COMPOSITION OF THE SUSPENDED LOAD AS A MEASURE OF STREAM HEALTH

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PROJECT SUMMARY:

Objectives of this exploratory research were: 1) to characterize the contribution of size-specific and total concentrations of organic and inorganic components to the suspended load during high and low flow periods in 4 streams in coastal northern California; and 2) to evaluate relationships between composition and nutritive quality of the suspended load with feeding efficiency and condition of salmonid fishes and the abundance of their invertebrate prey. In addition, we conducted laboratory feeding trials to evaluate the effects of suspended sediment concentration, organic: inorganic particle ratios, and their interaction on feeding rates of juvenile steelhead trout. Two levels of suspended sediment concentration (producing turbidities of approximately 25 and 50 NTU's), and three levels of organic: inorganic particle ratios (25,50, and 75% organic suspended sediments) were tested.

Suspended sediments, macroinvertebrates, and salmonids were sampled from 200-m reaches in North Fork Caspar and South Fork Caspar creeks (Caspar Creek basin in Mendocino County), and Little Lost Man and Upper Prairie creeks (Redwood Creek basin in Humboldt County) in three high flow and three low flow periods from October 2002 through December 2003. Stream sites differed in size and in riparian vegetation and land use history, and were chosen to represent a range of discharge and suspended load conditions.

Masses of organic and total suspended sediments (mg/L) were greater at high than at low flows. Within the size particle range of > 0.7 - 1µm , but not in the >1 µm – 1mm range, flow categories also affected both mass and percentage of organic suspended sediments. However, in the >1 µm – 1mm range, total suspended sediments were greater at high than low flows. Mass and percentage of organic sediments (total or by particle size class) did not detectably differ among the 4 streams or with a site*flow interaction. The total suspended load was moderately predicted by turbidity, but the addition of the percentage of organic particles did not improve the model fit. The percentage of organic suspended sediments was weakly correlated with turbidity. The contribution of algal particles, indexed by chlorophyll *a* concentration in suspension, to the suspended load was greatest in the reach where canopy coverage was least, but did not differ between high and low flow periods. In contrast, microbial respiration associated with organic sediments was greater at low than at high flows, but did not differ among sites.

Macroinvertebrate biomass was not predicted by mass or percentage of organic sediments. Biomass of filtering collectors was modestly positively related to chlorophyll concentration of the suspended load. The interaction of site and flow also affected the biomass of filtering collectors. At high flows, filtering collector abundance was greatest in the most pristine of the

sites (Upper Prairie Creek). The percentage of drifting macroinvertebrates (drift/ benthic + drifting invertebrates), by mass, was modestly related to the suspended load of organic particles, but not to the total suspended load.

Gut fullness and feeding activity of juvenile salmonids were not affected by mass or percentage of organic suspended sediments, and they did not detectably vary among sites or high and low flows. Underwater observations were made of at least some feeding activity at each site on each of the sampling dates, at turbidities ranging from 4 – 123 NTU, although salmonids available for observation were much more sparse at higher turbidities. Condition of coho salmon at the end of the overwinter period did not differ among sites. In lab feeding trials, individual steelhead consumed twice as many prey under low than high suspended loads, but differing fractions of organic particles within the suspended load did not affect their efficiency of prey consumption.

Although this study failed to detect a response by salmonid fishes or their invertebrate prey to the organic component of the suspended load, it is premature to dismiss the potential importance of organic sediments in affecting stream biota for at least two reasons. First, organic sediments provide food for filtering and gathering-collector invertebrates that are often common in fish diets. Second, because organic particles weigh less than do inorganic particles of the same size, organic particles likely contribute differentially to turbidity, which may affect both fish feeding efficiency and in-stream primary production. Biotic response is likely better revealed in time-integrated sampling than in small numbers of point samples of the suspended load. We recommend continued study of biotic response to organic and inorganic components of the suspended load, and inclusion of the organic fraction of the sediment load in analyses of suspended-sediment concentrations conducted for stream monitoring programs.

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INTRODUCTION

For over three decades, geologists, hydrologists and stream ecologists have shown significant interest in suspended load in running waters (e.g. Waters 1995). Physical scientists have focused on development of sediment-rating curves and estimation of sediment yields, often as an indicator of changing land uses (e.g. Beschta 1996). Over the same period, the interest of stream ecologists on sediments has often focused on the role of suspended sediments in water quality degradation, for example its deleterious impacts on biological communities (e.g. Waters 1995). However, stream ecologists have also studied the beneficial roles of the suspended load, or its surrogate turbidity) in providing basal resources to fluvial food webs and as the major pathway of organic matter transport that links upstream and downstream reaches (Minshall et al. 1983, Minshall et al. 1985, Wallace et al. 2006). The organic carbon portion of turbidity has been modeled, along with other components, as nutrient spiraling, in which materials are continuously taken up by stream biota, released, and transported downstream (e.g. Webster and Patten 1979, Webster and Valett 2006). Differences in the focus of studies on suspended load between physical and biological scientists have resulted in very different methodologies. In most cases, physical scientists have removed organic components in suspended load samples by ashing or chemical digestion, and they have discarded data on the organic fraction (ash- free or carbon digested). However, stream ecologists, while concentrating on the importance of the organic fraction of suspended load as a food resource for aquatic macroinvertebrates, have discarded information on the mineral fraction (ash or digestion residue). When data are reported on suspended load, derived from turbidity readings, it is seldom made clear whether reported values have been “corrected” for the organic fraction or whether, as is the usual case, both inorganic and organic components of the sample are combined as dry mass.

Failure to distinguish between organic and inorganic components of the suspended load or to consider the full suite of information present in suspended sediment samples has hindered full understanding of sediment dynamics as it affects stream health and reflects watershed condition (e. g. Minshall 1996). For example, because organic sediments remain in suspension longer than do similarly sized inorganic particles, and therefore ultimately contribute more to turbidity, they may have a greater overall effect on light reduction. An increased proportion of suspended organic sediments would be expected to reduce light penetration to the stream bottom over a longer period and could result in decreased primary production This could lead to a loss of macroinvertebrate scrapers that feed on periphytic algae. At the same time, an increased proportion of organic suspended sediments, in the appropriate size range and of sufficient quality, may benefit filter-feeding invertebrates (filtering collectors; Wallace and Merritt 1980, Benke et al. 1984). Deposition of organic sediments may enhance food resources for the gathering collectors, which feed within the benthos. Along with some scrapers, filtering and gathering collectors are often important prey items in the diets of juvenile anadramous and resident salmonids and other drift-feeding fishes. At present, the net effect of suspended organic: inorganic ratios on prey availability for fish is not known. Apart from effects on fish through their food base, the effect of an increased percentage of suspended organic sediments on light attenuation would also directly impact fish because of reduced visibility that would impact their feeding efficiency and feeding rate (Sweka and Hartman 2001a). This in turn could result in depressed growth rate of the fish (e.g. Barrett et al. 1992, Sweka and Hartman 2001b).

The particle size distribution of the suspended load (turbidity) is another important attribute that usually is not explored in analyses of suspended sediments. The majority of organic particles transported by most streams during baseflow conditions are < 50 µm in diameter (Sedell et al 1978, Naiman and Sedell 1979a & b, Wallace et al 1982), although in some cases, seston particle size varies with stream size. Wallace et al. (1982) showed that smaller headwater streams draining forested areas have larger median seston particle sizes than larger rivers downstream. While particle size composition of the mineral sediment portion provides insight into sediment transport hydraulics and likely sediment source areas, the particle size distribution and qualitative nature (e.g. microbial activity and relative amounts of plant, animal, and detrital material) of the constituents of the organic fraction of the suspended load may predict the response of macroinvertebrate filtering or gathering collectors. The organic fraction of the suspended load, or seston, is generally composed of fine particulate organic matter (FPOM) in the size range of > 0.45 µm to < 1000 µm (1 mm), with size fractions sometimes further subdivided into categories of medium-large (250 – 1000 µm), small (100-250 µm), fine (45-100 µm), very fine (25-45 µm), and ultrafine (0.45-25 µm). FPOM originates from a variety of sources, including mechanical breakdown of larger particles, animal consumption, microbial processes, flocculation of dissolved organic matter, and terrestrial inputs (Wotton 1984). The source and nutritional value of FPOM varies among size fractions. Generally, bacterial cells fall within the ultrafine fraction, macroinvertebrate feces within fine or larger fractions, algal detritus in the small fraction, and small leaf fragments within the medium-large fraction (Bisson and Bilby 1998). Small filtering collectors, such as blackflies (Diptera: Simuliidae), philopotamid caddisflies (Trichoptera), and certain chironomids (Diptera) such as *Rheotanytarsus*, are not selective of the quality of seston that they harvest, but select food only on the basis of particle size (Cummins and Klug 1979). For example, the majority of particles ingested by larval blackflies are < 10 µm (Merritt et al. 1982), on the component of the seston that is most nutritionally consistent and abundant component (Wallace et al. 1982). Other filtering collectors, including hydropsychid caddisflies (Trichoptera), feed on particles several hundred or larger micrometers, in a seston range that is more nutritionally variable . Evidence exists that this group may exhibit selectively capture larger particles (Edler and Georgian 2004, Brown et al. 2005). Inasmuch as the suspended load reflects the smaller particle component of the bed load, attributes of the organic fraction may also affect the response of the gathering collectors. We suggest that separation of suspended load material into inorganic and organic fractions, and detail on the particle size distribution of both fractions, together with qualitative aspects of the organic fraction, would provide a far greater resolution of physical and biological conditions relevant to juvenile salmonids and their prey base in a watershed than is currently available.

Objectives of this research were: 1) to characterize the contribution of size-specific and total concentrations of organic and inorganic components to the suspended load during high and low flow periods in 4 streams in coastal northern California; and 2) to evaluate relationships between composition of the suspended load with feeding efficiency and condition of salmonid fishes and the abundance of their invertebrate prey. Suspended sediments, macroinvertebrates and salmonids were sampled from two stream sites each within the Caspar Creek (Mendocino County), and Redwood Creek (Humboldt County) basins in coastal northern California over a two year period.

METHODS

STUDY SITES

Study sites within the Caspar Creek basin included North Fork Caspar Creek and South Fork Caspar Creek. These are tributaries in the headwaters of the 21.7km^2 Caspar Creek basin, situated within the Caspar Creek Experimental Watersheds in the Jackson Demonstration State Forest. Study sites within the 725 km^2 Redwood Creek basin included Upper Prairie Creek (UPC) and Little Lost Man Creek (LLM). Both sites are within the Prairie Creek watershed, which is tributary to Redwood Creek within the lower third of the basin. Upper Prairie and Little Lost Man creeks are within the boundaries of Redwood National and State Parks. Study sites were selected that were fish-bearing, for which records of continuous water discharge and periodic suspended load were available, and that offered the opportunity to explore effects of riparian composition and catchment area on composition of the suspended load. The North and South Forks of Caspar Creek are of equivalent catchment area, but differ in that riparian composition is dominated by second growth conifers in the North Fork and by red alder (*Alnus rubra*) and other hardwoods in the South Fork. The catchment areas of Little Lost Man and Upper Prairie creeks are each approximately twice as large as those of the North and South Forks of Caspar Creek, with riparian vegetation dominated by old-growth conifers. Salmonid fishes in each creek included steelhead (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*). In Little Lost Man and Upper Prairie creeks, cutthroat trout (*Oncorhynchus clarkii*) were also found within the reaches.

