THE EFFECTS OF FINE SEDIMENT PULSE DURATION ON A STREAM INVERTEBRATE ASSEMBLAGE AND GROWTH AND MORTALITY OF RAINBOW TROUT

by

E. AL SHAW

B.Sc., University of Guelph, 1994

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
THE FACULTY OF FORESTRY
Department of Forest Sciences

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
July 1999

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Department of Forest Sciences

The University of British Columbia
Vancouver, Canada

Date Aug 27/99
Abstract

Elevated fine inorganic sediment supply in streams may impair many biological functions, however the contribution of exposure duration to altering these functions has not been previously considered. I evaluated the effects of fine sediment pulse duration on invertebrate assemblages and rainbow trout growth and mortality. I constructed streamside flow-through channels at Moffat Creek in the central interior of British Columbia for this experiment. Fourteen experimental channels, each containing invertebrates and 10 rainbow trout swim-up fry, received fine inorganic sediment treatments of a constant concentration but varied in pulse duration, ranging from 0 to 6 hours per pulse. A pulse was initiated every second day for total of ten pulses over 19 days. Benthic invertebrate abundance and family richness declined (both $r^2=0.77$, $P<0.01$) as sediment pulse duration increased. Similarly, the family richness of invertebrate drift declined as pulse duration increased ($r^2=0.20$, $P=0.04$), however, drift abundance increased with increasing pulse duration ($r^2=0.35$, $P<0.03$). Drift samples were numerically dominated by the family Chironomidae (midges) comprising up to 99% of the drifting insects within the high pulse duration channels. Principal components analysis (PCA) of invertebrate family presence/absence revealed that the primary variation in the drift assemblage (PC1, 27%) was attributed to variation in the presence/absence of Simuliidae; longer pulse duration resulted in the disappearance of Simuliidae ($r^2=0.44$, $P<0.01$). The primary variation in the benthic assemblage (PC1, 38.8%) was described by the presence/absence of Elmidae, Nemouridae, Baetidae, Leptophlebiidae and Heptageniidae; increasing pulse duration resulted in the virtual disappearance of those families ($r^2=0.79$, $P<0.01$). Rainbow trout length and mass linearly declined ($r^2=0.69$, $P<0.01$; $r^2=0.70$, $P<0.01$ respectively) with increased
sediment pulse duration. There was no significant relation (P>0.05) between sediment pulse duration and trout mortality. Analysis of variance revealed that invertebrate, drift, benthos and trout growth were significantly affected by sediment exposure time. Relative to the controls, significant negative changes occurred between the three and five-hour treatments. The hypothesis that trout growth was more affected by direct effects of sediment (e.g. impaired visual feeding ability, physiological stress), than indirectly (through modification of the prey abundance or composition) was tested using path analysis. The results indicate that direct effects were the primary influence of sediment on trout growth although significant alterations of the invertebrate community were observed.
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ACKNOWLEDGEMENTS

First, I would like to thank John Richardson who took a chance on me, allowing me to be a part of his newly forming lab. The experience and knowledge gained from our diverse group has been vast; I only hope I gave as much as I learned. Thanks to the entire Richardson lab for an excellent learning and fun graduate school experience.

The rest of my advisory committee has been extremely helpful in guiding my project to the point where I feel it is a contribution that others may find insightful and useful; thank you Dr. Scott Hinch, Dr. Peter Kiffney and Dr Olav Slaymaker.

Many people helped me through a tough, nearly fruitless, field season in Horsefly. In particular Manfred Mulheisen allowed me to render the view from his cabin wildlifeless for the entire summer, Pat Teti (BC Ministry of Forests) and Rob Dolighan (BC Ministry of Environment Lands and Parks) in Williams Lake truly went out of their way to make this project possible; thank you.

From the Richardson lab Jessica Kaman and Kelly Kreiger helped with the microscope work and in the field. Fellow graduate student Jill Melody shared the good times and bad.

I would also like to thank my family (Dad, Mom, Janice, Duane, Rachel and Dylan) for supporting me along the way. Visits will become more frequent now, I promise. Last I would like to thank my future wife Bev; thank you for help, support and understanding. Woof to Aipa!

Finally, I would like to acknowledge Forest Renewal British Columbia who funded my research through a grant to Dr.J.S. Richardson.
CHAPTER 1: Effects of fine inorganic sediment on stream invertebrate assemblages: implications of exposure duration

Introduction

Sediment is a universal feature of lotic ecosystems. All rivers erode, transport and deposit sediment. Accelerated erosion occurs for two primary reasons; climatic forces, such as wind and rain, and disturbance by land-use activities. The severity of disturbance by activities such as timber harvesting and livestock grazing, is considerable. These practices tend to increase the sediment load within streams and rivers, as well as incur long-term effects through physical degradation of the channel and streambank.

