

QUANTITATIVE LINKAGES BETWEEN SEDIMENT SUPPLY, STREAMBED FINE SEDIMENT, AND BENTHIC MACROINVERTEBRATES IN THE KLAMATH MOUNTAINS, NORTHERN CALIFORNIA

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Abstract: Predicting the cumulative watershed effects of forest management on stream ecosystems requires a quantitative understanding of the linkages between hillslope sediment supply, streambed response, and biological effects. Here we examine the relationships between sediment supply, streambed fine sediment, and benthic macroinvertebrate assemblages in six streams in the Klamath Mountains of Northern California. Sediment supply has increased by 2-4 times over background rates in some drainage basins. Reach-averaged V^* , a measure of pool infilling by fine sediment that ranged from 5-20%, was strongly correlated with sediment supply, fine sediment in riffles, and excess transport capacity. Two biological metrics, Chironominae/Chironomidae (-, sign indicates response to fine sediment) and Orthocladiinae/Chironomidae (+), and four taxa, *Arctopsyche* (-), *Attenella delantala* (+), Chironominae (-), and Oligochaeta (+), responded as predicted in previous studies and were strongly related to fine sediment on the surface of the streambed. Many biological metrics commonly used in biomonitoring, such as taxonomic richness, exhibited poor or unexpected relationships with fine sediment. The quantitative relationships described in this study add to our understanding of the linkages between hillslopes, stream channels, and aquatic biota and identify areas where process-based understanding can be improved.

Key Words: sediment supply, V^* , fine sediment, benthic macroinvertebrates, substrate, mountain streams, gravel-bed streams, cumulative watershed effects.

INTRODUCTION

Cumulative watershed effects are significant, adverse influences on water quality and biological resources that arise from the ways watersheds function and 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 mountainous, forested watersheds. In order to improve capabilities to predict cumulative watershed effects the quantitative linkages between sediment supply, channel conditions, and stream biota need to be better understood.

In this paper we examine the relationships between sediment supply, streambed fine sediment, and benthic macroinvertebrate assemblages in streams in the Klamath Mountains of Northern California. The objective of this study was to examine if increased rates of sediment supply result in increased levels of streambed fine sediment, and if this in turn is correlated with altered benthic assemblages. Additionally, we attempted to identify the quantitative relationships between hillslopes, streambeds, and biota, in order to examine whether there are thresholds at which increased sediment supply results in significant changes in stream condition and biotic communities. We examined the hypothesis that high sediment supply to mountain stream channels leads to high levels of fine sediment in the streambed, resulting in a reduction in benthic macroinvertebrate diversity and altered community composition.

METHODS

Study Area: Sampling of channel conditions and benthic macroinvertebrates was performed in 6 streams in the Klamath National Forest (KNF) in fall 2003 (Table 1). Streams were selected based on the following criteria: (1) moderate gradient (2-4%), (2) gravel and cobble substrate, (3) bedrock that produced abundant fine sediment (predominantly granitics), (4) no recent channel-scouring debris flows, (5) known anadromous fisheries, and (6) minimal human land use other than forest management activities. The sites were selected to reflect the endpoints of sediment supply, based on qualitative assessments of streambed fine sediment by KNF personnel and sediment

supply models developed by KNF geologist Juan de la Fuente (see below). Study reaches were 0.5 – 2.0 km in length, and contained a minimum of 15 pools.

Sediment Supply: The KNF has developed two models of sediment delivery to stream channels, one to predict episodic inputs from landslides and one to predict chronic inputs of fine sediment. The fine sediment model uses estimates of surface erosion from the Universal Soil Loss Equation based on the spatial distribution of roads, timber plantations, wildfires, and terrain and soil types. The landslide sediment supply model is based on empirical relationships derived from air photo landslide assessments in the Salmon River subbasin during the period 1970 – 1975, a moderately wet period following a period of intensive timber harvest across the forest (de la Fuente and Haessig 1993). Future sediment delivery is predicted for each of 11 geomorphic terrain types, based on the frequency and size of landslides during the reference period. Data from the Salmon River drainage are then extrapolated using GIS to predict sediment delivery rates throughout the west side of the KNF. Risk ratios, defined as the ratio of anthropogenic to background rates of sediment supply divided by a constant (2 for the landslide model and 8 for the USLE model), were used with the qualitative assessments of fine sediment to categorize each site as high or low sediment supply (Table 1). Thus, sediment supply was characterized using two quantitative variables (the USLE model surface erosion prediction and the landslide sediment delivery prediction) and one quantitative categorical variable (high/low sediment supply).

