Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival

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Abstract: Elevated concentrations of inorganic sediment supply in streams may impair many biological functions. However, the contribution of exposure duration to the observed impacts has not been previously considered. We evaluated the effects of sediment pulse duration using 14 streamside flow-through experimental channels, each of which contained a naturally colonised invertebrate assemblage and 10 rainbow trout (*Oncorhynchus mykiss*) fry. Channels were exposed to fine sediment pulses of constant concentration but varied pulse duration (ranging from 0 to 6 h) every second day over 19 days. Total abundance of benthic invertebrate and family richness declined as sediment pulse duration increased. Invertebrate drift total abundance increased as pulse duration increased; however, family richness of drift decreased. Trout length and mass gain over the 19-day period was negatively correlated with pulse duration. Path analysis suggests that the direct effects of fine sediment on trout (impaired vision leading to reduced prey capture success and (or) increased metabolic costs from physiological stress) are more important to trout growth than indirect effects (decreased drift and benthic invertebrate richness and drift abundance).

Résumé : Les concentrations accrues des apports de sédiments inorganiques dans les cours d'eau peuvent perturber de nombreux processus biologiques. Cependant, les impacts de la durée de l'exposition n'ont pas été examinés jusqu'à maintenant. Nous avons évalué les effets de la durée de l'afflux de sédiments au moyen de 14 canalisations expérimentales installées en bordure d'un cours d'eau, chacune colonisée naturellement par une communauté d'invertébrés et dix alevins de Truite-arc-en-ciel (*Oncorhynchus mykiss*). Les canaux ont été exposés à des afflux de sédiments fins à concentration constante, mais dont la durée variait de 0 à 6 heures tous les 2 jours sur une période de 19 jours. L'abondance totale des invertébrés benthiques diminuait en fonction de l'allongement de la durée de l'afflux de sédiments et la richesse en familles déclinait. La densité totale de la dérive des invertébrés augmentait avec la durée de l'afflux, mais la richesse en familles diminue. La croissance en longueur et en masse des truites pendant la période de 19 jours était en corrélation négative avec la durée de l'afflux. Une analyse des coefficients de direction laisse croire que les effets directs des sédiments fins sur la truite (une vision réduite qui diminue le succès de la capture des proies et/ou des coûts métaboliques accrus dus au stress physiologique) affectent plus la croissance que les effets indirects (diminution de la dérive, de la richesse des invertébrés benthiques et de la densité de la dérive).

[Traduit par la Rédaction]

Introduction

The effects of increased fine inorganic sediment loads on stream communities have been well documented (summaries in Newcombe and MacDonald 1991; Newcombe 1994; Waters 1995). Many studies have reported a decrease in invertebrate abundance and a change in community composition resulting from several sediment-mediated mechanisms. Culp et al. (1986) showed that invertebrates become dislodged into the water column by rolling or saltating particles. Many taxa rely on a filter-feeding apparatus to remove fine particulate organic matter from the water column, and these can become clogged by sediment, thereby reducing feeding efficiency. Also, the distribution of grazing invertebrates may be affected by the smothering of algal habitat and abrasion of cells by elevated sediment concentration (Vuori and Joensuu 1996). Regardless of the particular mechanism, in all cases an increase in fine sediment load generally causes invertebrates to enter the water column and drift.

Changes to the quantity and composition of available food resources (e.g., aquatic invertebrates) can directly influence the growth of resident fish. Sediment can also indirectly

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affect fish growth through modifications of behaviour and habitat. At relatively low suspended sediment concentrations, turbid conditions may be viewed as cover for foraging fish (Gregory and Northcote 1992), leading to increased foraging effort because of a perceived reduction of predation risk (Gregory and Levings 1996). In contrast with elevated feeding effort is a severe reduction in foraging efficiency with increased turbidity (Vogel and Beauchamp 1999). Direct effects of increased sediments on fish vary with suspended matter concentration (Newcombe 1994), degree of sediment deposition (Chapman 1988), particle size distribution and type of sediment (Lake and Hinch 1999), and life stage at which the fish is exposed (Servizi and Martens 1990). Sediment-induced mortality and decreased survival rates have been noted in only a few studies (Sigler et al. 1984; McLeay et al. 1986), although the concentration administered to cause mortality greatly exceeds elevated field levels and could only be achieved in experimental situations (Lake and Hinch 1999). Suspended sediments in streams can induce coughing or gill flaring (Berg and Northcote 1984) and decrease respiratory capabilities through gill abrasion (Herbert and Merkins 1961). Even relatively low amounts of deposited sediment can limit inter-gravel water exchange, reduce interstitial dissolved oxygen, and effectively smother developing eggs and alevins (Scrivener and Brownlee 1989). Early life stages tend to be more susceptible to sediment due to their limited movement and tolerance (Servizi and Martens 1990).

Newcombe and MacDonald (1991) proposed that sediment in streams be viewed as eliciting a dose-dependent response, incorporating both concentration and duration of exposure when predicting an organism's reaction. The dose model is used frequently by toxicologists describing biological responses to chemicals in the environment (Liber et al. 1992). With few exceptions (Newcombe 1994; Larkin et al. 1998), duration of exposure to sediments is rarely evaluated or even noted. Newcombe and MacDonald (1991) suggested a stress index to rank any potential impacts of sediment based on the dose–response model. When studies were reanalysed using estimates of duration, the new model suggested dose was a better indicator and predictor than concentration alone. Although many of the studies that were used to derive the stress index compared several concentrations and types of sediment, no study has exclusively tested the contribution of sediment pulse duration to changes in stream communities.

