The effect of sediment characteristics and a fine sediment pulse on invertebrate distributional patterns

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Abstract

The amount of fine sediment entering river systems has increased dramatically in the last century and this has been recognised as a leading cause of ecological degradation and water quality impairment. In order to monitor and manage this problem more effectively further research is needed in to the quantitative, mechanistic relationships between the amount of fine sediment delivery in to river systems and the response of the lotic freshwater community. At present, this lack of information is problematic for environmental managers and regulators as they attempt to meet the challenges posed by this issue.

This thesis aimed to address this research gap by using stream mesocosms to investigate the response of invertebrates to a fine sediment pulse. It was unique in considering the effect of prior exposure to increased fine sediment deposition, whilst examining the response of benthic, hyporheic and drifting invertebrates concurrently. The research also set out to assess the effectiveness of fine sediment biomonitoring approaches, comparing them with more traditional metrics, it also investigated the power of a functional trait approach to discriminate fine sediment stress.

The results detailed in this thesis demonstrate that biomonitoring approaches have the ability to identify fine sediment stress more effectively than traditional taxonomic metrics (e.g. abundance and taxonomic richness), particularly when applied to invertebrate communities which are relatively tolerant of fine sediment stress. This was one of the first studies to identify the effects of prior fine sediment deposition on the response of invertebrates to a fine sediment pulse, finding that this factor plays an important role in their response, providing important evidence which may be used to better tailor our fine sediment management strategies. Examining, in tandem, the effects of a fine sediment pulse on invertebrate drifting behavior and their use of the hyporheic zone identified taxa-specific responses to fine sediment which will be useful to further refine our understanding of the mechanistic relationship between increased amounts of fine sediment and

invertebrate communities. This information will help to inform the refinement of functional trait databases, which has been identified by the work in this thesis as one of the major factors limiting their effective use.

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List of abbreviations

BSTI	Biological Sediment Tolerance Index
CCA	Canonical correspondence analysis
CoFSI	Combined Fine Sediment Index
DEFRA	Department for Environment, Food and Rural Affairs
EPA	US Environmental Protection Agency
E-PSI	Empirically-weighted PSI
EPT	Ephemeroptera, Plecoptera and Trichoptera
FBA	Freshwater Biological Association
FDR	False discovery rate method
FSSR	Fine Sediment Sensitivity Rating
GES	Good Ecological Status
GLM	General Linear Model
IMS	Industrial methylated spirits
LIFE	Lotic-invertebrate Index for Flow Evaluation
NMDS	Non-metric multidimensional scaling
OFSI	Organic Fine Sediment Index
pCCA	Partial canonical correspondence analysis
PSI	Proportion of Sediment-sensitive Invertebrates
SAC	Special Area of Conservation
SE	Standard error
SIMPER	Similarity percentage
SSSI	Site of Special Scientific Interest
TMDL	Total Maximum Daily Load
ToFSI	Total Fine Sediment Index
WFD	EU Water Framework Directive
WHPT	Whalley, Hawkes, Paisley and Trigg

1. Introduction

1.1. Background

Freshwater ecosystems are being degraded at a rapid rate, and have been identified as some of the most impacted ecosystems on a global scale (Sala *et al.*, 2000; Dudgeon *et al.,* 2006; Kingsford *et al.*, 2011; Sánchez-Bayo and Wyckhuys, 2019). A rising global human population and greater socio-economic development is likely to further increase this degradation of freshwater ecosystems (Sala *et al.*, 2000). Key threats to freshwater ecosystems include habitat loss and degradation, flow modification, agricultural intensification, water pollution, and climate change (Dudgeon *et al.,* 2006; Kingsford *et al.,* 2011; Reid *et al*., 2018). These issues affect the functioning of freshwater ecosystems and degrade their ability to provide important ecosystem services, such as the provision of water for domestic use, irrigation, recreation, fisheries, transportation and power generation (Millennium Ecosystem Assessment, 2005).

Almost 6% of the total global species described by scientists are supported by freshwater ecosystems, despite them only covering less than 1% of the planet's surface, making them one of the most diverse ecosystems globally (Hawksworth and Kalin-Arroyo, 1995; Carrizo *et al.*, 2017). However, this biodiversity is declining at much greater rates in freshwater ecosystems than even the most impacted terrestrial ecosystems (Ricciardi and Rasmussen, 1999; Sala *et al.*, 2000; Sánchez-Bayo and Wyckhuys, 2019). Agricultural intensification has been identified as a key threat to freshwater ecosystems as it is a major source of diffuse contamination to surface waters, elevating the amount of fine sediment entering watercourses to far above natural levels, so that it becomes harmful to aquatic communities (Jones *et al.*, 2012a; Foucher *et al.*, 2014). Due to these elevated sediment loads and the negative effects to freshwater ecosystems, fine sediment has been identified as being one of the leading causes of water quality impairment (Richter *et al.*, 1997; USEPA 2000).