Elevated levels of sediment in streams have the potential to impact stream organisms (Waters 1995). The effects of increased fine sediment loads on stream invertebrate communities have been well documented (summaries in Cordone and Kelley 1960, Newcombe and MacDonald 1991, Newcombe 1994, Waters 1995, Anderson et al. 1996). Many studies have reported a decrease in abundance and a change in community composition resulting from several sediment-mediated mechanisms. Culp et al. (1985) showed that invertebrates may 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. Increased suspended sediments tend to clog these feeding structures reducing feeding efficiency (Richardson and Mackay 1991). Also, the smothering of algal interstices and abrasion of cells may be an important factor affecting the distribution of periphyton and grazing invertebrates (Vuori and Joensuu 1996). Regardless of the particular mechanism, in all cases increases in fine sediment (<0.25 mm diameter) loads generally cause...
invertebrates to enter the water column and drift to a potentially better habitat.

What is clear from the literature is that elevated levels of fine sediment have the potential to negatively impact each component of the food web. 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 re-analysed 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 utilised to derive the stress index compared several concentrations and types of sediment, no study has exclusively tested the contribution of fine sediment pulse duration to changes in invertebrate abundance and richness of drifting and benthic assemblages.

The purpose of this study was to determine if fine sediment pulse duration had an effect on the abundance and richness of drifting and benthic invertebrate assemblages. I accomplished this by exposing invertebrates to pulses of fine sediment, ranging in duration from 0 to 6 hours, while sediment concentration remained constant at 700 mg·L⁻¹. A pulse was administered every second day for a total of ten pulses over 19 days. Invertebrate abundance and richness of drift and benthic assemblages were monitored prior to, and throughout the experiment.
Methods

Study Site

The 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 and into the Fraser River. The Fraser Plateau is covered by unconsolidated geologic materials in the form of fluvial, lacustrine and colluvial deposits (Lord 1984). Lacustrine and fluvial deposits tend to be easily disturbed during natural and anthropogenic events, becoming entrained and transported in the water column. Riparian and upslope areas surrounding Moffat Creek are moderately impacted. Generally, there is little riparian canopy as much of the land has been cleared to the stream for livestock grazing and hay crops.

Experimental Design

To test the effects of fine sediment pulse duration on invertebrate assemblages, a replicated, multi-treatment experiment was conducted using prefabricated stream channels. A combined analysis of variance and regression design was used allowing seven treatments (exposure duration), each replicated twice. Treatments consisted of a sediment pulse duration ranging from 0 (control) to 6 hours, pulsed every second day for 19 days (Table 1). The dose regime was intended to mimic a disturbance activity, such as regular movement of cattle through riparian areas, timber harvesting and frequently occurring thunderstorms which repeatedly introduce excess sediment over an extended period of time. In order to exclusively test pulse duration, sediment concentration entering the stream channels was held constant at 700 mg L$^{-1}$ throughout the dosing periods. This concentration has been shown to induce a response in fish and invertebrates at similar and elevated exposure durations (McLeay et al. 1986, Newcombe and MacDonald 1991). Also, a permanent BC Ministry of
Forests water quality monitoring station, situated downstream from my site, has recorded this particular concentration during many rain events.

Table 1. Fine sediment treatments applied to experimental channels. Each treatment was replicated twice giving 14 experimental units. Dose is given as the total administered over the entire experimental period and is calculated as the product of the number of pulses, concentration and duration.

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<th>Pulse Duration (hours)</th>
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<th>Number of Sediment Pulses</th>
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Experimental Stream Channels

Experimental stream channels were constructed immediately adjacent to Moffat Creek. Water flow was redirected from the creek through 250 m of 15 cm diameter, sewer-grade PVC pipe (gravity feed) and partitioned into two 500 L headtanks. Each headtank supplied water to eight experimental channels, 16 total, at approximately 0.5 L·sec⁻¹. Fourteen channels were used for sediment treatments and 2 channels were devoted to measuring invertebrate immigration. All channels had a surface area of 1.5 m² (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. After passing through the channel, water was collected in a settling pool before re-entering Moffat Creek. Substrate for the channels was collected from a local quarry. Particles were sieved to fit the gravel/pebble range (6.4 mm - 20 mm, -1 to -4 phi) approximating the substrate of Moffat Creek. Substrate depth was approximately 8 cm throughout. Wire mesh (1 cm × 1 cm) was placed over the intake pipe to prevent leaves from clogging the inflow and restrict resident stream fishes from entering the experiment. Further description of the experimental setup is provided in Appendix 1.
Invertebrates

Invertebrate assemblages were established in the channels through active addition and by natural drift. Kick samples (250 μm mesh), equivalent to the area of the channels (1.5m$^2$) and 10 cm deep, were collected from Moffat Creek and released along the length of the experimental channels. This was completed on two occasions before treatments began. Invertebrates could also immigrate into the channels by drifting through the water intake pipe. Invertebrates were allowed to colonise for three weeks before the experiment began. Benthos sampling baskets (12 per channel) were constructed out of 500 ml, clear plastic containers (surface area=104 cm$^2$). Each basket contained approximately 35 holes (7.5 mm diameter) and was buried flush with the surface of the substrate to allow free movement of invertebrates. During each sampling event, three baskets were removed from the channels and individually placed on a 425 μm sieve. Each sample was placed in a labeled plastic jar and 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 hours; thus including invertebrates, that drift during darkness. All drift samples were washed into a labeled 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 collected in these fractions were identified using Merritt and Cummins (1996).

