Benthic Biological Community Responses to Sediment Loading in Experimental Stream Mesocosm Channels

Report 4 of 4

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SUMMARY

1) The objectives of this study were to examine the effect of sediment dose and duration (pulse vs. press) on benthic communities inhabiting different in-stream habitats (riffle vs. pool) among replicate treatments over a 6-week exposure period, and after nearly one year.
2) Experiments were conducted in outdoor mesocosm stream channels at the Sierra Nevada Aquatic Research Laboratory (SNARL), Mammoth Lakes, CA. Pulse experiments consisted of a single 100 or 1000 liter dose of sediment (dry volume) and a control channel. Press experiments were composed of 10 repeated doses (at four-day intervals) covering a cumulative range of 100, 250, 500, and 1000 liters of sediment (dry volume) and a control channel.
3) Invertebrate drift increased in all but the lowest dose treatment and did not appear to result in mortality but drift emigration was low compared to benthic densities.
4) Mobilization and export of CPOM increased in proportion to sediment dose.
5) Algae chlorophyll biomass (green filamentous forms) was highest where most sediment was already present or was added in the greatest amount.
6) No effect of sediment was observed in changing density or richness, but multivariate analysis revealed increasing dissimilarity in overall community composition relative to initial stating conditions at higher doses.
7) The effect of sediment was more pronounced in pools where deeper, slow flows accumulated more sediments compared to riffles.
8) Long term samples taken 11 months after initial dosing indicated significant reductions in density and richness of benthic communities within riffle habitats. It is the longer-term legacy effects of sedimentation that appear to alter recruitment and result in patch-scale and reach-scale restrictions on distribution, abundance and composite community complexity.

INTRODUCTION

The effects of sediment as a pollutant on water quality and biological health are often difficult to assess because transport and deposition of sediment is a natural process of streams. Sediment derived from the landscape contributes to the dynamic processes of building, shaping, and renewing stream channels. Sediment fractions of fine, sand and gravel sizes contribute to the dynamic ecological function of streams, often forming the matrix substratum of stream bed habitat for periphyton, invertebrates, and fish. However, excess sediment supply to a stream, at levels exceeding natural background contributed by anthropogenic disturbances, can impair indigenous stream communities and interfere with their ecological function. The challenge for researchers and managers seeking to understand the effects of watershed disturbance and excess sediment loading on a stream is to determine: (1) whether impairment to aquatic life is occurring; (2) what portion of observed impairment can be attributed to excess sediment; and, (3) the degree to which sediment loads must be reduced to improve habitat quality and beneficial uses.

Many studies have examined the relationship of the physical substrate of the stream bed to benthic life (Minshall 1984; Waters 1995; Allen and Castillo 2007). Field studies of substrate associations with benthic invertebrates, algae and fish are confounded though by many environmental covariates, including current, depth, organic matter, and the patchiness of distributions across heterogeneous microhabitats. To control background sources of variation, experimental studies of substrate influence on stream invertebrates have typically examined either the colonization of introduced substrates of differing size and variety, or the responses of established replicate communities to sediment addition. Experiments have the advantage of manipulating the frequency, duration and intensity of exposure that form the elements of the stress regime of sedimentation. As with many other ecological experiments, results are limited by the relatively small scale and short time frame over which manipulations can be conducted and that responses are conditional on the community profile of taxa present in treatment units. Stream mesocosms are an advantage over laboratory microcosms in that they are nearer the natural scale of habitat units where experimental subjects reside, and are in operation for weeks to months, rather than hours or days, covering a greater length of the life history for organisms such as aquatic invertebrates (Cooper and Barmuta 1993).

Background

Sediment supply, transport, deposition and predicted effects on benthic biota

Stream sediment is supplied from sources both external and internal to the stream channel (Gordon et al. 2004; Gomi et al. 2005). External sources include bank erosion, mass movement, roads and trails, and surface erosion on slopes, while internal sources include material stored within the channel system in perennial and ephemeral reaches and their floodplains. Anthropogenic activities in the watershed can influence both the sediment supply and hydrologic conditions of a stream, affecting the quantity and quality of external sediment sources, as well as the transport and storage capacity of a stream. Watershed or stream disturbance that increase rates of erosion and the rate of sediment delivery to a stream will increase the external sediment supply. Internal storage and transport capacity will also be influenced by activities in the watershed, including the construction of impervious surfaces, the removal of vegetative cover, and the construction of dams, all of which alter the timing, duration, and magnitude of flow events. Changes in within-channel sediment storage may delay and attenuate sediment waves introduced from external sources (Hassan et al. 2005). Thus, the effects of increased sediment supply to a stream are complex and cannot necessarily be decoupled from alterations to its hydrology.

Wash material, functionally defined as fine sediment particles that are transported in suspension, comprises the major portion of total sediment load in most river systems, and strongly influences the physical and biological structure of streams (Gomi et al. 2005; Hassan et al. 2005). During transport events, wash material scours stream channels and can lead to temporarily turbid, inhospitable conditions for many organisms. At lower flows, wash material will be deposited within the interstices of coarser bed material, and, when in sufficient supply, even cover or bury bed material under surficial patches of fine sediment (Lisle and Hilton 1999). For a given hydrologic regime, as sediment supply increases fine particles will become more abundant on the bed surface (Dietrich et al. 1989). Generally, wash material will be transported directly through a reach without being deposited in the main channel. However, such fine sediment may be deposited in portions of a stream where channel velocities are lower than the settling velocities of these particles; in pools, along the channel margins, and upstream of flow obstructions such as boulders or large woody debris. In these locations, it is expected that the effects of deposition from excess sediment supply will most influence benthic habitat. In particular, as sediment supplies increase, the substrate quality in channel margins is likely to shift from a heterogeneous mixture of largely coarse bed materials, to a more homogenous matrix dominated by deposited wash material, with a corresponding shift in benthic biological communities (Fig. 1). While physical disturbance of benthic organisms may occur during both sediment transport and deposition processes, long-term effects from excess sediment supply will be most evident along channel margins where bar formations develop in zones of low power.

The effects of sediment supply may also vary longitudinally along a stream where flow power declines (pools, low gradient, flow separation), and due to variability in the location and extent of sediment sources and fluvial processes such as sorting and abrasion that influence the deposition of sediment spatially. While locations with substantial bank erosion and other direct contributions of sediment to a stream may be important, it is expected that watershed disturbance will particularly influence sediment supplies from tributaries. It has been asserted that tributary confluences can result in abrupt changes in bed sediment character and water quality in a main channel, depending on the volume and character of the water and sediment a tributary delivers (Rice et al. 2001). These changes also have implications for a number of important habitat characteristics. Abrupt changes in sediment supply and discharge may cause adjustments in channel form (slope, width, depth), bed sediment character (size, sorting, shape), and channel hydraulics (near-bed velocity and shear stress fields). Such effects will also vary downstream from a confluence due to sorting and abrasion processes that cause a downstream "fining" of channel substrates as finer sediment particles are preferentially transported and eventually deposited (Rice and Church 1998). This longitudinal variability presents an additional challenge to measuring biological impairment from sediment, one that requires appropriate sampling frequency and site selection. But it also presents the potential opportunity to detect variable effects from each tributary, such that a range of sediment "doses" might be detected.

Experimental studies of sediment effects on benthic macroinvertebrates communities

Considering how sediment is added, both the exposure time and concentration may be important to the biological effects observed. In one study, drift increase occurred only with prolonged exposure even at high concentrations, and with little mortality among communities (Shaw and Richardson 2001; Molinos and Donohue 2009). Others have observed immediate drift as either the concentration or duration of sediment exposure was increased relative to controls (Rosenberg and Wiens 1978; Doeg and Milledge 1991; Shaw and Richardson 2001; Suren and Jowett 2001). Some of these studies also reported declining density of benthic invertebrates and periphyton with sediment addition (Suren and Jowett 2001; Molinos and Donohue 2009). The survival of benthic macroinvertebrates in most experimental exposures to sediment suggests that short-term responses are mediated through drift rather than mortality (Culp et al. 1986). A number of studies have examined the effects of sediment transport and deposition processes on benthic macroinvertebrates. During sediment transport, both the duration and magnitude of an event will determine its effects. Macroinvertebrates may be impacted by abrasion, reduced visual efficiency in feeding, and interference with food gathering, which has been shown to induce many animals to drift downstream (Waters 1995) . These effects may be temporary, as macroinvertebrate communities can be expected recover rapidly if habitat and substrate characteristics are restored to pre-event conditions and intact colonization sources persist upstream.

The effects of sediment deposition on benthic macroinvertebrate communities are often more substantial, and presumably detectable long after an event. As described above, excess sediment deposition can alter the particle-size distribution of streambed substrate through the addition of fine particles. Macroinvertebrate abundance and community composition are often dependent on substrate particle size, such that a gradient of abundance of particular taxa is observed across the series of particle sizes (Waters 1995). Especially sensitive to substrate particle size are many mayfly (Ephemeroptera), stonefly (Plecoptera), and caddisfly (Trichoptera) taxa, collectively referred to as EPT, that often inhabit interstitial spaces of coarse substrate. Several studies have demonstrated that EPT abundance is best correlated to a mixture of heterogeneous gravel, pebbles, and cobbles (Bjornn et al. 1977; Ciborowski et al. 1977; Rutherford and Mackay 1986). Taxa that inhabit the hyporheic zone and depend on the flow of oxygen-containing water through interstitial spaces are affected by substrate particle size (Waters 1995), where more than 10 to 20 percent fine sand and silt (*i.e.*, <0.25 mm) can cause a significant reduction in the oxygen content within the substratum (Eriksen 1966).

Although individual taxa may be particularly sensitive to excess sediment inputs, the effect of excess sediment may be best characterized in terms of a shift in overall community composition (Waters 1995). Dominant species types and diversity may change as excess sediment inputs convert the dominant substrate from coarse to fine particles. A response often observed is a change from a community dominated by larger surface-dwelling taxa to one dominated by smaller burrowing macroinvertebrates (Suttle et al. 2004) such as Oligochaeta (segmented worms) and Chironomidae (midges). Sediment sufficient to change the dominant substrate type to sand-silt may change the number and type of taxa, altering community composition and structure, with variable effects on overall density (Lenat et al. 1981).

The objectives of this study were to improve on previous research by increasing the scale and duration of sediment exposure while contrasting the specific effects of press and pulse disturbances, partitioning these effects by habitat type. A better understanding of how sediment affects stream resources and dynamics, directed at what levels of sedimentation elicit changes in community structure and function, will aid researchers and managers in discerning the relative impacts of shorter term sedimentation events compared to longer term chronic delivery, and how invertebrate communities respond to the legacy of past deposition.

METHODS

Experimental design

Experiments to test the effects of suspended and deposited sediments on invertebrate communities were conducted in the outdoor mesocosm stream channels at the Sierra Nevada Aquatic Research Laboratory (SNARL) in July and September of 2008 (Fig. 2). These experiments were designed to test the effects of both pulse and press exposures of resident invertebrate assemblages to a range of sediment additions. In one experiment, using three channels, sediment was added as a single pulse exposure of a low dose (100 liter dry volume), high dose (1000 liter), and a control channel. In the second experiment using six channels, sediment was added gradually over 40 days with ten repeated additions every four days that covered a cumulative range of 100, 250, 500 and 1000 liters of sediment added. In all cases, sediment was added over a fixed duration of two hours during which time the volume for each treatment was delivered evenly through perforated buckets at the top of each experimental channel.

The SNARL mesocosm stream channels, located in the eastern Sierra Nevada at 7000 ft elevation, are each 50 m in length, surface slope 0.1%, and are comprised of seven riffle sections alternating with six pools in a sinuous form (mean riffle width 1m, max pool width 1.45 m). Channels are divided into two independent groups of six channels, and three channels, with source water originating from separate reservoirs. Flow is maintained in the channels year-round and natural recruitment of invertebrates occurs through both drift and colonization from adjacent Convict Creek. Trout were removed one month prior to the beginning of the experiment but did have access to the channels from Convict Creek. Although trout were able to move in or out of any of the channels, they were only transient occupants.