Both the Caspar Creek and Redwood Creek basins are within a geologic province characterized by some of the highest rates of erosion in the United States (Brown and Ritter 1971, Milliman and Meade 1983). High erodibility results from inherently weak rock units situated in a tectonically active area with a Mediterranean climate (Nolan et al. 1995). In both basins, extensive timber harvest activities have accelerated naturally high rates of erosion. Both basins are underlain by rocks of the Franciscan assemblage. Dominant rock types in Caspar Creek are well consolidated marine sedimentary sandstone with intergranular clay, silt, and feldspatic sandstone (Cafferata and Spittler 1998). In Redwood Creek, the Grogan fault bisects the basin, juxtaposing sedimentary rocks to the east against metamorphic rocks to the west (Pitlick 1995).

Forest vegetation in Caspar Creek and the lower Redwood Creek drainage is dominated by coast redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menzieii*), with an understory of evergreen huckleberry (*Vaccinum ovatum*), Pacific rhododendron (*Rhododendron macrophyllum*), and sword fern (*Polystichum munitum*). Virgin forest in the Caspar Creek basin was extensively logged in the late 1800's; logging of second-growth began in the 1960's. The entire watershed of South Fork Caspar Creek was selectively harvested and tractor yarded in 1971-1973. The watershed of North Fork Caspar Creek was clearcut logged (46%) in large patches during 1989-1991. Commercial timber harvest in the Redwood Creek basin did not begin until the 1930's (Best 1995). Twenty percent of the basin, nearly all of it within Redwood National and State Parks, remains as uncut virgin forest. Of the two Redwood Creek sites, Upper Prairie Creek is the most pristine, as Little Lost Man Creek contains evidence of an historical debris flow.

Sites in both basins lie within a predominantly maritime climate with warm, dry summers and cool, wet winters. Average annual precipitation is 120 cm (Caspar Creek) and 170 cm (Prairie Creek State Park), with most occurring as rainfall between October and April. This study was conducted from October 2002 through December 2003, during water years that experienced average precipitation based on a 70-y record at Prairie Creek Redwoods State Park. Recurrence intervals for peak flows in Little Lost Man Creek were 2 and 25 y for water years (Oct 1 – Sep 30) 2002 and 2003, respectively. Recurrence intervals for peak flows in the Caspar Creek drainage were 1.5 and 2.5 y respectively for these same years.

A 200-m study reach was established in each stream within the vicinity of previously established gauging stations. At each site, stream gradient over lengths of about 30 bank full widths and one to three cross sections were surveyed using standard surveying equipment. Percent canopy cover was measured at each cross section with a spherical densitometer. Dominant overstory riparian vegetation type and substrate size categories (following Cummins 1964) were estimated by visual inspection. Site characteristics are described in Table 1.

FIELD SAMPLING

Each study reach of Upper Prairie Creek, Little Lost Man Creek, North Fork Caspar Creek and South Fork Caspar Creek was sampled six times between October 2002 and December 2003, with 3 sampling events during times of low flows (< 1 cfs in North and South Fork Caspar Creeks, < 4 cfs in Little Lost Man Creek, and ≤ 10 cfs in Upper Prairie Creek), and 3 sampling events during higher flows (Table 2). A sampling event included collections of the suspended load, benthic and drifting macroinvertebrates, and juvenile salmonids. Underwater observations by snorkeling were also made of salmonid feeding behavior.

The suspended load at the time of biological sampling was measured from water samples collected with a 1-liter Horizontal Beta Plus™ grab sampler. Water samples were collected at 0.6 depth within the thalweg at three randomly chosen locations within the 200-m reach.

Current velocity at each location was measured with a Marsh-McBurney™ digital flowmeter. After collection, a sample was poured into a sealed, black 1-liter container that was continuously stirred with a magnetic stirrer to keep particles in suspension. Turbidity (NTU), chlorophyll *a* (mg/L, measured as fluorescence), and dissolved oxygen (DO, in mg/L), were measured with a YSI 6600™ sonde. DO measurements were tracked over a 5-min period to estimate microbial respiration, expressed as O_2-mg · L^{-1}· min^{-1}, from reductions in DO concentrations. Each sample was separated into inorganic and organic fractions. The organic fraction was decanted off, and the two fractions were placed in containers with distilled water added to bring volumes back to 1 liter. Samples were re-suspended with the magnetic stirrer, and DO and turbidity were again measured. Water samples were shielded from ambient light sources with black plastic sheeting and continuously stirred with an enclosed battery powered magnetic stirrer during measurements. Samples were saved on ice in a cooler, and brought to the lab for analysis of the mass of organic and inorganic fractions and particle sizes.

Suspended sediment samples were analyzed at the Soil Sciences Laboratory on the Humboldt State University campus to measure ash-free dry mass (AFDM) of size-specific organic and inorganic fractions of the suspended load. Particles > 1mm in diameter were removed by filtering a sample through a 1 mm sieve. Samples were then filtered through pre-weighed 1.0 µm and 0.7 µm glass fiber filters using a vacuum pump, and filters were oven-dried at 50 °C for 24 h, dessicated for 24 h, and weighed on an analytical balance (± 1 µg). Dry-weighed samples and filters were ashed in a muffle furnace at 550 °C, rewetted with distilled, deionized water to restore waters of hydration, and oven-dried (50 °C for 24 h), dessicated (24 h), and weighed on an analytical balance. Masses obtained provided measures of AFDM of the organic load (dry mass – ash mass) and inorganic load (ash mass) for each particle size range (>0.7 – 1 µm, and >1-1000µm), in mg/L . The choice of particle size ranges was constrained by availability of filter sizes.

Macroinvertebrates were sampled with a collection device designed by Cummins and Wilzbach to separately sample drifting and benthic macroinvertebrates from the same location (Fig. 1). The sampler was a square plexiglass box (0.18 m^2) with a center divider. A 5 cm flange around the outside of the box and a 2.5 cm flange on the bottom of the center divider had an attached layer of foam that provided a seal with the substrate when the box was in sampling position. The front of the box had a large panel of 250 µm mesh screening to allow current to pass through both sides of the box and out two ports, one on each side at the rear of the box. Each port was fitted with a cylinder onto which a 250 µm mesh, 1-m long drift net was fitted. Wing deflectors positioned on the front of the box increased flow through the front mesh panels. Two partitioning samplers were positioned within a reach on each sampling event, with drift nets attached that collected drift for a 1 hr period at dusk. Current velocity was measured at the mouth of the drift net ports at the end of the sampling period. After 1 h, the nets (n = 4) were removed and the contents of each washed onto a 250 µm sieve. Samples were transferred to a sample container, labeled, and preserved with 70% ethanol. Drift nets were then repositioned on the sampler, and the bottom sediments enclosed on each side of the partitioning sampler were disturbed, including hand washing the cobbles, to dislodge invertebrates into the attached nets (n = 4). The sampling device allowed for replicated comparison of drift and benthos collected from the same confined area, with the first set of nets collecting animals drifting from the known area of bottom, and the second set representing animals that did not drift during the drift-sampling period. Preserved animals were returned to the laboratory, where they were sorted under a dissecting microscope, identified, measured, and assigned to functional feeding groups of scrapers, shredders, predators, filtering collectors and gathering collectors following the designations in Merritt et al. (2008). Taxonomic resolution was at the level of genus where possible, or higher levels. Individual body lengths were converted to estimates of dry mass using taxon-specific relationships based on unpublished data of Cummins and Wilzbach (Appendix B).

To assess the feeding activity of salmonid fishes, we snorkeled each 200 m reach for a 30 minute period during daylight hours. Microhabitats (e.g. pools) that were found to hold two or more salmonids were observed for 3-minute periods each. Individuals were enumerated and the total number of prey captures observed by all individuals within a microhabitat during an observation session was recorded to determine mean prey captures per individual per minute. Individuals were not identified to salmonid species during the observations.

Following the period of underwater observation, juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) within each reach were captured with a backpack electro-shocker to collect a sample of individuals for assessment of fish condition and diet analysis by gastric lavage. Reaches were not systematically sampled. Rather, our goal was to obtain at least 10 fish for diet analysis from each of the six sampling events, and at least 50 individuals for assessment of fish condition during sampling events in October 2002 and June 2003. Condition measured in October provided an indication of growth potential during low flows of the previous summer, while condition measured in June suggested growth potential during the previous winter and spring high flow periods. Following capture, fish were anaesthetized with Alka-Seltzer™ tablets prior to measuring fork length to the nearest mm, and wet mass to the nearest 0.01g. Gut contents were sampled by gastric lavage, and fish were returned to the site of capture after they had recovered from CO_2 anaesthesia and handling. Gut contents were collected on a 250 µm mesh sieve, preserved in 70% ethanol, and returned to the laboratory for sorting and identification. Macroinvertebrates in gut contents were identified, measured, and classified by functional feeding group under a dissecting microscope. Diet samples from steelhead and coho salmon were pooled for analysis. Coho salmon dominated the salmonid assemblage in each site, comprising 65% (n = 216), 83% (n = 315), 58% (n = 390), and 86% (n = 297) of salmonid numbers in North Fork Caspar, South Fork Caspar, Little Lost Man, and Upper Prairie creeks, respectively.

DATA ANALYSIS

Suspended sediment composition was characterized by a) organic and inorganic mass, and b) the percentage of organic particles by mass. The effects of site (n = 4), flow category (low and high), and the interaction of site and flow on response variables were analyzed by 2-way ANOVA for each particle size category (0.7-1µm and 1 – 1000 µm) and the total sediment sample . To meet assumptions of normally distributed variables, organic and inorganic mass were $\log_{10}$ transformed, and the percentage of organic particles was transformed with an arcsine square root transformation. As land use managers are often interested in the ability of turbidity to predict the suspended sediment load, we explored the relationship between turbidity and total suspended sediment concentration by linear regression. Turbidity and total suspended sediment concentration were $\log_{10}$-transformed. We also evaluated the correlation between turbidity and percentage of organic suspended sediments, and asked whether the addition of percentage of organic sediments improved the fit of the predictive model for suspended sediment concentration.

Nutritional quality of the suspended sediment load for stream macroinvertebrates was assessed by comparing effects of site and flow on a) microbial respiration per gram of organic sediment, and b) chlorophyll *a* concentration. We compared microbial respiration per liter on organic and inorganic fractions of the suspended load with a paired t- test. Chlorophyll *a* concentrations were examined in relation to canopy coverage of the reaches. We evaluated the correlation between microbial respiration and chlorophyll a concentration of suspended sediments to test the hypothesis that the relationship between allochthonous (i.e. respiration) and authochthonous (i.e. chlorophyll) energy sources in flowing water ecosystems is inverse (Cummins and Wilzbach 2008).

Macroinvertebrate response variables included biomass, in g/m^2, of filtering collectors, all collectors (filtering + gathering collectors), scrapers, and all macroinvertebrates, and the percentage of drifting invertebrates by mass (drifting/ drifting + benthic invertebrates). Functional group biomass variables were log-transformed to meet normality assumptions; the percentage of drifting invertebrates was arcsine-transformed. We tested hypotheses that biomass of filtering collectors and other functional feeding groups could be predicted by mass (log-transformed) and percentage of organic suspended particles (arcsine-transformed) using least-squares linear regression. We also evaluated relationships between biomass of filtering collectors and nutritional quality (microbial respiration and chlorophyll content) of the suspended load. Effects of site, flow, and a site*flow interaction on biomass of functional groups and all macroinvertebrates were analyzed by 2-way ANOVA. We analyzed relationships between the percentage of drifting invertebrates with the total suspended load and with the organic suspended load.