Sediment

Sediment used in all treatments was 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 mixed with water in two 200 L tanks elevated at the upstream end of the channels. In order to achieve a concentration of 700 mg·L⁻¹, 1.6 kg of sediment was added to each tank and filled with water pumped from the creek. At this point the concentration of sediment in each mixing tank was 800 g·L⁻¹. Valves at the bottom of each mixing tank were set to deliver 50 ml·sec⁻¹ of sediment slurry to each channel. When combined with the 500 ml·sec⁻¹ inflow from the creek to each channel, the resulting concentration was 727 mg·L⁻¹. Allowing for a small amount of settling in the mixing tank, the average concentration measured entering the stream channels was 704 mg·L⁻¹. Each mixing tank was filled with water and sediment eight times during each day sediment pulses were administered. Re-filling the mixing tanks with water and sediment required three minutes.

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, during each sediment pulse. Twenty airstones powered by a 90 Watt aquarium pump, combined with a mechanical stirring device ensured consistent mixing and prevented buildup of sediment in the release valves.

In order to completely characterise the sediment used in the experiment, particle size distribution and concentration/turbidity relationships were determined. A column of sieves ranging from 355 μm to <63 μm was used to generate the particle size distribution. The mean ten samples was calculated. Many studies report turbidity, but not sediment concentration. In order to facilitate comparisons between studies reporting turbidity or suspended sediment concentration, a relationship was established between
the two measures for Moffat Creek sediments. A plastic bucket was filled with 20 L of water and 4 g of sediment was added to achieve a concentration of 200 mg\cdot L^{-1}. Turbidity was measured using a Quest turbidity probe while agitating the solution with a stirring rod to keep the particles suspended. Sediment was then added in 1 g increments, resulting in an increase of 50 mg\cdot L^{-1}. After each addition a turbidity measure was obtained using the turbidity probe. Sediment was added until the concentration reached 1000 mg\cdot L^{-1}. This procedure was repeated twice and the mean result calculated.

**Sampling Regime**

Sediment was delivered to each channel, with the exception of the controls, every second day for a total of ten pulses over nineteen 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 hours. 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**

Data were analysed using regression, analysis of variance (ANOVA), principal components analysis (PCA) and correlation analysis. To evaluate between treatment and between sampling date differences a repeated measures analysis was completed (Split plot ANOVA with sampling date as the sub-plot). To determine if a relationship
between sediment pulse duration and invertebrate (drift and benthos) abundance and family richness, regression analysis was performed on each of the four sampling days. I used ANOVA, on each sampling day, to reveal which pulse duration achieved significantly different mean abundance and richness measures in comparison to control. PCA, utilising the correlation matrix, was used to ordinate drift and benthic invertebrates presence/absence data. PCA was the multivariate technique chosen because of the consistency of results irrespective of the type of data standardisation used (Jackson 1993). Families which were not present in more than one of the 14 channels were excluded from the analysis. Also, families such as 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 treatments to determine if the pattern of invertebrate presence/absence was related to the experimental addition of sediment. This procedure was completed for both drift and benthos samples. The PCA scores for each channel were then correlated to the original insect presence/absence information. Correlation coefficients were used to identify taxa contributing significantly to the observed assemblage.

All requirements for regression analysis, analysis of variance, correlation and principal components analysis were considered and met according to Hicks (1993) and Gaugh (1982). All statistical analyses were performed using the GLM and PRIMCOMP procedures in PC SAS (1996) and utilised a 95% significance level ($\alpha = 0.05$). Significance levels were adjusted for multiple simultaneous comparisons (10 comparisons; $\alpha = 0.005$ for drift, 11 comparisons; $\alpha = 0.004$ for benthos).
Results

The distribution of sediment particles used in this experiment is reported in Figure 1a. Greater than 90% of the particles were <177 μm and 50% were <125 μm. Figure 1b shows the relationship between sediment concentration and turbidity for Moffat Creek sediments. The concentration of sediment used in this experiment, 714 mg·L⁻¹, corresponds to 23 nephelometric turbidity units (NTU). There were no significant differences among experimental channels for stream water temperature and discharge (Figure 2a and 2b), or invertebrate abundance and richness prior to the beginning of the experiment. Water temperature (P=0.96) and discharge (P=0.56) did not vary among experimental channels for the duration of the experiment (Figures 2a and 2b). Experimental applications of sediment were consistent in concentration throughout the experiment and did not significantly vary (P=0.53) among channels (Figure 2c).