Table 1 Channel slope and estimated sediment supply conditions for the six study streams.

Stream	Slope (%)	Landslide Risk Ratio	USLE Risk Ratio	Qualitative Fine Sediment	Sediment Supply Category
Elk Creek	4.3	0.22	0.00	Low	Low
Little North Fork Salmon River	2.5	0.54	0.19	Low	Low
Upper South Fork Salmon River	1.6	0.07	0.03	Low-Medium	Low
Beaver Creek	2.3	1.24	1.01	Medium-High	High
Grouse Creek	2.8	1.98	1.00	Medium-High	High
Taylor Creek	3.4	0.39	0.39	High	High

Streambed Measurements: V^* measurements were made in every pool in the study reach, following the methods of Hilton and Lisle (1993). Briefly, V^* is a measure of the volume of pools filled in by 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.

The proportion of fine sediment on the surface of the bed was measured in four riffles in each reach. A modified soccer net (9' x 4' with 5" grid, containing 220 intersections) was used to determine the spacing of measurements. At each grid intersection a chaining pin was placed on the bed and the presence or absence of fines at the tip of the pin was recorded. Fine sediment measurements were made along three transects in each riffle, in the same locations where macroinvertebrates were sampled. For each reach we determined the percentage of the bed covered by fine sediment in each of four riffles.

Grain size was assessed in each riffle via transect-based pebble counts (Bunte and Abt 2001). Particle diameter was measured every 0.3 m along transects using a gravelometer. The number and spacing of transects was determined at each riffle to obtain a minimum of 200 grain measurements. The embeddedness of each grain was characterized using a three category qualitative scale of the effort required to remove the grain: (1) "pick" particles are unembedded, loose particles on the surface of the bed, (2) "pluck" particles are moderately embedded, and (3) "pry" particles are highly embedded by fine sediment. We are primarily concerned with the embeddedness of coarse gravel and cobble; thus, for each riffle we calculated the percentage of 16-256 mm grains that were sitting freely on the bed, moderately embedded, and highly embedded.

Benthic Macroinvertebrate Sampling: Benthic macroinvertebrates were sampled from the same locations where fine sediment was measured. A timed 4 minute sample was made at each of 3 transects per riffle by disturbing the substrate upstream of a 500 micron mesh D-frame kick net. The 3 transect samples were composited into one sample container. Samples were elutriated to separate the organic and inorganic portions of the sample, and large

leaves and woody debris was 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 remainder of the organic 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).

For analyzing relationships between individual taxa abundances and measures of fine sediment we excluded taxa that were present at less than half the sites or 40% of the samples. From the taxonomic abundance data we calculated 58 common biological metrics, 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 sources of life history information (Merritt and Cummins 1996).

Statistical Analyses: We tested the hypothesis that high sediment supply is related to high levels of streambed fine sediment using three approaches. First, we examined whether measures of streambed fine sediment (V^* , surface fine sediment, and embeddedness) were higher at the qualitatively ranked “high” sediment supply sites than the “low” sites using the nonparametric Mann-Whitney test ($\alpha = 0.10$ to increase power). Next, we examined whether there was a positive relationship between quantitative predictions of sediment supply (from the USLE and landslide models) and 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 greater than zero (one-tailed, $\alpha = 0.05$). Finally, since 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 using linear regression. No data transformations were required to satisfy criteria for normality and homoscedasticity of residuals.

