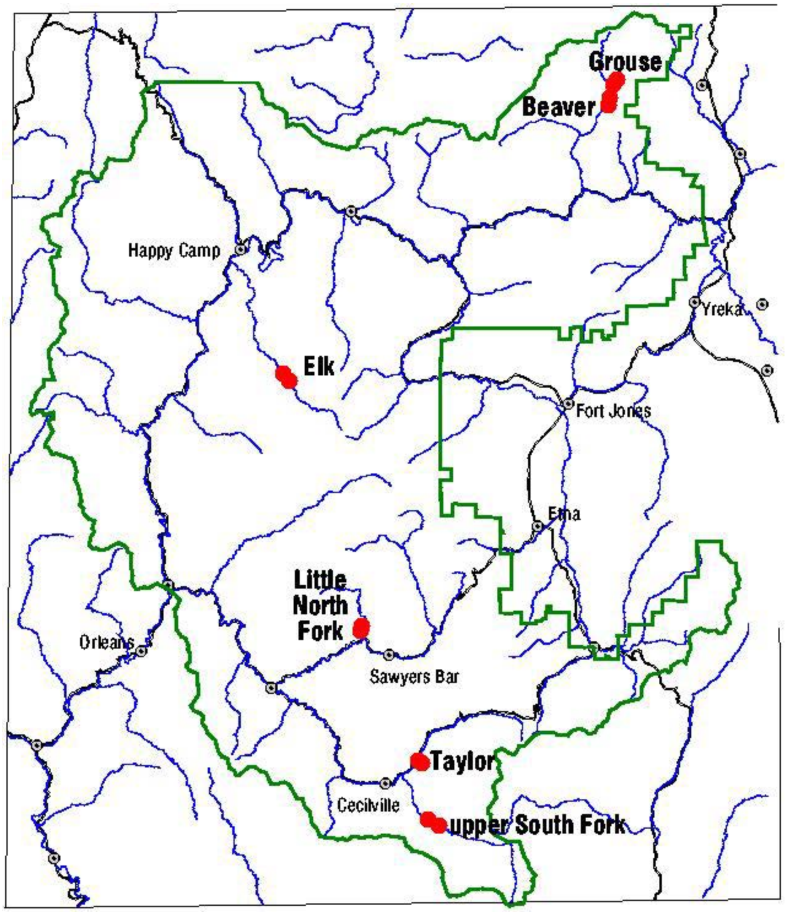

Figure 2. Map of study reaches (full/red circles) in the Klamath National Forest (outlined in solid/green line).

Table 1. Basin size and channel dimensions of study streams.

Stream	Drainage Area (km^2)	Channel Slope (%)	Stream Power Index	Bankfull Channel Width (m)	Bankfull Channel Depth (m)	Median Grain Size (mm)
Elk Creek	83	4.3	3.57	18.6	0.67	288
Little NF Salmon River	80	2.5	2.03	14.5	0.81	284
Upper SF Salmon River	157	1.6	2.45	19.0	0.60	169
Beaver Creek	93	2.3	2.14	10.4	0.47	121
Grouse Creek	26	2.8	0.74	5.5	0.44	54
Taylor Creek	47	3.4	1.63	7.5	0.65	135

Sediment Supply

KNF staff have developed two models for estimating sediment supply to stream channels in their forest-wide assessment of cumulative watershed effects. One model was developed to assess chronic inputs of fine sediment (USLE), and the other was based on episodic inputs from landslides (GEO). Both models are sensitive to past, present, and future management activities.

USLE Model

The fine sediment model uses estimates of surface erosion based on a locally-calibrated version of the Universal Soil Loss Equation (USLE). Results of this prediction are based on the spatial distribution of roads, timber harvest areas, wildfires, landforms, soil types, and rainfall patterns. Sediment delivery to stream channels is based on sediment production values and a delivery factor. The delivery factor is a spatially-uniform value of 30% for roads and 5% for hillslopes. Recent updates to the model consider traffic effects through a “use” factor and vary road sediment delivery from 15-40% based on aspects of the road template such as slope. These model updates incorporate recent insights into road erosion (e.g. Reid and Dunne 1984; Luce and Black 1999), but were implemented after this study was initiated and were therefore not included in the analysis.

In unmanaged basins, fine sediment supply is dependent on the proportion of the basin composed of highly weathered granitic plutons that produce an abundance of sand sized particles (**Table 2, Table 3**). In managed basins, the dominant source of fine sediment is road erosion (**Table 3**). Fine sediment supply estimates generated by the USLE model are reported in volumetric units per basin area per time interval ($m^3 \cdot km^{-2} \cdot yr^{-1}$); however, these predictions should only be considered as an index of potential supply and not as an absolute volume of sediment delivered to the channel.

GEO Model

The landslide sediment supply model (GEO) is based on empirical relationships derived from air photo assessments and limited field investigations of landslide occurrence in the Salmon River sub-basin from 1965 to 1975, a moderately wet period following a period of intensive timber harvest across the forest (de la Fuente and Haessig 1993). Based on landslide rates during these years, future sediment delivery was predicted for each of 11 geomorphic terrain types. Landslide rates in each terrain type were estimated for ‘undisturbed’ (areas that have not been logged or burned in the last 50 years) and ‘disturbed’ (affected by timber harvest or wildfire) conditions. After this study was initiated, the model was refined based on air-photo analysis of a large storm event (15-20 year recurrence interval) that occurred in 1997. Data from this event indicated that forest removal by timber harvest and wildfire was associated with an observed increase in landslide density of six times over undisturbed areas (KNF, unpublished data). Road-related landslides were associated with an increase in landslide density of 187 times over undisturbed conditions.

To predict sediment delivery over a broader spatial area, data from the Salmon River drainage were extrapolated using GIS to predict sediment delivery rates throughout the west side of the KNF. This approach assumes that (1) future storms will produce landslides at rates similar to past events, (2) empirical relationships developed in one basin can be extrapolated to other basins, (3) recovery of intensively logged or severely burned land occurs in 50 years, (4) the shape of the recovery curve has been correctly identified, and (5) roads increase landslide rates in ways that do not recover through time. Predictions from this model are reported in terms of volumetric units per basin area per time interval ($m^3 \cdot km^{-2} \cdot yr^{-1}$). Model-based estimates were made for both undisturbed conditions and present-day conditions (accounting for the effects of forest management activity and natural disturbances such as fire) (**Table 2**). Model-based estimates for areas outside the Salmon River drainage and time periods other than 1965-1975 should only be considered as an index of potential sediment supply because estimates are not based on the actual occurrence of landslides and debris flows.

Estimates of sediment supply from both models were scaled by the stream power index (SPI), which represents the product of reach-scale slope and drainage area.

Table 2. Measures of sediment supply for the six study streams.

Stream	**GEO Sediment Supply ($m^3\ km^{-2}\ yr^{-1}$)**	**USLE Sediment Supply ($m^3\ km^{-2}\ yr^{-1}$)**	**GEO Increase Over Undisturbed (%)**	**USLE Increase Over Undisturbed (%)**	**Qualitative Fine Sediment Supply[1]**	**Qualitative Sediment Supply[1]**
Elk Creek	69	4.98	44	0	Low	Low
Little NF Salmon River	98	9.06	109	148	Low	Low
Upper SF Salmon River	61	5.04	14	24	Low-Medium	Low
Beaver Creek	151	13.95	248	811	Medium-High	High
Grouse Creek	156	13.48	397	800	Medium-High	High
Taylor Creek	72	11.27	79	310	High	High

[1] *A priori* categorization based on field observations and professional judgment of KNF staff

Table 3. USLE model predictions of sediment sources.

Stream	Plutons[1] (% of watershed area)	Undisturbed (% of total sediment supply)	Fire (% of total sediment supply)	Timber Harvest (% of total sediment supply)	Roads (% of total sediment supply)
Elk Creek	65	100	0	0	0
Little NF Salmon River	57	40	28	2	30
Upper SF Salmon River	49	81	0	0	19
Beaver Creek	52	11	0	1	88
Grouse Creek	99	11	0	1	88
Taylor Creek	50	24	0	3	73

[1] Plutons are granitic terrain with the potential for high sand production if deeply weathered.

Bed Surface Fine Sediment

The volumetric proportion of each pool filled with fine sediment (V*; Hilton and Lisle 1993; Lisle and Hilton 1992, 1999*)* was measured in every pool in the study reach that met a minimum size criteria of being at least twice as deep as the average riffle crest depth and containing the majority of flow (following the methods described by Hilton and Lisle (1993), and detailed in the protocol document prepared by Northern California Resource Center (2003)). Briefly, V* is a measure of the volume of a residual pool filled with fine sediment, and is determined by measuring the water depth and the depth of fine sediment deposited at multiple locations on the bottom of a pool (Lisle and Hilton 1999). V* values from all of the pools in a reach were averaged to obtain one reach-wide V* value.

Within each reach, four riffles were selected for intensive sampling of surficial fine sediment, grain size, and benthic invertebrates. The steepest and shallowest gradient riffles in each reach were selected for sampling, as well as two moderate gradient riffles that were randomly chosen. The proportion of fine sediment on the surface of the bed was measured in each of the four riffles by placing a large sampling grid on the streambed (2.8 m x 1.25 m with 13 cm grid spacing, containing 220 intersections). At each grid intersection, a point count was taken by placing the point of a steel pin on the bed and noting the presence or absence of fine sediment (<4 mm) at the tip of the pin. Point counts ranged from 5,330 to 16,850 per reach, depending on channel width. The distribution of fine sediment on the streambed was partitioned into five categories: (1) interstitial spaces, (2) boulder wake zones, (3) free-formed surficial patches, (4) bank drapes, and (5) wood-forced patches. Although we differentiated among these depositional micro-sites of fine sediment, we consider only the total amount of fines in our statistical analyses. Fine sediment measurements were made along three equally-spaced transects that spanned the full width of the channel in each riffle. Bankfull width and depth measurements were also made at one cross-section per riffle.