Fish response variables included a) feeding activity, measured as number of prey captures per minute per individual; b) gut fullness, measured as mg invertebrates in gut contents per gram of fish; and c) fish condition. Relationships between gut fullness and feeding activity with turbidity, mass of organic suspended sediments, or percentage of organic suspended sediments were analyzed by least-squares linear regression. Effects of site and flow were analyzed using 2-way ANOVA. Differences in fish condition among sites and sampling dates were analyzed by comparing slopes and intercepts of log-transformed length-weight regressions. Analyses of fish condition were restricted to coho salmon, as sample sizes of steelhead from some sampling events were too small to be legitimately analyzed.

FLUME EXPERIMENT OF FISH FEEDING EFFICIENCY

The effect of suspended sediment concentration and organic: inorganic particle ratios on feeding rates of juvenile steelhead trout were measured in short-term feeding trials conducted in artificial stream channels located outdoors at the Humboldt State University (HSU) fish hatchery. Trials were conducted at two levels of suspended sediment concentration, and three levels of organic: inorganic ratios. Suspended sediment concentrations were high (averaging 0.54 mg/L, SD = 0.38), producing turbidities ranging between 44-67 NTU; or low (averaging 0.22 mg/L, SD = 0.11), producing turbidities ranging between 24-31 NTU. Organic to inorganic particle ratios varied as 0.75 to 0.25, 0.50 to 0.50, and 0.25 to 0.75 by dry mass. Each treatment combination was replicated 5 times (number of trials = 30). During a feeding trial, live invertebrate prey were introduced to an experimental arena containing a solitary trout. The number of prey captured and consumed by the trout during a 3-minute period was determined.

Five artificial channels used for feeding trials were each 9 m long, 0.41 m wide, and 0.19 m deep. Each channel had a reservoir with a submersible pump that re-circulated filtered water derived from Fern Lake, which supplies freshwater for the hatchery facility. Ambient water temperatures ranged from 14-16 ° C during the trials. The channels were covered with 1 cm mesh plastic screening to exclude the introduction of plant debris and terrestrial invertebrates from the surrounding vegetation. Feeding trials were conducted within a 1.5 m section of each channel, which was bounded with 3 mm mesh screening at the upstream and downstream end. Velocity through the experimental section was 8.0 cm/s.

Turbidity was created in the channels by introducing mixtures of inorganic and organic particles. Clay (bentonite) < 62 µm in diameter was used as the source of inorganic particles and alder leaf fragments were used as the source of organic particles. Organic particles were prepared from leached and dried leaves that were ground to pass through a 62 µm sieve. Pumps that re-circulated the water in the flumes maintained the particles in suspension and the resulting turbidity (NTU) was continuously measured with a YSI™ 6600 sonde throughout a feeding trial.

Juvenile steelhead used in the experiments were provided by the HSU hatchery, and ranged in size from 85 to 97 mm fork length (mean = 90 mm; SD = 3). Fish were held without food in the artificial channels at 14-16 ° C during a 5-day acclimation period prior to the beginning of trials. Pilot studies established that the trout began feeding on live *Gammarus* after a 5 day period. Each fish was used in only one feeding trial. During a trial, fish were offered live amphipods (*Gammarus* sp.). Amphipods were collected from Prairie Creek (Redwood National and State Park near Orick, CA) and cultured in aquaria at the HSU hatchery. Mean body length of *Gammarus* used in feeding trials was 5 mm (SD = 0.3).

Feeding trials were conducted between 0700-900 h in August 2003. Sixty amphipods were introduced to a channel in groups of 5-10 individuals at the beginning of a trial. Prey were released into the upstream end of the experimental section of a channel, and they drifted in the water column through the section. At the termination of a trial, each test fish was captured and its stomach contents were sampled by gastric lavage to determine the number of *Gammarus* ingested. Feeding activity of the fish was also filmed using an Aqua-View ™ underwater camera connected to a videorecorder.

Number of prey captured by the steelhead during trials was subjected to a two-way analysis of variance having two levels of suspended sediment concentration (low, high), and three levels of percentages of organic particles (25,50, and 75%). Effects were determined to be significant at the 0.05 significance level.

RESULTS

CHARACTERIZATION OF THE SUSPENDED LOAD

Mass of both total and organic suspended sediments differed between low and high flow periods ($F_{1,16}$ = 9.42, P = 0.01 for total suspended sediments; $F_{1,16}$ = 4.87, P = 0.04 for organic seston), but not among sites or the interaction of site and flow (all $P \geq 0.50$). Concentrations of organic and inorganic components were greater during high than low flows. Total suspended sediments averaged 6.7 mg/L (SD = 3.7, n = 12) at low flows among the 4 sites, and 19.5 mg/L (SD = 14.5, n = 12) at high flows. Organic seston averaged 3.17 mg/L (SD = 3.01, n = 12) during low flows, and 9.22 (SD = 7.92, n = 12) at high flows (Fig. 2). Neither site nor flow had a detectable effect on the (arcsine-transformed) percentage of organic sediments by mass (all $P >$ 0.3). The percentage of suspended sediments composed of organic particles averaged 53% (SD = 34, n = 24), over a range extending from 0.3 to 100%.

Response of total and organic suspended sediments to flows differed among size classes. In the particle size range of 0.7 µm – 1.0 µm, flows affected both mass and percentage of organic particles ($F_{1,16}$ = 5.09, P = 0.04 for mass and $F_{1,1,6}$ = 5.48, P = 0.03 for percentage organics). Concentrations of organic seston were greater during high than low flow periods (average = 0.42mg/L, SD = 0.32, n =12 at low flows, and 1.35 mg/L, SD = 2.05, n = 12). Within this size range, organic particles averaged 40% (SD = 29) of the total suspended load by mass at low flows, and 70% (SD = 37) of the total load at high flows. Neither site nor site*flow interaction were significant (all $P \geq 0.22$). Within the particle size range of >1.0 µm – 1.0 mm, neither mass nor percentage of organic particles were affected by flow period, site, or their interaction (all $P \geq 0.18$). However, effects of flow (but not site or a site*flow interaction) were significant for total suspended sediments ($F_{1,1}$6 = 12,04, P < 0.01). At low flows, total suspended sediments in this larger size class averaged 5.20 mg/L (SD = 3.97, n = 12); at high flows, total suspended sediments averaged 15.29 mg/L (SD = 9.16, n = 12).

Partitioning of the suspended load between size classes was similar between organic and inorganic sediments. Mass of inorganic sediments in the size range of >1.0 µm – 1.0 mm (mean = 4.93 mg/L) was greater than in the size range of 0.7 µm – 1.0 µm (mean = 1.96) (2-tailed paired t test, t = 2.71, df = 23, P = 0.01). Mass of organic sediments the size range of >1.0 µm – 1.0 mm averaged 5.31 mg/L, and was greater than the mass in the range of 0.7 µm – 1.0 µm (mean = 0.88) (t = -4.46, df= 23, P < 0.01).

Despite a small sample size (n = 24), the total suspended sediment load was moderately predicted by turbidity ($F_{1,22} = 17.34$, $p < 0.01$, $R^2 = 0.44$ on log-transformed variables; Fig. 3). The addition of the percentage of organic suspended sediments did not improve the ability of turbidity to predict the concentration of total suspended sediments (t = -1.032, $P = 0.31$). The percentage of organic suspended sediments was weakly correlated with turbidity (R = 0.27). In this study, the US EPA (1986) recommended maximum turbidity of 25 NTU was exceeded on 2 of 6 sampling events (Jan and Apr 2003) in the North and South Forks of Caspar Creek, and on 1 of 6 sampling events (Nov/Dec 2003) in Little Lost Man and Upper Prairie creeks.

Microbial respiration was greater in association with organic (mean = 0.39 mg O_2 consumed $min^{-1}L^{-1}$, SD = 0.10) than inorganic (mean = 0.21, SD = 0.23) suspended sediments (1-tailed *t* test, df = 23, $p < 0.01$). Per mg of organic sediments, respiration differed between high and low flow periods ($F_{1,16} = 7.28$, $P = 0.02$, $R_2 = 0.36$), but not among sites or the interaction of site and flow (all $P > 0.73$). Respiration was greater during periods of low flow (mean = 0.22 mg $O_2 min^{-1}$mg organic sediments^{-1}, SD = 0.16) than high flow (mean = 0.08, SD = 0.10). In contrast, concentrations of chlorophyll *a* differed among sites ($F_{3,16} = 4.22$, $P = 0.48$), but not among flow categories or the site*flow interaction (all $P > 0.29$). Chlorophyll *a* concentration in suspended sediments was greatest in Upper Prairie Creek, where canopy coverage was least (Fig. 4). We observed a negative correlation between chlorophyll and respiration at the same site (R = -0.48, n = 24, Fig. 5).

MACROINVERTEBRATES

Characteristics of the suspended load were not detectably related to macroinvertebrate assemblages. Macroinvertebrate taxa that were collected from the study sites are listed in Appendix 1. Contrary to our hypothesis, biomass of filtering collectors was not related to either mass of organic suspended sediments ($R^2 = 0.00$, $P = 0.93$) or to percentage of organic suspended sediments ($R^2 = 0.05$, $P = 0.31$). Nor did data suggest relationships between mass or percentage of organic suspended sediments with biomass of scrapers, total collectors (gathering and filtering collectors), or the entire macroinvertebrate assemblage (all $R^2 < 0.10$, $p > 0.20$). Mass of the total suspended load (inorganic plus organic) also did not explain variation in biomass of macroinvertebrate assemblages.

Biomass of filtering collectors was modestly positively related to the chlorophyll concentration of the suspended load ($R^2 = 0.20$, $P < 0.03$), but not to microbial respiration ($R^2 = 0.01$, $P = 0.61$). Filtering collector biomass also differed among sites ($F_{3,16} = 15.92$, $P < 0.01$), flow periods ($F_{1,16} = 14.76$, $P < 0.01$), and the interaction of site and flow ($F_{3,16} = 13.46$, $P < 0.01$). During low flow periods, differences in filtering collector biomass among sites were slight (Fig. 6). During high flow periods, filtering collector biomass was substantially higher in Upper Prairie Creek than in the other three sites. Larvae of the caddisflies *Chimarra* (Philopotamidae) and *Hydropsyche* (Hydropsychidae) were the primary contributors of filtering collector biomass at all of the sites. Biomasses of scrapers, total collectors, and all macroinvertebrates were not affected by site, flow, or their interaction (all $P > 0.06$).

The percentage of drifting macroinvertebrates (drift/ benthic + drifting invertebrates), by mass, was modestly related to the suspended load of organic particles ($R^2 = 0.41$, $P < 0.01$; Fig. 7), but not to the total suspended load.

FISH

Gut fullness of juvenile salmonids was not detectably related to turbidity, mass of organic suspended sediments, or percentage of organic suspended sediments (all $R^2 < 0.03$, $P > 0.43$). Gut fullness did not differ between sites, flow, or with a site*flow interaction (all $P > 0.54$). An average of 9 diet samples (SD = 3) were analyzed from each site on each date, with the exception of the February 2003 sample from North Fork Caspar Creek, when no fish were captured. Fish from which diet samples were obtained ranged in fork length from 70 – 144 mm. Over all dates and sites, gut fullness averaged 3.6 mg of prey per gram of fish (SD = 3.5, range = 0.25 – 14.96, n = 206). Fish diets were dominated by non-feeding invertebrates (pupae and adults of aquatic origin, as well as terrestrial taxa), and filtering collectors were the least represented functional feeding group by biomass (Fig. 8). Filtering collectors did not comprise more than 3% of any diet sample. Macroinvertebrate taxa identified from salmonid gut contents are described in Appendix A.