A total of 31 different families of invertebrates were identified in the drift and benthic samples (Appendix 2). Chironomidae was the most abundant taxa and was the only family to occur in all samples, both drift and benthos. Baetidae and Limnephilidae were the next most abundant taxa, each accounting for 12.2% of all invertebrates sampled. An average of 65 animals were collected in each 24 hour drift sample and 255 animals (8950 animals·m⁻²) in each benthic sample. For analysis, each 24 hour drift sample was considered individually. The sum of the three benthic samples, taken on each sampling day from each channel, was used in analyses.
Figure 1. Characteristics of sediments used in experiment. a. shows the particle size distribution. Note that greater than 50% of the sediment mass is composed of particles 125 μm and finer. b. shows the relationship between turbidity (NTU) and sediment concentration (mg·L⁻¹). Note that the sediment concentration applied to the experimental channels, 700 mg·L⁻¹, corresponds to a turbidity value of 23 NTU.
Repeated measure analysis (split plot ANOVA) revealed a significant subplot (sampling date) effect (benthos $F= 9.92 \, p=0.001$, drift $F= 4.79 \, p=0.008$), 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 is a significant interaction term, analysis can continue by evaluating relationships within a single treatment over time, or across treatments on a single sampling day.

Linear regression showed significant relationships between the fine sediment pulse duration (independent variable) and total abundance for both drift (Figure 3) and benthic invertebrates (Figure 4) by day 9. All regression results are summarised in Appendix 3.

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. Samples collected on day 9 revealed significant negative relationships for total invertebrate abundance, drift and benthos, and for benthos family richness (Figures 3 and 4) when regressed against sediment treatments. Following day 19 all invertebrate measures showed significant relationships with sediment treatments. Linear regressions models became stronger and accounted for more variation as the number of sediment pulses increased. The only exception was drift abundance. The relationship between the abundance of invertebrates and sediment treatments was driven by the abundance of Chironomidae. The abundance of Chironomidae in drift samples collected on day 9 and 19 showed significant linear relationships with sediment treatments (Figure 5). Also, as sediment treatments increased, the proportion of the drift samples composed of Chironomidae increased. Drift and benthos total abundance significantly vary from control abundance between the 3 and 4 hour treatments on day 9 and between the 4 and 5 hour treatments on day 19 (ANOVA and Duncan's multiple
Figure 2. Experimental trough conditions prior to and during the experiment. Mean daily temperature (a.), discharge (b.) and sediment concentration (c.) did not vary significantly, between or within channels, at any time. The overall mean and ANOVA statistics are given in the top right corner, for detecting differences between channels. Confidence limits (95%) are given around daily mean values in each plot.
Figure 3. Changes in drift total abundance and family richness over the duration of the experiment. Solid lines represent least-squared regression lines for total abundance (closed circles) and dashed lines for family richness (open squares). Regression statistics in lower left corner correspond to total abundance and upper right refer to family richness.
Figure 4. Changes in benthos total abundance and richness over the duration of the experiment. Solid lines represent least-squared regression lines for total abundance (closed circles) and dashed lines for family richness (open squares). Regression parameters in lower left corner correspond to total abundance and upper right refer to family richness.
Figure 5. Total number of insects (solid line,●) and total number of Chironomidae (dashed line,□) in each drift sample, 9 and 19 days after sediment pulses 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).
range test).

The data also showed that for families other than Chironomidae, the change in abundance would not describe the patterns of variation as well as a measure of presence/absence as some taxa disappeared as sediment pulse duration increased. Principal components analysis (PCA) was performed using the invertebrate samples from the final day of the experiment to summarise and organise the variation in invertebrate family richness for both drift and benthic samples and reveal which families were most important in the assemblage. Results for drifting insects showed that PCA axis 1 summarised 27% (Figure 6a) of the total variation and was dependent on variation in Simuliidae (nymphs and pupae). PCA axis 1 for the benthic assemblage summarised 38.8% (Figure 6b) of the variation and was dominated by the presence/absence of the families; Elmidae, Nemouridae, Leptophlebiidae, Baeotidae and Heptageniidae. Significant negative relationships were found between both drift and benthic PCA axis 1 scores and sediment pulse duration (Figure 6a and b).

Discussion

In this study, I have shown that the duration of a fine sediment pulse, given a constant concentration, had a negative effect on the richness and abundance of both benthic invertebrates and family richness of drifting invertebrates, while the total abundance of drifting invertebrates increased. Despite extensive literature describing the effects of fine sediments in aquatic ecosystems, no previous studies have addressed the contribution of pulse duration to changes in abundance and richness of invertebrate assemblages exposed to episodes of fine sediment. My results, using a replicated, multi-dose, experiment utilising a single concentration of sediment, conclusively validated the dose-response model as an improved predictor for the
Figure 6. 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. Family names in the right margin indicate their Pearson correlation to PC1.
response of stream invertebrates exposed to fine sediment events.