Grain Size

Grain size distribution was measured in each riffle via transect-based pebble counts (Wolman 1954). Particles were measured every 0.3 m along transects using a gravel template (Bunte and Abt 2001). The number and spacing of transects was determined at each riffle to obtain a minimum of 200 equally spaced grain measurements. Cumulative frequency distributions were developed to calculate the D_{16} (grain size for which 16% of the sampled particles were finer), D_{50} (median grain size), and D_{84} (the grain size for which 84% of the sampled particles were finer).

The embeddedness of each grain was characterized using a three category qualitative scale of the effort required to remove the grain: (1) loose, unembedded particles on the surface that could be easily 'picked' off the bed; (2) particles that were moderately embedded and needed to be 'plucked' from the streambed; and (3) tightly embedded particles that needed to be 'pried' from the bed. It should be noted that this qualitative measure of embeddedness reflects both the interlocking of coarse grains and partial burial in fine sediment. Because we are primarily concerned with the embeddedness of gravel and cobble particles, we calculated the percentage of 16-256 mm grains that were sitting freely on the bed, moderately embedded, and highly embedded.

Theoretical predictions of the reach-averaged median grain size were calculated from a depth-slope product derived by inverting the Shields equation (Dietrich et al. 1996). The predicted grain size can be calculated from the simplified equation:

$$D_{50} = \rho g h \mathrm{S} / \tau^{*}_{c50} (\rho_s - \rho) g$$

Where ρ and ρ_s are the fluid and sediment densities (1000 and 2650 km/m^3, respectively), g is gravitational acceleration, h and S are the reach-averaged bankfull depth and channel slope, respectively, and τ^{*}_{c50} is the bankfull bed stress, which is approximately equal to the boundary shear stress for low-roughness channels and was set to a value of 0.047 (for further discussion see Buffington and Montgomery 1999a and 1999b). Field measured values of bankfull depth and channel slope were used in this calculation.

Spawning Gravel Permeability

Spawning gravel quality was assessed by direct measurements of gravel permeability during the summer of 2004 using a modified version of methods described by Barnard and McBain (1994). Reach-average permeability was calculated from measurements made in each of the four 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 80mm in median particle size. At each site a perforated stand pipe was driven into the streambed to a depth of 36 cm, representing a sampling depth from 14 to 22 cm below the bed elevation. This depth and grain size was chosen because it represents average egg pocket depth and substrate size utilized by several species of anadromous salmonids for spawning (Kondolf and Woman 1993). Water was pumped out of the standpipe with a battery powered vacuum pump and into a measurement chamber. The rate at which interstitial water refilled the void was measured, with five replicate samples drawn for each standpipe location. Survival to emergence for salmonid eggs was calculated from the observed permeability rates and a regression analysis performed on three datasets reviewed by Chapman (1988), which accounted for 85% of the observed variation in survival-to-emergence in previous studies.

Benthic Macroinvertebrates

Benthic macroinvertebrates were sampled along the same transects where riffle fine sediment was measured on the sampling grid. A timed four-minute sample was made at each of three transects per riffle by disturbing the substrate upstream of a 500 micron mesh D-frame kick net. The three transect samples were composited into one sample container. Samples were elutriated in the field to separate the organic and inorganic portions of the sample, and large leaves and woody debris were removed from the organic portion of the sample. The inorganic portion of the sample was carefully examined for benthic organisms such as cased caddisflies, which were added to the organic portion of the sample. The organic portion of the sample was preserved in 95% ethyl alcohol.

In the laboratory, benthic invertebrates were removed from the sample under a dissecting microscope at 10x magnification. The subsampled fraction ranged from 7-100%, and the number of identified organisms ranged from 541 to 1443. Organisms were identified to the lowest practical taxonomic level, usually genus or species, except for Chironomidae (subfamily), Collembola (order), Trombidiformes (order), Oligochaetes (class), Ostracoda (class), Turbellaria (class), and Nemata (phylum). Laboratory sorting and identifications were performed by the National Aquatic Monitoring Center (Utah State University, Logan, Utah).

Fifty-eight common biological metrics were calculated from the raw taxonomic abundance data, including measures of richness, abundance, diversity, functional feeding groups, and pollution tolerance. To understand how altered benthic assemblages could affect prey availability for salmonids, we classified taxa by their availability to benthic-feeding fish. Following Suttle et al. (2004), each invertebrate taxa was classified as burrowing, armored, or vulnerable, based on life history information (Merritt and Cummins 1996).

Other Reach-Scale Measurements

A continuous longitudinal profile, based on the water surface slope, was measured along the full length of each study reach. Slope for 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.

Canopy cover was calculated from digital photography using methods described by Engelbricht and Herz (2001). A digital camera was held on an extension rod that was level with the water surface. The top of the camera was oriented north so that the long axis of the camera followed the east to west solar pathway. A remotely triggered photograph was taken in the middle of the stream in each riffle transect where fine sediment and benthic invertebrates were sampled. Each photograph was converted into a black-and-white image in Adobe Photoshop by adjusting the contrast and brightness. The resulting image consisted only of black and white pixels, representing foliage and canopy gaps respectively. The percentage of each image composed of black pixels was used to calculate canopy cover.

Water chemistry parameters, including specific conductivity and alkalinity were measured at the mid-point of each sample riffle. Conductivity was measured with a YSI model 30 instrument and calibrated for water temperature. Alkalinity was measured via titration with a La Motte field test kit.

Statistical Analyses

We tested the hypothesis that high sediment supply is related to increased levels of streambed fine sediment using three approaches. First, we examined whether measures of streambed fine sediment (V*, surficial fine sediment in riffles, and embeddedness) were higher at the sites that were considered (based on field observations and professional judgment) to have "high" sediment supply than at the "low" sediment supply sites (**Table 2**). Because the low sample size ($n = 3$ for each category) underestimates variability in the data, we used the nonparametric Mann-Whitney test ($\alpha = 0.10$ to increase power). Second, we examined whether quantitative predictions of sediment supply (from the USLE and landslide models) were correlated with reach-averaged measures of streambed fine sediment (V*, riffle surface fine sediment, and embeddedness). Here we used linear regression to test whether the slope of the line was statistically different than zero (two-tailed, $\alpha = 0.05$). Finally, because V* has been shown to be a useful predictor of sediment yield (Lisle and Hilton 1999), we examined whether V* was positively related to riffle surface fine sediment and embeddedness, also using linear regression.

To examine the relationships between benthic macroinvertebrates and fine sediment, we began by reviewing the available literature on the topic, with a focus on studies from the Pacific Northwest, USA (e.g. Angradi 1999, Hawkins 1984, Relyea et al. 2000, Suttle et al. 2004, Waters 1995). We selected 25 taxa and 8 metrics that were identified in the literature as being especially responsive to fine sediment additions as hypotheses to be tested (**Table 4**). Because individual hypotheses were made for each *a priori* identified metric and taxon, the statistical tests are considered independent of one another and the experiment-wise false positive rate (α_e) was not adjusted using the Bonferroni Criterion.

We first used partial correlation to examine the relationships between each of the biological response variables and fine sediment, while accounting for the effects of other environmental variables. Both the variables of bed surface fine sediment and D_{16} grain size were separately considered as response variables because they both reflect levels of fine sediment. Environmental variables that were held constant in the partial correlation include five riffle-scale variables (riffle slope, canopy cover, D_{84} grain size, specific conductivity, and sampling date) and one reach-scale variable (drainage area). Several other potential variables, including bankfull width, elevation, and alkalinity, were excluded from the analysis because of multicolinearity. We compared the results of the sixth-order partial correlation to those from a zero-order linear regression of biological response variables and measures of fine sediment, in order to examine whether the two approaches had similar results. We also performed partial correlation analyses on 52 metrics for which no *a priori* hypotheses were made using the Bonferroni-corrected false-positive error rate of $\alpha_e = 0.001$

We used multiple regression to model the metrics and taxa identified in the literature using the same explanatory variables as above. Although there are no firm rules for the number of variables to use in multiple regression, one conservative approach is to use no more than one explanatory variable for every 6 to 10 observations (Neter et al. 1996.). Because of the relatively small number of data points (16), using 7 potential explanatory variables increases the probability of overfitting the model. To reduce this possibility, we examined all 128 possible models for each modeled metric and taxon and used Mallow's C_p criterion to select the model that most reduces squared-error while minimizing p, the number of explanatory variables in the model (Mallows 1973). This method produces models that are often similar to those produced using stepwise forward selection of variables, except that Mallow's C_p criterion is often more conservative in adding additional variables.

For all linear regression analyses we assessed whether data transformations were necessary to approximate linear relationships between the variables and satisfy criteria for normality and homoscedasticity of residuals. For example, sediment supply estimates did not meet assumptions of normality because stream power-adjusted sediment supply estimates for both the GEO and USLE models were two to three times higher at Grouse Creek than the other five sites. Reach- and riffle-scale sediment supply estimates, riffle-scale percent fines, gravel permeability, and predicted over observed grain size data were log-transformed (ln) for the statistical analyses. When two variables were both log-transformed we present power-law relationships on log-scaled axes. Raw taxon abundance data was transformed using the ln(x+1) transformation to prevent negative values.

Table 4. Predicted responses of biological metrics and benthic macroinvertebrate taxa to increased levels of fine sediment as reported in other studies.