To examine relationships between benthic macroinvertebrates and fine sediment we began by reviewing the available literature on this topic, with a focus on studies from the Pacific Northwest, USA. We identified relationships of three types (Waters 1995): (1) correlations between the presence or abundance of individual taxa with substrate size (e.g. grain size preferences), (2) changes in community metrics and taxa abundance following experimental additions of fine sediment, and (3) descriptive changes in taxonomic composition following changes in substrate conditions (Table 2). We examined each of the hypotheses identified in the literature by viewing bivariate plots of the biological variables versus riffle surface fine sediment. We choose not to examine biological variables relative to V^* or embeddedness because V^* is a reach-averaged value ($n=6$) and is well correlated with riffle surface fine sediment, and embeddedness is poorly correlated with any of the other measures of sediment supply or fine sediment. We used linear regression to test the significance of the hypothesized relationships between biological metrics or abundance of individual taxa and surface fine sediment (one-tailed, $\alpha = 0.05$). As the analysis progressed it became clear that many of the relationships between individual macroinvertebrate taxa and fine sediment were sub-optimally characterized by linear regression. Thus, in addition to linear regression we used partitioned linear regression, or factor-ceiling analysis (Thomson et al. 1996). Partitioned linear regression is a method using successive regressions through a cloud of data. The choice of the upper quantile is arbitrary; we used the upper quartile (75%) as a compromise between ability to identify the upper ceiling of the distribution and relatively few data points.

All of the tests described above are considered independent of one another, since individual hypotheses were made for each statistical test. The second phase of our analysis included identification of relationships between sediment and biological variables that were not explicitly tested above. Since these were multiple unplanned tests (two-tailed), the experiment-wise false positive rate ($\alpha_e = 0.05$) was adjusted using the Bonferroni Criterion, whereby the false positive rate for individual tests was $\alpha = 0.001$.

RESULTS AND DISCUSSION

Linkages Between Sediment Supply and Streambed Fine Sediment: Reach-averaged V^* was significantly higher in streams judged to have high sediment supply (0.141 ± 0.029 (Mean \pm SE)) than streams with low sediment supply (0.064 ± 0.008) (Mann-Whitney, $\alpha = 0.10$). Similarly, bed surface fine sediment was also significantly greater in streams with high sediment supply ($14.0\% \pm 2.1\%$ vs. $7.5\% \pm 1.9\%$). Thus, 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. The three embeddedness categories, however, exhibited similar values at sites with high and low sediment supply.

Quantitative estimates of surface erosion from the USLE erosion model exhibited marginally significant positive linear relationships with V^* ($p = 0.047$, $r^2 = 0.55$) and surface fines ($p = 0.052$, $r^2 = 0.52$), but were poorly related to measures of embeddedness. Estimates of sediment delivery from the landslide model exhibited positive relationships with V^* and surface fines that were not statistically significant ($p = 0.08$ and $p = 0.21$, respectively). Fine sediment delivery in the USLE model is primarily a factor of road density, while the landslide model uses extrapolations of empirical observations of landslide delivery volumes in various terrain types, but does not explicitly consider roads. Since landslides in forested watersheds are often associated with roads, by accounting for watershed road density the USLE model may reflect both surface erosion and, indirectly, landslide delivery of sediment.

All three embeddedness categories were uncorrelated with categorical and model-based sediment supply estimates, as well as bed surface fine sediment. Of the three in-stream measures of fine sediment, V^* and bed surface fine sediment reflect increased sediment supply fairly well while embeddedness measures were poorly related. Gravel and cobble embeddedness, as measured in this study, may reflect both embeddedness from fine sediment as well as the interlocking of grains with other large particles, and thus may not be the best measure of interstitial crevices.

Lisle and Hilton (1999) described a logarithmic increase in watershed sediment yield with increasing V^* . Based on their relationship between V^* and sediment yield, the range of V^* values in this study implies at least an order-of-magnitude difference in basin sediment yield between the sites with the highest and lowest V^* . Reach-averaged V^* values exhibited a strong, statistically-significant linear relationship with bed surface fine sediment ($p = 0.016$, $r^2 = 0.72$) (Fig. 1). The linear regression model predicts approximately a 1:1 positive relationship (slope = 76.5 ± 23.8) between volume of pools filled with fine sediment and surface area of riffles covered by fine sediment. Alternatively, the data also suggests the possibility of a riffle-surface fine sediment threshold near 15%, above which increases in sediment supply continue to cause infilling of pools but do not cause increased coverage of riffle surfaces (Fig. 1). 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 the turbulent, high velocity zones of steep gravel-bed streams, and is generally only deposited in the wakes and crevices of coarse grains. As flood flows decrease below the point of gravel entrainment, sand can be transported out of riffles and into pools (Lisle 1989). Fine sediment in riffles, then, is expected to increase rapidly as sediment supply increases, but plateau as interstitial spaces are filled with sand.