Preliminary conditions and preparation of experimental mesocosm channels

In fall 2007, prior to the summer 2008 experiments, substrate and depth profiles were characterized to determine adjustments that might be necessary to equalize conditions across the channels in riffles and pools. Particle size distribution and water depths were measured along five transects of 5 points each, within each riffle and pool. Substrate was added or removed from channels as necessary, and flow gate openings set to distribute flow equally across channels. Adjusted conditions were maintained through the winter and spring preceding the experiments. Spring floods brought fine sediments into the outer channel of the upper set of six, so this channel began with an elevated burden of fine sediment, especially in pools. Initial conditions in riffles at the start of the experiment were a geometric mean particle size of 38.1 mm (95% CI 0.93) and mean water depth of 8.4 cm (SD 3.2).

Experimental treatments

Sediment particles were obtained from a nearby commercial sand and gravel yard. Only particles passing through a 2 mm sieve were used in the experiment (Fig. 3). We found that the organic content of this material was less than 0.2% AFDM, and even the smallest fraction was only 1% organic. On each day of sediment dose addition, the appropriate volume of sediment for each channel was measured and mixed with water in a five gallon bucket to create a slurry. This slurry was added manually to each channel at a constant rate over a two hour period. Larger particles within the size range settled out as bedload while smaller particles remained in suspension and passed through the system as washload. A discharge of approximately 30 L/sec (velocity = 25 cm/sec) was selected as the highest discharge that could be maintained throughout the experiment as the natural flow of Convict Creek was reduced through the summer.

The levels of sediment exposures tested were 100, 250, 500, and 1000 liters (1 L = 1.64 kg) of inorganic sediment. This was delivered in the 3-channel set as a single pulse event of 100 and 1000 liters plus an untreated control (pulse dose experiment treatments referred to here as 100/1, 1000/1, and 0/1), and in the six-channel set as ten event pulses given at 4 day intervals (press dose experiment referred to hereafter as 0/10, 100/10, 250/10, 500/10, and 1000/10. Treatments were assigned randomly to channels, with one control for each treatment group. Possibly related to spring floods that ran over the ground surface in this area, channel 6 (see Fig 2) exhibited high fine sediment and algal cover prior to the start of the experiment. In this channel we repeated the 250 liter treatment (coded as 250/10*) so that responses in this channel could be contrasted with the other 250 liter treatment channel. While this problem prevented us from assigning another dose level, it afforded the opportunity to observe the effect of sediment addition to an already sediment-loaded system.

Physical habitat description

Surveys of water depth and substrate particle size (intermediate width axis) were taken at five equidistant transects within each riffle and pool section. Each transect consisted of five equally spaced point-intercepts. These measures permitted comparison of the extent of treatment effects on channel substrate composition, and were made on day 0, 30, and 60 of the experiment. In addition, current velocity and depth measures were taken at the mid-channel thalweg at 1, 25 and 46 days after treatments had begun. During the initial sediment addition, turbidity measurements were taken at 30, 60, and 90 minutes in the upper and lower portions of each channel to establish the wash load carried for each treatment event.

The cover of fine and sand particles (<0.25 mm and 0.25 – 2 mm, respectively) along each experimental channel was also measured before sediment was added, and in conjunction with each invertebrate sampling event. A 30 × 30 cm grid frame with 25 cross points was centered over six alternating left and right half channel positions within each of the six riffle segments sampled, for a total of 900 point counts per channel. The fine-sand counts were made using a plexiglass tube-scope to view the channel bottom.

Biological sampling

Beginning July 24, 2008 benthic invertebrate samples were sampled using a 20 x 20 cm Surber-type frame completely enclosed on all sides by 250 micron mesh netting.

An aquarium net 20 cm wide with 100 micron mesh net was placed at the downstream side and the substrates within the frame disrupted by hand to dislodge organisms that were swept by the current or hand into this net. Samples were taken on the day before addition of sediments (day 0), and then on day 1, 10, 30, and 45. The sampling design divided each channel into an upper, middle, and lower section containing two riffles each. Four samples were collected from each section (two per riffle, 400 cm^2 area each) and combined into a single collection. The exact location of each sample was recorded to avoid re-sampling the same area of substrate on subsequent sample dates.

Drift samples were collected over a 24 hour period using a 250 micron drift net one day before and one day after the initial addition of sediments. Drift nets captured 100% of channel flow and all invertebrates. Samples were preserved in 100% ethanol. All invertebrate samples were identified in accordance with the standard level of taxonomic effort established by the Southwest Association of Freshwater Invertebrate Taxonomists (SAFIT, 2006), with the exception of Chironomidae not being identified beyond family. Sub-sampling was conducted using a Folsom plankton splitter to obtain a minimum count of 250 individuals removed from at least 1/16 or more of any sample.

Benthic algae (periphyton) samples were collected on day 0 and 60. From each of the lower, middle and upper riffle sections, two cobble-size rocks were selected at random from the 2 riffles in each section. These rocks were combined in a tub and all surfaces scrubbed clean with a nylon bristle brush into a small volume of water in the tub. Rock surfaces were rinsed into the pan and their length (L), perpendicular width (W), height (H), and longest perimeter (LP) dimensions of each were measured to estimate total surface area (upper surface area = $(L*W + L*H + W*H)*(LP/(2(L+W))$. The sample volume was adjusted to a fixed volume of 150 ml and this was then homogenized in a blender for 30 seconds. Sub-samples of the homogenate were removed with a 20 ml syringe and this was filtered through 25mm type A/E glass fiber filters (1 micron pore size), fit in a filter holder, to obtain a sample of algae sufficient for fluorometric analysis (usually 5-10 ml volumes filtered). Sample filters were kept in darkness, frozen within 2 hours of collection and analyzed after storage. Frozen filters were ground in 95% ethanol, stored for 12 hours in cold and darkness, mixed and centrifuged for 4 minutes. The supernatant was read in a Turner model TD-700 fluorometer, and then re-read after acidification with 6 drops of 0.1 N HCl (to determine phaeophytin content), and the readings calibrated to chlorophyll standards.

To examine the long term effects of sediment, a set of “legacy samples” were collected in early June 2009, 11 months after the start of the experiment. Samples were collected from the control channel (0/1) and the largest pulse dose channel (1000/1). Two replicate samples were collected from the upper end of each of six riffle sections per channel (n=12 per channel). Within a 30 x 30 cm area, counts of fine and sand substrate were made at intersecting grid points (as described previously) prior to collecting invertebrates from this same location using a D-frame net.

Statistical and exploratory analysis

Richness values were rarefied at our minimum count of 230 organisms using EcoSim700 (Gotelli and Entsminger 2001) with 1000 iterations of Monte Carlo randomizations. Rarefied Ephemeroptera, Plecoptera, Trichoptera (EPT) richness was derived from output provided by EcoSim of the final iteration which listed all taxa, their original richness, and the rarefied richness for that iteration. Indicator taxa were identified from the indicator taxa analysis routine in PC ORD 5 (McCune and Mefford 2006), using sediment dose as the grouping variable. Total density, rarefied total richness, and rarefied EPT richness estimates were based on an average of the upper, middle, and lower sections of each treatment channel. Samples from the upper, middle, and lower sections do not represent replicates but more accurately capture the average community structure and illustrate within channel variability as affected by both suspended load and bed load introduced. This channel average was calculated only for riffle habitats where all channel section samples were processed. Pool samples represent only a single value from the upper sections. Dissimilarity among all samples of composite channel section for each treatment through time was calculated in PC ORD 5 using Bray-Curtis distances. Figures illustrate the amount of cumulative dissimilarity in macroinvertebrate community structure with respect to the initial community structure (day 0) before treatments were applied. Non-metric multidimensional scaling (NMDS) was conducted in PC ORD 5 to identify which taxa were driving the observed dissimilarity by examining differences between the highest dose level (1000 liters) compared to control channel changes at the final sample date (day 45) when differences were most pronounced. Time (day of experiment) was included as a quantitative variable, and taxa with high time axis correlations and that were both abundant and common were then examined to determine if they were increasing or decreasing over the course of the experiment. Differences in legacy samples were tested for using t-tests assuming unequal variance at a significance level of 0.05. Differences in velocity and depth were tested for using two factor repeated measures ANOVA conducted in R. Differences in accumulated fines and sand from day 0 levels were tested for using paired t-tests in R.

RESULTS

Physical habitat changes

Current velocities varied between 25-35 cm/sec and did not differ among channels or over time (two factor ANOVA, $p = 0.44$ and $p = 0.73$ respectively). Depths ranged from 8-10 cm and did not differ among channels or over time (two factor ANOVA, $p = 0.89$ and $p = 0.35$ respectively). Although flow and depths were not altered, sediment treatments changed the physical environment of the experimental channels in several ways. In riffle habitats, mean values of fines and sand increased in all but the lowest treatment by day 30, however, this was only significant for 250/10 and 1000/1 treatment (4.7 to 15.9% and 3.2 to 32.6% respectively, $p < 0.05$ for both; Fig. 4). Control channel 0/1 also showed a significant increase in fines and sand by day 30 and may reflect natural background accumulation associated with higher summer flows, although this was not observed in the 0/10 control. By day 60 fines and sand remained high in the 250/10, declined in the 1000/1, and increased significantly over day 0 levels in the 1000/10, and 100/1 treatments (4.1 to 66.6%, and 4.8 to 20.1% respectively, $p < 0.05$ for both). In pool habitats, mean values of fines and sand also increased in all but the lowest treatment by day 30 with significant increases in the 250/10, 1000/10, 100/1, and 1000/1 treatments (Fig 4). By day 60, fine and sand levels remained high in 1000/10 and 1000/1 but declined in the 100/1 and 250/10 treatments. Geometric mean particle size declined in all treatments after sediment addition was reduced from 44 to 13 mm at the highest (1000/1) dose level (mostly due to deposition in the upper riffles), and mean pool particle size was reduced from 1.9 to 1.3 mm. The channel with preexisting high sediment (250/10*) accumulated more fine and snd sediment than the matched treatment with an increase in fines and sand from 4.7 to 15.8% for the channel with lower initial fines and sand, and 25.6 to 35.1% in the channel with preexisting fines and algae.

The coverage of fines and sand were attenuated downstream from the application point, but over the experimental period, sediments were transported out of portions of the upper and into lower riffles, partly uncovering the rock present on the bed. In the pulse exposures, the 100 and 1000 liter loads both showed initially high FS compared to control levels but the high dose FS levels gradually migrated downstream and out of the channel (Fig. 4). In the press exposures, the gradual additions of sediment resulted again in higher cover in the upper riffles, accumulating most extensively in the early stages in the 250/10* treatment which had preexisting high sediments, and also at the 1000/10 treatment where sediments continued to build to high coverage over the length of the channel (Fig. 4). Turbidity measurements showed that suspended sediment concentration was elevated during additions of sediment as a function of treatment level (Fig. 5).

Sediment treatments affected the mass of course particulate organic matter (CPOM) exported from channels. During the first addition of sediment (day 1) CPOM exported from channels corresponded roughly to dose (Fig. 6). The mass of CPOM exported from the 1000/1 treatment was more than 7 times greater than that of the 100/1 treatment and 15 times greater than that of the control. Organic matter samples taken three months after the first sediment deliveries indicate a continued depletion in CPOM with increasing dose and little effect on FPOM (Fig. 7). The lack of overlap between the means and confidence intervals for the press control relative to both 250* and 1000 liter dose levels suggest these reductions are statistically significant.

Biological responses

Prior to the application of sediment treatments, channel 6 (see Fig. 2, channel schematic), where high levels of sediment were already present, had noticeably greater levels of filamentous green algae on day 0 (Fig. 8). Remaining channels had growth of epilithic diatoms but little filamentous algae. In press exposures, chlorophyll *a* appears to increase slightly over the course of the experiment with no effect of sediment treatments relative to the control except for channel 6 which received a 250 liter dose over the 45 day experiment, but where more sediment appeared to accumulate and was trapped in algae. In this channel chlorophyll *a* increased at an initially higher rate then declined after day 30 to levels similar to the control (Fig. 8). In the pulse exposure, chlorophyll *a* also increased over time with change to both the 100 and 1000 liter treatments being similar to that of the control for the first ten days. Beyond day 10, chlorophyll *a* in the 1000 liter treatment continued to rise with increasing variability then decline after day 30 but always remaining higher than the control. Filamentous green algae dominated the periphyton.