Metrics and Taxa	**Predicted Response**	**Source of Prediction**	**Study Locations**
Taxa Richness	-	Waters 1995	widespread
Total Abundance	-	Angradi 1999	West Virgina
EPT Richness	-	Angradi 1999	West Virgina
EPT Abundance	-	Waters 1995	widespread
% Burrowing	+	Suttle et al. 2004	Eel River, CA
% Vulnerable	-	Suttle et al. 2004	Eel River, CA
Chironominae/Chironomidae	-	Angradi 1999	West Virgina
Orthocladiinae/Chironomidae	-	Angradi 1999	West Virgina
Antocha spp.	-	Relyea et al. 2000	Pacific Northwest
Arctopsyche spp.	-	Relyea et al. 2000	Pacific Northwest
Attenella delantala	+	Hawkins 1984	Oregon
Caudatella spp.	-	Relyea et al. 2000, Hawkins 1984	Pacific Northwest
Chironomidae	+	Waters 1995	widespread
Chironominae	-	Angradi 1999	West Virgina
Cinygmula spp.	-	Relyea et al. 2000	Pacific Northwest
Dicranota spp.	+	Relyea et al. 2000	Pacific Northwest
Drunella doddsi	-	Relyea et al. 2000, Hawkins 1984	Pacific Northwest
Epeorus spp.	-	Relyea et al. 2000	Pacific Northwest
Glossosoma spp.	-	Relyea et al. 2000	Pacific Northwest
Hesperoperla pacifica	-	Relyea et al. 2000	Pacific Northwest
Hexatoma spp.	+	Relyea et al. 2000	Pacific Northwest
Isoperla spp.	+	Relyea et al. 2000	Pacific Northwest
Lepidostoma spp.	+	Relyea et al. 2000	Pacific Northwest
Malenka spp.	+	Relyea et al. 2000	Pacific Northwest
Neophylax spp.	-	Relyea et al. 2000	Pacific Northwest
Oligochaeta	+	Waters 1995	widespread
Optioservus spp.	+	Relyea et al. 2000	Pacific Northwest
Rhithrogena spp.	-	Relyea et al. 2000	Pacific Northwest
Rhyacophila Betteni grp.	-	Relyea et al. 2000	Pacific Northwest
Rhyacophila Hyalinata grp.	-	Relyea et al. 2000	Pacific Northwest
Simulium spp.	+	Relyea et al. 2000	Pacific Northwest
Zapada cinctipes	+	Relyea et al. 2000	Pacific Northwest
Zapada columbiana	+	Relyea et al. 2000	Pacific Northwest

3. Results

Sediment Supply Model Estimates

Log-transformed estimates of basin area-adjusted sediment supply from the GEO and USLE models were well correlated ($p = 0.044$, $r^2 = 0.68$). When sediment supply estimates are scaled by stream power, estimates from the two models exhibited a much stronger linear relationship ($p = 0.003$, $r^2 = 0.93$). Because estimates from the two models are so well correlated, we describe the relationships between both models and other variables but only display charts featuring sediment supply estimates from the USLE surface erosion model. *A priori* categorization of streams with 'low' and 'high' sediment supply, based on field observations and professional judgment by KNF staff, corresponded reasonably well with model predictions (**Table 2**).

Linkages Between Sediment Supply and Streambed Fine Sediment

Reach-averaged residual pool volume (V*) ranged from 0.05 to 0.17. Reach-averaged V* exhibited a strong positive correlation with fine sediment supply estimates from the USLE model scaled by the reach-averaged stream power index ($p = 0.011$, $r^2 = 0.92$) (**Figure 3**). Likewise, V* was strongly correlated with sediment supply predicted from the GEO model ($p = 0.015$, $r^2 = 0.81$). V* was significantly higher in streams judged by KNF staff to have 'high' sediment supply category (0.141 ± 0.029 (Mean ± SE)) than in streams with 'low' sediment supply (0.064 ± 0.008) (Mann-Whitney, $\alpha = 0.10$).

The quantity of fine sediment on the bed surface of individual riffles ranged from a low of 2% to a high of 23% of the riffle surface area, while reach-averaged values ranged from 4% to 16%. Fine sediment in riffles exhibited a highly significant positive power-law relationship with fine sediment supply predicted from the USLE model scaled by the stream power index calculated for each riffle ($p < 0.0001$, $r^2 = 0.60$) (**Figure 4**). Similarly, there was a highly significant relationship between riffle-scale fine sediment and GEO model estimates of sediment supply, but the correlation was not as strong ($p = 0.0004$, $r^2 = 0.45$). The proportion of the riffle surface that was covered in fine sediment was significantly higher in streams categorized as having 'high' sediment supply (14.0% ± 2.1% vs. 7.5% ± 1.9%).

Channel width was strongly correlated with streambed fine sediment, with the smallest streams having the highest levels of fine sediment ($p = 0.0009$, $r^2 = 0.40$). Small streams also tended to be higher elevation. These trends are likely an artifact of site selection and the small number of sites, because sites judged to have the highest sediment supply were also the smallest streams included in the study.

The majority of fine bed material was stored in interstitial spaces among prominent particles (**Figure 5**). A smaller fraction of fine sediment was stored in boulder wake zones, free-formed surficial patches, and along the channel banks. No fine sediment patches forced by wood were observed.

Reach-averaged V* values exhibited a strong, statistically-significant linear relationship with bed surface fine sediment ($p = 0.032$, $r^2 = 0.72$) (**Figure 6**). The linear regression model predicts approximately a 1:1 positive relationship (slope = 76.5 ± 23.8) between percent volume of pools filled with fine sediment and percent surface area of riffles covered by fine sediment.

Comparisons of reach-averaged predictions of the median grain size (D_{50}) to the observed value were inversely correlated with sediment supply estimates from USLE modeling (**Figure 7**). Values < 1.0 for observed versus predicted grain size (y-axis) represent reaches that were coarser than predicted, whereas values > 1.0 represent reaches that were finer grained or under-predicted. The inverse power-law relationship is weakly correlated (r^2=0.37) but suggests that reaches become finer than predicted as sediment supply increases.

All three embeddedness categories were uncorrelated with categorical and model-based sediment supply estimates, as well as bed surface fine sediment ($r^2 < 0.1$, $p > 0.1$ for all tests). However, it should be noted that gravel and cobble embeddedness, as measured in this study, reflects both embeddedness from fine sediment as well as the interlocking of grains with other large particles.

Subsurface flow rates (i.e., gravel permeability) measured in potential salmonid spawning gravels decreased with increases in predicted volumes of fine sediment supply (**Figure 8.A**). Inferences from laboratory studies suggest this may result in a corresponding decrease in salmonid egg survival (Chapman 1988). Inferred egg survival ranged from a high of 39% to a low of 15% (**Figure 8.B**).

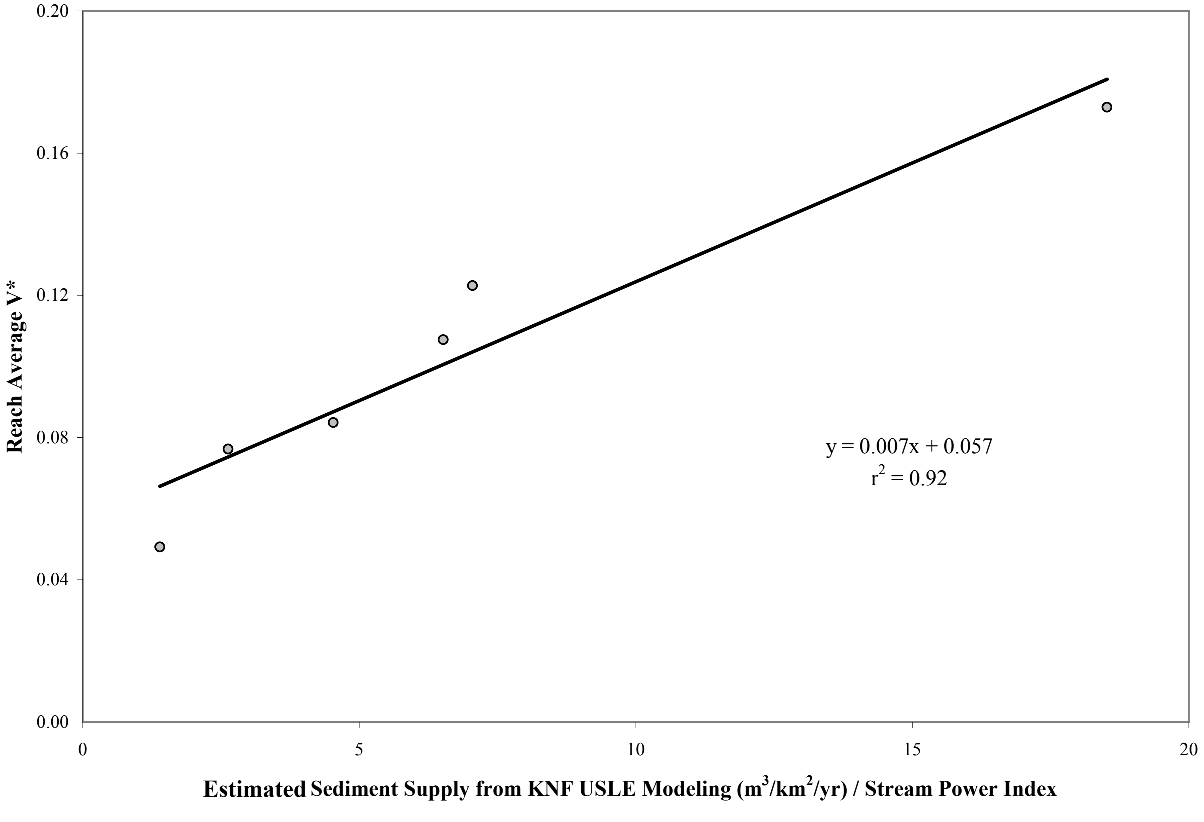

Figure 3. Linear relationship between estimated sediment supply from the KNF USLE model (scaled by reach-scale stream power index) and reach average fine sediment stored in pools (V*).