Increased sediment supply can cause a fining of the surface of the streambed as particle size adjusts to offer less resistance to transport (Dietrich et al. 1989, Lisle et al. 2000). The ratio of the median grain size predicted by the Shields equation (D_{50}^*) (based on bankfull depth measurements and assumed critical shear stress of 0.045) to the measured D_{50} is a relative indicator of excess transport capacity. The ratio of predicted D_{50}^* to measured D_{50} exhibits a very strong positive linear relationship with V^* ($p = 0.004$, $r^2 = 0.90$) (Fig. 2). This implies that the bed surface gets finer (and is mobilized more frequently) as V^* , a proxy for sediment supply, increases.

Linkages Between Streambed Fine Sediment and Benthic Macroinvertebrates

From our survey of empirical relationships between benthic macroinvertebrates and fine sediment, we identified 8 metrics and 25 taxa that were common in our dataset (we excluded taxa occurring at less than half of the sites or less than 40% of samples) (Table 2). Of the 8 metrics we tested, four responded as predicted: total abundance, EPT abundance, Chironominae/Chironomidae, and Orthocladiinae/Chironomidae (Table 2). Our results are in strong agreement with the findings of Angradi (1999) with regards to the response of the Chironomidae to fine sediment.

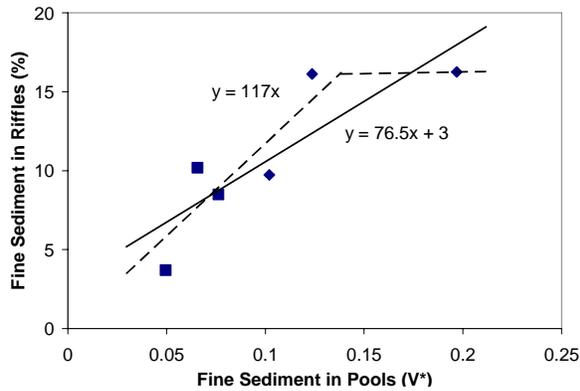


Figure 1 Percentage of riffle bed surface covered by sediment versus reach-averaged V^* . Two models are presented, a linear regression (solid line) and a broken-stick regression (dashed line).

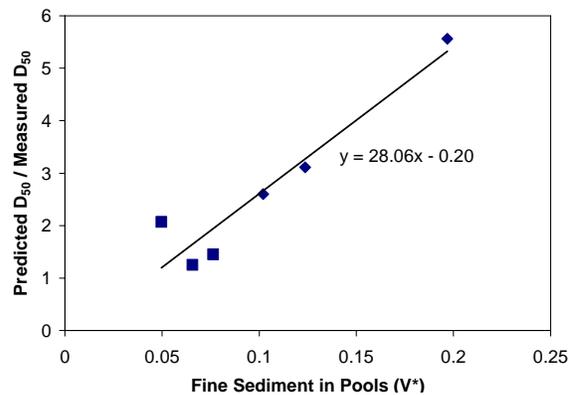


Figure 2 Ratio of predicted median grain size to fine measured median grain size, versus reach-averaged V^* .

The fraction of chironomids composed of the sub-family Chironominae was negatively related to increasing fines, while the fraction made up of Orthocladiinae increased strongly (Table 2, Fig. 3). 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), respond negatively to deposits of fine sediment. In this study, fine sediment is primarily composed of inorganic deposits of coarse sand, suggesting that this substrate is not suitable for Chironominae. As predicted, total abundance and EPT abundance were negatively related to fine sediment, but the relationships were not statistically significant at $\alpha = 0.05$ (Table 2).