The purpose of this study was to address two key questions regarding the biological impacts of sediment in lotic ecosystems. First, we sought to determine the effects of fine sediment pulse duration on drifting and benthic invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) fry growth and mortality. The second objective was to quantify and compare the direct and indirect (mediated through the invertebrate food supply) effects of sediment exposure on fish growth.

Methods

Study site

This experiment was performed at Moffat Creek near Horsefly, British Columbia, approximately 80 km east of Williams Lake. Moffat Creek is a third-order tributary of the Horsefly River, which flows through Quesnel Lake into the Fraser River. The Fraser Plateau is covered by unconsolidated geologic materials in the form of fluvial, lacustrine, and colluvial deposits (Lord 1984), which tend to be highly mobile and become entrained and transported in the water column. Generally, there is little riparian canopy as much of the land has been cleared to the streambank for livestock grazing and hay crops.

Experimental design

To test the effects of fine sediment pulse duration on invertebrate assemblages and fish growth, an experiment was conducted by creating a gradient of duration treatments. Treatments consisted of seven sediment pulse durations ranging from 0 (control) to 6 h, pulsed every second day for 19 days (Table 1). All sediment pulses were initiated at 1000 h and continued for the predetermined duration. Each treatment was replicated twice. The dose regime was intended to mimic a typical disturbance activity, such as regular movement of cattle through riparian areas, riparian timber harvesting and frequently occurring thunderstorms which repeatedly introduce excess sediment pulses over an extended period of time. To exclusively test pulse duration, the concentration of each sediment pulse entering the stream channels was held at approximately 700 $mg \cdot L^{-1}$ throughout the dosing periods. This concentration has been shown to induce a response in fish and invertebrates (McLeay et al. 1986; Newcombe and MacDonald 1991). Also, a permanent B.C. Ministry of Forests water-quality monitoring station, situated downstream from our site, has often recorded this concentration and higher during rain events.

Experimental stream channels were constructed immediately adjacent to Moffat Creek. Water flow was redirected from the creek in polyvinyl chloride (PVC) pipe and partitioned into two 500-L headtanks. Each headtank supplied water to eight experimental channels, 16 in total, at approximately 0.5 $L \cdot s^{-1}$ each. Fourteen channels were used for sediment treatments and two channels were devoted to measuring invertebrate immigration. All channels had a surface area of 1.5 m^2 (7.5 m long × 0.2 m wide × 0.2 m deep) and were set to a 1% slope to mimic the local stream gradient. Substrate particles were sieved to fit the gravel–pebble range (6.4 mm to 20 mm) approximating the substrate of Moffat Creek. Substrate depth was approximately 8 cm throughout and no alteration of the substrate was initiated prior to the experiment. Small pool and riffle areas were created naturally around fish cover objects (10-cm section of PVC pipe cut along its length) placed in each of the channels (10 per channel). Water depth was approximately 2.5 cm at the upstream end and 10 cm at the outflow.

Invertebrates

Invertebrate assemblages were established in the channels through active addition of kick samples collected from Moffat Creek, and by natural drift through the intake pipe. Invertebrates were allowed to colonise for three weeks before the experiment began. Benthos-sampling baskets (surface area, 104 cm^2; volume, 500 mL; 12 per channel) were made from clear plastic tubs, which contained numerous holes over their entire surface, and were buried flush with the substrate surface to allow free movement of invertebrates. During each sampling event, three baskets were removed from the channels and the contents preserved with a 5% formaldehyde solution.

Drift nets (250-μm mesh; 1 per channel) were placed on the downstream end of the channels. During sampling events, drift nets were set at the beginning of the sediment pulse and remained in place to collect invertebrate drift for 24 h, thus including invertebrates that exhibit a delayed response to disturbance. All drift samples were washed into a labelled plastic jar and preserved with a 5% formaldehyde solution. In the laboratory, each invertebrate sample was rinsed through a 2-mm and 425-μm sieve. The invertebrates retained by these sieves were enumerated and identified using Merritt and Cummins (1996).

Table 1. Fine sediment treatments applied to experimental channels.

Pulse duration (h)	No. sediment pulses	Mean sediment concentration ($mg{\cdot}L^{-1}$)	Standard error	Number of replicate channels	Dose ($mg{\cdot}L^{-1}{\cdot}h^{-1}$)
0	N/A	N/A	N/A	2	0
0.5	10	695.0	15.8	2	3 475
1.0	10	699.0	14.7	2	6 990
3.0	10	701.5	17.9	2	21 045
4.0	10	704.5	12.1	2	28 180
5.0	10	702.0	13.8	2	35 100
6.0	10	705.0	13.7	2	42 300

Note: Each of the seven treatments was replicated twice giving 14 experimental units. Dose is given as the total administered over the duration of the 19-day experiment and is calculated as the product of concentration and duration (product of pulse length and number of pulses). N/A, not applicable.

