

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 accrues 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).

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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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Table 1. Fine sediment treatments applied to experimental channels.

Pulse duration (h)	No. sediment pulses	Mean sediment concentration (mg·L ⁻¹)	Standard error	Number of replicate channels	Dose (mg·L ⁻¹ ·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 electro-fishing 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·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- μ m 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·L⁻¹). Twenty air-stones 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·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 μ m to <63 μ m. 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 $\alpha = 0.05$. Significance levels were adjusted for multiple simultaneous comparisons (10 comparisons, $\alpha = 0.005$ for drift; 11 comparisons, $\alpha = 0.004$ for benthos).

Results

There were no significant differences among experimen-

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.

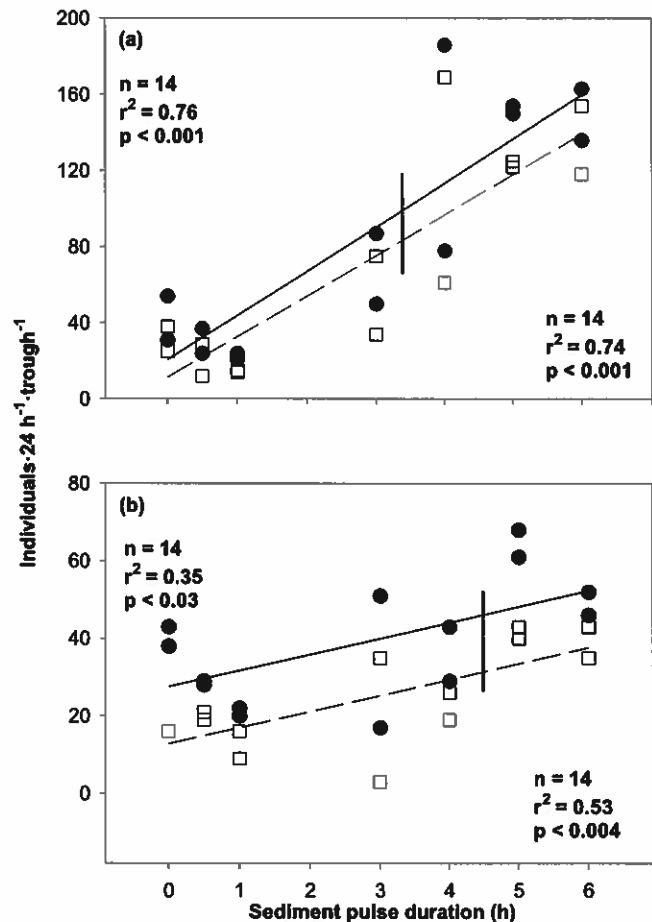
Repeated measures analysis revealed a significant sampling date effect (benthos $F = 9.92$, $p < 0.001$; drift $F = 4.79$, $p < 0.01$), a significant treatment effect (benthos $F = 13.41$, $p < 0.001$; drift $F = 9.4$, $p < 0.001$), and a significant interaction (benthos $F = 6.1$, $p = 0.001$; drift $F = 4.84$, $p = 0.001$). 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. 4a) of the total variation and was dependent on variation in Simuliidae (larvae and pupae). PCA axis 1 for the benthic assemblage summarized 39% (Fig. 4b) 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. 4a and 4b).

Regression analysis of mass and length gain of rainbow trout fry revealed a linear relationship with sediment pulse duration (Figs. 5a and 5b). 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. 5a and 5b). 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. 5a and 5b). This value is similar to the results for changes in abundance and richness of invertebrates. Trout mortality was not influ-

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).

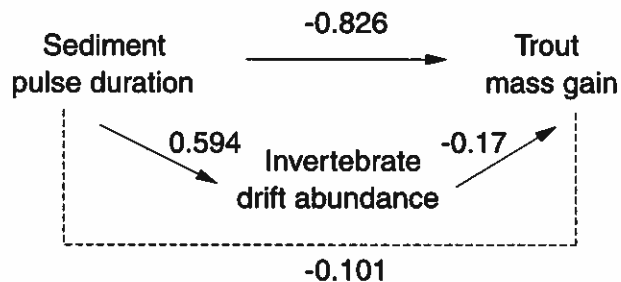


enced by the sediment treatments (ANOVA $F_{6,7} = 0.14$, $p = 0.71$; Fig. 5c).

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. Wootton, 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. 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), Elmidae, 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 bio-monitoring 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.

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