Immediately following sediment delivery there was an increase in drift rate of invertebrates (Fig. 9). Initial drift rates are presented over a gradient showing both press and pulse experiments because some applications were the same (e.g., the 100/1 and

1000/10 treatment each received the same 100 liter volume dose on Day 1 and are labeled 100-pulse and 100-press respectively). Drift rate increased on day 1 in all treatment channels and controls. Control channels showed drift increases of 40-50%. The smallest increase in drift (7%) occurred in the channel receiving 10 liters of sediment while the largest increase (235%) occurred in the channel with preexisting high sediments receiving 25 liters. The other treatment adding 25, and at 50 liters, showed drift increased about 80-90%, while those receiving 100 liters of sediment increased by over 100% and remained at this level in the 1000 liter addition. Three taxa dominated the drift, together comprising nearly 75% of the total: *Simulium* (26%), Chironomidae (26%), and *Baetis* (21%). Collectively, the drift of these taxa increased on average from day 0 to day 1 about twice as much among all treatments excluding the lowest (100/10) compared to the control channels (means of 59 to 149 $m^{-3}hr^{-1}$ in treatments and 65 to 111 $m^{-3}hr^{-1}$ in controls). Relative to controls on day 0, no changes in the taxonomic richness of drifting invertebrates occurred after the initial pulse of sediment (Figure 9b). The per capita drift emigration rates, as a fraction of overall benthic densities, were less than just 1% export per day (using riffle area densities and one-half the area of pools to be conservative).

The degree to which macroinvertebrate community structure was altered by sedimentation was influenced by habitat type (riffle vs. pool), duration of delivery (pulse vs. press), and magnitude of the dose. Generally, pool habitats were more altered by sedimentation than riffle habitats, and continuous press delivery changed benthic communities to a greater extent than did a one time pulse of the same magnitude (Fig. 10). In terms of a habitat specific response, alteration of community structure relative to initial pre-dose conditions occurred on day 1 in pools following the first of ten press deliveries and continued to change by day 30 for both the press and pulse (Fig. 10b & d) Riffle habitats, by contrast, changed little on day 1 and did not accrue noticeable alteration until day 30-45, and only in the high press exposure (Fig. 10). The effect of dose was mixed across habitat types with little change in community structure occurring for the 100, 250, or 500 liter dose in riffle habitats (Fig. 10a) compared to noticeable change for the same dose levels in pools (Fig. 10b). NMDS analysis identified several dominant taxa that appear to be driving patterns in community dissimilarity. For example, *Diphetor* whose densities increased in control riffles over time as well as the 1000/1 exposure, remained constant in the 1000/10 exposure. Midges (Chironomidae) were unchanged in riffle habitats; but in pools they increased by 430% in the single pulse exposure, and were reduced by 88% in the press exposure, but showed little net change in controls. Flat worms (class Turbellaria) were also relatively unaffected in riffle habitat but were eliminated in pools receiving the 1000 liter dose regardless of press or pulse exposure. Several taxa in riffle habitat increased in density in the presence of sediments. For example, in the 1000 liter press exposure aquatic mites, *Baetis*, and *Optioservus* increased from 20.3 to 96.0, 10.6 to 101.3, and 26.6 to 314.6 individuals per m^2 respectively over 45 days. These same taxa also increased in the high dose pulse exposures relative to pre-treatment levels.

Benthic densities of control channels exhibited a gradual increase over the course of the 45 day experiment with a spike in density at Day 30 (Fig. 11). Some substantial differences existed in mean values both within control channels and between channel sections of controls on day 0 and day 1. These differences were inconsistent in direction and suggest a highly variable and patchy distribution of invertebrates within and between channel sections. In the case of both press and pulse deliveries, sediment appears to have had little affect on benthic densities of riffle communities (Fig. 11a & c). The 100 and 500 liter doses appear to have caused an increase in pool densities on day 1 (Fig. 11b). This is possibly an artifact of the channel design where sediment delivery was occurring directly above the first sampled pools (see Fig. 2, channel schematic) and may have been driving invertebrates from the upper riffle into these upper pools. This result was temporary as densities declined by day 30 resulting in a change similar to the control. The pool under the 1000-lieter pulse exposure showed a marked decrease in density on day 1, recovering by day 30 (Fig. 11d). This was not a recovery of community composition but of density only as it was driven by two opportunistic taxa, midges and Oligochaete worms. Both taxa were reduced in density by roughly 95% on day 1 followed by a 95X increase by day 30 for Chironomidae and a 32X increase for Oligochaetes. Remaining taxa changed little or were reduced in density.

Rarefied total taxonomic richness was not influenced by sediment in riffles, but pools were depleted at high doses. At the 1000 liter dose level, the press pool decreased in total richness from 18 to 5 taxa over 30 days (Fig. 12b), and from 20 to 10 taxa in the pulse pool. In comparing among channel treatments, rarefied EPT taxonomic richness was far more variable among pools than riffles (Fig. 13). Similar to total richness, EPT richness showed no influence of dose relative to controls in riffles, but the press-exposed 1000-liter pool showed a richness decrease from 8 to 0 EPT taxa over 30 days (Fig. 13b).

Influence of preexisting high sediment levels

Biological response to sediment differed between the two channels receiving a 250 liter treatment, one with high initial sediment and algae (250/10*) and the other with lower levels (250/10). Benthic density was initially higher in the 250/10* channel and exhibited the largest increase in density compared to any other treatment channel at day 30. This high density on day 0 appears to be driven by tolerant dipteran taxa as *Bezzia*, *Limnophora*, and Chironomidae as well as higher densities of *Physa* snails and an absence of *Ameletus* present in the 250/10 channel. Total and EPT richness (Fig. 14b & c respectively) appear to have been only slightly reduced if at all by the pre-existing high sediment and algae conditions. Cumulative dissimilarity (Fig. 14d) shows a higher degree of community alteration over time in the 250/10* channel compared to the 250/10.

Legacy samples 11 months later

Physical habitat measures such as velocities and depths were not measured during the 11 month post experiment period, however, channel gate controls remained the same and any variations in flow to these channels occurred equally. All density and richness metrics (total density, EPT density, Chironomidae density, total richness, EPT richness, and Chironomidae richness) were found to be lower in the 1000/1 dose channel compared to the 0/1 control channel 11 months after the dose delivery (two sample t-test, $p < 0.0001$ for all; Fig 15). Fine and sand substrate concentrations ranged from 0 to 32% for control samples and 8 to 64% for dose samples, and all biological metrics declined over this range of sediment cover. Where FS cover overlapped, the dose channel was still depleted in numbers and richness relative to the control.

DISCUSSION

Biological responses to increased sediment loads observed in this experiment suggest that for a given concentration (dose), the various combinations of exposure time (press vs. pulse) and habitat (riffle vs. pool) can elicit a different response from individual taxa and from the community as a whole. Further, impacts to these communities may not be immediately evident as mature larvae can exhibit a strong degree of resilience to sediment loads. It may take a full season before impacts to benthic communities, through reduced recruitment, are realized. The sediment treatments were effective in changing the particle size distribution of experimental channels but despite this, and while invertebrate drift increased two-fold, benthic densities were not altered in riffles and most pools as per capita drift rates of the standing stock abundance were much less than 1% per day. Only under severe loading of the pulse treatment in pools was there a reduction in density on day 1 that was restored by day 30. Sediment addition did induce an initial proportionate drift export of CPOM, and treatments remained deficient in stored organic matter in the bed even 3 months after the dosing. This suggests that organic matter resources in streams may become depleted as a result of sediment flux. Habitat specific responses differed, with density and diversity unaffected in riffles, and pools losing diversity under both sediment press and pulse. Community composition though did change as cumulative dissimilarity was most pronounced at the highest press in riffles, and with high press and pulse in pools. Changes were more immediate in pools, gradual in riffles, and were related most to increases in certain tolerant taxa, but also to loss of EPT diversity in press pools. The shift observed at the high 1000-liter doses (both press and pulse) and not in others suggests that the increase in average FS cover here from 4.1 to 33.9% for press and 3.2 to 32.6% for pulse in riffles over the first 30 days corresponds to a level where limits of tolerance and habitat suitability exceed the ecological capacity to maintain biological integrity (report 3 of this series). Field data corroborate this assertion as biological thresholds of sediment were found to be in the range of 30 to 40% FS for measures at both point-transect and patch-scale. At the high 1000-liter dose, the continued increase in FS cover by day 60 in the press exposure compared to a reduction in the pulse may indicate that without continued inputs, even at low flows, FS will migrate downstream and sediments will move out from the reach localities where deposition occurred. Episodic high flows near bankfull will have an even more important influence, and such flushing flows are considered important for rejuvenating habitats exposed to sediment loading (Gordon et al. 2004)

The channel laden with sediment at the start of the experiment (#6) harbored the highest invertebrate densities and algal chlorophyll biomass over all other treatments. Dosed at the same level as another channel not having high starting sediment, neither showed much response, suggesting that these sediment additions (250 liter) were not enough to produce changes even where initial density of invertebrates or sediment cover was high. The high sediment levels created in the high pulse dose were also associated with higher levels of chlorophyll than seen in other channels. The higher levels of chlorophyll *a* and the dominance of filamentous forms is consistent with related work which has shown this algae type to be not only tolerant of sedimentation but of unremitting chronic delivery (Riddle et al. 2009). Filamentous algae also appears to entrain fine sediment particles which are later released with seasonal senescence (see Fig. 4 and Fig. 8 for correlated reduction in sediments and algae by day 60 in 250*/10).

The long-term limitation of the legacy of sedimentation was evident in the samples taken nearly one year after the experiment was begun. The high pulse channel appeared to be unsuitable for colonization as FS cover remained elevated and CPOM resources had been depleted, limiting the recruitment potential. Immigrant propagules may not persist above 30-40% FS, where most diversity and density was lost. Even where FS overlapped the lower range of FS found in the adjacent control channel, the high dose channel was still depauperate in taxa and numbers. The sediment legacy appears to impede recovery and is consistent with results from field data where locations with FS cover above 30-40% have reduced invertebrate richness (report 3).

The main effect of excess sediment on benthic stream invertebrates has been characterized as a shift in overall community composition (Waters 1995) but variable effects on overall density (Lenat et al. 1981). Our results refine how these changes may be related to sediment delivery (timing) and habitat type (erosional riffles and depositional pools). Univariate metrics based on density or richness should be used cautiously in evaluating the effect of sediment on benthic communities as the various responses from individual taxa owing to their relative tolerance to sediment and particular substrate habitat needs can result in misleading patterns of overall community response. For example, the recovery in density at day 30 in pool habitats exposed to a single high dose pulse (1000/1) was attributable to only two taxa groups, Chironomidae and Oligochaeta that often inhabit sediments and are generally more pollution-tolerant. This response is consistent with other findings (Suttle et al. 2004) showing that smaller burrowing taxa can tolerate sediment and take advantage of this niche space, but does not represent a recovery of community structure. This lack of recovery in high pulse pool habitat community composition was reflected in cumulative dissimilarity which was higher on day 1 and persisted at the same level through day 30 compared to control or low pulse pools. The more pronounced response by benthic invertebrates to the additions of sediment in pools supports the expectation that locations with lower velocities would accumulate greater amounts of deposited sediments and would have more influence on benthic communities compared to riffle areas of higher velocity and lower settling rates.