Four metrics responded in the opposite direction as predicted: taxa richness, EPT richness, percent burrowing and percent vulnerable (Table 2). Whereas other workers have observed decreased richness in response to large increases in deposited sand, especially in the Ephemeroptera, Plecoptera, and Trichoptera (EPT) insect orders (Angradi 1999), we observed strong positive relationships between both total taxa richness and EPT richness and fine sediment (Table 2, Fig. 4). When recalculated using a two-tailed test, both of these metrics exhibited statistically significant positive slopes (taxa richness: $p = 0.012$, EPT richness: $p = 0.022$). Rather than resulting in an overall reduction in taxa richness, higher levels of fine sediment in these steep mountain streams may provide habitat for many psammophilic taxa such as Oligochaeta, Gomphidae (Odonata), the ephemereid mayflies *Attenella* and *Serratella*, the stoneflies *Yoraperla* (Peltoperlidae) and *Doroneuria* (Perlidae), and the caddisfly *Dolophilodes* (Philopotamidae). Two caddisflies that build portable cases out of fine sediment, *Gumaga* (Sericostomatidae) and *Pedomoecus sierra* (Apataniidae), are 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. The percent burrowing metric exhibited a weak negative relationship with fine sediment, while percent vulnerable was weakly, positively related.

None of the metrics for which a priori predictions were not made were significant at the Bonferroni-corrected false-positive error rate of $\alpha_c = 0.001$. The strongest relationships among these metrics were the abundance of predators and the abundance of filter-feeding organisms, both of which decreased with increasing fine sediment. The declining trend in filter-feeders reflects low abundances of simuliid blackflies and hydropsychid caddisflies in riffles with greater than 15% surface fine sediment. Likewise, decreasing predator abundance resulted from declines in perlid caddisflies, particularly *Calineuria californica*, and rhyacophilid caddisflies. Pollution tolerance metrics and other measures of community composition were weakly related to sediment supply and levels of fine sediment.

Of the 25 taxa with a priori predictions, only 14 responded in the expected direction with increasing fine sediment (Table 2). Of these, only four taxa had statistically significant relationships with fine sediment: the net-spinning caddisfly *Arctopsyche* (Hydropsychidae), the ephemereid mayfly *Attenella delantala*, the midge subfamily Chironominae, and Oligochaeta, aquatic worms (Table 2, Figs. 5 and 6). *Arctopsyche* was identified by Relyea et

Table 2 Predicted and measured responses of biological metrics and benthic macroinvertebrate taxa to increased levels of fine sediment. The P-Value is calculated based on the predicted slope using a one-tailed test. Statistically significant relationships are in bold.