Rainbow trout

To examine the effect of sediment pulse duration on rainbow trout we collected swim-up fry, using baited minnow traps and electrofishing gear, from the Horsefly River sockeye spawning channels in the town of Horsefly, B.C. (Quesnel Lake stock). Swim-up fry (n = 140) were anesthetized with MS222, mass and length measured, examined for signs of disease, and then randomly placed in the experimental channels five days prior to treatment. Each channel contained 10 fish, giving a density of 6.7 $fish{\cdot}m^{-2}$. This stocking density is similar to or less than other studies examining the effects of sediment on fish growth (Sigler et al. 1984; McLeay et al. 1986). A single pretreatment mortality was removed and replaced. The average size of trout prior to treatments was 45.8 mm and 1.04 g. Because of their small size, fry were not individually marked; mean mass and length within channels were used for statistical analysis (in all cases n = 14). At the conclusion of the experiment, fish were removed from the channel, immediately anesthetized, and mass and length recorded.

Sediment

Sediment particles used in all treatments were collected from an exposed streambank 2 km downstream from the experimental stream channel site. This material commonly enters Moffat Creek at several points along its length. Particles passing through a 425-µm sieve (medium sand – silt) were included in the experimental treatments. Prior to entering the channels sediment was combined with stream water in two 200-L tanks (approximately 30 $g{\cdot}L^{-1}$). Twenty airstones powered by a 90-W aquarium pump, combined with a mechanical stirring device ensured consistent mixing and prevented buildup of sediment in the release valves. When mixed with the incoming stream water, the concentration measured entering the stream channels averaged 704 $mg{\cdot}L^{-1}$ (Table 1). Sediment concentration was determined by filtering a 500-mL sample, collected where the stream water and sediment slurry combined, through a Whatman GF/C filter. Samples were collected randomly, from all channels, once during each sediment pulse. Sediment pulses were consistently initiated at 10:00 during each sediment event and continued for the designated duration.

To completely characterise sediments used in the experiment and facilitate comparison between studies, the particle size distribution and concentration–turbidity relationships were determined using a standard column of sieves ranging from 355 µm to <63 µm. The mean of 10 samples was calculated.

Sampling regime

Sediment was delivered to each channel, with the exception of the controls, every second day for a total of 10 pulses over 19 days. Invertebrates were collected on four occasions; two days before the first pulse and following the first (day 1), fifth (day 9), and tenth pulses (day 19). Both drift and benthic samples were collected at these times. Drift nets were set on the sampling days just prior to the start of the sediment pulse and were collected after 24 h. A total of 64 drift samples were collected during the experiment. Three benthic samples were randomly collected during each of the four sampling occasions, resulting in 168 samples. Sediment samples and discharge measures were collected during each sediment event. Temperature was constantly monitored with data logging temperature probes placed in the headtanks and the terminal end of two experimental channels.

Statistical analyses

We evaluated between treatment and between sampling date differences using repeated measures analysis of variance (ANOVA). To determine if a relationship exists between sediment pulse duration and invertebrate (drift and benthos) abundance and family richness, regression analysis was performed on each of the four sampling days. We used ANOVA, for each sampling day, to reveal which pulse duration achieved significantly different mean invertebrate abundance and richness measures as well as fish length and weight gain, in comparison to control.

Principal components analysis (PCA), using a correlation matrix, was used to ordinate drift and benthic invertebrates presence–absence data from the final day of the experiment. Families that were not present in more than one of the 14 channels were excluded from this analysis. Also Chironomidae, which appeared in each sample, would not contribute to a PCA based on presence–absence and were therefore excluded. Following the ordination, PCA scores for the primary axis were regressed against pulse duration to determine if the main pattern of invertebrate presence–absence was related to addition of sediment. This procedure was completed for both drift and benthic samples. Correlation coefficients (structure coefficients) were used to identify taxa contributing significantly to the observed assemblage.

Trout body condition was compared between treatments by establishing linear relationships between mass and length gain for each treatment and subsequently tested for similarity in slopes and intercepts using analysis of covariance (ANCOVA). Path analysis was performed using sediment pulse duration, trout mass gain, and invertebrate drift abundance data to quantify and compare direct versus indirect effects of sediment on fish growth.

Prior to conducting analyses, assumptions of normality and heteroscedasticity were tested and natural log transformations were applied where appropriate (Gauch 1982). Only trout mass required transformation. All statistical analyses were performed using the GLM and PRINCOMP procedures in PC SAS (ver. 6.12, SAS Institute Inc., Cary, N.C.) and utilised α = 0.05. Significance levels were adjusted for multiple simultaneous comparisons (10 comparisons, α = 0.005 for drift; 11 comparisons, α = 0.004 for benthos).

Results

There were no significant differences among experimen-

Fig. 1. Relationship between sediment treatments and drift total abundance or family richness at pretreatment (*a*), day +1 (*b*), day +9 (*c*), and day +19 (*d*). Solid lines represent least squared regression lines for total abundance (●) and broken lines for family richness (□). Regression statistics for each line are shown in the upper (abundance) and lower (richness) right corner. In each panel n = 14.