Feeding activity of juvenile salmonids was not related to turbidity, total suspended sediment load, or suspended organic sediments (all $R^2 < 0.12$, $p > 0.10$). Nor did feeding rates of fish vary consistently among sites or dates. Averaged over all sites and dates, fish were observed to make 0.5 captures per fish per 3 minute observation (SD = 0.3, range = 0.07 - 1.07, n = 24). Total number of fish observed within 10 pools of each reach on each date averaged 72 (SD = 49, range = 2-186), but fewer than 10 fish per reach were detected in January 2003 in North Fork Caspar and Little Lost Man creeks, and in April 2003 in South Fork Caspar Creek. However, at least some feeding activity was observed at each site on each of the sampling dates, at turbidities ranging from 4 – 123 NTU (Table 2).

Length-weight relationships for coho salmon among sites differed between October and June. In October, slopes of ln-transformed length-weight regression lines differed among sites (site*length interaction, $F_{3,214} = 2.68$, $P = 0.05$; Fig. 8A.), indicating that the effect of site on fish growth differed with fish size. In June, both slopes (site* length interaction $F_{3,207} = 0.47$, $P = 0.70$) and intercepts ($F_{3,207} = 0.58$, $P = 0.62$) of the length-weight relationships were similar among sites (Fig. 8B).

FLUME EXPERIMENT

Prey capture by individual steelhead in lab feeding trials differed between high and low total suspended sediments ($F_{1,24} = 48.70$, $P < 0.01$), but not among levels of organic: inorganic ratios ($F_{2,24} = 2.40$, $P = 0.11$). The interaction of total suspended sediments and organic: inorganic ratios was also not significant ($F_{2,24} = 0.08$, $P = 0.92$). Steelhead consumed twice as many prey at low than at high suspended loads (Fig. 10A). While average prey consumption appeared to be lower at a fraction of 25% than at 50 or 75% organic suspended particles (Fig. 10B), suggesting a greater deleterious impact of inorganic than organic materials on feeding efficiency, the difference in means was insufficient to override individual variation.

DISCUSSION

The high variability in concentrations and percentages of organic seston that we observed among sampling dates and sites likely reflects sample sizes too small to reveal any patterns that may exist. Variability in both total and organic suspended loads was greater during periods of higher than lower flows (e.g., Fig. 2). This may be attributable to differences in seston concentrations and composition that have been observed between leading and trailing edges of individual storm events. Several studies have reported increases in seston concentration during the rising limb of a storm events, and that peak concentrations usually occur before peak discharge (e.g. Webster et al. 1990, Wallace et al. 1991). Our sampling was limited because of logistical constraints in sampling stream biota concurrently with suspended sediments, and an inability to sample or observe biota during large storms. Finer resolution of temporal variability in suspended load concentrations and composition is best accomplished with automated sampling devices such as ISCO samplers. As a separate part of this study, we analyzed the organic composition of ISCO-taken storm samples collected at the study sites by the US Forest Redwood Sciences Laboratory (North and South Forks of Caspar Creek) and Redwood National and State Parks (Little Lost Man and Upper Prairie creeks) personnel. Preliminary analysis of this larger dataset supported a finding that organic content was higher on early rising hydrograph limbs, as well as on late falling limbs. Organic materials also tended to be more abundant in water samples collected during early-season storms. On an annual cumulative basis, most organic flux occurred during a few days of high flow. By weight, the inorganic component of suspended sediment dominated the annual sediment flux in three of the catchments, but organics represented more than half the suspended sediment load in the most pristine old growth redwood stream (Upper Prairie Creek, unpublished data). This is consistent with a finding of Webster and Golladay (1984) that percent ash (i.e., inorganic fraction) was positively related with long-term forest disturbance. However, they also reported a higher mass of organic seston in summer than in winter, which they attributed to biological activity. This is contrary to our finding (from point samples) of higher organic loads in winter high flows. It is important to note that automated suspended load sampling is usually terminated at low flows, which have very low turbidity values, at times when essentially the only particles in suspension are organic. Excluding this seasonal difference will always give an annual bias to inorganic sediment in the suspended load. This is particularly true if all comparisons are on a mass per volume basis.

While automated sampling should be employed to better characterize temporal variability in both organic and inorganic components of the suspended load, monitoring programs and analytic procedures currently in place may require design modifications. For example, the USGS National Water Quality laboratory considers sediment concentrations of <10 mg/L to be below reliable analytical capabilities. Thus a larger volume of sampled water, or combining of filters, may be required to increase sediment volumes. Estimation of organic content requires that sediment samples be processed immediately or kept chilled and in the dark to reduce microbial respiration or photosynthesis. Size fractions chosen for particle size analysis should be standardized among laboratories to allow for site comparisons.

Because organic particles remain in suspension longer than similar-sized inorganic sediments, we expected that the ability of turbidity to predict suspended sediment concentrations would be improved by the addition of percent organics to the model. Although conclusions are limited by a small sample size, our data did not support this expectation. However, we also note that assessing the relative roles of inorganic vs. organic particles in contributing to turbidity or suspended sediment concentrations is problematic when done on a mass per volume basis. Such a comparison needs to be made on a volume per volume basis (e.g. number of particles in a given size range per volume of water). After roughly separating the organic from inorganic particles by decanting, number of particles per volume could be determined by running samples through a Coulter counter. To our knowledge, this has never been done. Until such analyses are conducted, it will be difficult to accurately evaluate the relative importance of the organic portion of the suspended load to stream biota.

Our finding of greater masses of organic and inorganic particles in larger (>1 - 1,000 µm) than smaller (0.7 – 1.0 µm) size classes is inconsistent with literature reports that the majority of seston is in the smallest size fractions. Sedell et al. (1978) found that > 70% of particulate organic matter in transport was in the size range of 0.45 – 53 µm. In setting the lower limit of our analyses at 0.7 µm, we likely missed the bulk of sedimentary particles, and conclusions regarding size-class partitioning are likely immaterial. In this study, separation of size classes for analysis was constrained by filter availability and small volumes of our water samples. A more meaningful separation would distinguish size classes based on ranges of sizes used by differing taxa of filtering collectors, or that differ in nutritional quality. Wallace et al. (2006) suggested a minimum of three size fractions: 0.45 – 250 µm, 250-500 µm, and 500 - 1000 µm. They added that, because particle-size distributions are strongly skewed toward smaller size fractions, larger quantities of water (i.e. > 1 L) need to be sampled to obtain accurate concentration estimates for seston particle sizes > 250 µm.

Seston particle size rather than quality serves as the basis of food selection for macroinvertebrates in the collector functional group, including both gathering collectors (e.g. Mattingly et al. 1981, Ward and Cummins 1978, Ward and Cummins 1979) and filtering collectors. Because of this, it is likely that concentrations of organic seston or its surrogate turbidity will predict the food supply and abundance of collectors (especially filtering collectors) only when the quality of the suspended material is taken into account. The correlation we observed between biomass of filtering collectors with chlorophyll *a* concentrations of suspended sediments and biomass of filtering collectors, but not with organic seston loads, is a case in point. Because macroinvertebrate abundance generally reflects variation in environmental conditions over periods of at least the previous several weeks or longer, it is also likely that relationships with suspended sediment composition would be best detected by time-integrated rather than point sampling.

Taxonomic richness and overall abundance of filtering collectors at our study sites, and in other small watersheds that we have sampled in coastal northern California, was quite low relative to other regions. Filter-feeders at our sites were limited to sparse populations of *Hydropsyche* (Trichoptera: Hydropsychidae), *Chimarra* (Trichoptera: Philopotamidae), *Tanytarsini* (Diptera: Chironomidae), and blackflies (Simuliidae). In other river systems, filter-feeders also include, among others, representatives of the trichopteran families Psychomiidae and Polycentropidae, representatives of other dipteran families including Dixidae and Culicidae, as well as bivalve mollusks and freshwater polychaetes. The filtering functional group plays an important role in stream ecology, particularly in tightening the spirals of particulate organic matter with an increase in efficiency to the entire ecosystem (Wallace et al. 1977). The seeming paucity of filtering collectors in northern California streams may reflect an overriding limitation from high suspended loads of inorganic sediments.

Results of our flume experiment also suggested that fish feeding may be more adversely affected by suspended inorganic than organic particles. However, a revised experimental design that compared relative roles of organic and inorganic particles on a volume per volume basis, as discussed above, would be required to strengthen this conclusion. Our field observations of salmonid feeding activity and analyses of gut fullness suggest that turbidity does not inhibit salmonid feeding to the extent often assumed, at least within the range of turbidities encountered. Similar findings have been recently reported (DeYoung 2007, White and Harvey 2007).

We suggest that a more complete understanding of stream biotic response to suspended sediments will require the development of a conceptual model that highlights the importance of, and link between, the suspended and deposited organic particulate resources. Both particle size partitioning among collector macroinvertebrate taxa and the quality of particles in different size ranges need to be incorporated in such a conceptual model. One contrast could be between: 1) the more immediate effect of the ratio of organic to inorganic particles in suspension (transport) and the size and quality of those organic particles on filtering collector populations; and 2) the effect of the ratio of the organic to inorganic particles deposited in the sediments (bed load), again by size and quality, on the gathering collectors. Over longer timeframes, but not during high flows, the amount of deposited organic particles in storage would exceed those in suspension. The longer residence time of organic particles in storage would be expected to provide a larger and better conditioned particle resource, which is utilized by gathering collectors. The organic particulates stored in the sediments would represent the largest year-round, utilizable food resource for macroinvertebrates, except for the period of leaf litter drop in the autumn. For open streams, and in the early spring and late autumn in those streams with a heavy deciduous riparian cover, an algal food base may exceed the stored particulate organic resource in importance. But, even in such streams, on an annual basis the sedimentary organics may dominate. The ubiquitous and abundant organic particulate food resource available to macroinvertebrates on and in the sediment, coupled with a lack of specialized feeding behaviors to harvest the fine particulate resource, likely explains the usual dominance by the gathering collector functional feeding group in stream invertebrate assemblages.

Future research should first establish the linkage between the quantity and quality of organic particles in transport and in storage in a stream with the macroinvertebrate taxa that are supported by this organic particulate resource. Establishing the relative importance of these taxa as food for salmonids can then provide the linkage between the quality and quality of the suspended load or turbidity with the abundance and growth of stream salmonids.

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TABLE 1. Characteristics of stream study sites.

Basin	Caspar Creek		Redwood Creek	
Site	North Fork	South Fork	Upper Prairie	Little Lost Man
Watershed area (km^2)	3.94	4.24	10.52	8.96
Stream gradient (%)	1.5	0.8	1.0	2.6
Elevation (m)	86-317	48-329	85-432	15-591
Dominant overstory riparian vegetation	2nd growth redwood	red alder	old- growth redwood, Douglas-fir forest	old- growth redwood forest
Canopy cover (%)	87	91	80	83
Dominant substrate	cobble, pebble	pebble	pebble, sand	cobble, pebble

TABLE 2. Discharge, turbidity, mass of total suspended sediments (TSS), and percent by mass of TSS comprised of organic particles on sampling dates in North Fork (NFC) and South Fork (SFC) Caspar Creek, and in Little Lost Man (LLM) and Upper Prairie (UPC) creeks.