Little attention has been given to examining the longer term effects of sediment on the recolonization of systems recently impacted by sediment. In this experiment, the long term effects of excess sediment supply were more evident in riffle areas than were the immediate short-term effects. For example, in the 1000/1 dose treatment no change to Chironomidae density was observed in riffle habitat throughout the 45 day experiment. However, 11 months later Chironomidae density was significantly reduced in riffle habitat relative to the control. Moreover, density and richness of the community as a whole, and EPT taxa in particular had been reduced, a response also not observed in the initial 45 day experiment. This delayed legacy of sediment is important to consider and suggests that short term experiments may not capture the full scope of impacts. Along with persistent FS deposits in the high dose channel, organic matter food resources may be deficient because large amounts of CPOM were flushed from the system during the initial dosing (Fig. 6). Reduced amounts of CPOM persisted 90 days later suggesting that sediments prevent subsequent retention and storage of CPOM as interstitial spaces became filled (Fig. 7). The flushing event may also have removed early instar larvae and eggs from the channel. Though FPOM storage was apparently not reduced in the high pulse, it and CPOM were reduced as press exposures increased, suggesting that the mechanics of organic matter mobilization may depend on the relative volume and timing of sediments entering a channel. A huge influx of sediment in the high pulse, consisting of 75% sand (Fig. 3), mobilized the large particle fraction of organic matter in a massive export from the channel. Sand acts as a lubricant, being the most transportable particle size fraction. The gradual addition of sand in the press treatments resulted in lower levels of CPOM export, but ultimately depleted all organic matter fractions in these channels. Low abundance of few taxa in the high pulse channel suggests that would-be colonists were deprived of food resources in an inhospitable habitat of persistent FS cover. While sand loading of stream channels may generate local export and depletion of CPOM, as seen in our mesocosm channel results, it is also important to recognize that large wood debris (LWD) jams in small channels leads to the retention of sand and sediment in steep headwater forest streams (Hassan et al. 2005) . So there may be a dynamic interaction between the retention of organic matter and sediment as sand entry may trigger transport of CPOM and LWD debris flows under high loading, while jams dam sediment movements under lower discharge conditions.. Episodic discharges resulting from snow melt and precipitation events can release these debris dams and accumulated sediments.

The most immediate biological response following sediment additions was elevated invertebrate drift. Results from our longer term, larger scale experiment were similar to the Molinos and Donohue (2009) laboratory findings where increased drift was seen in the first 24 hours following dosing. Increases in drift were observed in all but the lowest treatment level relative to controls. However, drift did not increase with dose indicating that drifters may be induced at some lower threshold of suspended particles, but then saturates at some constant level despite continued increases in suspended particles (Gibbins et al. 2007). This differed from the relationship between CPOM and sediments where mobilization of CPOM appears to be proportional to sediment dose. Drift rates roughly doubled for all channels receiving 25 liters of sediment (dry volume) or more but, as the numbers of drifting individuals were roughly two orders of magnitude lower than the benthic density, this increased rate of drift on day 1 was insignificant in reducing benthic densities to any detectable degree. In our experiment, the highest drift rates occurred in the channel with preexisting high sediments and invertebrate density, consistent with density-dependence of drift (Hildebrand 1974). Filter feeding *Simulium* had one of the highest drift rates of any taxa supporting the idea that interference with food gathering can be a major contributor to drift behavior (Waters 1995).

Field studies show that while some tolerance indicators exhibit a monotonic responses to sediment, diversity drops at thresholds of 30-40% combined fine and sand substrate measured at both reach and patch-scales (report 3 of this series). The experimental mesocosm results are also consistent with the reach-scale findings that low stream power permits greater deposition for local conditions, but that for equal power, test streams in disturbed landscapes accumulate more sediment and support less diversity. The depositional pools of the mesocosms similarly showed most of the biological impact over the short-term exposure period, but biotic limits were also realized over the long-term in sediment-laden riffles. These experiments corroborate field studies of sediment limitations, adding certainty to the applicability of results in natural stream systems for resource management decisions and developing numeric criteria for sedimentation.

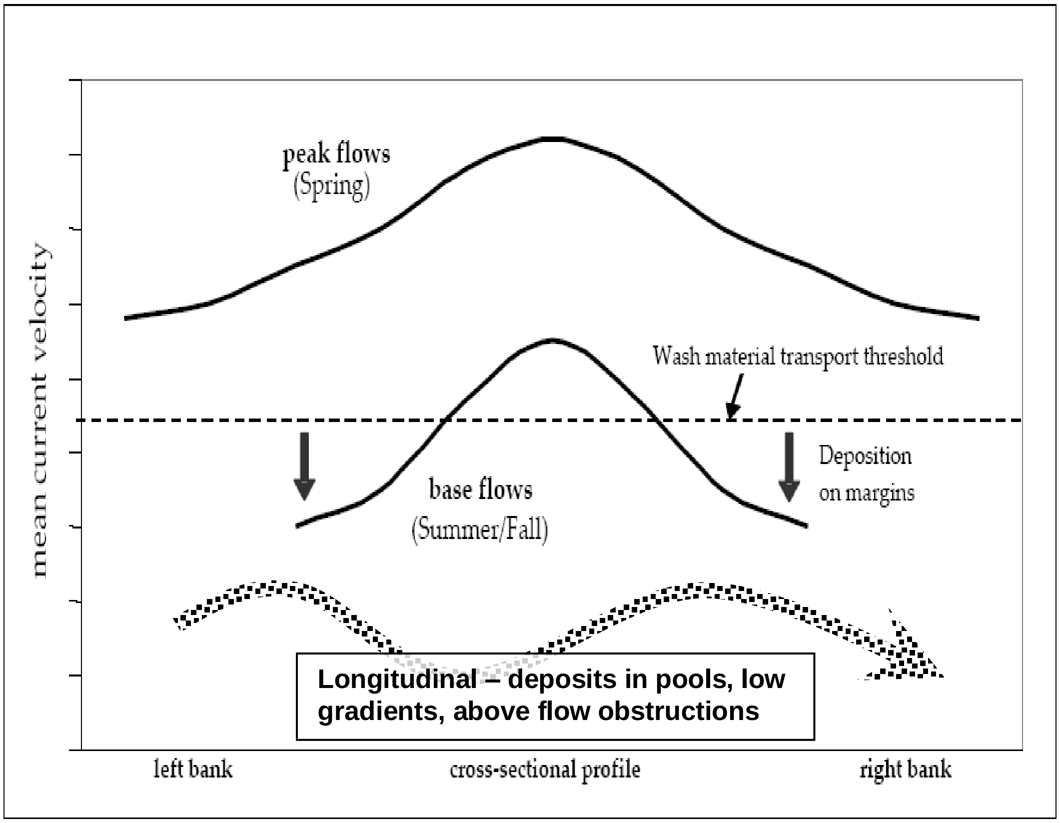

Figure 1. Deposition occurs across the lateral profile of a channel as a function of changes in the transport energy of current velocity declining at the margins, and with seasonal decreases in flow. Deposition along the longitudinal flow profile occurs where riffles flow into pools, from steeper to lower gradient reaches, and upstream of boulders and large wood debris (flow separation).

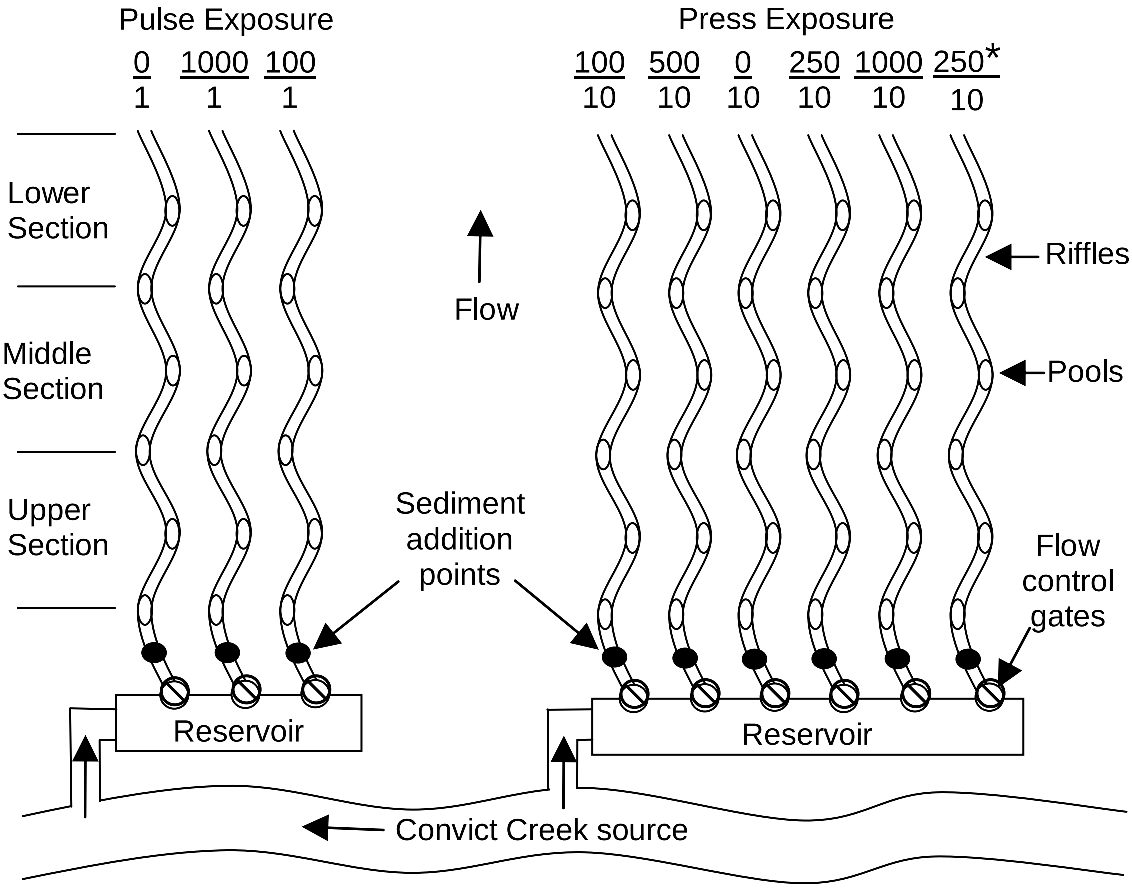

Figure 2. Experimental stream channel schematic illustrating stream flows and sediment dosing design for independent pulse and press exposures. Numerator indicates total sediment dose delivered (volumetric liters) and denominator indicates number of dosing events to deliver that total. 250* is the outer channel with preexisting high sediment and algae concentrations for contrast to the 250 treatment without prior sediment loading.

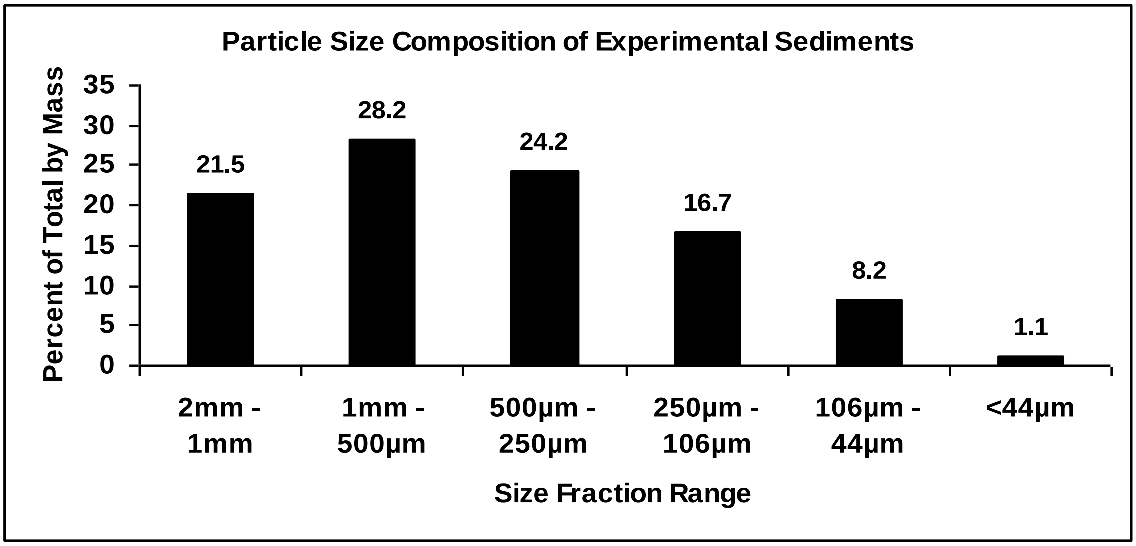

Figure 3. Particle size composition of sediments used for experimental treatments.