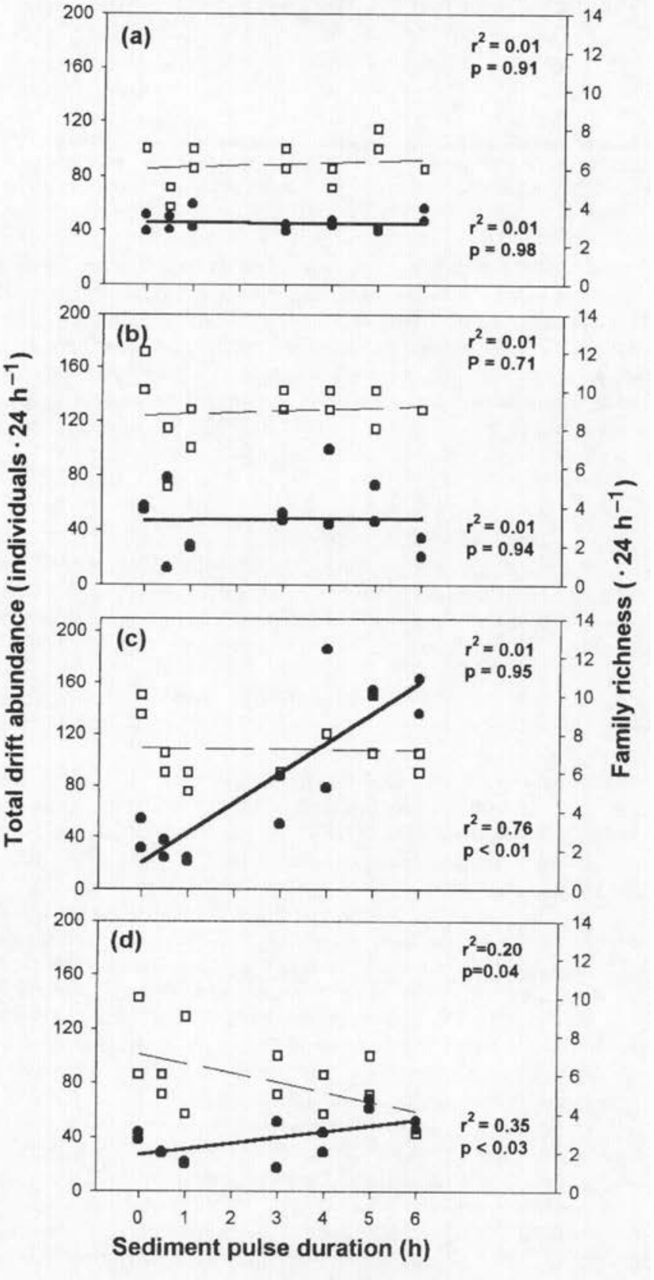
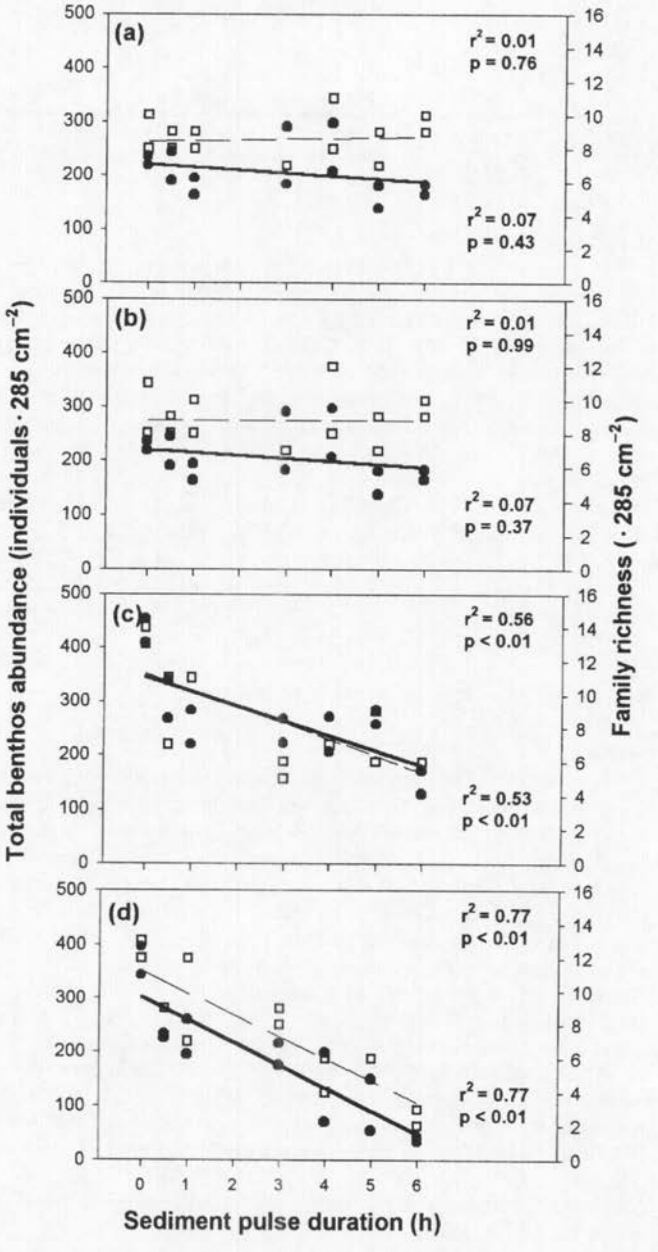


Fig. 2. Relationship between sediment treatments and benthos total abundance or family richness at pretreatment (*a*), day +1 (*b*), day +9 (*c*), and day +19 (*d*). Solid lines represent least squared regression lines for total abundance (●) and dashed lines for family richness (□). Regression statistics for each line are shown in the upper (abundance) and lower (richness) right corner. In each panel n = 14.



tal channels prior to the beginning of the experiment for stream water temperature, discharge, invertebrate abundance and richness (Figs. 1 and 2), or fish mass (ANOVA $F_{6,7}$ = 1.02, $p > 0.43$) and length (ANOVA $F_{6,7}$ = 1.6, $p > 0.15$). Water temperature (p = 0.96), discharge (p = 0.56), and sediment concentration (p = 0.53) did not vary among experimental channels for the duration of the experiment. Greater than 90% of the sediment particles, by weight, used in our treatments were <177 μm and 50% were <125 μm. Direct laboratory comparisons of sediment mass per volume and turbidity revealed that the mean sediment concentration administered in our experiment, 704 mg·L^{-1}, corresponds to 23 nephelometric turbidity units (NTU).