1.2. The importance and value of fine sediment

The erosion and transport of sediments are a key component of the global biogeochemical cycle, due to the fact that Al, Fe and Mn do not fully dissolve in water, meaning that suspended and particulate sediments are responsible for removing these elements from the land (Schlesinger and Bernhardt, 2013). Another role that sediment has in the global biogeochemical cycle is in the transport of phosphorous, which, when dissolved, reacts with soil minerals to form phosphorous enriched sediments, which may subsequently be transported by rivers (Schlesinger and Bernhardt, 2013).

Uncontaminated sediment is not a stressor on freshwater ecosystems, and under natural conditions, the erosion and deposition of fine sediments (defined as inorganic and organic particles <2mm) are an inherent aspect of hydro-geomorphic processes which shape freshwater ecosystems (Owens *et al.,* 2005). Fine sediment is also vital for the ecological functioning of rivers, supplying nutrients, creating physical habitat, increasing substrate heterogeneity, and providing refugia and spawning grounds for biota (Baron *et al*., 2003; Owens *et al*., 2005).

1.3. Sources of fine sediment

The sources of fine sediment entering surface waters may be split in to point sources and diffuse sources (Figure 1.1). Point sources encompass inputs from sewage treatment works and industry, whereas diffuse sources include erosion from agricultural land, or eroding channel banks. Diffuse sources are typically spread over a wider area than point sources, which makes diffuse sources more difficult to identify and control (Bilotta *et al.*, 2010). In the UK, most fine sediment entering river systems is from agricultural sources (76%), with other sources including eroding channel banks (15%), diffuse urban sources (6%) and point source discharges (3%; Collins *et al*., 2009).

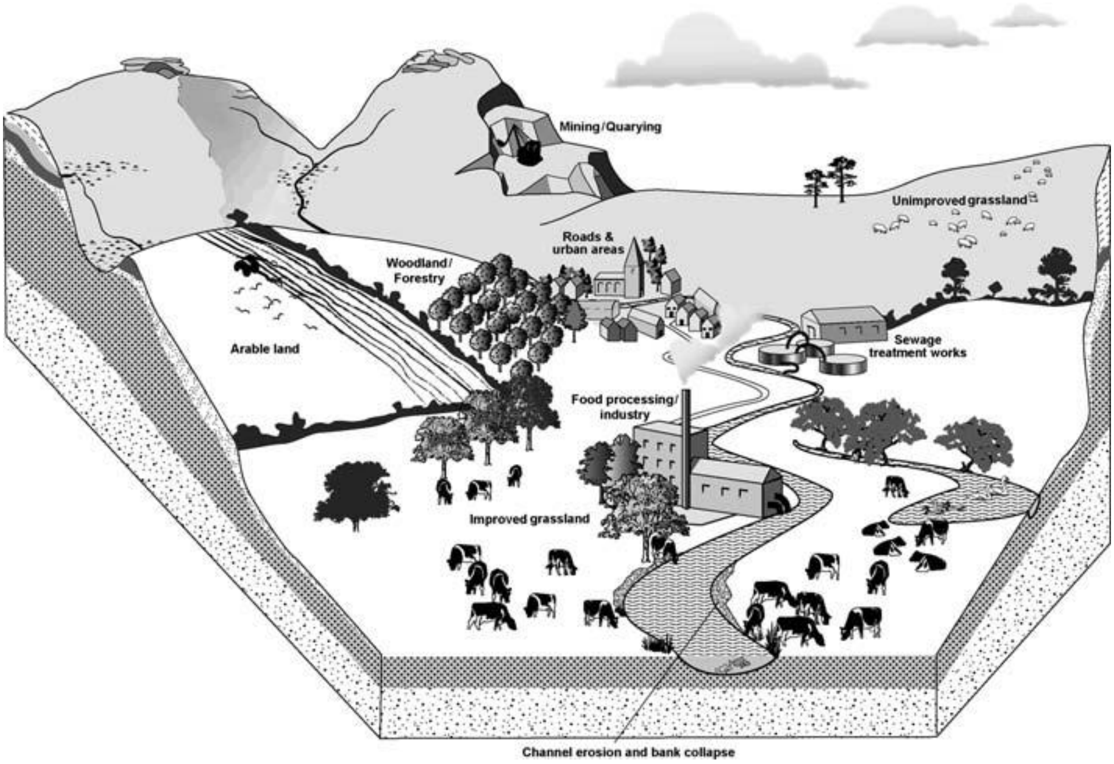

Figure 1.1 A conceptual diagram detailing the potential sources of fine sediment in a typical catchment (Bilotta *et al.*, 2010).

The term 'sediment load' describes the quantity of sediment being transported by a river and is different to 'sediment yield' which describes the total amount of sediment discharge through a river outlet, with the term 'specific sediment yield' being a measure of sediment export per unit area per unit time (Dutta, 2016). Sediment load may be split in to three categories (Crawford, 1998):

1. Bedload is the fraction of the sediment load transported on the riverbed by saltation and usually consists of coarser-grained, heavier material.
2. Suspended load describes particulate sediment carried within the water column and is usually made up of lighter-weight, finer-grained particles. The suspended load usually accounts for the greatest fraction of the sediment load in a typical river.
3. Dissolved load describes the material being carried by a river in solution and is usually formed from common ions, such as potassium sulphate, calcium bicarbonate and chloride.