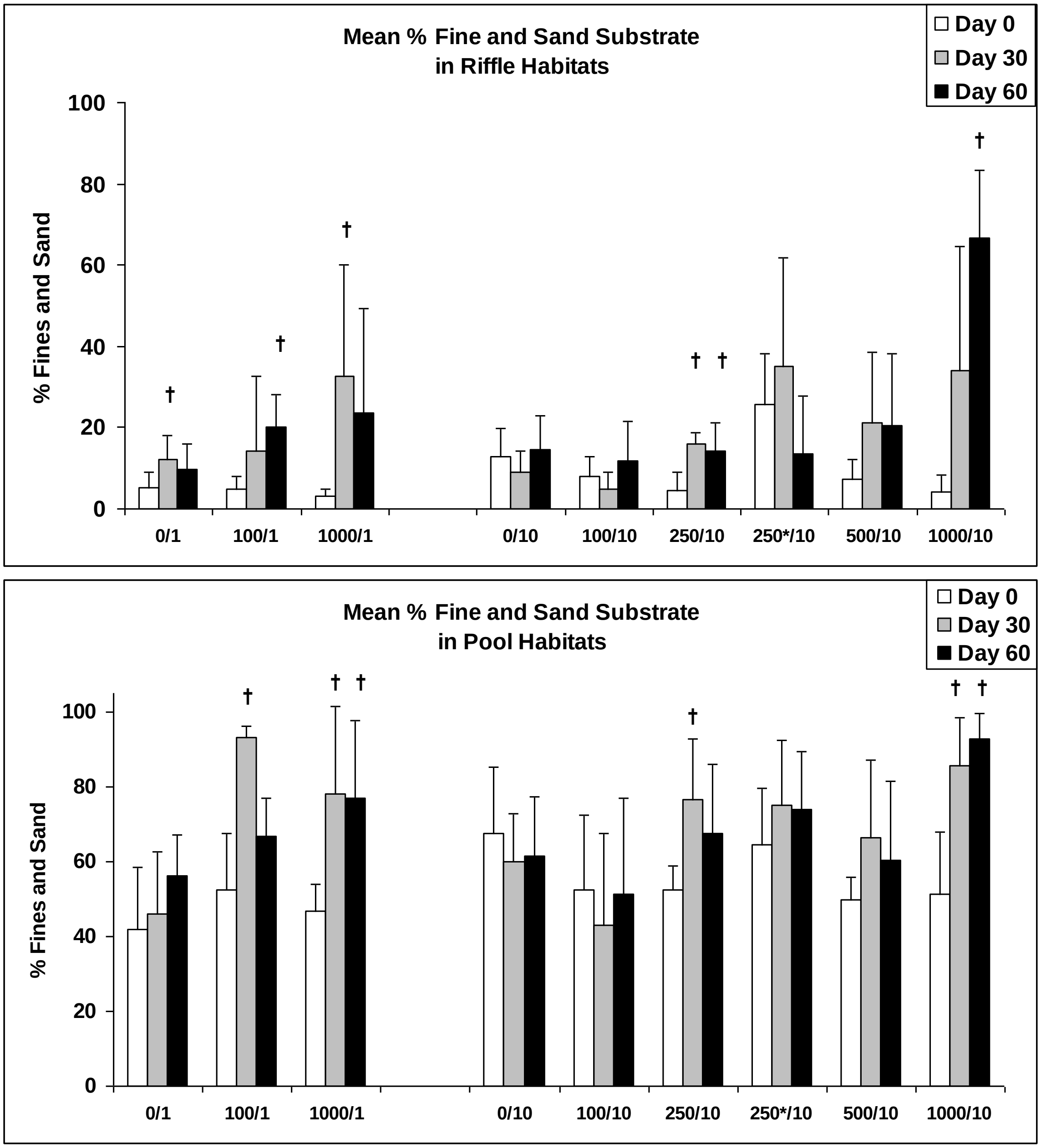

Figure 4. Mean percent fine and sand substrate (n=6, ± 95% CI) for days 0, 30, and 60 for riffles and pools in press and pulse experimental treatments. * Denotes the 250 liter treatment assigned to the channel exhibiting pre-existing high fines and algal densities at the beginning of the experiment, for contrast with the randomly assigned 250 liter treatment channel. Within each treatment, † symbol indicates significant differences ($p < 0.05$) from day 0.

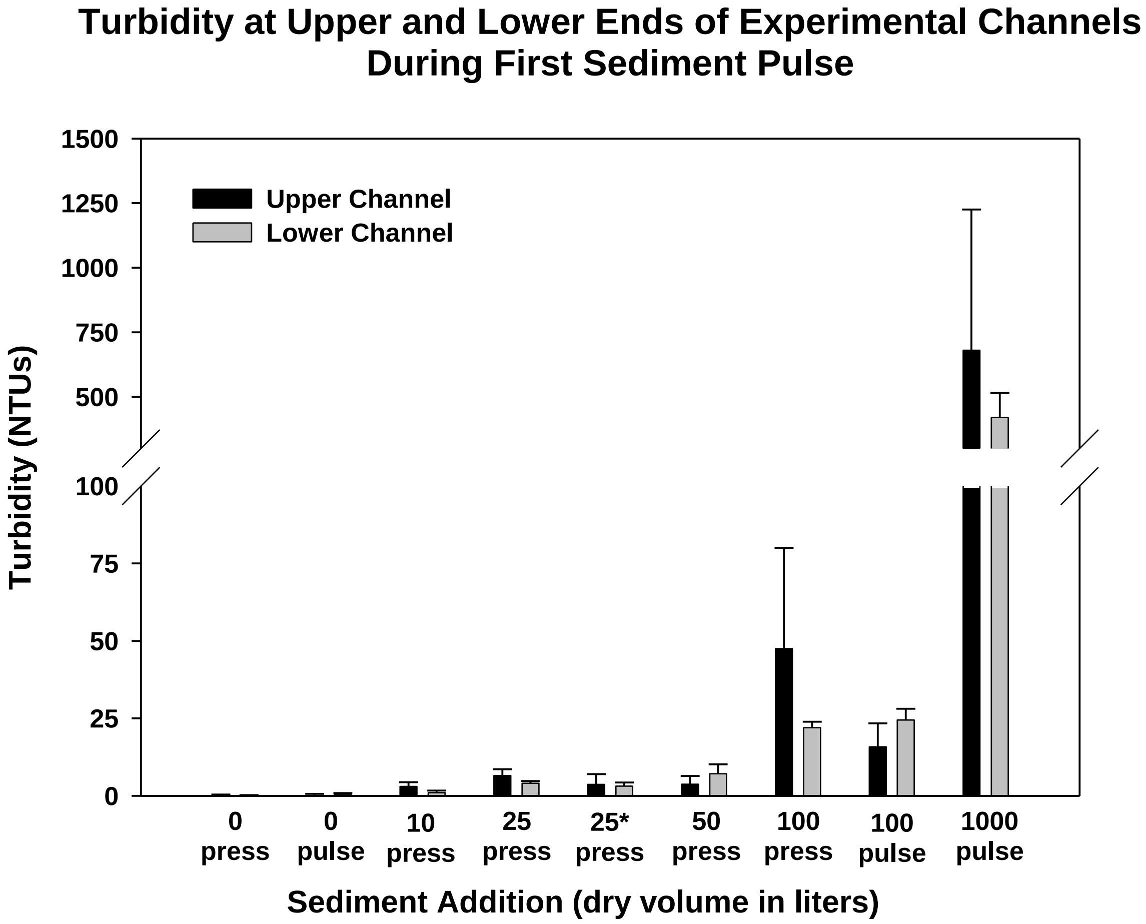

Figure 5. Mean turbidity (n=3, ± 1SD) measurements made at 30, 60, and 90 minutes into the first two hour sediment pulse at the upper and lower channel sections. Treatment channels are labeled on the X-axis with the volume (in liters) delivered that day and the experiment assignment, denoted as press or pulse. * Denotes the 25 liter treatment (first sediment pulse period only) assigned to the channel exhibiting pre-existing high fines and algal densities at the beginning of the experiment, for contrast with the randomly assigned 25 liter treatment channel.

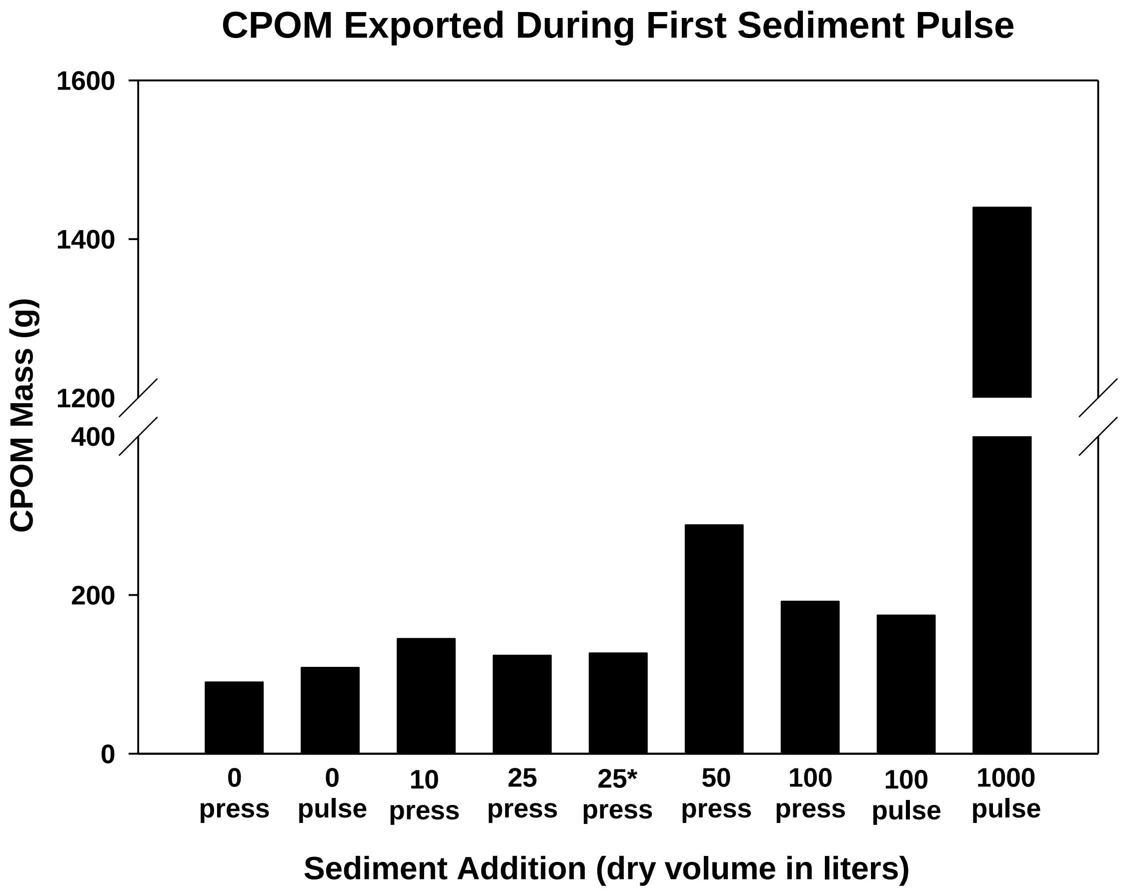

Figure 6. CPOM export from experimental channels during first sediment pulse on Day 1. Treatment channels are labeled on the X-axis with the volume (in liters) delivered that day and the experiment assignment, denoted as press or pulse. * Denotes the only replicated treatment assigned to a channel exhibiting pre-existing high fines and algal densities at the beginning of the experiment for contrast with the randomly assigned 25 liter treatment channel.