Site	Date	Discharge (cfs)	Turbidity (NTU)	TSS (mg/L)	Percent Organic
NFC	10/26/02	0.10	4	6.54	5.35
NFC	02/15/03	7.42	123	17.35	13.96
NFC	04/19/03	27.1	80	15.45	13.70
NFC	06/09/03	7.70	16	15.86	0.56
NFC	8/21/03	0.32	5	3.81	1.35
NFC	11/20/03	0.42	6	2.03	0.01
SFC	10/25/02	0.04	4	8.71	3.06
SFC	01/08/03	4.14	104	31.47	26.70
SFC	05/16/03	21.3	46	24.70	19.58
SFC	06/27/03	3.90	18	22.09	2.05
SFC	08/03/03	0.30	5	2.79	1.69
SFC	11/03/03	0.39	2	9.03	0.03
LLM	10/20/03	0.02	4	10.02	9.06
LLM	01/08/03	28.30	9	6.82	5.14
LLM	5/06/03	31.20	8	7.79	3.46
LLM	06/27/03	4.00	7	11.21	1.02
LLM	08/17/03	1.01	5	1.86	0.76
LLM	11/28/03	22.00	30	27.10	6.78
UPC	10/28/02	2.10	4	5.07	3.19
UPC	01/08/03	16.50	6	3.49	3.19
UPC	04/01/03	41.80	10	5.64	5.46
UPC	06/16/03	10.46	5	12.45	7.92
UPC	08/15/03	6.54	6	6.3	4.64
UPC	12/10/03	41.84	53	55.6	10.11

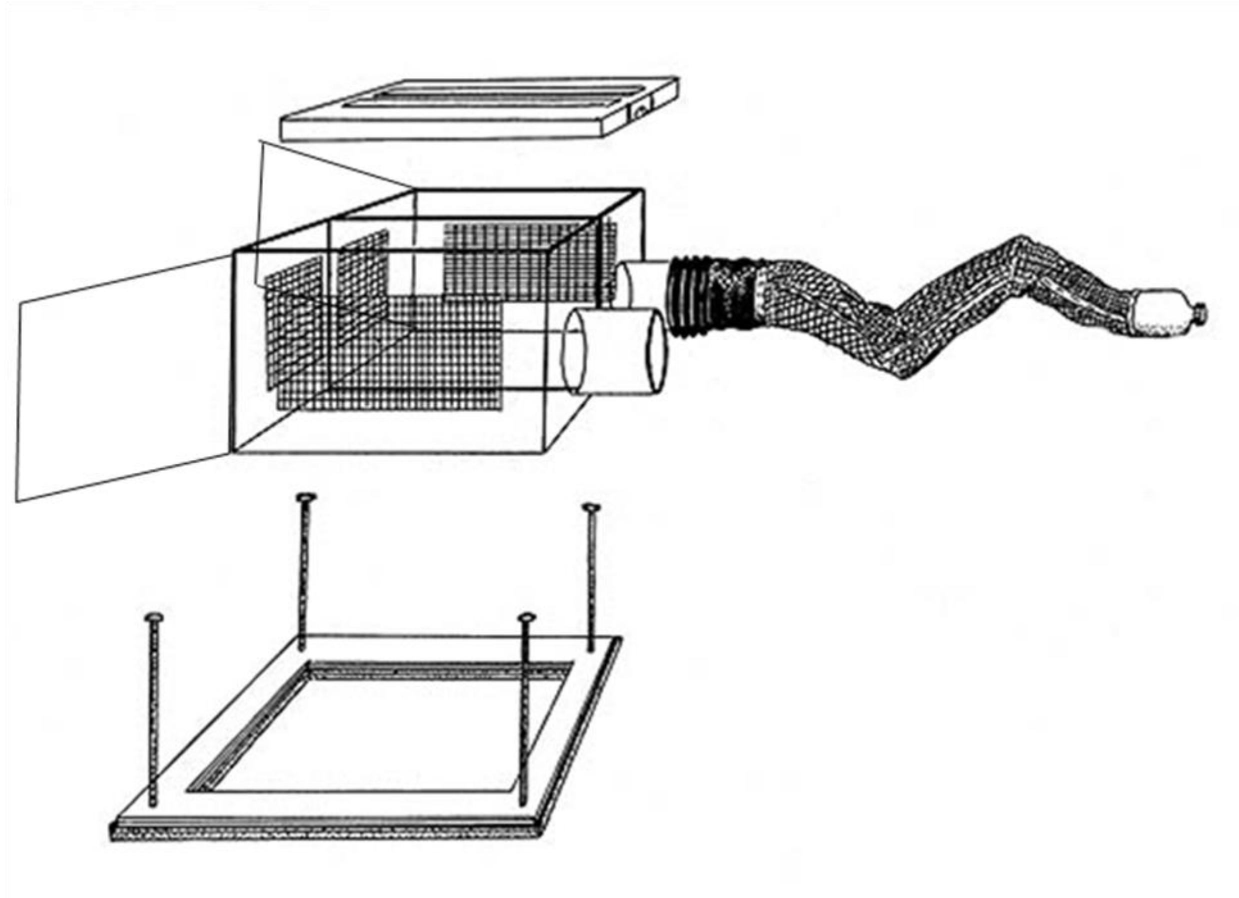

Figure 1. Drift-benthic partitioning sampler used in collecting aquatic macroinvertebrates. The sampler is divided with a central partition that allow for replicated comparison of drift and benthos collected from the same confined area. Panels of 250 µm mesh netting on the front, sides, and top allow flow to pass through the box. Wing flanges attached to the leading edge of the box ensure flow through the box. Drift nets positioned over the ports at the back of the box are 250 µm mesh wind-sock type, 0.75 µm in length. Samples retrieved from nets collect animals drifting from a known area of bottom during the sampling period; subsequent samples collected by disturbing bottom sediments into the nets sample animals that did not drift during the sampling period.

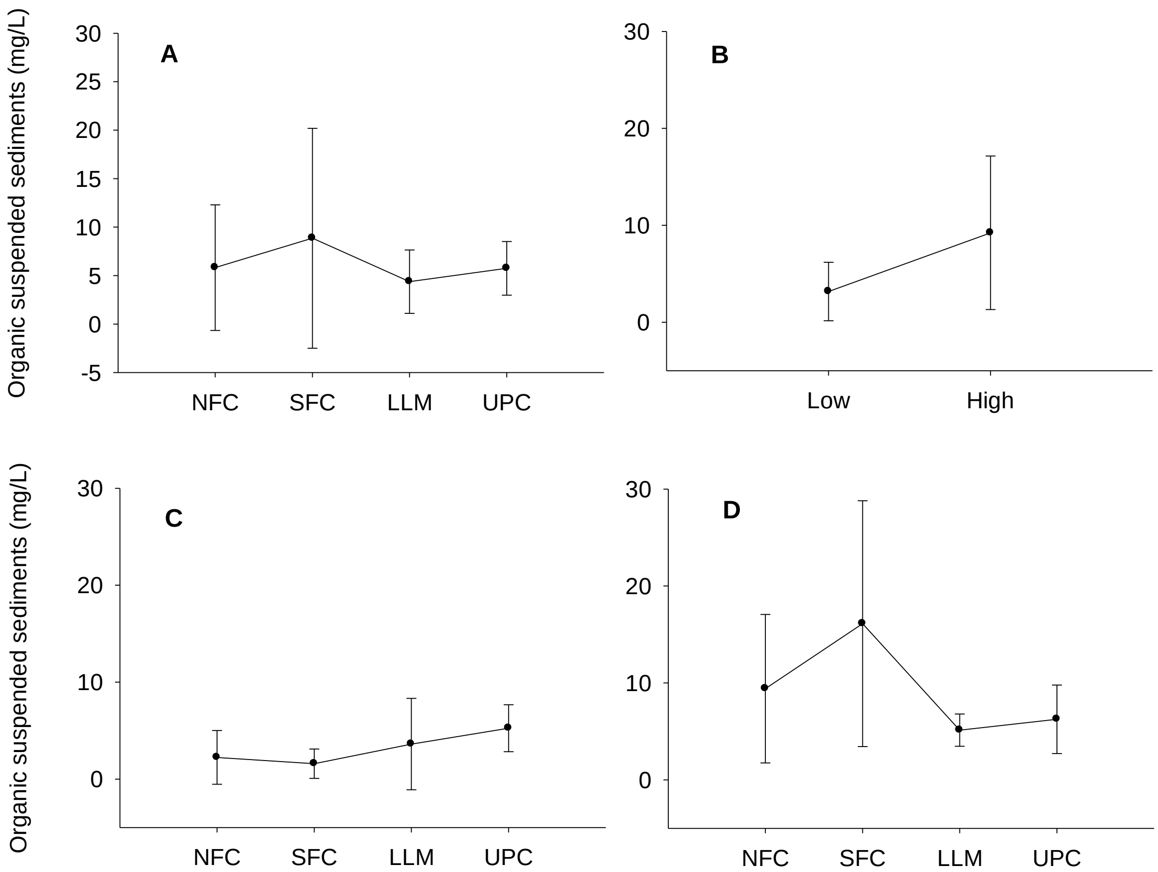

Figure 2. Mean concentration of organic suspended sediments: A) among sites (n = 6 samples per site), B) between low and high flows (n = 12 samples at each flow period), C) among sites during low flows (n = 3 samples at each site), and D) among sites during high flows (n = 3 samples at each site). Site abbreviations: LLM = Little Lost Man Creek; NFC=North Fork Caspar Creek; SFC = South Fork Caspar Creek; UPC = Upper Prairie Creek. Vertical lines represent standard deviation.

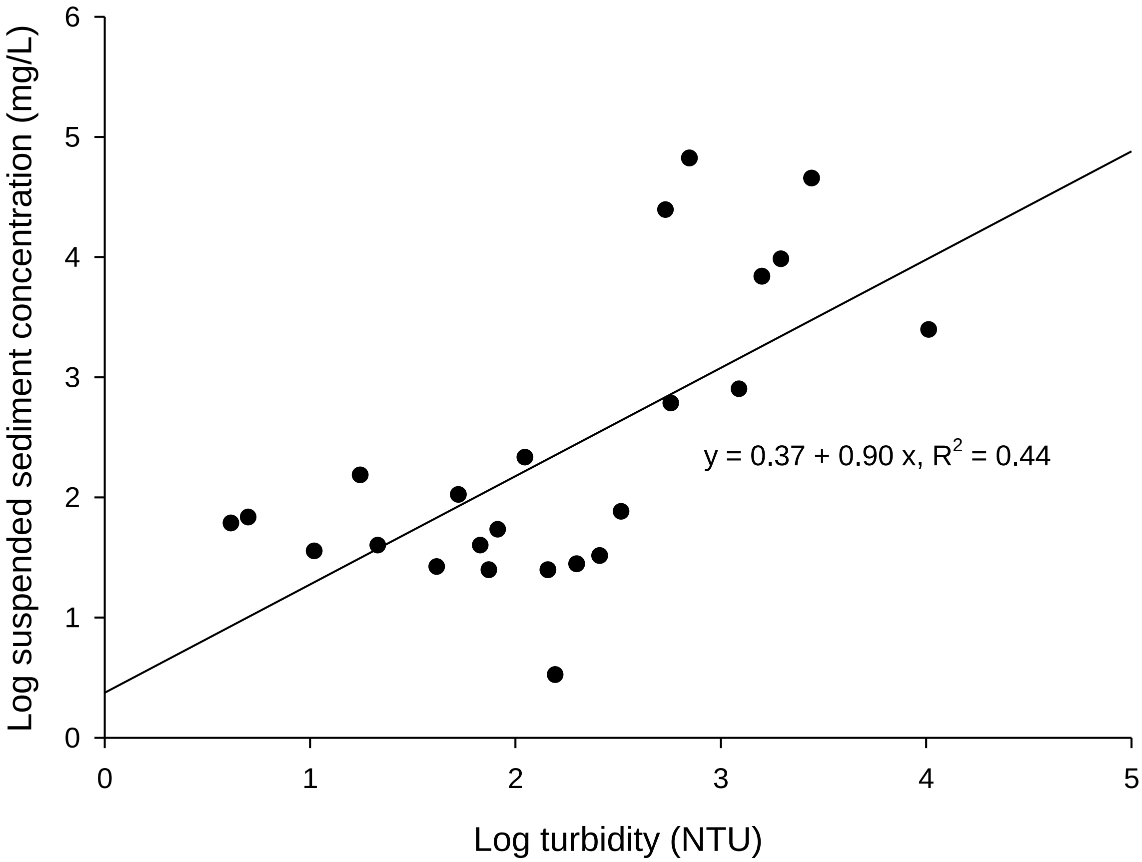

Figure 3. Relationship between turbidity and total suspended sediment concentration at the four study sites over six sampling dates.