Metrics and Taxa (Predicted Response)	Measured Response	Slope (SE)	Predicted Response P-Value	Source of Prediction
Taxa Richness (-)	+	0.72 (0.27)	0.99	Waters 1995
Total Abundance (-)	-	-92.8 (66.3)	0.088	Angradi 1999
EPT Richness (-)	+	0.39 (0.16)	0.99	Angradi 1999
EPT Abundance (-)	-	-47.8 (54.2)	0.19	Waters 1995
% Burrowing (+)	-	-0.40 (0.25)	0.93	Suttle et al. 2004
% Vulnerable (-)	+	0.43 (0.38)	0.88	Suttle et al. 2004
Chironominae/Chironomidae (-)	-	-0.021 (0.008)	0.004	Angradi 1999
Orthocladiinae/Chironomidae (+)	+	0.022 (0.008)	0.007	Angradi 1999
<i>Antocha</i> spp. (-)	-	-0.46 (0.78)	0.28	Relyea et al. 2000
<i>Arctopsyche</i> spp. (-)	-	-1.50 (0.55)	0.006	Relyea et al. 2000
<i>Attenella delantala</i> (+)	+	2.00 (0.40)	<0.0001	Hawkins 1984
<i>Caudatella</i> spp. (-)	-			Relyea et al. 2000, Hawkins 1984
	+	0.31 (0.79)	0.65	
<i>Chironomidae</i> (+)	-	-29.1 (11.0)	0.99	Waters 1995
<i>Chironominae</i> (-)	-	-18.3 (6.3)	0.004	Angradi 1999
<i>Cinygmula</i> spp. (-)	+	1.34 (1.13)	0.88	Relyea et al. 2000
<i>Dicranota</i> spp. (+)	-	-0.34 (0.15)	0.98	Relyea et al. 2000
<i>Drumella doddsi</i> (-)	-			Relyea et al. 2000, Hawkins 1984
	+	0.062 (1.22)	0.52	
<i>Epeorus</i> spp. (-)	-	-4.95 (5.57)	0.19	Relyea et al. 2000
<i>Glossosoma</i> spp. (-)	+	1.20 (0.80)	0.92	Relyea et al. 2000
<i>Hesperoperla pacifica</i> (-)	-	-0.60 (0.52)	0.13	Relyea et al. 2000
<i>Hexatoma</i> spp. (+)	-	-0.026 (0.255)	0.54	Relyea et al. 2000
<i>Isoperla</i> spp. (+)	-	-0.66 (0.76)	0.80	Relyea et al. 2000
<i>Lepidostoma</i> spp. (+)	-	-3.59 (3.13)	0.87	Relyea et al. 2000
<i>Malenka</i> spp. (+)	+	0.32 (0.43)	0.76	Relyea et al. 2000
<i>Neophylax</i> spp. (-)	-	-0.13 (0.60)	0.59	Relyea et al. 2000
Oligochaeta (+)	+	1.19 (0.56)	0.023	Waters 1995
<i>Optioservuis</i> spp.(+)	-	-0.63 (0.37)	0.95	Relyea et al. 2000
<i>Rhithrogena</i> spp. (-)	+	4.45 (2.44)	0.96	Relyea et al. 2000
<i>Rhyacophila</i> Betteni grp. (-)	-	-0.20 (0.50)	0.65	Relyea et al. 2000
<i>Rhyacophila</i> Hyalinata grp. (-)	-	-0.17 (0.27)	0.27	Relyea et al. 2000
<i>Simulium</i> spp. (+)	+	0.06 (0.41)	0.56	Relyea et al. 2000
<i>Zapada cinctipes</i> (+)	+	0.03 (2.32)	0.51	Relyea et al. 2000
<i>Zapada columbiana</i> (+)	+	0.58 (0.75)	0.22	Relyea et al. 2000

al. (2000) as being very intolerant to 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. *Attenella delantala* had the most upstream distribution of 12 species of Ephemeroptera in the McKenzie River, Oregon, but was commonly found in patches of sand and gravel < 20 mm diameter (Hawkins 1984), suggesting a preference for fine sediment. As discussed

above, Angradi (1999) also found that Chironominae exhibited a strong negative response to fine sediment. Most oligochaetes are obligate burrowers in fine sediment; they are often reported to increase in abundance with fine sediment additions, although one group of Oligochaetes, the Lumbricina, are considered moderately intolerant (Relyea et al. 2000).

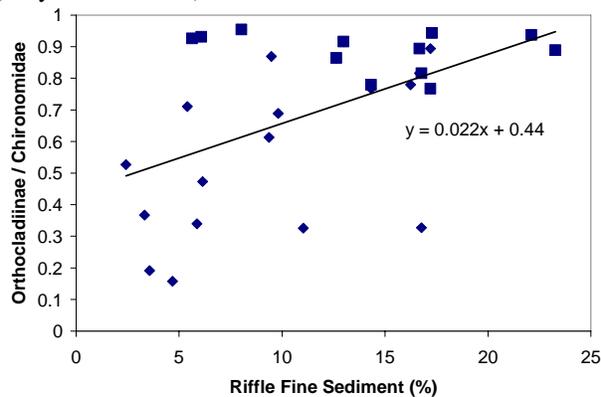


Figure 3 Fraction of Chironomidae composed of Orthocladiinae versus percentage of riffle bed surface covered by fine sediment.

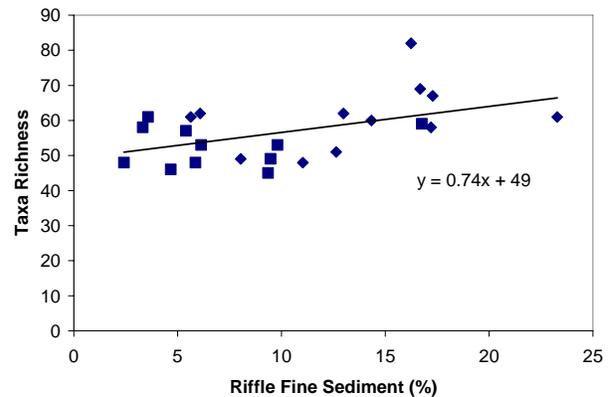


Figure 4 Benthic macroinvertebrate taxa richness versus percentage of riffle bed surface covered by fine sediment.