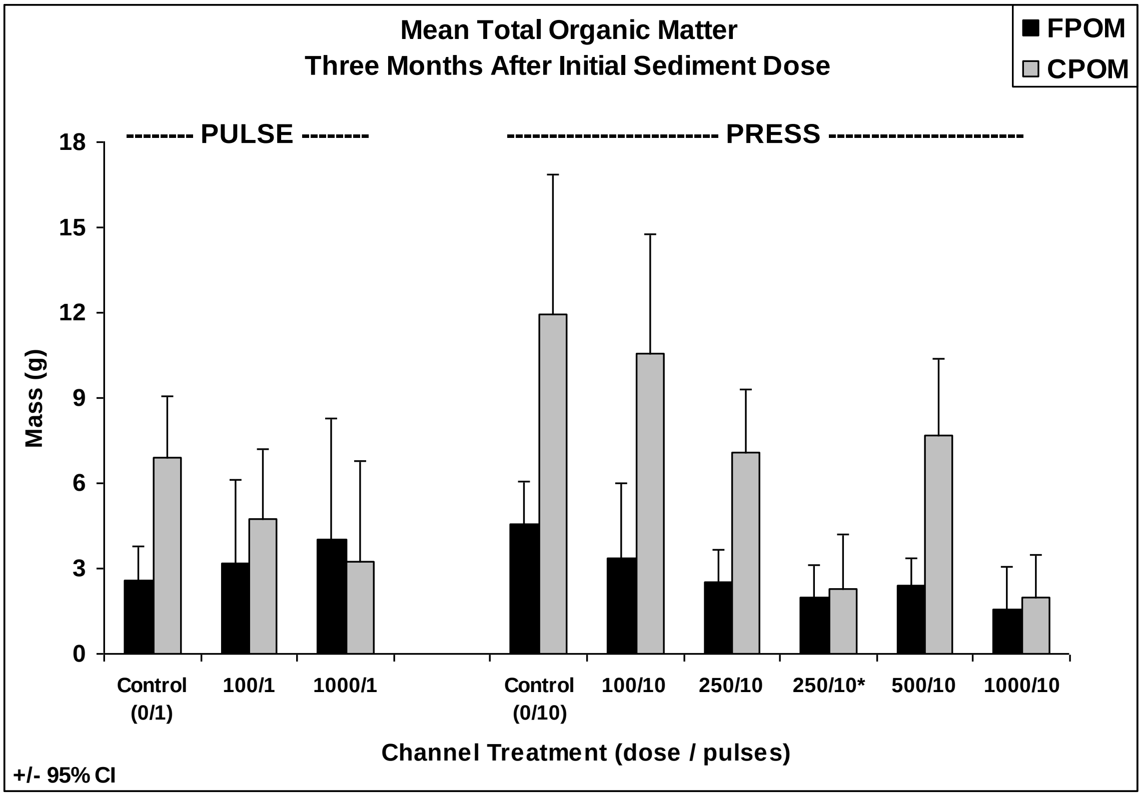

Figure 7. Mean total organic matter (n=6, ± 95% CI) collected within each of six riffle segments of experimental treatment channels three months after initial dose delivery.

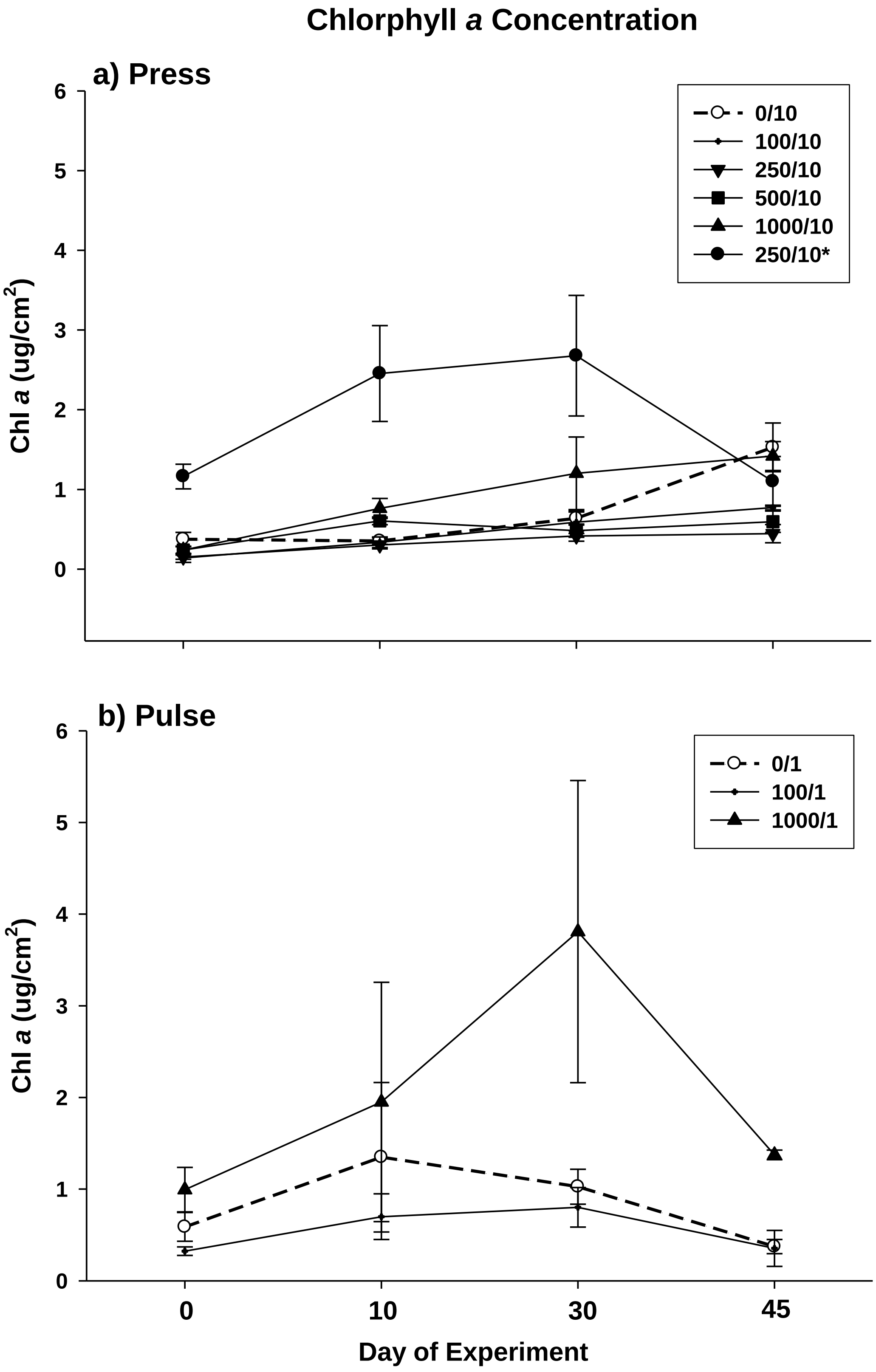

Figure 8. Mean chlorophyll *a* (n=3, ± 1 SE) for a) press and b) pulse exposures on days 0, 10, 30, and 45.

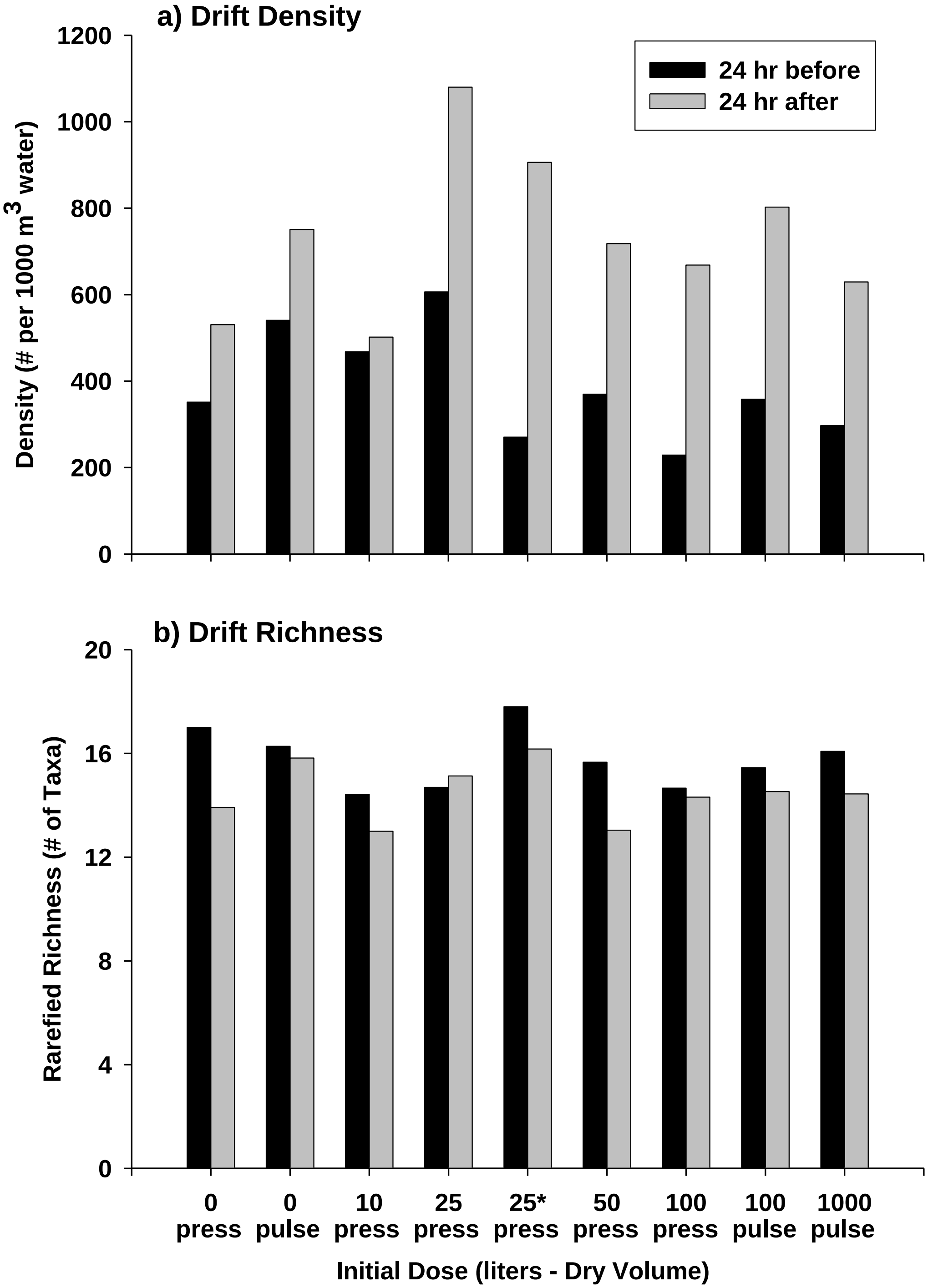

Figure 9. a) Drift density and b) taxonomic richness for samples collected in the 24 hours leading up to the first sediment delivery (Day 0) and the 24 hours following the first delivery (Day 1). X-axis labels represent the volume (in liters) delivered that day and the experiment assignment, denoted as press or pulse. * Denotes the 250 liter treatment assigned to the channel exhibiting pre-existing high fines and algal densities at the beginning of the experiment, for contrast with the randomly assigned 250 liter treatment channel.