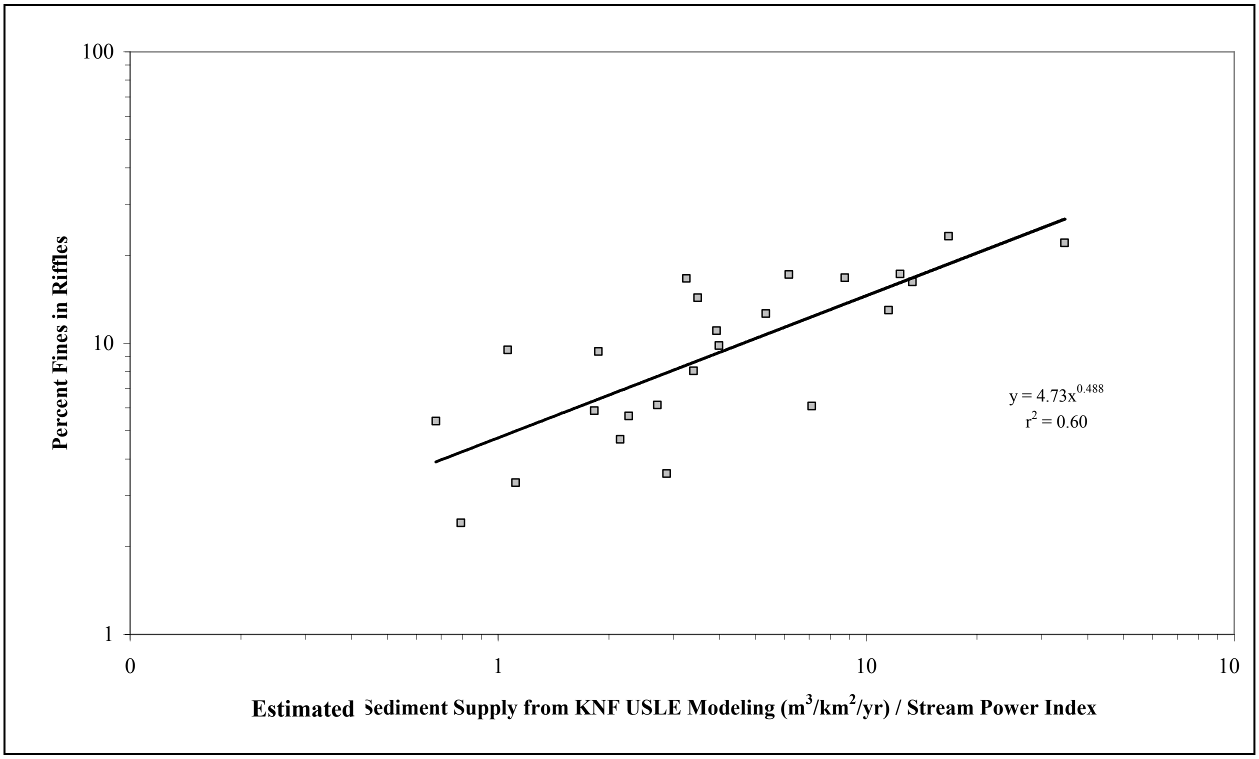

Figure 4. Power-law relationship between estimated sediment supply from the KNF USLE model (scaled by riffle-scale stream power index) and the percent of riffle surface area covered by fine sediment.

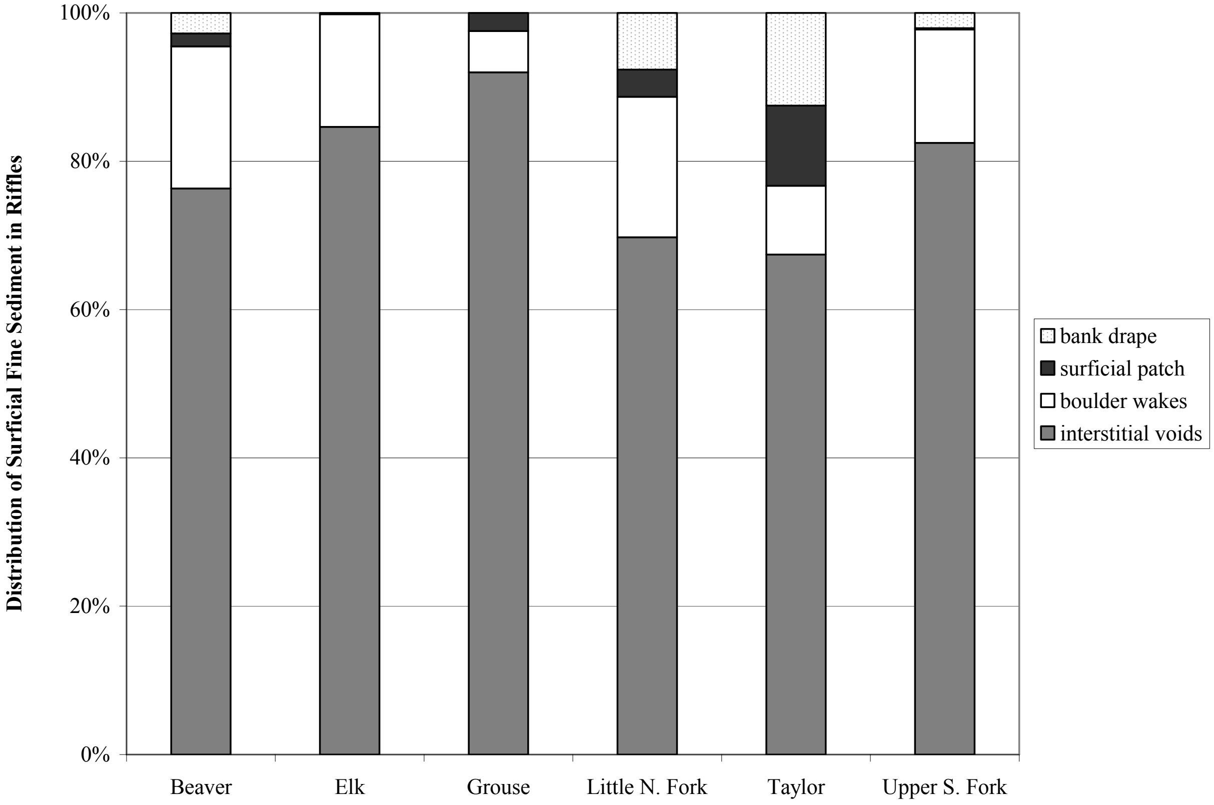

Figure 5. The distribution of micro-sites where fine sediment was stored in riffles.

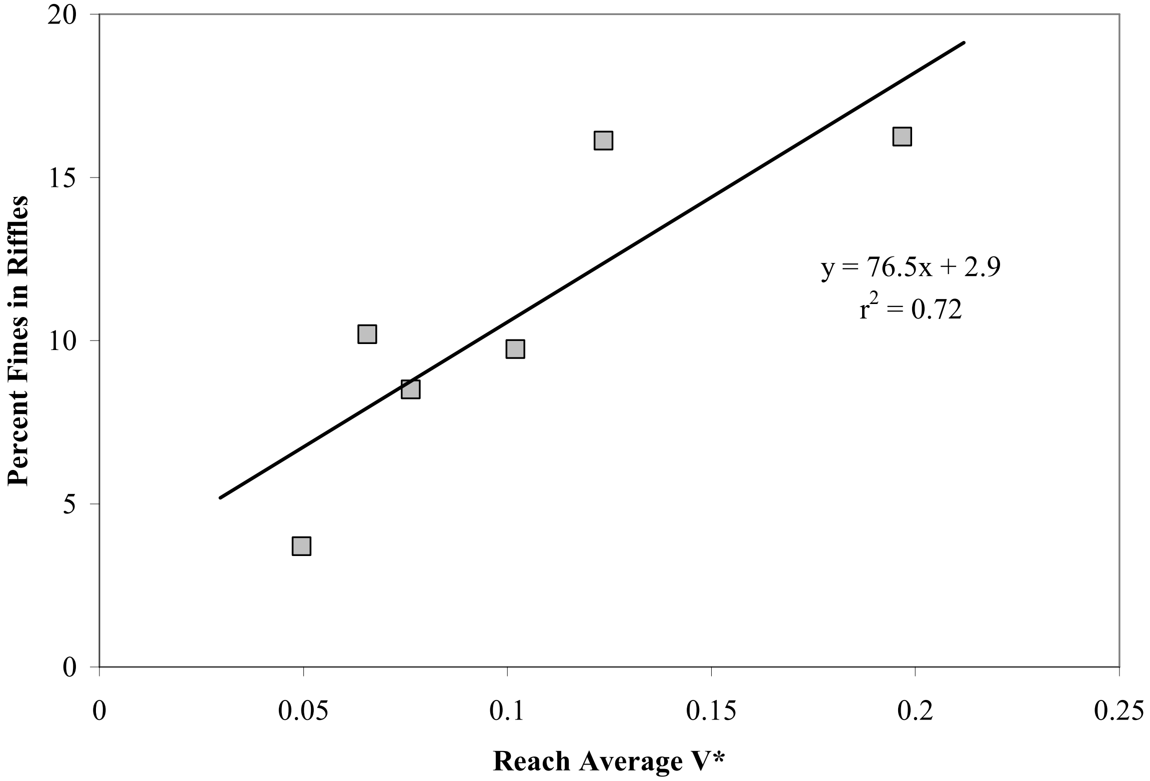

Figure 6. Linear relationship between reach average fine sediment in pools (V*) and the percent of riffle surface area covered by fine sediment.