A total of 31 different families of invertebrates were identified in the drift and benthic samples. Chironomidae was the most abundant taxon and was the only family to occur in all samples. Baetidae and Limnephilidae were the next most abundant taxa, each accounting for 12% of all invertebrates collected. An average of 65 animals total were collected in each 24-h drift sample and 255 animals (8950 animals·m^{-2})

were collected in each benthic sample. For analysis, each 24-h drift sample was considered individually. The sum of the three benthic samples taken from each channel on each sampling day was used in analyses.

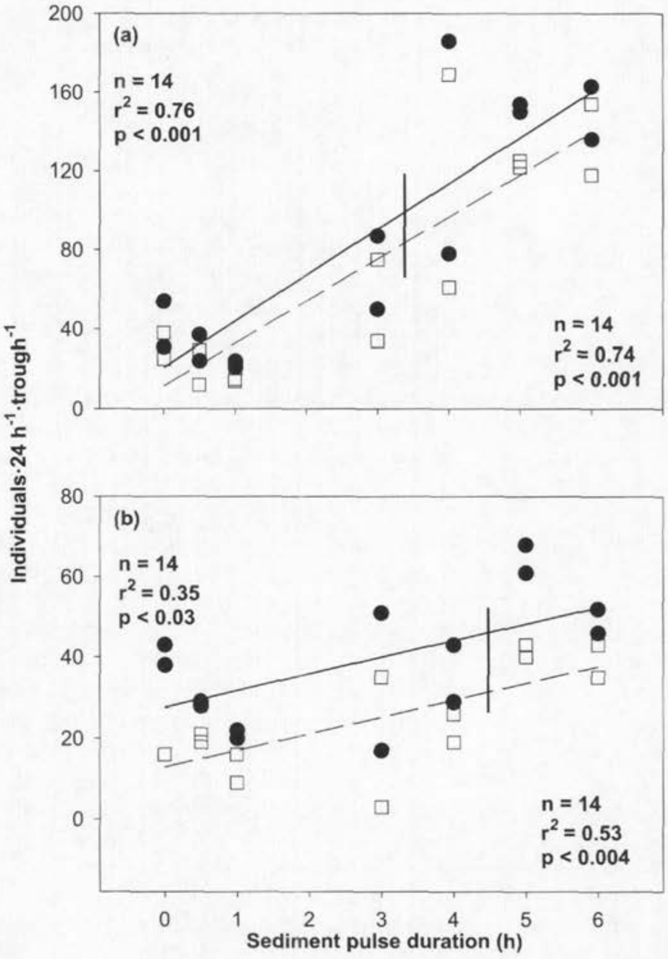
Repeated measures analysis revealed a significant sampling date effect (benthos F = 9.92, $p < 0.001$; drift F = 4.79, $p < 0.01$), a significant treatment effect (benthos F = 13.41, $p < 0.001$; drift F = 9.4, $p < 0.001$), and a significant interaction (benthos F = 6.1, p = 0.001; drift F = 4.84, p = 0.001). As there was a significant interaction effect, analysis continued by evaluating relationships within a single treatment over time, or across treatments on a single sampling day.

Linear regression analyses found significant relationships between the sediment pulse duration and total abundance for both drift (Fig. 1) and benthic invertebrates (Fig. 2) by day 9. No significant linear relationships, with respect to pulse duration, were found for drift or benthic samples collected prior to the initial pulse or after the first sediment pulse. However, following day 9, abundance and richness in both the drift and benthos showed significant relationships with sediment treatments. Treatment effects became stronger as the number of sediment pulses increased over the duration of the experiment. The only exception was drift abundance, which peaked on day 9. The relationship between the abundance of drifting invertebrates and sediment treatments was driven by the family Chironomidae. The abundance of Chironomidae in drift samples collected on day 9 and 19 showed significant linear relationships with sediment treatments (Fig. 3). Also, as exposure duration increased, the proportion of the drift samples composed of Chironomidae increased. Drift and benthos total abundance significantly varied from control abundance between the 3- and 4-h treatments on day 9 and between the 4- and 5-h treatments on day 19 (ANOVA and multiple range test).

For families other than Chironomidae, the change in abundance did not describe the patterns of variation as well as a measure of presence–absence, as some taxa disappeared as sediment pulse duration increased. PCA axis 1 for drifting insects summarized 27% (Fig. 4*a*) of the total variation and was dependent on variation in Simuliidae (larvae and pupae). PCA axis 1 for the benthic assemblage summarized 39% (Fig. 4*b*) of the variation and was dominated by the presence–absence of the families Elmidae, Nemouridae, Leptophlebiidae, Baetidae, and Heptageniidae. Significant negative relationships ($p < 0.01$) were found between both drift and benthic PCA axis 1 scores when regressed with sediment pulse duration (Figs. 4*a* and 4*b*).