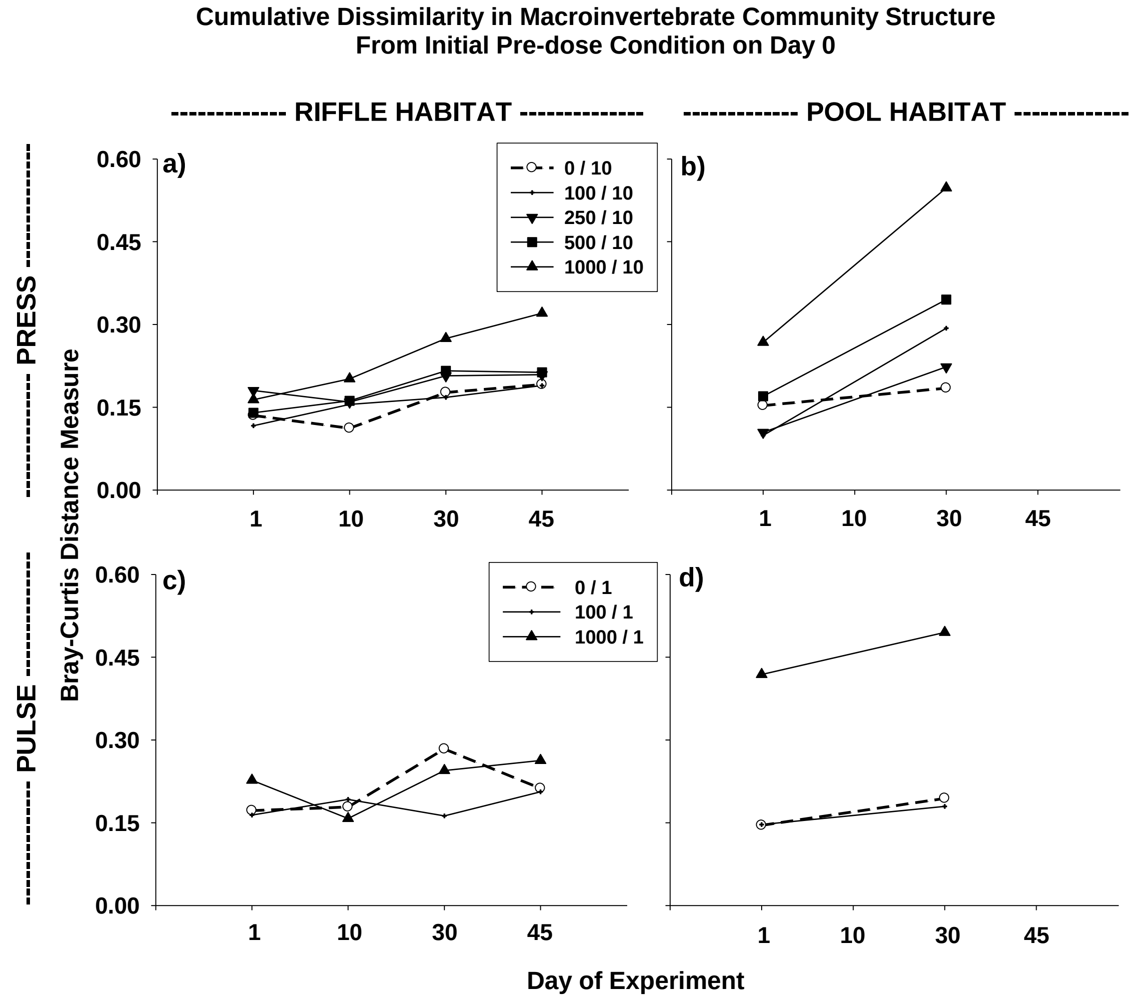

Figure 10. Cumulative dissimilarity over time from initial community structure on day 0 among sediment treatments organized by habitat (riffle vs. pool) and sediment delivery (press vs. pulse). Figures represent differences from experimental days 1, 10, 30, and 45 for riffle habitats (a & c) and days 1 and 30 for pool habitats (b & d).

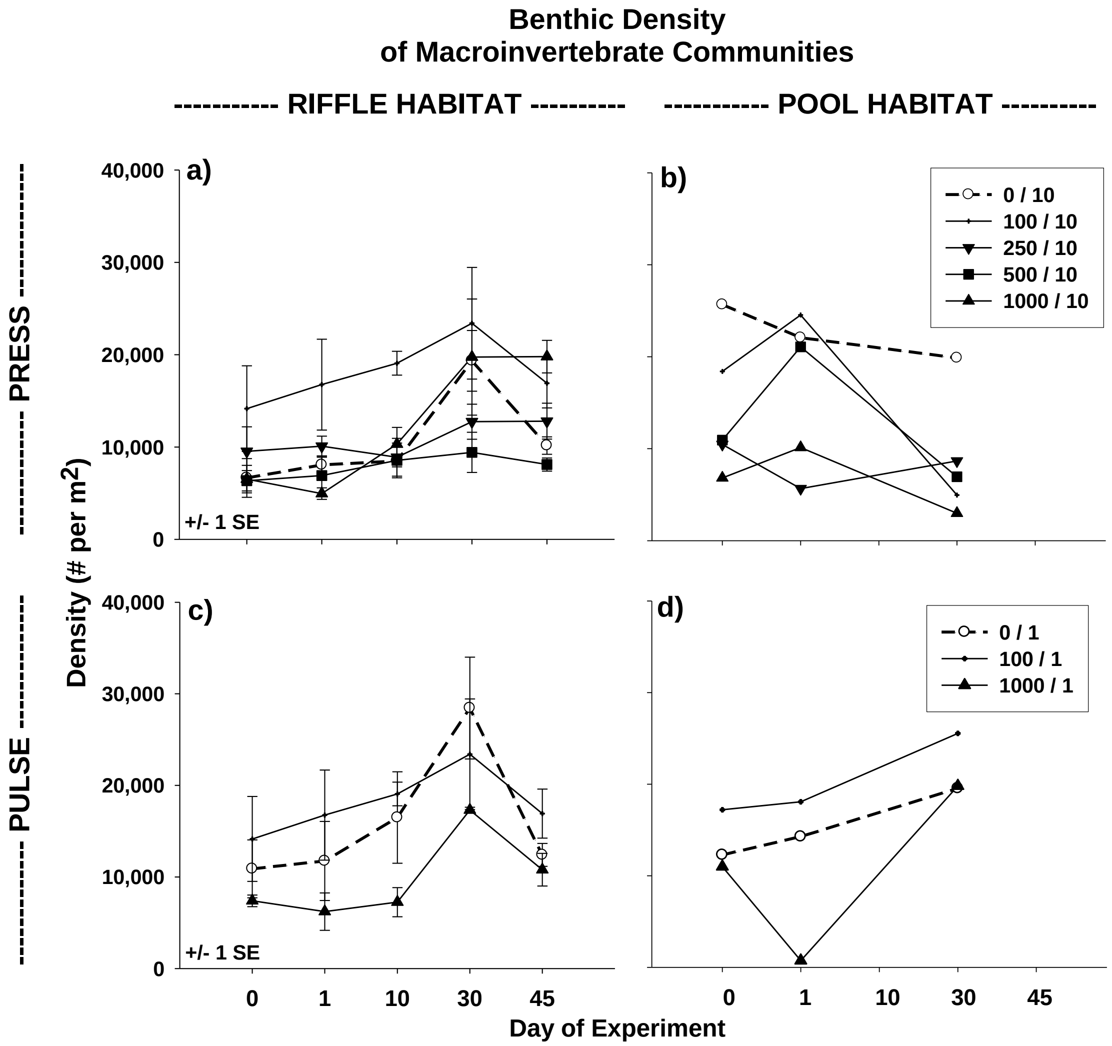

Figure 11. Benthic density among sediment treatments organized by habitat (riffle vs. pool) and sediment delivery (press vs. pulse). Figures represents samples from experimental days 0, 1, 10, 30, and 45 for riffle habitats (a & c) and days 0, 1, and 30 for pool habitats (b & d). Values from riffle habitats represent an average of upper, middle, and lower sections (n=3, ± 1 SE) within channel treatments, values from pool habitats represent the upper section only. Legend text represents the total dose delivered over the number of incremental pulses to deliver that total.

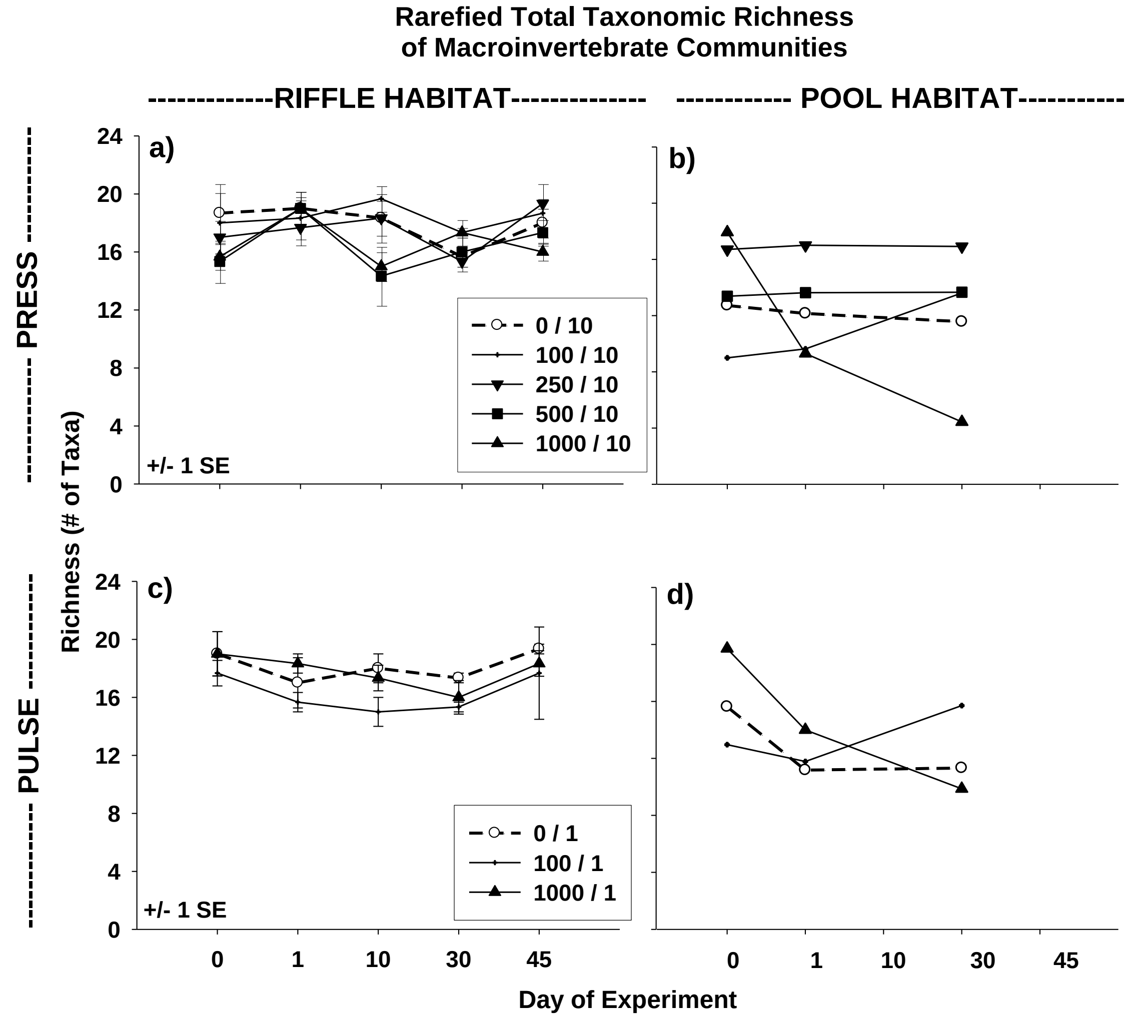

Figure 12. Rarefied total taxonomic richness among sediment treatments organized by habitat (riffle vs. pool) and sediment delivery (press vs. pulse). Figures represents samples from experimental days 0, 1, 10, 30, and 45 for riffle habitats (a & c) and days 0, 1, and 30 for pool habitats (b & d). Values from riffle habitats represent an average of upper, middle, and lower sections (n=3, ± 1 SE) within channel treatments, values from pool habitats represent the upper section only. Legend text represents the total dose delivered over the number of incremental pulses to deliver that total.