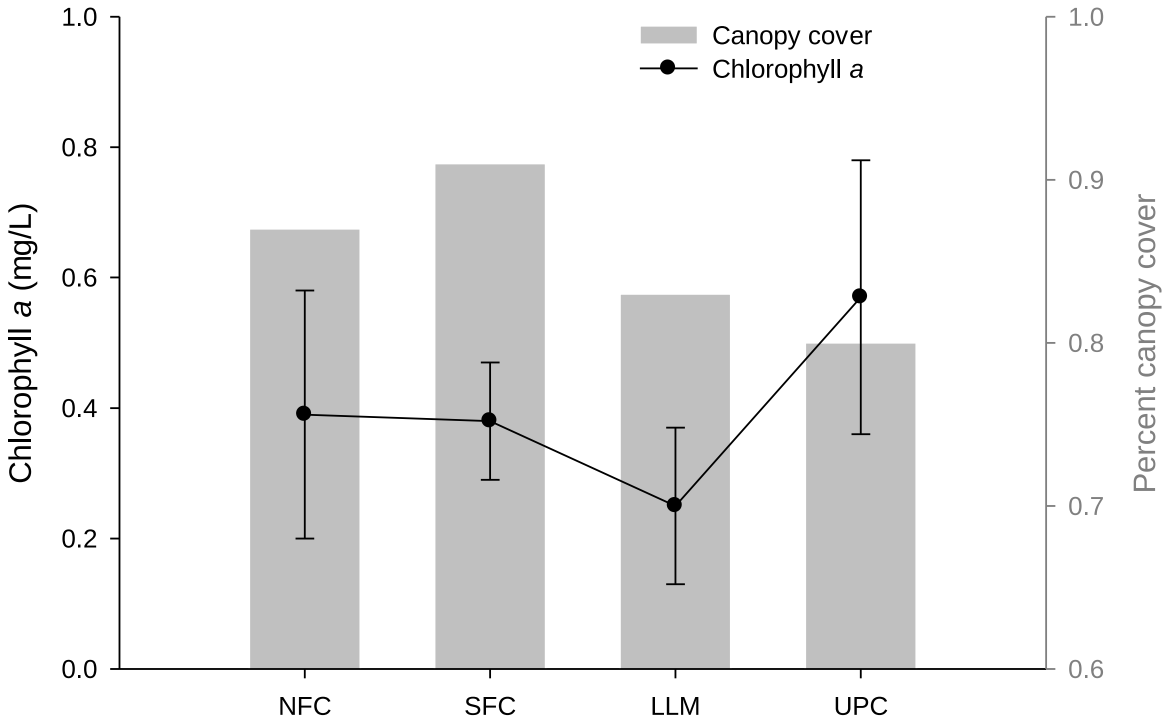

Figure 4. Concentration of chlorophyll *a* (closed circles, with vertical lines representing standard deviation) in samples of the total suspended load, and percentage of canopy cover (vertical bars) in each of the four sites (NFS= North Fork Caspar Creek, SFC = South Fork Caspar Creek, LLM = Little Lost Man Creek, and UPC = Upper Prairie Creek). Chlorophyll *a* concentrations were averaged over 6 sampling dates between October 2002 and December 2003.

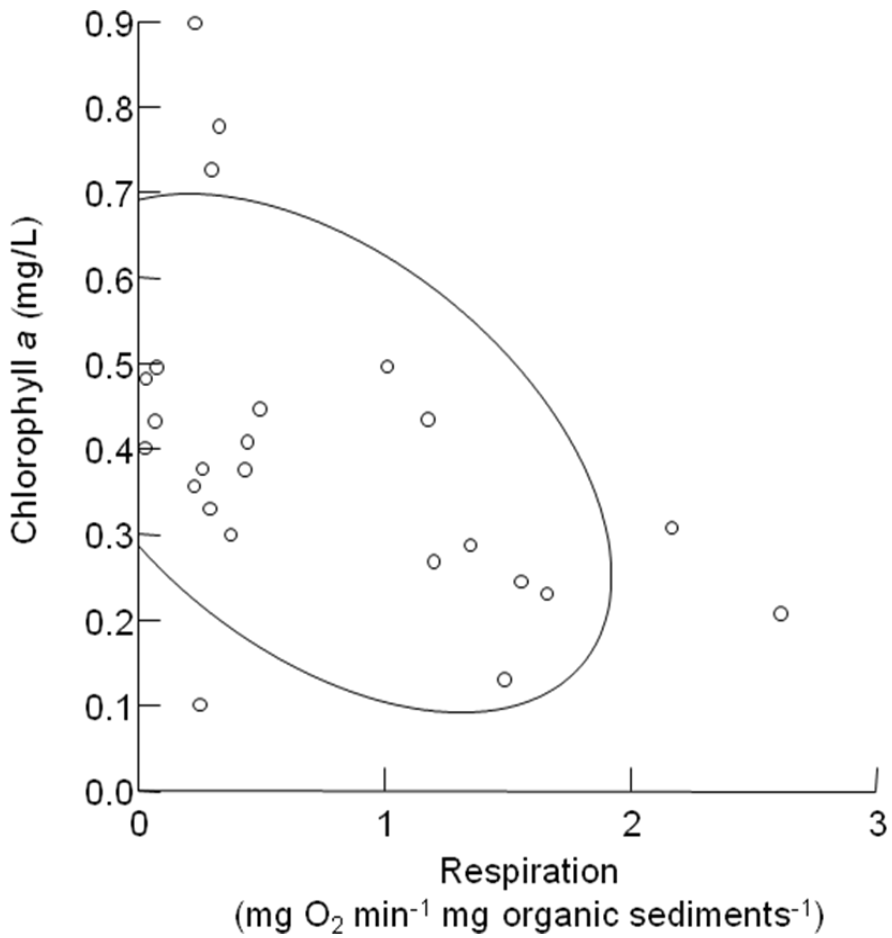

Figure 5. Relationship between respiration, as mg O_2 consumed per mg of suspended organic sediments, and chlorophyll (mg/L) in the four study sites on six sampling dates (R = -0.48, n = 24). The ellipse is drawn centered on means of chlorophyll and respiration, with its size and orientation representing unbiased standard deviations with a probability of 0.68.

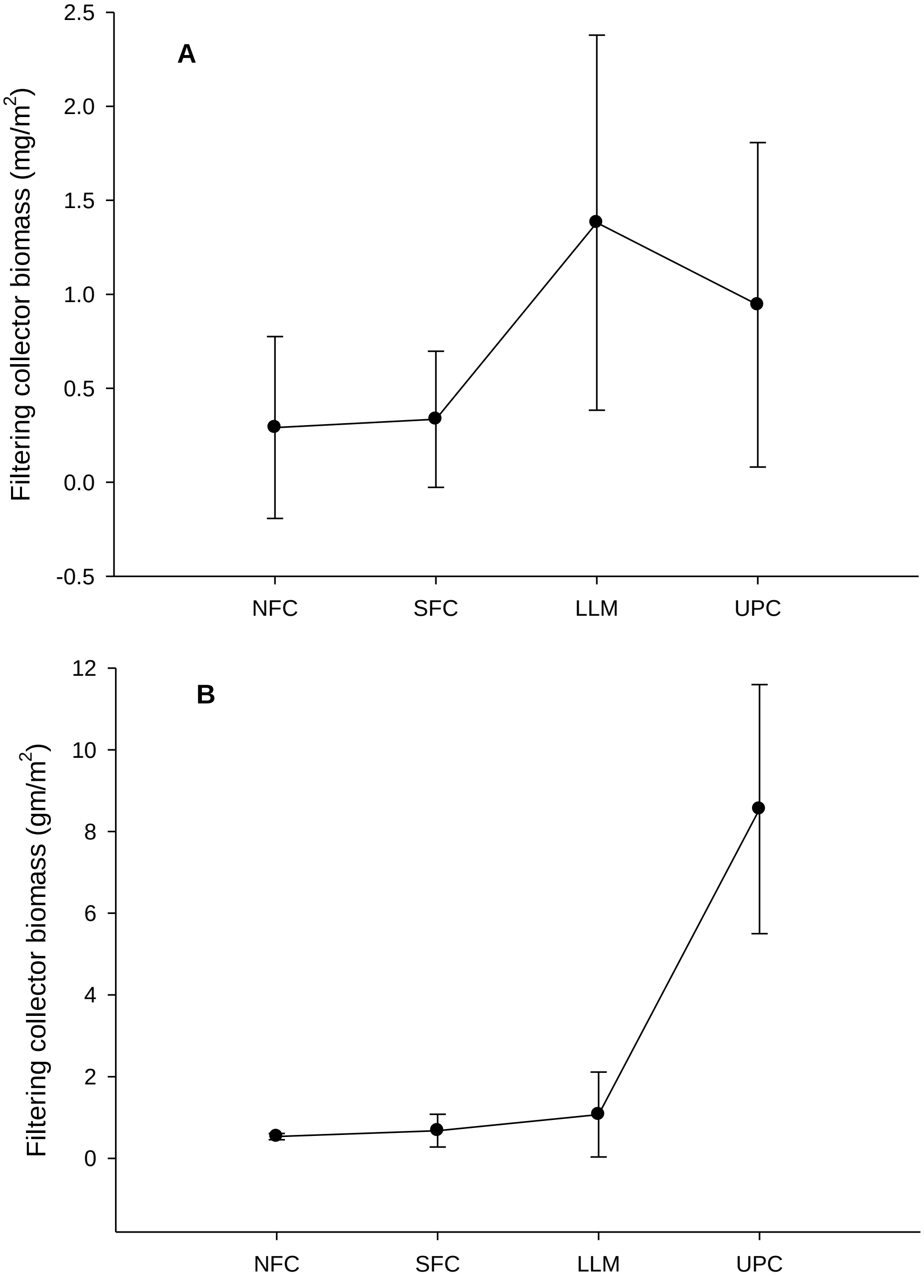

Figure. 6. Biomass of invertebrate filtering collectors among sites during A) low flow periods, and B) high flow periods. Sites are abbreviated as: Little North Fork Caspar Creek (NFC), South Fork Caspar Creek (SFC), Lost Man Creek (LLM), and Upper Prairie Creek (UPC). Biomass during each flow period was estimated from 4 samples on each of 3 dates at a site. Vertical lines represent 1 standard error.