Duration of sediment exposure influenced the abundance and composition of invertebrate communities in the experimental channels in comparison to control channels. Significant changes in total abundance and composition of drift and benthic invertebrate assemblages were not identified following the first addition of sediment. Culp et al. (1986) also noted no measurable short-term impact on five of the six most numerically dominant taxa exposed to saltating sediment particles. The area surrounding our experimental site is mostly agricultural, both hay and livestock, revealing an already disturbed environment. Invertebrates may have been previously exposed to sediment events of short duration and therefore may not immediately react to a pulse of sediment. This may also explain the relatively poor diversity of disturbance sensitive taxa (i.e. Ephemeroptera, Plecoptera and Trichoptera).

A dose-dependent response was first noted on day 9. At this point both drift and benthos abundance and benthos family richness were affected. Drift abundance rose significantly with treatments while benthic abundance and family richness declined. By day 19, abundance and family richness of both drift and benthic samples showed a response directly influenced by fine sediment exposure. These findings are consistent with Newcombe and MacDonald (1991) who stated that the currently used concentration-response model provides little predictability, as it neglects the contribution of pulse duration in eliciting an organism's response. Based on the concentration-response model, the expected outcome of this study would be that all treatments would impact the invertebrate assemblage in a similar fashion, as the concentration of fine sediment entering the channels was similar. Clearly the assemblages reacted relative to the administered dose. The use of the stress index, proposed by Newcombe and MacDonald (1991), although a much-improved version is
still limited. Just as there was a need to incorporate the contribution of pulse duration to more accurately predict an organism or assemblage response to fine sediment, there is a need to incorporate a component describing the physical characteristics of sediment. Many studies report an elevated response of invertebrates with an increase of fine particles in the water column (Chutter 1968, McClelland and Brusven 1980, Waters 1982, Culp et al. 1986, Angradi 1998). A measure of the distribution of particle sizes, along with discharge measurements, to better understand the amount of entrained and deposited solids, may enhance the predictability of the stress index.

Principal components analysis revealed a number of invertebrate taxa which were predominantly affected by fine sediment addition. As the sediment pulse duration increased, Simuliidae (larvae and pupae) were present in fewer drift samples. Similarly, Elmidae, Nemouridae, Baetidae, Leptophlebidae and Heptageniidae were identified in fewer benthic samples as exposure to fine sediment increased. In the literature, members of the families Baetidae (Lemly et al. 1981, Culp et al. 1985, Vuori and Joensuu 1996) Simuliidae (Lemly 1982, Gurtz and Wallace 1984) and the order Plecoptera (Gurtz and Wallace 1984, Culp et al. 1985, Vuori and Joensuu 1996) show a significant negative impact when exposed to fine sediment. These taxa may be useful as indicators for biomonitoring purposes. Conversely, Chironomidae tend to increase in abundance or remain unchanged with fine sediment exposure (Culp et al. 1985, Vuori and Joensuu 1996). In my experiment, Chironomidae was the only taxon to increase in abundance with elevated sediment pulse duration.

The potential trade-offs exist for invertebrates entering the drift. Finding a more suitable habitat (reduced competition and/or less disturbed environment) and dispersal are the potential benefits to entering the drift, while predation and locating an unsuitable habitat are potential drawbacks. As previously stated, these invertebrates inhabit a
moderately disturbed environment and did not immediately drift with the onset of the first sediment pulse. Drifting was not the best option as short-term sediment events often pass through the area. As the pulses continued the likelihood of survival and reproduction in this habitat are reduced to such a degree that entering the drift is the best option.

Resource managers could use this information to model invertebrate responses to sediment pulses, using dose, the product of concentration and duration, and not concentration alone. This would require more frequent monitoring to better characterise the temporal changes of fine sediment flux in streams. I have shown in this experiment that pulse duration is a significant factor, contributing to the effects of sediment on stream invertebrate assemblages.
CHAPTER 2:

Effects of sediment pulse duration on rainbow trout growth and survival: importance of direct and indirect effects

Introduction

Species communities have long been viewed as complex and interdependent, suggesting that interactions between organisms may be direct or indirect. Modeling multiple species in a community and quantifying indirect effects has been poorly addressed in the literature because of the complex mathematics involved and the number of possible influential factors mediating interactions between species. Controlled field experiments have been paramount in demonstrating indirect effects and revealing their importance in community ecology (Power 1990, Werner and McPeek 1994, Wooton 1994). The possibility of indirect effects makes paired species experiments difficult to interpret; therefore experiments that monitor multiple members of the community, while disturbing the environment, are preferable (Bender et al. 1984).

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 (Redding and Schreck 1987), and life stage exposed (Servizi and Martens 1990). Sediment-induced mortality and decreased survival rates have been noted in 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. 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 levels of deposited sediment can limit inter-gravel water exchange,
reduce interstitial dissolved oxygen and effectively smother developing eggs and alevin (Chapman 1988). Studies from the Carnation Creek Watershed project concluded that reductions in both coho (Onchorhynchus kisutch) and chum (O. keta) salmon egg survival were attributable to reduced permeability and oxygen levels in redds (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).