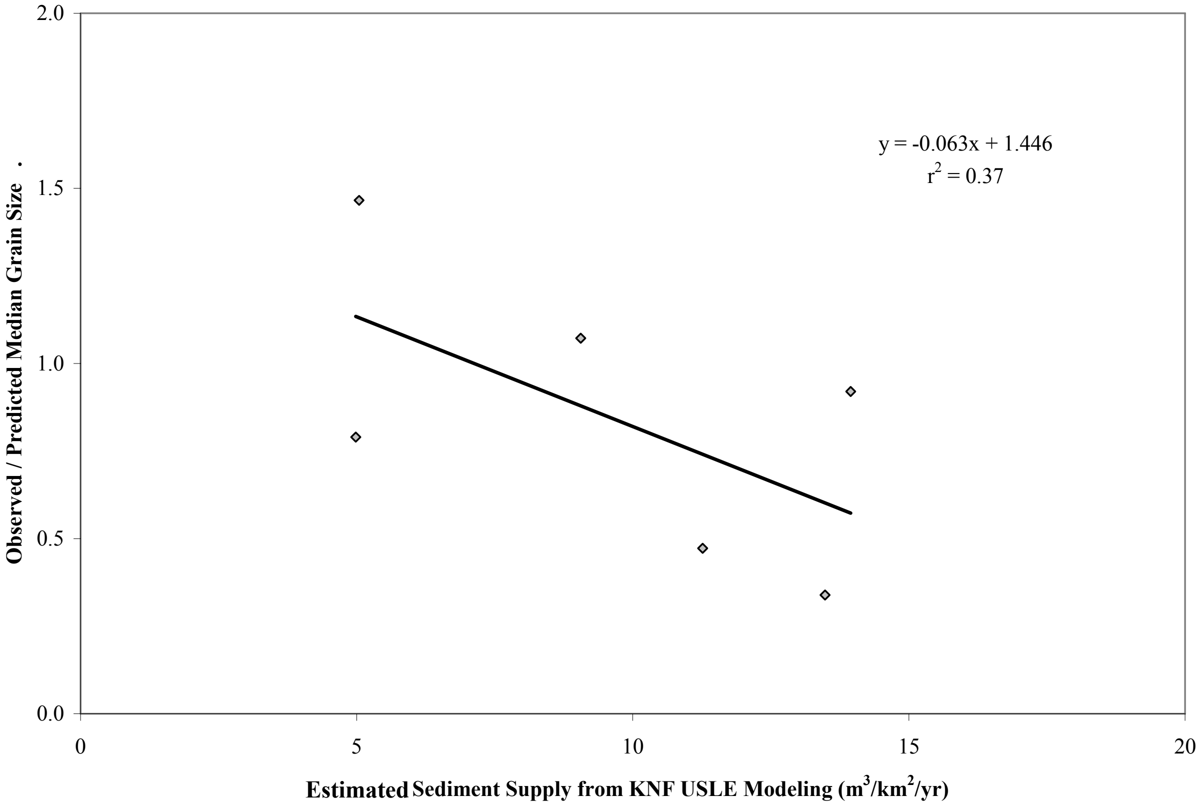

Figure 7. Inverse power-law relationship exhibited for the ratio of observed to predicted median grain size (D_{50}) relative to estimated fine sediment supply.

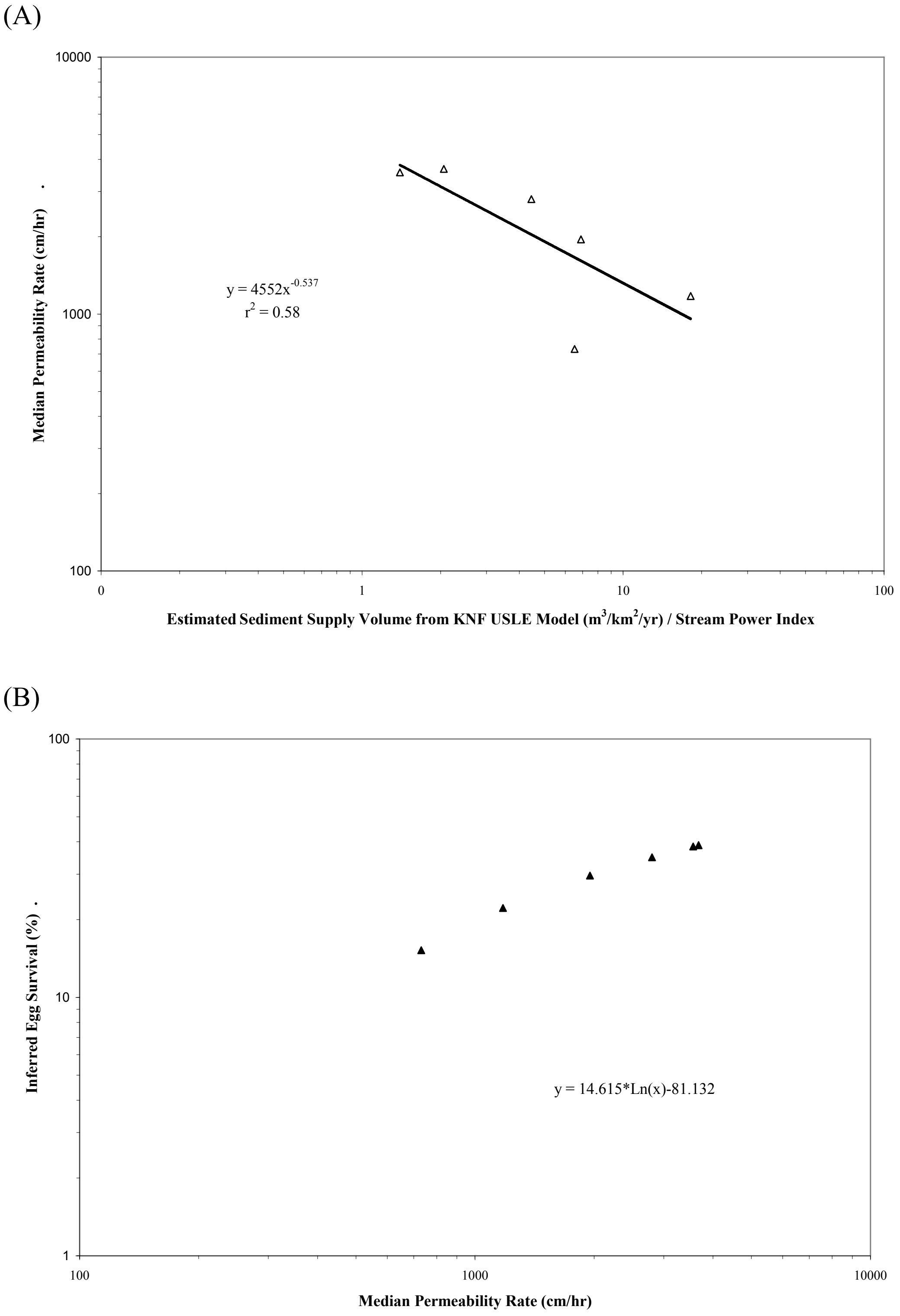

Figure 8. (A) Inverse relationship between subsurface flow rates and estimated sediment supply in the six study reaches. (B) Percent egg survival inferred from regression analysis developed by Chapman (1988).

Linkages Between Streambed Fine sediment and Benthic Macroinvertebrates

Benthic Macroinvertebrate Metrics

Of the eight biological metrics we identified based on a literature survey of invertebrate assemblage responses to fine sediment, only two exhibited strong, statistically significant responses that agreed with predictions: the fraction of Chironomidae as Chironominae was negatively related to increasing fines and the fraction of Chironomidae as Orthocladiinae increased with fine sediment. Both metrics exhibited highly significant strong correlations with fine sediment in both the partial correlation (**Table 5**) and the multiple regression models (**Table 6**), and were also significantly correlated with the D_{16} grain size. Because other groups of chironomids are present at very low abundances, the fraction of Chironominae and Othocladiinae are strongly inversely related.

Of the six other metrics with *a priori* hypotheses, only half responded as predicted in the partial correlations with fine sediment, although none of these relationships were statistically significant at $\alpha = 0.05$ (**Table 5**). Likewise, fine sediment was not an important predictor variable for any of the other six metrics in the multiple regression models (**Table 6**). Instead, variables such as drainage area, conductivity, and slope were significant predictors for many of the metrics.

Other than the chironomid-based metrics, percent burrowers exhibited the strongest relationship in the partial correlation with fine sediment ($r = 0.40$, $p < 0.1$). While percent burrowers is negatively related to fine sediment in the simple linear regression model, when other environmental variables are accounted for in the partial correlation model it is positively related with fine sediment, as was predicted (Suttle 2004) (**Table 5**).

None of the metrics for which *a priori* predictions were not made were significant at the Bonferroni-corrected false-positive error rate of $\alpha_e = 0.001$. The strongest partial correlation relationship among these other metrics was shredder abundance, which was negatively correlated with fine sediment ($r = -0.67$, $p = 0.002$). Pollution tolerance metrics and other measures of community composition were weakly related to levels of fine sediment.

Benthic Macroinvertebrate Taxa

Of the 25 taxa with *a priori* predictions, only three exhibited statistically significant partial correlation coefficients with fine sediment in the direction predicted (**Table 5**): the midge subfamily Chironominae ($r = -0.70$, $p = 0.001$), the heptageniid mayfly *Epeorus* spp. ($r = -0.66$, $p = 0.003$), and Oligochaetea, aquatic worms ($r = 0.55$, $p = 0.018$) (**Table 5**). Fine sediment was included in the multiple regression models for each of these three taxa (**Table 6**).

D_{16} grain size had a statistically significant partial correlation with the heptageniid mayfly *Cinygmula* spp. ($r = 0.55$, $p = 0.018$). Two other multiple regression models used fine sediment as a statistically significant predictor variable: the ephemerellid mayfly *Attenella delantala* and the nemourid stonefly *Zapada columbiana* were positively related to fine sediment (**Table 6**). The variables drainage area, sampling date, conductivity, and channel slope were all more frequently significant predictor variables than fine sediment.

Table 5. Predicted and measured responses of biological metrics and benthic macroinvertebrate taxa to increased levels of fine sediment. The significance probability (sig. prob.) is the probability of obtaining a correlation with greater absolute value than the computed value if no linear relationship exists. Note that a positive (+) response to D_{16} indicates a negative (-) response to fine sediment, and vice versa. Correlation coefficients that agree with the predicted response and have significance probabilities <0.05 are in bold.