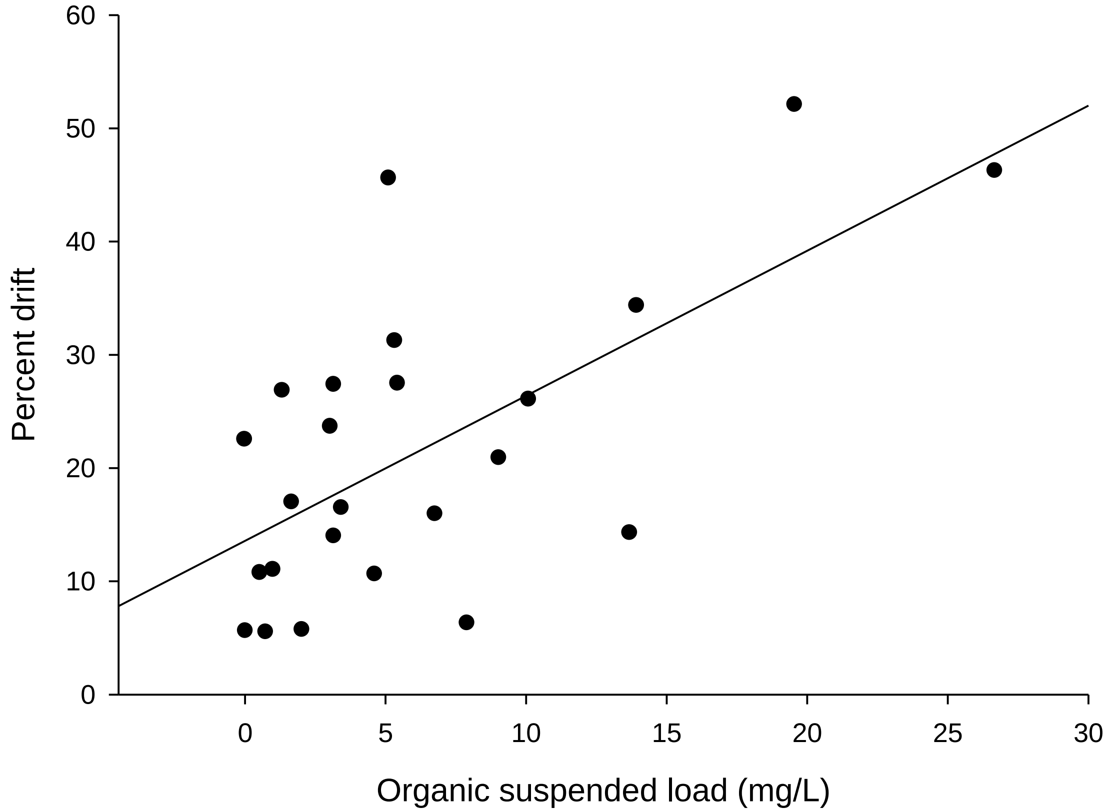

Figure 7. Relationship between concentration of the organic suspended load and the percent of invertebrates collected that were captured in the drift. Percent drift was arcsine transformed.

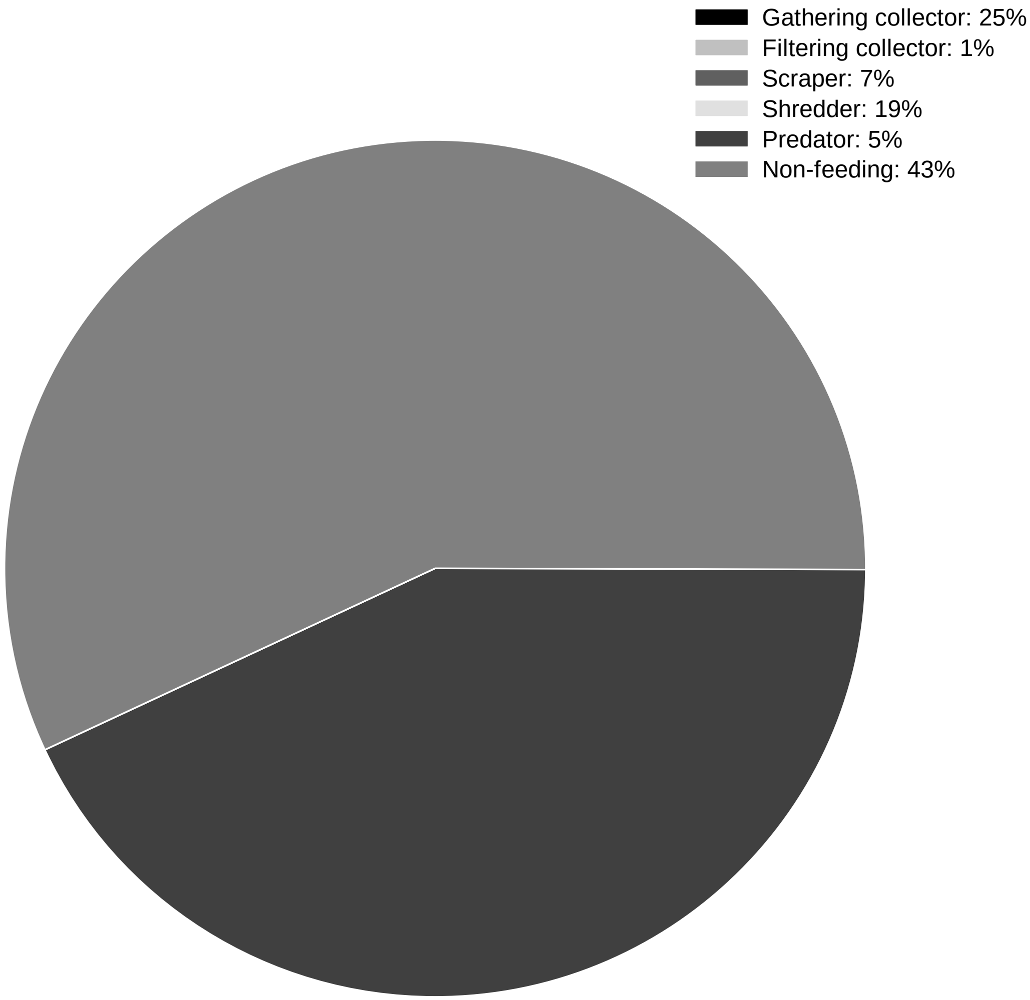

Figure 8. Representation of macroinvertebrate functional feeding groups within the diets of steelhead and coho salmon, averaged among creeks and dates (n = 206 diets analyzed). The non-feeding category includes pupae and adults of aquatic origin, together with all terrestrial taxa.

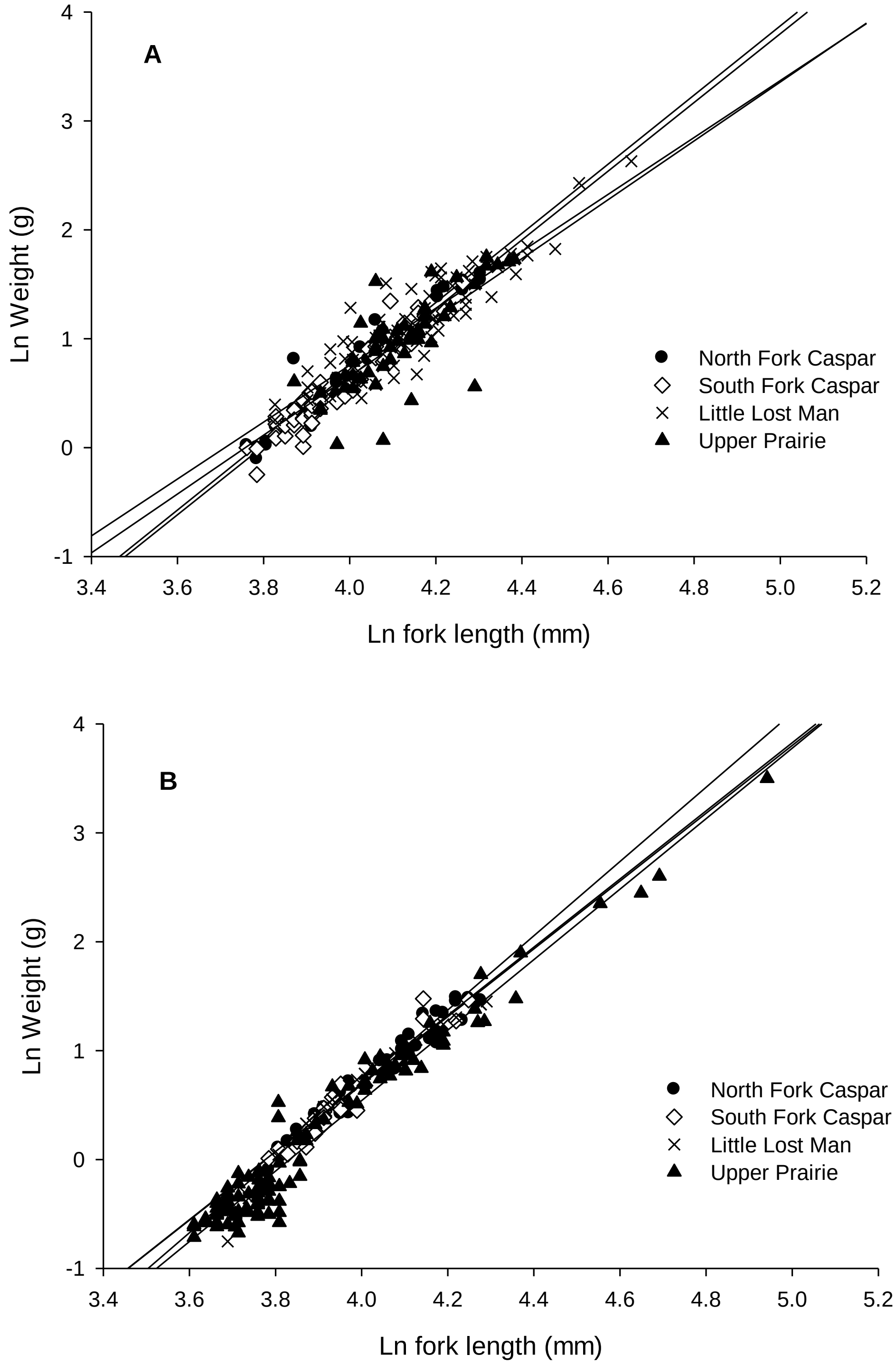

Figure 9. Length-weight relationships for coho salmon from the four study sites in A) October 2002 and B) June 2003.