Indirectly, sediment can affect fish growth through modifications of behaviour, habitat and food resources. 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). At moderately elevated sediment levels young coho attempt to avoid impacted areas (Bisson and Bilby 1982). This may lead to the displacement of otherwise resident fish (McLeay et al. 1986). This displacement was attributed to a reduction in the quantity and quality of habitat available for spawning and rearing. Berg and Northcote (1985) observed a breakdown of juvenile coho territories when exposed to short-term pulses of suspended sediment. All of these behavioural modifications may increase stress, alter migration patterns and foraging effort, and potentially impact growth rates. For many salmonid species, slower growth rates result in poorer territories, increased time to smoltification and outmigration, and decreased overwinter survival (Holtby 1988). Although most experimental fish studies utilise manufactured fish foods or single invertebrate species as prey, it has been speculated that a change in the abundance or composition of the invertebrate food resource may impact fish growth independently of reduced visual ability. No experiment to date has combined natural invertebrate communities, fish and sediment in a partially controlled stream environment.
The purpose of this study was to determine the influence of sediment pulse duration on growth and mortality of rainbow trout (Oncorhynchus mykiss) and to compare and quantify direct and indirect effects imposed by sediment exposure. In particular, the indirect influence of an altered invertebrate food resource, caused by the experimental addition of sediment, will be assessed in comparison to the direct effect of sediment on fish stress and visual ability to capture prey. Each of these factors will be analysed in relation to fish growth.

Methods

All experimental methods are identical to the methods section of chapter 1. Only procedures specifically pertaining to fish are expanded in this section.

For this experiment I used swim-up fry from the Quesnel Lake rainbow trout stock of the central interior of British Columbia. These trout are highly prized as sport fish as there is only one stock in British Columbia, the Gerrard stock in Kootenay Lake (maximum 16 kg), which produces larger fish than the Quesnel Lake stock (maximum size 14 kg). An unusual migration pattern brings sub-adults into tributary streams during the summer and fall which provides excellent opportunity for stream angling large trout (Rob Dolighan, Ministry of Environment, Lands and Parks, pers. comm.). What makes this stock a conservation concern beyond heavy angling pressure, is the lack of accurate enumeration, a recent decrease in spawner and juvenile densities, and their reproductive history. Quesnel Lake rainbow trout are a genetically unique, late-maturing strain; sexual maturity occurs in their sixth, seventh and occasionally eighth year (Rob Dolighan, Ministry of Environment, Lands and Parks, pers. comm.). Immature trout may be quite large but have not yet spawned. As a result this stock is extremely sensitive to exploitation and disturbance.
Trout were captured, using baited minnow traps and electrofishing gear, from the Horsefly River sockeye spawning channels in the town of Horsefly, British Columbia. Swim-up fry (n=140) were transported in aerated containers approximately 15 km to the experimental stream channels on Moffat Creek. No mortality was noted from either the collection method or transportation. All individuals were anaesthetised with MS222, mass and length measured, examined for signs of disease, then randomly placed in the experimental channels five days prior to treatment. Each channel contained ten fish at a density of 6.7 fish m\(^{-2}\). This stocking density is similar to other studies examining the effects of sediment on fish growth (Sigler et al. 1984, McLeay et al. 1986). A single pre-treatment mortality was removed and replaced. The average size of trout prior to treatments was 45.8 mm and 1.04 g. Due to their small size, fry were not individually marked; mean mass and length within channels was used for statistical analysis (in all cases N=14). At the conclusion of the experiment, fish were removed from the channel, immediately anaesthetised with MS222 and mass and length were measured.

This experiment was based on a combination regression and analysis of variance (ANOVA) designs. This hybrid approach allowed the use of both statistical methods for evaluation, gaining the benefits of each (Liber et al. 1992). Analyses were performed to determine the relationship between sediment pulse duration and trout growth (mass and length gain) and mortality (regression), and describe which pulse duration treatments showed significantly different trout growth measures in comparison to controls (ANOVA, Duncan's multiple range test). Trout body condition was compared between treatments using ANCOVA (Cône 1989). Linear relationships were established between mass and length gain for each channel and were subsequently tested for similarity in slope and intercept using ANCOVA. Finally, to evaluate direct versus indirect effects of fine sediment addition on fish growth, path analysis was
performed using trout mass and invertebrate drift abundance. Angradi and Griffith (1989) identify drift as the primary source of forage for rainbow trout; therefore drift abundance was used in the analysis. Path analysis is a statistical technique applied to assess the covariation of species to reveal important linkages in community structure (Wooton 1994, Shipley 1997). This technique provides the opportunity to make inferences about very complex systems with many interacting species and provide much stronger inferential ability than studies utilising regression analysis alone (Wooton 1994). Essentially, path analysis is a series of correlation and multiple regression analyses, with path coefficients being the standardised regression and correlation coefficients.