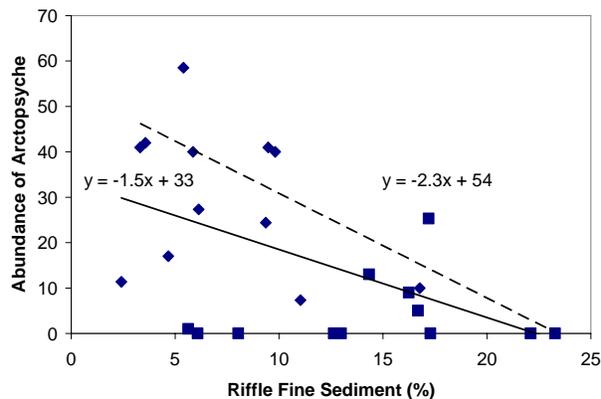


Figure 5 Abundance of *Arctopsyche* versus percentage of riffle bed surface covered by fine sediment. Two models are presented, a linear regression (solid line) and a partitioned linear regression (dashed line).

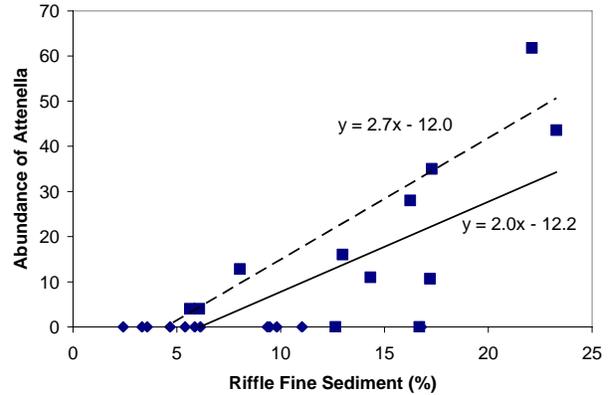


Figure 6 Abundance of *Attenella* versus percentage of riffle bed surface covered by fine sediment. Two models are presented, a linear regression (solid line) and a partitioned linear regression (dashed line).

CONCLUSIONS

Estimates of sediment supply from quantitative models and V^* measurements suggests that sediment delivery to streams in the Klamath Mountains has increased several times over background rates in some drainage basins. Increases in sediment supply in steep, mountain streams can result in predictable increases in fine sediment in pools and riffles. Precise quantification of these relationships is hampered by the difficulty in accurately measuring sediment delivery to stream channels over decadal time scales, however. V^* , bed surface fine sediment, and excess transport capacity all are potentially useful indicators for linking hillslopes and biota because they respond predictably to increased sediment supply and result in direct biological consequences.

The effects of increased sediment supply on benthic macroinvertebrate communities are more subtle than the effects of water quality impacts from urbanization or agriculture. Diversity and tolerance metrics that are useful for detecting the effects of water chemistry pollutants may not be useful for assessing the ecological impacts of increased sediment supply. Benthic invertebrate taxa such as Chironominae, Oligochaeta, *Attenella*, and *Arctopsyche* respond predictably to levels of fine sediment and offer potential for improved monitoring and increased understanding of stream ecosystems. The quantitative relationships described in this study add to our

understanding of the linkages between hillslopes, stream channels, and aquatic biota and identify areas where process-based understanding can be improved.

ACKNOWLEDGEMENTS

The field crew was led by Sue Maurer and composed of Jeremy Warner, John Bowman and Wind Beaver. Don Elder served as the KNF liaison and worked with the field crew. Juan de la Fuente (KNF) developed the landslide and surface erosion models and provided assistance with the study design. Al Olson (KNF) and Brian Staab (USFS Regional Office) provided project leadership and oversight. Tom Lisle (USFS Redwood Sciences Lab) provided insight that improved the study design and Sue Hilton (USFS Redwood Sciences Lab) trained the crews in measuring V*. The USFS funded this research in the form of a grant to W.E.D. and V.H.R.

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