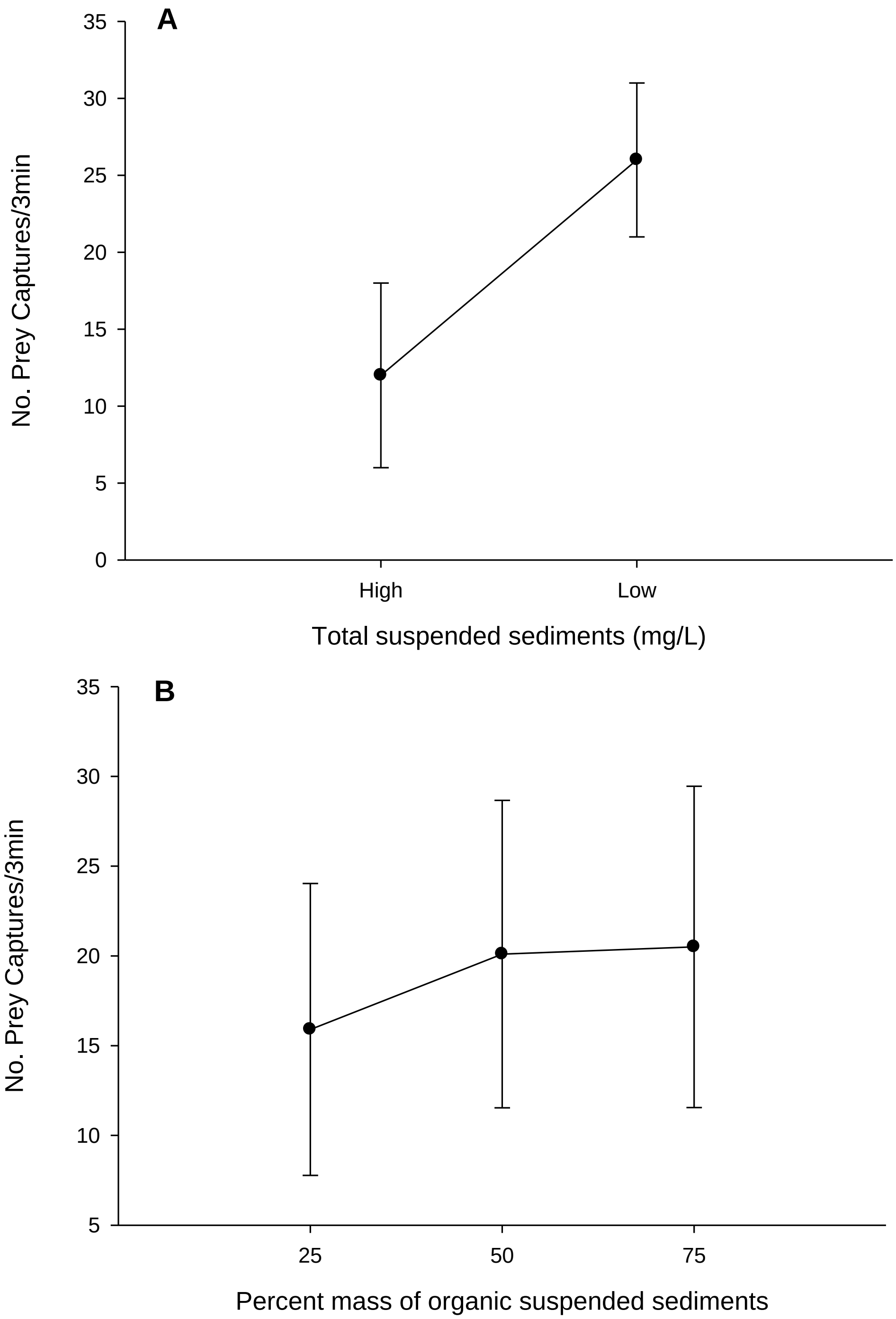

Figure 10. Average number of prey captures by solitary steelhead in 3 minute lab feeding trials at A) high and low suspended sediment concentrations, and B) under varying percentages by mass of organic suspended sediments. Vertical lines represent 1 standard deviation, n = 5 trials at each combination of suspended sediment concentrations and organic percentages.

Appendix A. Macroinvertebrate taxa collected from drift-benthos (x) and salmonid diet samples (d) from study reaches October 2002 to December 2003.

Taxa	NF Caspar	SF Caspar	Little Lost Man	Upper Prairie
Collembolla (springtails)	x,d	x,d	x,d	x,d
Isotomidae		x		
Porduridae	x,d	x,d	x	x
Pordura	x	x		x
Crustacea				
Amphipoda	d	x,d	x	d
Gammeridae	d	x	x	d
Gammarus	d	x	x	d
Copepoda		x		
Diplopoda		d		
Isopoda		d		
Odonata (dragonflies)				
Zygoptera				
Lestidae				d
Anisoptera				
Libellulidae				d
Ephemeroptera (Mayflies)				
Ameletidae	x,d	x	x,d	x
Ameletus	x,d	x	x,d	x
Baetidae	x,d	x,d	x,d	x,d
Baetis	x,d	x,d	x,d	x,d
Procoelon	x,d	x	x	
Ephemerellidae	d	x,d	x,d	x,d
Caudatella				x
Drunella		x,d	x	x

Taxa	NF Caspar	SF Caspar	Little Lost Man	Upper Prairie
Ephemerella				x
Serratella			x	
Timpanoga	x			
Heptagenaiidae	x,d	x,d	x,d	x,d
Cinygmula	x,d	x	x	x,d
Epeorus	x,d	x,d	x,d	x,d
Heptagenia		x,d		
Ironodes		d		
Nixe	d	x,d	d	x,d
Rithrogena			x,d	x,d
Stenonema	x	x	x	
Leptophlebiidae	x,d	x,d	x,d	x,d
Leptophlebia	x,d	x,d	x,d	x,d
Paraleptophlebia	x,d	x,d	x	d
Polymetrarcidae		d		
Tricorythidae		d		
Plecoptera (stoneflies)				
Capniidae	x,d	x,d	x,d	x,d
Capnia	x,d	x,d	x	x
Isocapnia			x	
Chloroperlidae	x,d	x,d	x	x
Haploperla		x		
Isoperla		x		
Kathoperla		x	x	
Paraperla	x,d			
Leuctridae	x,d	x,d	x,d	x,d
Perlomyia	x,d			

Taxa	NF Caspar	SF Caspar	Little Lost Man	Upper Prairie
Nemouridae	d	x,d	x,d	d
Peltoperlidae		x		x,d
Perlidae		x,d		x,d
Calineuria		x		
Hesperoperla				d
Perlodidae		x	x	x
Pteronarcydae	d	x		
Taeniopterygidae	d			
Hemiptera (true bugs)				
Corixidae	d			
Mesovellidae				d
Homoptera				
Aphidae				d
Trichoptera (caddisflies)				
Brachycentridae			x,d	x,d
Amiocentrus			x	x
Micrasema			d	x,d
Calamoceratidae	x	x,d	d	d
Heteroplecton	x	x	d	d
Glossosomatidae	x,d		x,d	x,d
Glossosoma	x,d		x,d	x,d
Hydropsychidae	d	x	d	x,d
Homoplectra				x
Hydropsyche			d	x,d
Lepidostomatidae	x,d	x,d	x,d	x,d
Lepidostoma	x,d	x,d	x,d	x,d
Leptoceridae				d

Taxa	NF Caspar	SF Caspar	Little Lost Man	Upper Prairie
Mystacides				d
Limnephilidae	d	x,d	d	x,d
Allocosmoecus	d	x		x
Dicosmoecus		x,d	d	d
Ecclisomyia		x		
Hydatophylax	d	x,d		x,d
Odontoceridae	d	x	x,d	x
Parthina		x,d		
Philipotamidae	x,d	x,d	x,d	x,d
Chimarra	x,d	x,d	x,d	x,d
Rhyacophilidae		x,d	x,d	x,d
Rhyacophila		x	x	
Sericostomatidae		x,d		x,d
Gumaga		x		x,d
Uenoidae				x,d
Neothremma				x,d
Lepidoptera				d
Thysanoptera	d	d	d	d
Megaloptera				
Calopterygidae		d		
Corydalidae	d		d	
Sialidae	x,d	x		x,d
Sialis	x,d	x		x,d
Coleoptera (beetles)				
Elmidae	x,d	x,d	x,d	x,d
Cleptelmis	x,d	x,d	x,d	x,d
Lara	x,d			x,d

Taxa	NF Caspar	SF Caspar	Little Lost Man	Upper Prairie
Narpus	x			
Hydraenidae				d
Psephenidae	x		x,d	x,d
Psephenus	x		x,d	x,d
Staphylinidae	d		x	
Stenus			x	
Hymenoptera				
Formicidae (ants)	d	d		
Vespidae (wasps)				d
Diptera (flies)				
Athericidae			x	
Blephariceridae		d	x	
Blepharicera			x	
Ceratopogonidae	x,d	x,d	x,d	x,d
Bezia	x,d	x,d	x	x,d
Chironomidae	x,d	x,d	x,d	x,d
Chironomini	x	x	x,d	x,d
Tanytarsini	x	x,d		x,d
Orthocladiinae	x,d	x	x,d	x,d
Tanypodinae	x,d	d	d	x,d
Culicidae	d			
Deuterophlebiidae		d		
Dixidae	x,d	d	x,d	x,d
Pelecorhynchidae	d			
Psychodidae		x	d	x
Psychomyidae	d			
Simuliidae	d	x,d	x	x,d

Taxa	**NF Caspar**	**SF Caspar**	**Little Lost Man**	**Upper Prairie**
Stratiomyidae	x,d	d	x	
Syrphidae		d		
Tabanidae		d		
Tipulidae	x,d	x,d	x,d	x,d
Arachnida	d	d		d
Hydracarina	x,d	x,d	x,d	x,d
Gastropoda				
Pleuroceridae				x
Juga			x	x
Chilopoda		d	d	d
Oligochaeta	x	x	x	X

Appendix B. Regression coefficients (a, b) used in estimation of biomass (W) from length (L) measurements of invertebrate taxa using the formula $W=aL^b$, based on unpublished data of Cummins and Wilzbach.

Coefficient a	Coefficient b	Invertebrate taxa	Life stage
0.001230	3.5800	Ephemeroptera	Adult
0.001849	3.4570	Ephemeroptera	Larvae
0.002809	3.0360	Plecoptera	Adult
0.004303	3.0610	Plecoptera	Larvae
0.017650	2.9030	Trichoptera	Adult
0.002299	3.0790	Trichoptera	Larvae
0.037140	2.3660	Diptera	Adult
0.001135	2.7508	Diptera	Larvae
0.000115	3.4780	Diptera	Pupae
0.002581	2.9930	Collembola	Adult
0.004303	3.0610	Isopoda	Adult
0.003300	2.3200	Diplopoda	Adult
0.003300	2.3200	Chilopoda	Adult
0.004303	3.0610	Amphipoda	Adult
0.004303	3.0610	Megaloptera	Larvae

Coefficient a	Coefficient b	Invertebrate taxa	Life stage
0.017650	2.9030	Lepidoptera	Adult
0.047360	2.6810	Coleoptera	Adult
0.001453	3.6110	Coleoptera	Larvae
0.085350	0.2160	Coleoptera (terrestrial)	Adult
0.044780	2.9290	Araneae	Adult
0.020838	2.4070	Hymenoptera	Adult
0.020838	2.4070	Hymenoptera	Larvae
0.039726	2.7610	Acari	Adult
0.049887	2.2700	Hemiptera	Adult
0.049887	2.2700	Hemiptera	Larvae
0.036589	2.6960	Homoptera	Adult
0.036589	2.6960	Homoptera	Larvae
0.002809	3.0360	Thysanoptera	Adult
0.001135	2.7508	Pulmonata	Adult
0.287200	1.0000	Hirudinea	Adult
0.003300	2.3200	Oligochaeta	Adult