Mass gain was taken as the mean final mass, in each channel, minus the pre-treatment mass; length gain was similarly obtained. A loge transformation of the trout mass data was necessary to bring about equality of variance and satisfy all assumptions of the regression and ANOVA models (Hicks 1993). All subsequent analysis and interpretations were performed with the transformed mass data.

Regression, ANOVA, ANCOVA and correlation analyses were performed using PC SAS (1996). A significance level of 95 % (α=0.05, n=14) was used in all circumstances.

**Results**

There were no significant difference within or between channels for initial fish mass (ANOVA F_{6,7} = 1.02, P > 0.43) and length (ANOVA F_{6,7} = 1.6, P > 0.15). As previously mentioned, channel discharge, water temperature (Chapter 1, Figures 2a and 2b) and invertebrate abundance and richness (Chapter 1, Figures 3 and 4) did not differ significantly between channels prior to sediment treatment application.

Following 19 days (10 sediment pulses) there were significant 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 comparing treatments and controls (Figures 7a and 7b). Duncan's multiple range test revealed differences between the four and five hour treatments for length gain, and the five and six hour treatments for mass gain, when compared to the control. This value is similar to the results for changes in abundance and richness of invertebrates (Chapter 1, Figures 5a and 5b). Trout mortality was not influenced by the sediment treatments (ANOVA $F_{6,7} = 0.14$, $P = 0.71$, Figure 7c).

Trout body condition was evaluated as a change in the linear relationship between length and mass among treatments, but there was no significant relation; 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. Regression analysis revealed a linear relationship between both mass and length gain and sediment pulse duration (Figures 7a and 7b). All regressions are summarised in Appendix 3.

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. The path coefficient between sediment pulse duration and drift abundance is the correlation coefficient between the two variables. The relative
Figure 7. Effect of pulse duration on, (a.) the change in length, (b.) change in weight and (c) mortality of trout, over the course of the experiment. Vertical lines indicate significant differences in (a.) length and (b.) weight in comparison to control (Duncan's multiple range test). Each point represents mean value for each channel.
strength of the indirect path is the product 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 trout mass, has a higher path coefficient than the complete indirect path coefficient, indicating greater importance (Figure 8).

Figure 8. Diagram representing the direct and indirect effects of sediment 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).

Discussion

The biological and ecological consequences of suspended sediment concentration have been the focus of several studies (Cordone and Kelley 1960, Bruton 1985, Redding and Schreck 1987, Servizi and Martens 1990, Newcombe and MacDonald 1991). However, there have been no studies to evaluate the contribution of sediment pulse duration to the effects observed on fish or to evaluate the importance of direct and indirect mechanisms of sediment effects on fish.

My results clearly showed that fish growth was depressed as the duration of
sediment exposure increases, despite fixed concentration. The observed level of impairment is consistent with the predictions of Newcombe and MacDonald (1991), who suggest physiological stress, histological changes and reduced growth rates for fish exposed to the dose administered in this study. McLeay et al. (1987) also reported a 6-33% reduction in growth rate of arctic grayling exposed to placer mining sediment of similar dose to this experiment, and Crouse et al. (1981) reported growth reduction in juvenile coho exposed to fine sediment deposition.

The dose-dependent response (pulse duration) exhibited by rainbow trout growth in this experiment can be explained by a number of hypotheses. First, suspended particles may come in direct contact with fish gills, causing abrasion, leading to decreased foraging and reduced growth rates. Exposed gill tissue would also provide an entry for toxic chemicals, either bound to the sediment or in solution, to enter the bloodstream and further impair growth. There is little support for this hypothesis, as visual inspection of each test fish revealed no gill tissue abrasion. Similarly, other studies which have exposed fish to an equivalent, or even higher, dose of sediment reported no gill damage (Goldes et al. 1988, McLeay et al. 1986), including highly angular, anthropogenically-derived, sediments (Lake and Hinch 1999).

A second hypothesis is that direct visual impairment, when exposed to suspended sediments, may alter behaviour or stress fish in a way that reduces foraging activity and 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 (Vinyard and O'Brien 1976) and rainbow trout (Barrett et al. 1992). At moderate turbidity levels suspended material may also incur a perceived reduction in predation risk, causing fish to exhibit higher foraging rates (Gradall and Swenson 1982, Gregory 1994). During this experiment, fish were
observed feeding in all channels prior to the addition of sediment. After the addition of
sediment, fish in channels subject to high sediment dose were noticeably more reactive,
and were quick to retreat under cover objects, reducing their forage time, providing
support for this hypothesis. In this experiment sediment treatments began at 9:00 am
while maximum forage effort is generally between 10 am and noon (Angradi and Griffith
1989). Therefore trout exposed to sediment treatments greater than 1 hour, were
potentially disrupted during prime foraging times.