Regression analysis of mass and length gain of rainbow trout fry revealed a linear relationship with sediment pulse duration (Figs. 5*a* and 5*b*). Following the experiment (19 days, 10 sediment pulses) there were significant negative impacts of sediment pulse duration on trout mass (ANOVA $F_{6,7}$ = 4.52, $p < 0.03$) and length gained (ANOVA $F_{6,7}$ = 5.04, $p < 0.03$) when treatments and controls were compared (Figs. 5*a* and 5*b*). Duncan's multiple range test revealed that significant differences occurred between the 4- and 5-h treatments for length gain, and the 5- and 6-h treatments for mass gain, when compared to the control (Figs. 5*a* and 5*b*). This value is similar to the results for changes in abundance and richness of invertebrates. Trout mortality was not influenced by the sediment treatments (ANOVA $F_{6,7}$ = 0.14, p = 0.71; Fig. 5*c*).

Fig. 3. Total number of insects (solid line, ●) and total number of Chironomidae (broken line, ☐) in each drift sample, 9 and 19 days after sediment treatments began. Regression coefficients in the top left corner correspond to all insects (including Chironomidae) and bottom right refer to Chironomidae. Vertical lines indicate significant differences in total abundance and Chironomidae abundance in comparison to control (Duncan's multiple range test).



Trout body condition was evaluated as a change in the linear relationship between length and mass among treatments. When comparing the regression lines between treatments neither the slope ($F_{1,12}$ = 0.92, P = 0.49) nor the intercept ($F_{1,12}$ = 1.11, P = 0.36) was altered by sediment introduction.

Path analysis was performed using mean trout mass gain and invertebrate drift data. Path coefficients were calculated as the standardised partial regression coefficients of a multiple regression analysis with sediment pulse duration and drift abundance as the independent variables and trout mass gain ($\log_e$ transformed) as the dependent variable (J.T. Wooton, Department of Ecology and Evolution, University of Chicago, Chicago, Ill., personal communication). The path coefficient between sediment pulse duration and drift abundance is the correlation coefficient between the two variables. The relative strength of the indirect path is the product

Fig. 4. First principal component for invertebrate drift (*a*) and benthos (*b*) based on presence–absence regressed against sediment pulse duration. Regression statistics for each plot are located in top right corner. PC1 values for invertebrate drift increases with increasing presence of Simuliidae pupae and larvae, while PC1 values for benthos increase with the occurrence of Elmidae, Nemouridae, Baetidae, Leptophlebiidae, and Heptageniidae.

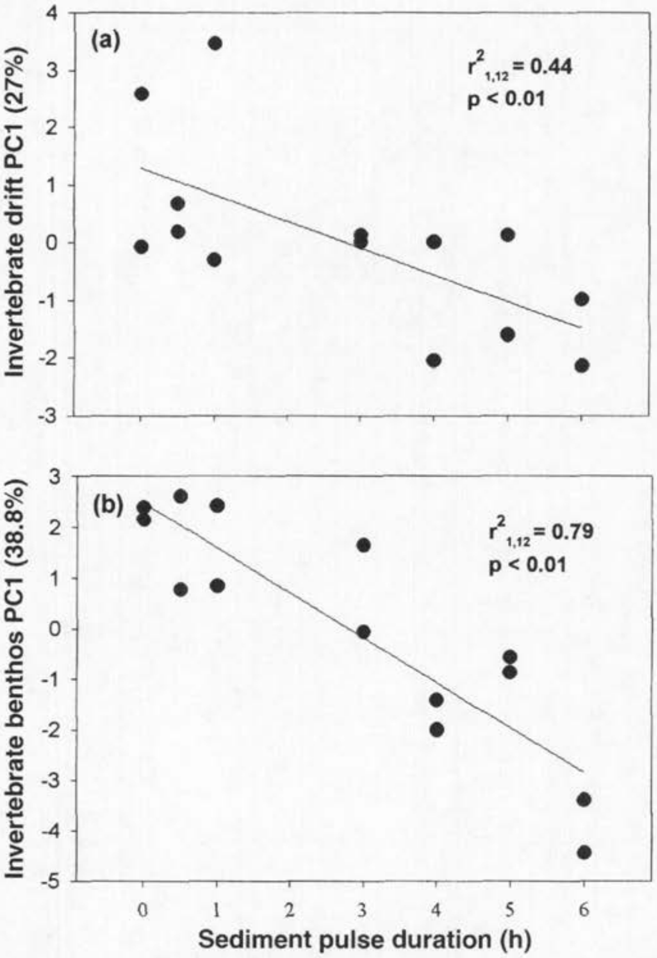
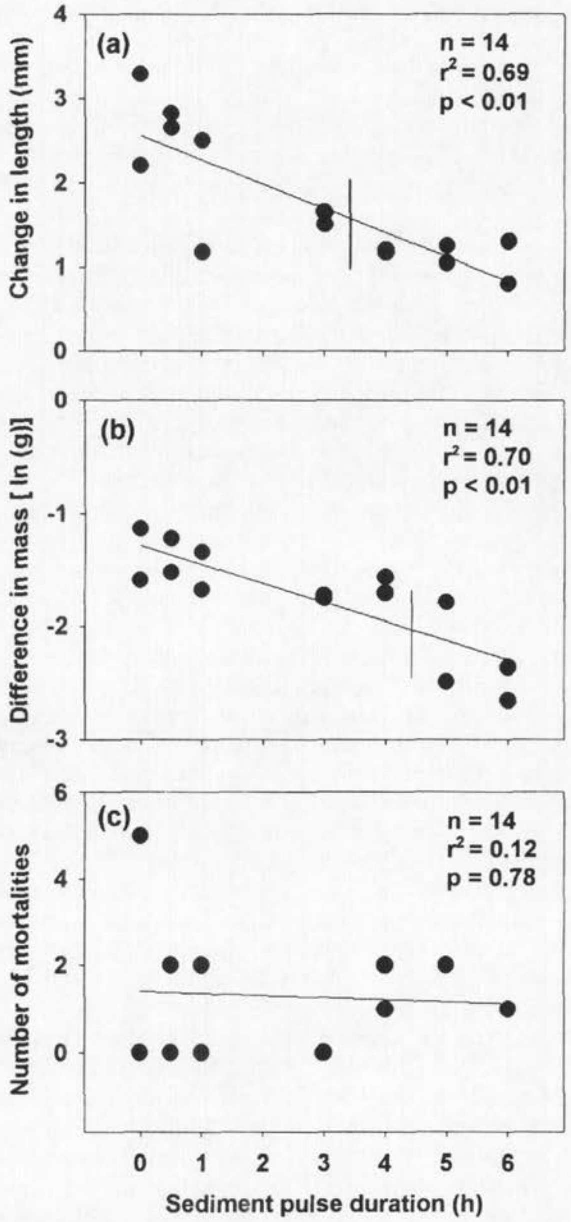