	Fine Sediment				**D16 Grain Size**			
	Simple Linear Regression		**Partial Correlation**		**Simple Linear Regression**		**Partial Correlation**	
Metrics and Taxa (Predicted Response to Fine Sediment)	r_{12}	**Sig. Prob.**	$r_{12.345678}$	**Sig. Prob.**	r_{12}	**Sig. Prob.**	$r_{12.345678}$	**Sig. Prob.**
Taxa Richness (-)	0.50	0.012	0.18	0.49	-0.38	0.064	-0.14	0.59
Total Abundance (-)	-0.29	0.18	-0.28	0.26	-0.02	0.91	-0.02	0.94
EPT Richness (-)	0.46	0.023	0.07	0.80	-0.37	0.073	-0.07	0.78
EPT Abundance (-)	-0.18	0.39	-0.08	0.78	-0.10	0.63	-0.11	0.65
% Burrowing (+)	-0.32	0.13	0.40	0.097	0.09	0.67	-0.31	0.20
% Vulnerable (-)	0.23	0.27	0.30	0.23	-0.39	0.056	-0.24	0.34
Chironominae/Chironomidae (-)	**-0.53**	**0.0082**	**-0.81**	**<0.001**	**0.64**	**0.0008**	**0.59**	**0.009**
Orthocladiinae/Chironomidae (+)	**0.50**	**0.014**	**0.79**	**<0.001**	**-0.63**	**0.0010**	**-0.57**	**0.014**
Antocha spp. (-)	-0.29	0.18	0.08	0.74	0.21	0.33	0	0.99
Arctopsyche spp. (-)	**-0.47**	**0.021**	-0.33	0.18	**0.59**	**0.0025**	0.29	0.24
Attenella delantala (+)	**0.67**	**0.0004**	0.45	0.061	**-0.59**	**0.0022**	-0.23	0.36
Caudatella spp. (-)	0.23	0.28	-0.06	0.80	-0.31	0.14	-0.07	0.79
Chironomidae (+)	-0.56	0.0044	-0.50	0.036	0.19	0.37	-0.16	0.52
Chironominae (-)	**-0.66**	**0.0005**	**-0.70**	**0.001**	**0.54**	**0.0063**	0.40	0.096
Cinygmula spp. (-)	0.16	0.47	-0.41	0.094	-0.20	0.36	**0.55**	**0.018**
Dicranota spp. (+)	-0.32	0.13	-0.13	0.60	0.09	0.67	-0.15	0.55
Drunella doddsi (-)	0.01	0.96	0.11	0.65	-0.13	0.54	-0.20	0.43
Epeorus spp. (-)	-0.28	0.19	**-0.66**	**0.003**	0.02	0.92	0.41	0.095
Glossosoma spp. (-)	0.39	0.060	0.02	0.92	-0.26	0.22	0.04	0.89
Hesperoperla pacifica (-)	-0.11	0.60	0.04	0.88	-0.26	0.59	-0.30	0.22
Hexatoma spp. (+)	0.01	0.95	-0.20	0.43	-0.23	0.27	0	0.99
Isoperla spp. (+)	-0.24	0.26	-0.13	0.62	-0.12	0.56	-0.12	0.64
Lepidostoma spp. (+)	-0.63	0.0009	-0.66	0.003	0.58	0.0030	0.42	0.079
Malenka spp. (+)	0.12	0.56	0.07	0.79	0.14	0.51	0.07	0.79
Neophylax spp. (-)	-0.07	0.76	-0.27	0.28	0	0.99	0.15	0.55
Oligochaeta (+)	**0.63**	**0.0011**	**0.55**	**0.018**	**-0.50**	**0.013**	-0.33	0.18
Optioservus spp.(+)	-0.40	0.054	-0.33	0.18	0.13	0.54	0.41	0.090
Rhithrogena spp. (-)	0.32	0.13	0.33	0.19	-0.18	0.36	0.03	0.91
Rhyacophila Betteni grp. (-)	-0.14	0.50	-0.30	0.24	-0.20	0.36	0.07	0.78
Rhyacophila Hyalinata grp. (-)	-0.15	0.48	-0.18	0.46	0.06	0.78	0.10	0.69
Simulium spp. (+)	-0.09	0.68	-0.29	0.24	0.23	0.28	0.15	0.54
Zapada cinctipes (+)	0.11	0.61	-0.46	0.054	0.33	0.11	0.22	0.37
Zapada columbiana (+)	0.31	0.14	0.36	0.14	**-0.53**	**0.0074**	-0.45	0.059

Table 6. Multiple regression models of benthic macroinvertebrate metrics and taxa. Models for which the variable fine sediment agrees with the predicted response and is statistically significant ($p < 0.05$) are shown in bold. In this table the significance probability reflects the probability that the regression parameter could be equal to zero due to chance alone.

Metric (Predicted Response to Fine Sediment)	**(Response) Sig. Prob.**	**Slope (SE)**	**Other Variables: (Response) Sig. Prob.**	**Model Cp**	**Model R2**
Taxa Richness (-)	NA	NA	Area: (-) 0.0042	-1.8	0.32
Total Abundance (-)	NA	NA	Area: (+) 0.009 Cond: (+) 0.004	2.7	0.45
EPT Richness (-)	NA	NA	Area: (-)0.0008	-1.9	0.41
EPT Abundance (-)	NA	NA	Area: (+) 0.0016 Cond: (+) 0.0011	2.0	0.50
% Burrowing (+)	NA	NA	Cond: (+) 0.010 D84: (+) 0.015	-0.96	0.33
% Vulnerable (-)	NA	NA	Date: (+) 0.002 D84: (-) 0.003 Slope: (+) 0.02	1.8	0.58
Chironominae/ Chironomidae (-)	**(-) 0.0001**	**-0.032 (0.006)**	Slope: (-) 0.0001 D84: (+) 0.002 Cond: (-) 0.003 Area: (-) 0.011 Canopy: (+) 0.08	7.8	0.86
Orthocladiinae/ Chironomidae (+)	**(+) 0.0001**	**0.032 (0.006)**	Slope: (-) 0.0001 D84: (-) 0.003 Cond: (+) 0.0007 Area: (+) 0.018 Canopy: (-) 0.06	6.6	0.87

Table 6 (continued)

Taxa (Predicted Response to Fine Sediment)	**(Response) Sig. Prob.**	**Slope (SE)**	**Other Variables: (Response) Sig. Prob.**	**Model Cp**	**Model R2**
Antocha spp. (-)	NA	NA	Area: (+) 0.02	-6.4	0.22
Arctopsyche spp. (-)	NA	NA	Area: (+) <0.0001 Date: (+) 0.06 Cond: (-) <0.0001	3.81	0.84
***Attenella delantala* (+)**	**(+) 0.0057**	**0.11 (0.036)**	Area: (-) 0.015 Cond: (+) 0.005	5.2	0.70
Caudatella spp. (-)	NA	NA	Cond: (+) <0.0001 Area: (-) 0.0034	2.9	0.69
Chironomidae (+)	(-) 0.0048	-0.093 (0.029)	Canopy: (-) 0.02 Cond: (+) 0.02 Slope: (-) 0.04	3.45	0.71
***Chironominae* (-)**	**(-) <0.0001**	**-0.15 (0.03)**	Slope: (-) <0.0001 D84: (+) 0.0003	2.6	0.82
Cinygmula spp. (-)	NA	NA	Cond: (+) 0.002 Area: (-) 0.005 Date: (+) 0.05	4.2	0.69
Dicranota spp. (+)	NA	NA	Date: (+) 0.005 Cond: (-) 0.003	-1.6	0.41
Drunella doddsi (-)	NA	NA	Cond: (+) 0.011 Area: (+) 0.018 Date: (-) 0.05	5.1	0.42
***Epeorus* spp. (-)**	**(-) 0.0014**	**-0.13 (0.03)**	Date: (+) 0.005 Area: (-) 0.013 Slope: (-) 0.013 Cond: (+) 0.04	5.0	0.73
Glossosoma spp. (-)	NA	NA	Area: (-) 0.014	0.17	0.24
Hesperoperla pacifica (-)	NA	NA	Area: (+) <0.0001 D84: (-) 0.003 Cond: (+) 0.007	0.49	0.77
Hexatoma spp. (+)	NA	NA	D84: (-) 0.011 Canopy: (-) 0.020	0.45	0.33
Isoperla spp. (+)	NA	NA	Date: (+) 0.006	-1.5	0.30
Lepidostoma spp. (+)	(-) 0.0001	-0.22 (0.04)	Slope: (-) 0.015 Cond: (-) 0.06	3.24	0.62
Malenka spp. (+)	NA	NA	Date: (-) <0.0001	-2.9	0.69
Neophylax spp. (-)	NA	NA	Slope: (-) 0.16	-0.30	0.09
Oligochaeta (+)	**(+) 0.0008**	**0.14 (0.042)**	Cond: (+) 0.02)	2.1	0.53
Optioservus spp.(+)	(-) 0.080	-0.075 (0.04)	Canopy: (-) 0.006 Area: (-) 0.018	2.6	0.46
Rhithrogena spp. (-)	NA	NA	Date: (+) 0.0012 Slope: (-) 0.0043	0.75	0.53
Rhyacophila Betteni grp. (-)	NA	NA	Date: (+) 0.0004 Cond: (+) 0.008 D84: (+) 0.07	3.4	0.73
Rhyacophila Hyalinata grp. (-)	NA	NA	D84: (+) 0.06 Cond: (+) 0.08	2.6	0.20
Simulium spp. (+)	NA	NA	Date: (-) 0.0022	1.8	0.35
Zapada cinctipes (+)	(-) 0.011	-0.14 (0.05)	Area: (-) 0.0001 Cond: (+) <0.0001 Slope: (-) 0.03	6.3	0.80
***Zapada columbiana* (+)**	**(+) 0.0064**	**0.14 (0.05)**	Slope: (+) 0.0017	2.0	0.44

4. Discussion and Management Implications

Sediment Supply and Streambed Fine Sediment

Basin area-weighted sediment supply estimates from the GEO and USLE models suggest a three-fold difference in sediment supply between the highest (Beaver Creek and Grouse Creek) and lowest (Elk Creek and Upper South Fork Salmon River) ranked basins. Lisle and Hilton (1999) found that the proportion of the residual pool volume filled with fine sediment (V*) is strongly correlated with annual sediment yield in basins that have a bedrock lithology that produces abundant sand-sized sediment. Based on their logarithmic relationship between V* and sediment yield, the range of V* values in this study implies approximately an order-of-magnitude difference in basin sediment yield between the sites with the highest (Grouse Creek) and lowest (Elk Creek) V* values.