A third hypothesis which may explain the observed dose-dependent response is
that the invertebrate food resource was depleted or the composition was altered as a
result of sediment introduction, causing a lower growth rate in comparison to fish not
exposed to sediment. Many studies agree that the density of benthic invertebrates is
greatly reduced (Culp et al. 1986, McClelland and Brusven 1980), and alterations to
species composition also occur following sediment events (Culp et al. 1986, Newcombe
and MacDonald 1991, Vuori and Joensuu 1996). In this study, there is good evidence
that the addition of sediment impaired the growth of rainbow trout fry and in chapter 1, I
showed that sediment also altered the abundance and species composition of drifting
invertebrates. After sediment addition the overall abundance of drifting insects actually
increased, although the resulting drift assemblage is composed primarily of
Chironomidae. Pinder (1986) suggests that many species of Chironomidae are quite
tolerant to various types of pollution, often remaining as the numerically dominant taxa.
In this experiment, path analysis suggests that the direct effect of sediment, acting to
stress and impair the vision of drift-feeding trout, is more important to trout growth than
the indirect alteration to invertebrate abundance and community composition. This is
consistent with the results of this experiment, which indicated that drift abundance
actually increased. However, it is unknown whether Chironomidae are as nutritious for
salmonids as a more diverse diet of invertebrates. Chironomidae often make up a large portion of salmonid gut contents in both lotic and lentic environments (Nilsson and Northcote 1981, Pinder 1986) along with Trichoptera (caddisflies) and Ephemeroptera (mayflies) (Angradi and Griffith 1989) suggesting they may be preferred forage. Although the results of the path analysis are convincing (i.e. the direct path coefficient was eight times higher than the indirect path) the assumptions of the analysis must be examined. A potential weakness is that all possible path linkages may not be represented in the diagram (Englund and Evander 1999). The interactions between sediment and fish could potentially be affected by components of the community not measured or interactions between invertebrate families or feeding groups may be pivotal in directing effects seen in fish. As suggested by Englund and Evander (1999), the results of path analysis should be regarded as hypotheses which direct further testing.

Management Implications

As in chapter 1, the ideal use for this information is for managers to view sediment in streams as eliciting a dose-dependent response from fish and incorporate this idea into sediment monitoring programs. This would include more frequent sampling of suspended and deposited sediment to evaluate pulse duration during heavy rainfall, spring freshets, and in response to livestock grazing and logging in riparian areas. Goals may be set for conservation initiatives regarding the Quesnel Lake stock of rainbow trout as results from this study show that growth of fry is negatively affected at a dose of sediment between 21420 and 35700 mg\(\cdot\)L\(^{-1}\)\(\cdot\)Hr. Again, this may lead to strict monitoring programs and improved sediment prevention and control measures in riparian and upland areas. Lloyd (1987) suggests that for protection of
salmonids in Alaska, water quality standards should not allow an increase of greater than 25 NTU above ambient turbidity in lotic systems. The Forest Practices Code of British Columbia does not suggest a turbidity or sediment concentration level not to exceed, but uses a number of indicators of soil erosion potential to establish a prescription for further development. This study suggests that turbidity levels below 25 NTU, depending on pulse duration, may significantly impact trout growth through the direct influence of sediment.
Literature Cited


APPENDIX 1. Detailed drawing of experimental stream channels (see photograph on next page for in situ view)

Notes:
- Wire mesh (0.5cm²) was placed over the opening of the water intake pipe and the terminal end of the experimental channels to prevent resident stream fish from entering the experiment and the experimental trout from emigrating.
- Cover objects for fish were constructed from 10 cm diameter pvc pipe, cut along the length. Each channel received 10 cover objects.
- Clear plastic mesh (2 cm²) was placed over all channels to prevent fish from jumping out of the channels and avian predators from taking experimental fish.
- The sediment slurry was kept in suspension by airstones powered by an aquarium pump and a stirring device made from a drill, fitted with a wooden paddle.
- Valves at the bottom of the sediment tank regulated the flow of the sediment slurry into the channels. As a treatment finished, the appropriate valve was closed and the remaining valves were adjusted, a to predetermined position, to maintain a consistent concentration.
### APPENDIX 2

Aquatic invertebrate families identified in drift and benthic samples. Structure coefficients are given for PC1 and PC2 if families were used in principal components analysis.

<table>
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<tr>
<th>Drift Samples</th>
<th>Numbers</th>
<th>% of Total</th>
<th>PC1</th>
<th>PC2</th>
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<td></td>
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<td></td>
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<td>2408</td>
<td>22.23</td>
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* Indicates significant structure coefficients ($\alpha=0.005$ for drift samples and $\alpha=0.004$ for benthic analyses)
APPENDIX 3 Summary of variables and statistics for all regression analyses. Only significant regressions are listed.

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<th>Std. Error Intercept</th>
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