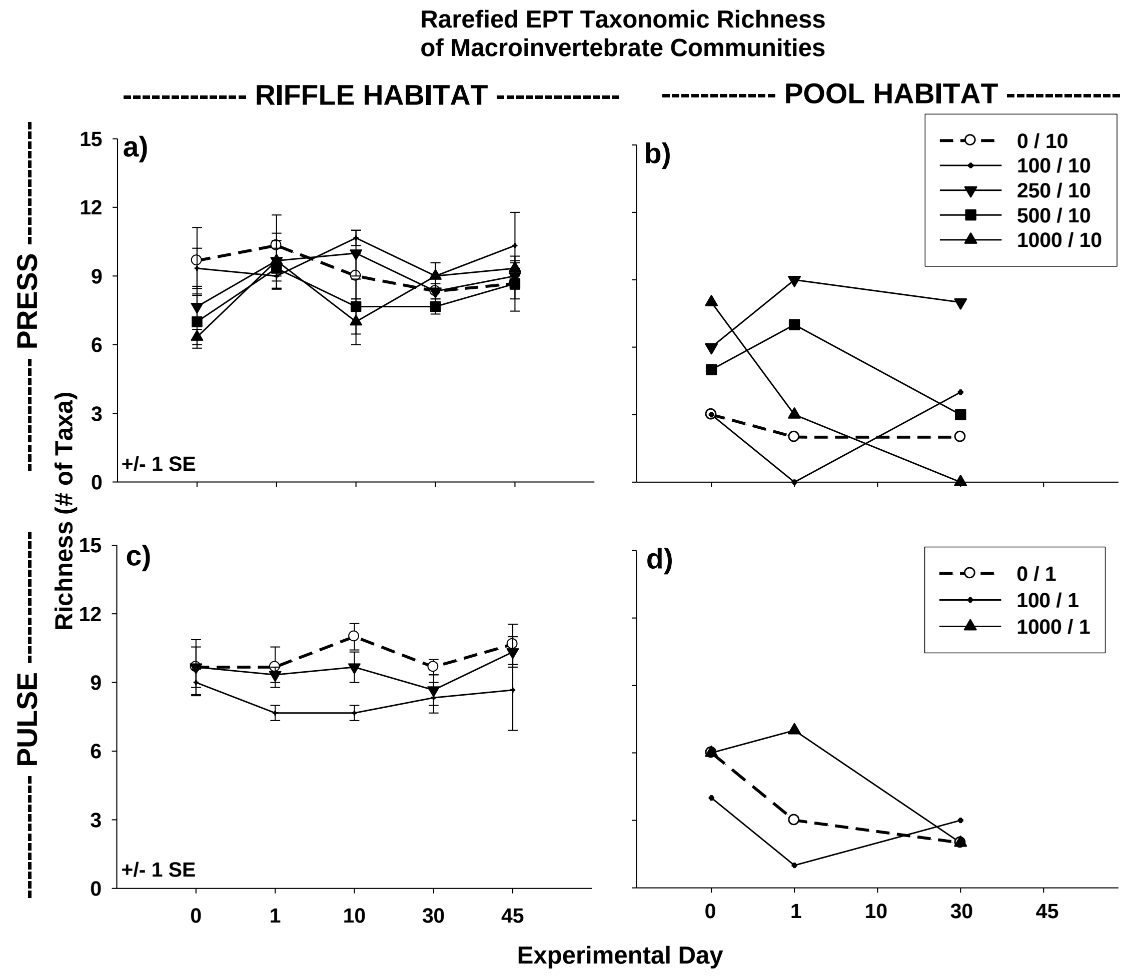

Figure 13. Rarefied Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness among sediment treatments organized by habitat (riffle vs. pool) and sediment delivery (press vs. pulse). Figures represents samples from experimental days 0, 1, 10, 30, and 45 for riffle habitats (a & c) and days 0, 1, and 30 for pool habitats (b & d). Values from riffle habitats represent an average of upper, middle, and lower sections (n=3, ± 1 SE) within channel treatments, values from pool habitats represent the upper section only. Legend text represents the total dose delivered over the number of incremental pulses to deliver that total.

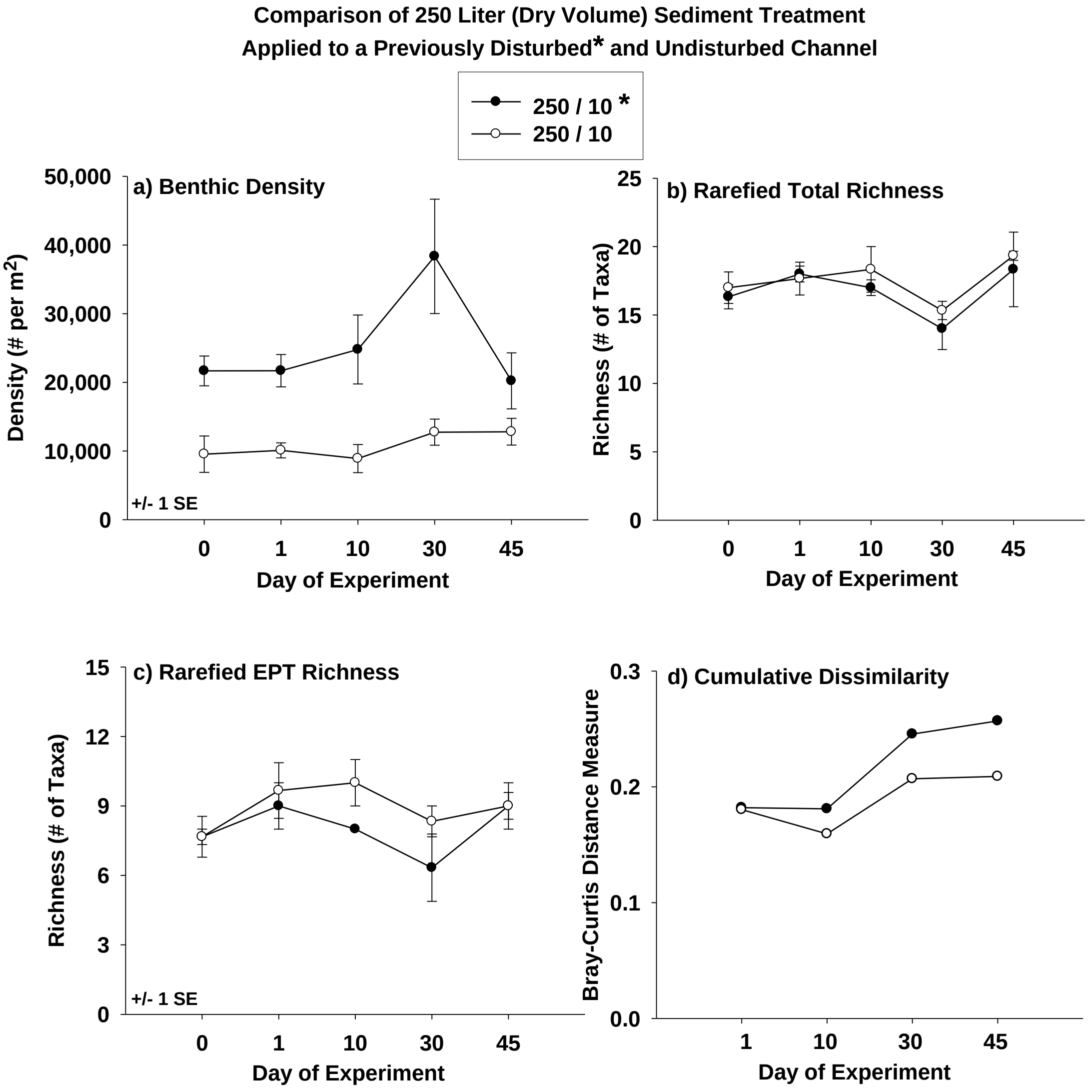

Figure 14. Influence of preexisting high sediment and algae concentrations on the effect of sediment on experimental day 0, 1, 10, 30, and 45 for mean values (n=3, ± 1 SE) of a) benthic density, b) taxonomic richness, c) and EPT richness and experimental day 0, 1, and 30 for d) cumulative dissimilarity. * indicates preexisting high sediment channel, both received 250 liters (dry volume) of sediment delivered over 40 days in 10 pulses.

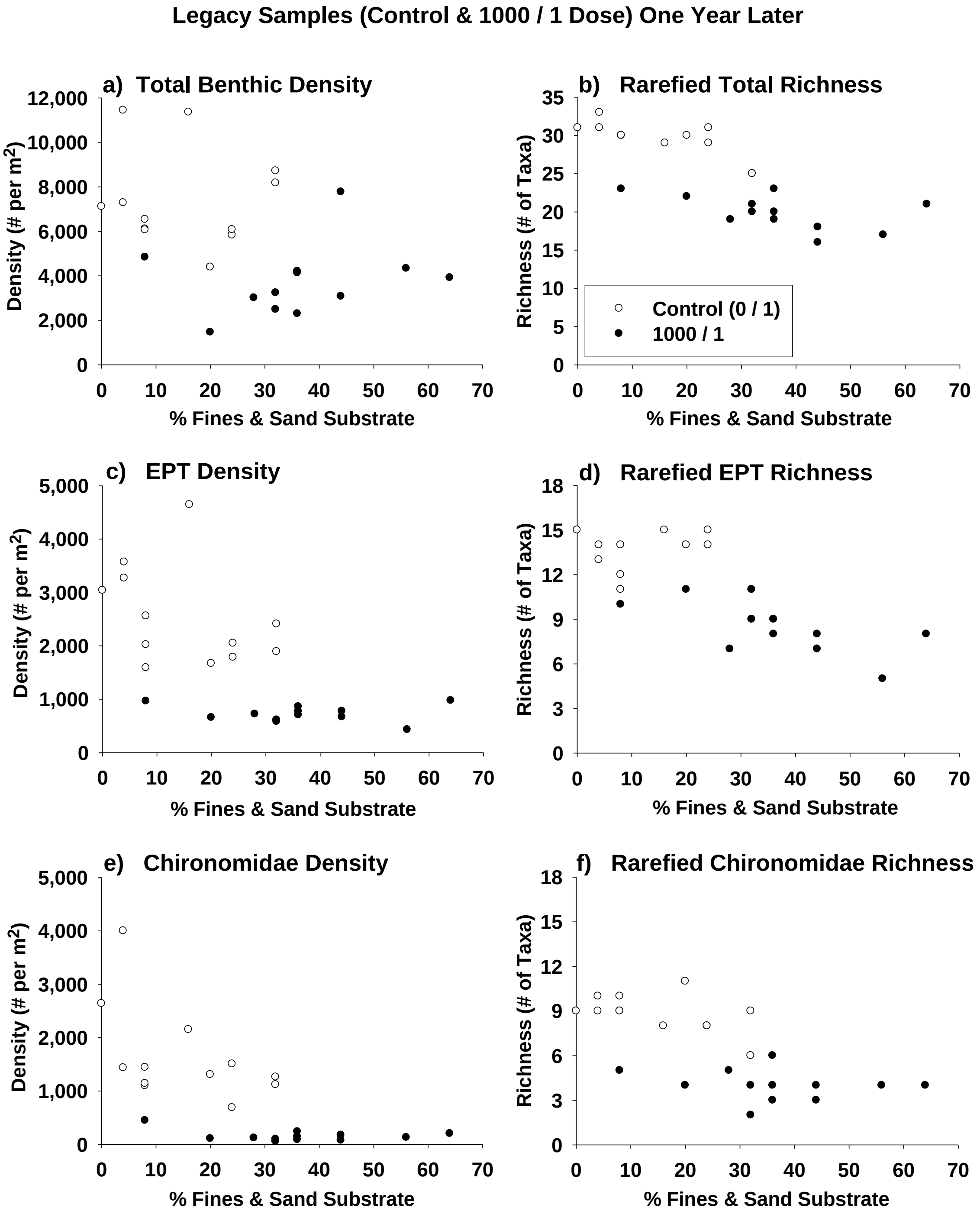

Figure 15. Legacy samples for control (n=12) and 1000/1 dose (n=12) 11 months after dose delivery. Figures represent a) benthic density, b) rarefied total richness, c) EPT density, d) EPT richness, e) Chironomidae density, and f) rarefied Chironomidae richness regressed against percent fine and sand substrate.

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