The GEO model estimates that sediment supply in individual basins has increased up to four times over undisturbed rates (Grouse Creek), while the USLE model suggests increases up to eight times (Beaver Creek and Grouse Creek) over undisturbed rates. These increases in both chronic inputs of fine sediment and episodic landsliding have resulted in detectable changes in channel conditions and aquatic biota. Some of the difference in these estimates is due to different processes, response times, and recovery rates in the GEO and USLE modeling approach. Both measures of fine bed material (V* and surficial fines in riffles) were sensitive to increases in supply estimated by the USLE and GEO modeling approaches; however, relationships were stronger for the USLE approach. This might be anticipated because landslides deliver both coarse and fine material, and the relative contribution of each is not known. The major source of model-estimated fine sediment in undisturbed areas was steep terrain composed of decomposed granite, which produces an abundance of sand sized particles. The primary source of fine sediment associated with management activities was road erosion, especially in granitic terrain.

Fine sediment in riffles and pools are both strongly correlated with increased sediment supply, adjusted by stream power. In this study of six basins, streams with the highest sediment supply were also the smallest and had lower stream power. It is unclear whether this trend is an artifact of site selection and a small sample size, or whether smaller streams are truly more sensitive to sedimentation. Smaller streams are often more tightly coupled with the surrounding hillslopes and may be more sensitive to direct effects of an increase in sediment supply; whereas hillslope inputs may be attenuated further downstream. Streams with low stream power throughout the channel network have less transport capacity and are more likely to accumulate fine sediment in response to increased sediment supply.

Biological Effects of Increased Fine Sediment

Salmonid Habitat

Increased supply of fine sediment can affect salmonid habitat by impairing spawning gravel quality, reducing food availability and foraging efficiency, and through the loss of rearing habitat. Fine sediment reduces subsurface flow rates in spawning gravels, which in turn reduces dissolved oxygen and the flushing of metabolic wastes from the egg pocket. Numerous studies have documented an inverse relationship between embryo survival and the percentage of fine sediment in spawning gravels (e.g., Koski 1966; Tagart 1976; McCuddin 1977; Cederholm et al. 1981; Chapman 1988; Bjornn and Reiser 1991).

Elevated levels of fine sediment can also cause physical entrapment of emerging fry, even in redds where emergence has occurred (Chapman 1988). Rearing habitat for juvenile fish is further affected by substrate embeddedness, which reduces the size and abundance of interstitial crevices and results in larger scale effects on channel morphology such as the infilling of pool habitat. Bed mobility may also be affected because increases in the sand fraction reduce the critical shear stress required for incipient motion (Wilcock and Kenworthy 2002). As the sand content approaches 10 to 30% the bed undergoes a transition from being 'framework supported' (the bed consists of a framework of interlocking gravel clasts) to being 'matrix supported' (the coarse grains are 'floating' in a matrix of sand). This change in the bed composition is related to an orders of magnitude increase in gravel transport rates (Wilcock et al. 2001). Increases in bed mobility may adversely affect egg survival by increasing the risk of redd scour and may affect food production by dislodging benthic organisms.

Our investigation sought to identify the direct linkages between fine sediment supply and channel conditions that are perceived to be limiting for salmonid fishes in the Klamath National Forest. The habitat parameters that we focused on included the infilling of pools by fine sediment, surficial fine sediment in riffles, permeability of spawning gravels, and the prey base of benthic invertebrates.

Pools provide important rearing habitat for numerous species and life stages of salmonids. Because V* is linked to sediment supply (Lise and Hilton 1999), V* has been widely used as a monitoring tool by state and federal agencies. However, prior to this study, the biological significance of this metric had not been previously established. Our study found that V* was positively correlated with surficial fine sediment in riffles, which in turn affected salmonid spawning gravel quality and benthic invertebrate assemblages. These results provide important empirical evidence for observable and biologically significant effects of increased sediment supply associated with forest management activities, especially those associated with roads.

Surficial fine sediment in riffles was strongly correlated with both V* and predicted sediment supply from the USLE and GEO models. Variation in surficial fines ranged from 2 – 23%. As the volumetric fraction of sand in the bed increases to between 10 – 30%, pore spaces between coarser sediments can become completely filled in, creating localized patches of fine grained sediment (Wilcock and Kenworthy 2002). Based on our observations of streams in the study area; however, sand tends to be flushed through these steep gravel-bed streams, and is generally only deposited in the wakes of boulders and interstitial spaces between coarse grains. As sediment transporting flows decrease below the point of gravel entrainment, sand can be transported out of riffles and into pools (Lisle 1989). Thus, fine sediment in riffles is expected to increase rapidly as sediment supply increases, but plateau as interstitial spaces are filled with sand.

The magnitude of a biological response to elevated levels of fine bed material is difficult to infer from previous studies. The majority of experimental studies use much higher concentrations of fine sediment than we observed (e.g., Crouse et al. 1981; Suttle et al. 2004) and often report fine sediment in units of volume instead of surface area (e.g., studies reviewed in Chapman 1988). The definition of what constitutes fine sediment also varies, with values in the literature ranging from particles <0.85mm to 8mm. The particle size distribution of fine sediment also affects the type and magnitude of response. For example, fine sand reduces the emergence success of salmonid eggs more effectively than coarse sand (Peterson and Metcalfe 1981). Even with these caveats, the majority of past studies have documented dramatic reductions in egg and embryo survival when the percentage of fine sediment in spawning gravels increases above 10-20% (see review by Chapman 1988).

Both physical factors, such as the quantity, quality, and mobility of spawning gravels, and biological factors, such as the effects of temperature on egg viability and the consumption of eggs by predators, can affect egg-to-fry emergence from redds. In areas with depressed population sizes, the quantity of spawning gravel of the preferred size range is rarely limiting. However, the quality of gravel, in terms of fine sediment concentration, permeability and mobility, is paramount in determining spawning success. The most effective way of directly measuring gravel quality is quantifying permeability in preferred spawning sites because field measurements of permeability can be directly correlated to egg survival rates measured in laboratory studies (Chapman 1988) and to growth rates of embryos (Koski 1966). Results from our investigation indicate that subsurface permeability is at best only of modest quality (median egg survival rate 30%) and individual sample sites were highly variable (minimum survival 15%, maximum survival 39%). Predicted fine sediment supply from the KNF sediment modeling efforts accounted for over half of the observed variation in reach-averaged permeability rates (**Figure 8**).

Grain Size

In addition to empirical correlations between sediment supply and channel conditions, theoretical predictions can be used to test for deviations from expected values. Theoretical predictions of the reach-averaged median grain size are calculated from a depth-slope product derived by inverting the Shields equation (Dietrich et al. 1996). The difference between predicted and observed values of the median grain size are an indirect measure of excess shear stress, which has been found to be a useful indicator of both sediment supply rates and bed load transport rates in equilibrium channels (Buffington and Montgomery 1999b). Deviations of predicted values from observed values may be indicative of changes in substrate size caused by land use impacts. Over-prediction of grain size can be a function of wood-controlled sediment storage (Buffington and Montgomery 1999b), high form roughness (Buffington and Montgomery 1999b), high sediment supply (Buffington and Montgomery 1999a), or errors in predicting channel slope from digital elevation models (DEMs). Under-prediction of grain size suggests that bed material was deposited by an atypical process (e.g., extremely high magnitude floods, landslide or debris flow inputs, or lag deposits from hydraulic mining), the reach is heavily influenced by tributary inputs that disrupt patterns of downstream fining (Rice 1998) or that the channel is sediment starved (e.g., below dams or diversions). Bed coarsening can also occur if there is a reduction in flow resistance associated with a loss of in-stream wood; however, the contrast of observed to predicted grain size will not be sensitive to this type of change, unless wood roughness is explicitly included in the calculation. With high wood loading, the channel would be finer than predicted and removal of wood would presumably result in the channel returning to its predicted value. Our study did not assess wood loading and thus cannot decipher the causal mechanisms for fining of the substrate. Substrate conditions were finer than predicted as sediment supply increased; however, the correlation was weak and results were highly variable.

Benthic Macroinvertebrate Assemblages

The effects of increased sediment supply on benthic macroinvertebrate communities are more subtle than the effects of water quality impacts commonly observed in urbanization or agriculture, which result from pollutants such as pesticides or metals (Waters 1995). Diversity and tolerance metrics that are useful for detecting the effects of water chemistry pollutants may not be as useful for assessing the ecological impacts of increased sediment supply. Benthic invertebrate taxa such as Chironominae, Oligochaeta, *Epeorus*, and *Attenella* respond predictably to levels of fine sediment and offer potential for improved monitoring and increased understanding of stream ecosystems.

Chironomid midges, in particular, may represent a particularly useful indicator taxa of fine sediment. Our results are in agreement with the findings of Angradi (1999), who observed differential responses among the Chironomidae to fine sediment additions in a West Virginia stream. Although Orthocladiinae are often the dominant chironomid on gravel and cobble (Pinder 1986), they appear to be resistant to the filling of interstitial spaces, perhaps because they reside on the upper surfaces of stones rather than in crevices. Chironominae, common in organic-rich silt (Pinder 1986), responded negatively to deposits of fine sediment. In streams of the KNF, organic-rich silt is probably most common in the interstices between cobble or on the surfaces of cobble. High levels of inorganic coarse sand tend to fill in interstices and abrade away organic silt deposits, reducing available habitat for Chironominae.

Whereas other workers have observed decreased taxonomic richness in response to large increases in deposited sand, especially in the Ephemeroptera, Plecoptera, and Trichoptera (EPT) insect orders (Angradi 1999), we found no clear relationships between either total richness or EPT richness and fine sediment (**Table 5**). Although both metrics had statistically significant simple linear relationships with fine sediment that were opposite in magnitude as expected, once other variables were accounted for in the partial correlations the positive relationships weakened and were no longer significant. Because of the high transport capacity and low background levels of fine sediment in these steep mountain streams, taxa richness might not respond in the same manner as in other, lower gradient systems. Rather than resulting in an overall reduction in taxa richness, higher levels of fine sediment could actually provide habitat for psammophilic (sand-loving) taxa that otherwise might not be present or as abundant. Two caddisflies that build portable cases out of fine sediment, *Gumaga* (Sericostomatidae) and *Pedomoecus sierra* (Apataniidae), were more common at sites with high levels of fine sediment, suggesting that the availability of small mineral grains for case construction could be a limiting factor for these taxa.