Fig. 5. Effect of pulse duration on (*a*) the change in length, (*b*) change in mass, and (*c*) mortality of trout, over the course of the experiment. Vertical lines indicate significant differences in (*a*) length and (*b*) mass in comparison to control (Duncan's multiple range test). Each point represents the mean value for each channel.



of the two coefficients deriving that path and is compared to the direct path, which has only one coefficient. The direct path, sediment pulse effects on change in trout mass, had a higher path coefficient than the complete indirect path coefficient, indicating greater importance (Fig. 6).

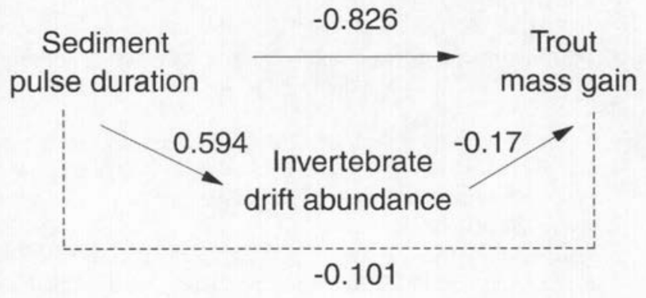
Discussion

By experimentally examining the effects of sediment pulse duration on invertebrate assemblages and trout growth and survival, we quantitatively tested a previously unconfirmed hypothesis and provided indirect evidence as to the mechanism of effect. In this experiment we have shown that the duration of a sediment pulse, given a constant concentration, had a negative effect on the richness and abundance of benthic invertebrates and the richness of drifting invertebrates. However, the total abundance of drifting invertebrates increased over the duration of the experiment. In addition, trout growth suffered as sediment pulse duration increased. Our study design was developed to compare the response of invertebrates and rainbow trout exposed to repeated pulsed-sediment episodes of contrasting duration. Unfortunately, it is not possible to discriminate between cumulative exposure over all pulses and the duration of individual pulses as being responsible for determining impacts on community structure and fish growth.

Benthic and drifting invertebrate assemblages

Duration of sediment exposure influenced the abundance and composition of invertebrate communities in the experimental channels relative to controls. However, the timing of the response was delayed. A dose-dependent response of invertebrate taxa was first noted following the fifth sediment

Fig. 6. Representation of the direct and indirect effects of fine sediment exposure on trout growth. Path analysis coefficients are given for each path. The complete indirect path coefficient is the product of the two coefficients making the path –0.101.



pulse (day 9). By this point, both drift and benthos abundance as well as benthos family richness were altered. Drift abundance rose with treatment severity while benthic abundance and family richness declined. Culp et al. (1986) also found no measurable short-term impact on five of the six numerically dominant taxa exposed to saltating sediment particles. The area surrounding our experimental site is mostly agricultural (both hay and livestock), suggesting a human-altered environment. In addition, exposed lacustrine sediment deposits located along the stream margin introduced particles during rain events (E.A. Shaw, personal observation). Invertebrates would have been previously exposed to sediment events of short duration and therefore may not immediately react to a pulse of sediment. Exposure to a constant source of sediment may also explain the relatively low diversity of disturbance-sensitive taxa (i.e., Ephemeroptera, Plecoptera, and Trichoptera). By day 19, abundance and family richness of both drift and benthic samples showed a response directly proportional to fine sediment exposure.

Ordination revealed a number of invertebrate taxa that were disproportionately affected by fine sediment addition. As sediment pulse duration increased, Simuliidae (larvae and pupae) were present in fewer drift samples. Similarly, Elmidae, Nemouridae, Baetidae, Leptophlebiidae, and Heptageniidae were at lower densities in benthic samples as exposure to fine sediment increased. Members of the families Baetidae (Culp et al. 1986; Vuori and Joensuu 1996), Simuliidae, and the order Plecoptera (Culp et al. 1986; Vuori and Joensuu 1996) have been shown to incur significant declines when exposed to elevated fine sediments. These taxa have been used as indicator organisms in various biomonitoring programs (Barton 1996; Somers et al. 1998) because of their sensitivity to disturbance and associations with clean, cool, running waters and substrates containing only small amounts of fine particles. Conversely, the family Chironomidae tends to increase in abundance or remain unchanged with fine sediment exposure (Culp et al. 1986; Vuori and Joensuu 1996). In our experiment, Chironomidae was the only taxon to increase in abundance with elevated sediment pulse duration.