Oligochaete abundance was strongly associated with fine sediment. Most oligochaetes are obligate burrowers in fine sediment, and are often reported to increase in abundance with fine sediment additions. One group of Oligochaetes, the Lumbricina, is considered moderately intolerant of fine sediment, however (Relyea et al. 2000).

Another taxa found to respond positively to fine sediment, *Attenella delantala,* had the most upstream distribution of 12 species of Epehemerellidae in the McKenzie River, Oregon (Hawkins 1984). It was commonly found in patches of sand and gravel < 20 mm diameter, suggesting a preference for fine sediment (Hawkins 1984). 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 may be due to the fact that *Attenella* is generally found only in headwater streams where fine sediment levels are usually low.

The hydropsychid caddisfly *Arctopsyche* exhibited strong linear relationships with fine sediment and D_{16}, but was better explained by environmental variables such as drainage area and conductivity (**Table 5, Table 6**). *Arctopsyche* was identified by Relyea et al. (2000) as being very intolerant of fine sediment. The larvae build and reside in fixed retreats downstream of their coarse-meshed nets, where they remain unless disturbed. Voelz and Ward (1996) found that larvae and pupae of *Arctopsyche grandis* are found almost exclusively on the undersides of large cobble, usually in pairs, particularly during the winter and spring in the Rocky Mountains. The large size of the larvae necessitates large crevice spaces beneath stones, only found in streams with low levels of fine sediment.

Similarly, heptageniid mayflies, such as *Epeorus*, are dorsoventrally flattened and cling to exposed surfaces of rocks, where they scrape algae. They may be especially prone to abrasion from saltating sand grains and filling of interstitial crevices.

Overall, changes in the benthic invertebrate assemblage that could be attributed to fine sediment were fairly subtle. Other impacts from forest management, such as increased temperature or increased primary production, may also play an important role in affecting benthic communities.

Macroinvertebrate Prey Availability for Salmonids

Changes in the benthic macroinvertebrate assemblage can affect the availability of food and survival of insectivorous fish such as salmonids. When invertebrate prey is scarce, salmon forage more often during the day, increasing their risk of predation (Metcalfe et al. 1999). Although we are unaware of salmonid prey consumption data from the Klamath National Forest, studies from elsewhere suggest that salmonids, especially older steelhead/rainbow trout, prefer to feed on large (5-20 mm), soft-bodied invertebrates that are available in the drift or on the surface of the benthos (Allan 1981). Stomach contents from one- and two-year old wild steelhead caught in the Trinity River in May were dominated by ants (Formicidae), hydropsychids and other caddisflies, ephemerellid and heptageniid mayflies, beetles (Coleoptera), the dipteran *Atherix*, stoneflies such as *Pteronarcys* and *Calineuria*, dragonflies (Odonata), and *Parargyracitas* (Lepidoptera) (Boles 1990). Other than ants, which are probably a seasonal terrestrial source of food, these taxa tend to be large, soft-bodied, and can be found clinging or crawling on the surfaces of stones. Small insects common in the drift such as chironomids and baetids were rarely consumed during low flow conditions in the Trinity River. Studies of insectivorous fish feeding from other areas often find that the most commonly ingested prey of trout and salmon are chironomid midges, baetid mayflies, and simuliid black flies (Radar 1997). A study of fall-run age-0 Chinook salmon feeding in the Feather River (California) in April found that the most common prey were chironomids, Cladocera, baetids, simuliids, hydropsychids, mites (Acari), and terrestrial insects (Esteban and Marchetti 2004). Invertebrate assemblages in this section of the Feather River are very different from tributaries to the Klamath River, however, as they contain zooplankton and are relatively depauperate with regards to sensitive EPT insects.

As discussed above, invertebrate taxa that decreased in abundance with increasing fine sediment include Chironominae, *Epeorus* (Heptageniidae), *Cinygmula* (Heptageniidae), and *Arctopsyche* (Hydropsychidae). Taxa that increased in response to fine sediment include Oligochaeta, *Attenella delantala* (Ephemerellidae), and *Zapada Columbiana* (Nemouridae). Radar (1997) developed an availability score for benthic invertebrates that reflects biological traits that are believed to make taxa more available for consumption by salmonids (e.g. drifting frequency, size, habit, etc.). Taxa that decreased in abundance are generally considered to be more available as prey to salmonids than taxa that increased in response to fine sediment, as judged by Radar's (1997) trait-based approach (**Table 7**). Taxa that decreased in abundance in response to fine sediment were larger in size than taxa that increased in abundance, except for Chironominae.

Additionally, the percentage of the assemblage that burrowed into the substrate and was unavailable as prey was positively correlated with fine sediment after other environmental variables were accounted for, although this relationship was not statistically significant. Suttle et al. (2004) reported similar findings from a manipulative experiment of fine bed material. These authors observed a linear decrease in juvenile steelhead growth with increasing levels of fine sediment resulting from a shift in available prey organisms to burrowing taxa that were mostly unavailable. Steelhead swimming, aggressive activity, and injury also increased with increasing levels of fine sediment. We conclude that higher levels of fine sediment result in reduced quantity and quality of prey available to salmonids, although the biological effects of these changes on salmonid growth are unknown.

Table 7. Size and prey availability scores of taxa with statistically significant responses to fine sediment, using the trait-based scoring system of Radar (1997).

Taxa	Response to Fine sediment	Size (mm)	Availability Score
Chironominae	-	2-8	70.5
Epeorus	-	7-18	63.6
Cinygmula	-	7-18	63.6
Arctopsyche	-	10-28	51.6
Oligochaeta	+	2-20	10.0
Attenella delantala	+	5-9	22.5
Zapada columbiana	+	5-10	52.6

Context and Extrapolation

When making inferences from empirical studies it is important to identify the contextual setting for which the inferences may apply. This is particularly important in a management setting because of the tendency to over-extrapolate results from one area to another. Relationships among sediment supply, channel conditions, and the biological responses that we investigated are limited to moderate gradient (1.5-4.5%), cobble-bed streams in basins that are underlain predominantly by highly weathered granite (>50% basin area). Similarly, previous studies of V* found that relevant comparisons can only be made for mid-order streams of moderate gradient in basins that produce abundant sand sized particles (Lisle and Hilton 1992). Likewise, an on-going study of spawning gravel quality in the KNF also found that the relationship between sediment supply and permeability did not extend to smaller, steeper streams or to larger streams that drained more resistant rock types (May, unpublished data).

Because all of the parameters needed to define the contextual setting (channel slope, drainage area, and proportion of the basin area composed of decomposed granitic terrain) and to predict supply and transport capacity (USLE model results and stream power index) can be assessed using DEM-based analysis and GIS software, these empirical linkages can be investigated across broad spatial scales. The output of this effort would depict frequency distributions of stream reaches predicted to have varying levels of pool infilling (V*), surficial fines in riffles, spawning gravel permeability, and altered benthic invertebrate assemblages within various watersheds. Such predictions would directly link sediment supply modeling with beneficial uses, and would provide a powerful and biologically relevant management tool that could be applied at multiple spatial scales.

5. Conclusions

Results of this study indicate that there are significant, measurable differences in streambed fine sediment levels between basins in the study area that were chosen as end-members of sediment supply. Estimates of sediment supply from the USLE and GEO models were related to channel conditions in the following ways:

1. directly correlated to fine sediment stored in pools (V*);
2. directly correlated with surficial deposits of fine sediment in riffles;
3. inversely correlated with deviations from median grain size predictions, resulting in a fining of the surface layer; and
4. inversely correlated with subsurface flow rates in spawning gravels.

Surficial deposits of fine sediment in riffles were related to stream biota in the following ways:

5. correlated with abundances of the benthic invertebrate taxa Oligochaeta, *Attenella delantala*, and *Zapada columbiana;*
6. inversely correlated with abundances of the benthic invertebrate taxa Chironominae, *Epeorus*, *Cinygmula*, and *Arctopsyche*; and
7. inversely correlated with presumed prey availability for salmonids.

These results suggest that V* and surficial fine sediment in riffles are potentially useful indicators for linking hillslope sediment supply and aquatic biota because they respond predictably to increased sediment supply and result in direct biological consequences in basins that drain highly weathered granitic terrain. Managers can use this information to explore the spatial distribution of stream reaches affected by elevated levels of fine sediment using these empirical linkages in a broad-scale DEM-based analysis. Likewise, several benthic invertebrate taxa are potentially useful indicators of fine sediment levels, and could be the focus of future monitoring efforts.

Future research will further examine the biological effects of increased sediment supply in the Klamath National Forest. In an ongoing study examining the effectiveness of best management practices (BMPs) to prevent excessive loading of fine sediment associated with road crossing construction activities, we are investigating how the size and amount of deposited fine sediment affects benthic invertebrate colonization. We are also sampling invertebrates residing underneath individual cobble with varying levels of embeddedness, in order to examine the effects of cobble embeddedness on invertebrate assemblages. Together, these investigations will allow us to better understand the microhabitat requirements of particular invertebrate taxa. Finally, in addition to focusing on fine sediment, we are examining other impacts of increased sediment supply. Landslides that occur during large flood events can result in debris flows that strip riparian forests and mobilize channel and valley floor deposits, causing widespread disturbance for long distances downstream. In summer 2005 we began a study examining the biological conditions of mid-sized streams affected by debris flows in the 1997 flood. This research reflects the necessity to improve our understanding of the effects of forest management on stream ecosystems by making quantifiable linkages between sediment supply, channel conditions, and the magnitude of biological response.

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