Rainbow trout growth

The biological and ecological consequences of suspended sediment on fish have been the focus of many studies. Our results clearly indicate that a negative relationship exists between fish growth was and sediment pulse duration, despite a fixed concentration. The observed level of impairment was somewhat consistent with the predictions of Newcombe and Jensen (1996), who have developed a series of six model equations to predict the severity of ill effect (SEV) caused by fishes exposed to sediments in lotic ecosystems. The six models were developed for a range of fish species, life stages, and sediment particle sizes. Based on the concentration and duration of exposure to sediment, the model output is a series of expected impairment. Using the SEV model equation developed for juvenile and adult freshwater salmonids exposed to fine or coarse particles, trout in the four highest exposure doses of the present experiment would have been expected to show indications of major physiological stress; long-term reduction in feeding rate; long-term reduction in prey capture success; and poor condition. Trout in our experiment clearly showed reduced growth rates compared to control, suggesting similar findings to the model predictions. A lack of studies that describe early life stages exposed to sediments is a key shortcoming that will likely be remedied in future versions of this widely applied and useful fisheries management tool. The SEV model effectively predicted a reduction in feeding rate and prey capture success for trout in this experiment, but does not give any indication of the underlying mechanism.

The dose-dependent reduction in rainbow trout growth observed in this experiment can be explained by a number of mechanisms. First, suspended particles may come in direct contact with fish gills, causing abrasion, leading to decreased overall fitness and growth rates. Exposed gill tissue would also provide an entry for toxic chemicals, either bound to sediments or in solution, into the bloodstream and further impair growth. There is little support for this mechanism of action in our experiment, as visual inspection of each test fish revealed no gill tissue abrasion. Similarly, other studies that have exposed fish to an equivalent or higher dose of sediment reported no gill damage (Goldes et al. 1988), including highly angular, anthropogenically derived sediments (Lake and Hinch 1999).

A second mechanism that may explain a reduction in trout growth is that suspended sediments may directly alter behaviour or stress fish in a way that reduces foraging activity and (or) prey capture success. Gregory and Northcote (1992) reported a log-linear decline in reaction distance of chinook salmon to prey as turbidity increased from control to 810 NTU. Similar results have been established for bluegill (*Lepomis macrochirus*, Vinyard and O'Brien 1976), rainbow trout (Barrett et al. 1992), and lake trout (*Salvelinus namaycush*, Vogel and Beauchamp 1999). At moderate turbidity levels suspended material may also incur a perceived reduction in predation risk, allowing fish to increase foraging rates (Gregory 1994). During this experiment, trout were observed feeding on the drift in all channels prior to the addition of sediment. After the addition of sediment, trout in channels subject to a high sediment dose were noticeably more reactive, moving between cover objects and feeding areas more frequently and were exposed to potential predators for a longer duration than control fish. This observation suggests that foraging was not as successful or efficient for trout exposed to sediment pulses, providing support for this mechanism.

A third potential mechanism for growth reduction is that the invertebrate food resource was depleted or the composition altered as a result of sediment introduction, resulting in reduced growth rates. Many studies have also found that the density of benthic invertebrates is greatly reduced (Culp et al. 1986), and alterations to species composition (Culp et al. 1986; Newcombe and MacDonald 1991; Vuori and Joensuu 1996) occur following sediment events. Our study also indicated significant changes to the drifting insect assemblage composition.

Simultaneously exposing invertebrates and trout to sediment within a single experimental system allowed us to evaluate the two primary mechanisms causing the sediment impact. Path analysis suggested that the direct effect of sediment, acting to increase physiological stress and impair the vision of drift-feeding trout, is more important to trout growth than the indirect alteration to invertebrate abundance, which increased in our experiment. The increase in drift abundance was most strongly influenced by the family Chironomidae, which often make up a large portion of salmonid diet in both lotic and lentic environments (Pinder 1986) along with Trichoptera (caddisflies) and Ephemeroptera (mayflies) (Angradi and Griffith 1989). Unfortunately, our study did not distinguish between the abundance of drifting insects during the day versus night. As visual feeders, trout consume most of their prey during daylight hours. Often as a response to poor conditions, insects will drift to new habitats at night to avoid predation. A predominance of night drift caused by increased sediment pulse duration in our experiment would have suggested that the abundance of drifting invertebrate prey decreased, potentially altering the conclusions of our path analysis. Time may have also limited the response of drifting invertebrates. The final day of the experiment showed a significant decrease in the abundance of drifting invertebrates in the high sediment duration treatments, in comparison with the abundance of the same group following day 9. Allowing the experiment to proceed further might have resulted in high exposure treatments to arrive at a lower equilibrium abundance, also potentially altering the conclusions of our path analysis. Although the results of the path analysis seemed straightforward (i.e., the direct path coefficient was eight times higher than the indirect path) the results should be regarded as hypotheses to direct further testing (Wooton 1994).

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