Sediment loads in rivers naturally vary spatially and temporally, both between and within catchments. For example, Bilotta *et al.* (2012) found that background suspended sediment loads varied by a factor of at least fifteen between 42 different ecosystem-types, in a temperate ecosystem. The differences in environmental characteristics driving these natural variations between catchments have been identified as climate, geology, channel hydromorphology and topography (Grove *et al.,* 2015). In addition to the natural drivers of differences in sediment loads, they may also be influenced to a large extent by anthropogenic factors (Grove *et al.*, 2015).

1.4. Elevated fine sediment loads in river systems

The load of fine sediment entering rivers has increased dramatically over the last century, with the majority of increases in the UK thought to be associated with forest management, changing agricultural practices and weather patterns (Foster and Lees, 1999; Evans, 2006). The potential impact of land use on suspended sediment loads is illustrated by the work of Groves *et al.* (2015) and Wass and Leeks (1999). Groves *et al.*, (2015) conducted an assessment of suspended sediment loads in ten reference condition rivers in the UK, and found large variations both temporally within the same river and spatially between different rivers. Mean suspended sediment loads of between 1 and 17 mg l^{-1} were recorded from these reference condition sites (Groves *et al.,* 2015). This contrasts with work by Wass and Leeks (1999) which examined the suspended sediment loads of 10 sites within the Humber catchment. In their study the highest mean suspended sediment loads were recorded from two rural, agriculturally dominated, catchments and ranged between 43 and 57.6 mg l^{-1}. These figures are only given to provide a snapshot of the potential differences in suspended sediment loads between impacted and non-impacted sites and it should be noted that the variation between the figures recorded by Groves *et al.* (2015) and Wass and Leeks (1999) may be due to some of the previously discussed environmental factors (e.g. climate, geology, channel hydromorphology and topography). These studies do however provide an illustration of the differences that land use can have on suspended sediment loads. These findings highlight that despite natural variation in background suspended sediment loads, anthropogenic influences, such as agricultural intensification, have caused substantial overall increases in sediment yield. This is demonstrated by the work of Foster and Lees (1999) which found that sediment yields in most UK catchments have increased by factors ranging from around 2 to 10 over the last century.

In the future, climate change is expected to result in an increase in high intensity rainfall events, which may cause more sediment to enter river systems (Lane *et al*., 2007; Wilby *et al*., 2010). Climate change is also predicted to increase low flow/drought occurrences during summer, which may lead to greater sediment deposition (Hakala and Hartman, 2004; Dewson *et al*., 2007). There is deep uncertainty regarding how climate change will act on regional weather patterns, so the exact nature of the impacts of climate change on river systems in different parts of the world is still unclear (Wilby *et al.*, 2010).

1.5. Impact of elevated fine sediment loads in rivers and difficulties associated with its management

Increased delivery of fine sediment to rivers is a major problem due to its wide range of effects on aquatic ecosystems and their functioning (Jones *et al.*, 2012a). Increased concentrations of suspended sediment cause increased turbidity, limited light penetration, and changes in water chemistry and temperature (Van Nieuwenhuyse and LaPerriere, 1986; Jones *et al*., 2012), which reduce primary productivity and affect the entire aquatic food chain (Davies-Colley *et al*., 1992). Deposited sediments clog substrate interstices, reduce interstitial volume, alter bed substrate composition and increase habitat homogeneity causing ecological impairment (Ryan, 1991; Niyogi *et al*., 2007; Bryce *et al*., 2010). Increases in sediment deposition can affect all trophic levels of the aquatic ecosystem, impacting fish, invertebrates, macrophytes and the phytobenthos (Owens *et al*., 2005).

Increased rates of fine sediment deposition and the range of negative effects on aquatic biota has meant that managing sediment inputs into river systems has become a priority for environmental regulators (Owens *et al*., 2005). However, at present, there is only a limited understanding of the quantitative relationships between freshwater community responses and levels of sediment delivery in to river systems (Walling *et al*., 2007; Jones *et al*., 2012). This lack of information is causing problems for environmental regulators aiming to define critical sediment values for river catchments (Walling *et al*., 2007).

Whilst the concentration of fine sediment strongly effects aquatic biota and ecological processes, other influential factors include the duration of exposure, fine sediment quality, particle size and hydrological conditions (Bilotta and Brazier, 2008). It is also important to note that focussing on the concentration of fine sediment only deals with suspended sediment loads, whereas deposited sediment causes the most marked impacts on freshwater ecosystems (Jones *et al.*, 2012a). Much of the existing water quality legislation focusses on the concentration-response model and ignores these other important factors, which brings in to question whether they are appropriate for the effective control of fine sediment to sufficiently prevent the damage it can cause to sensitive freshwater ecosystems (Newcombe and Macdonald, 1991). Recent work suggests that some aquatic biota may be adversely affected even by small amounts of fine sediment (Bilotta and Brazier, 2008; Jones *et al*., 2015). For example, Larsen and Ormerod (2010b) found that even short term, low-level, increases in fine sediment concentrations led to significantly raised drift rates in some species of mayfly (*Baetis rhodani* (Pictet, 1843: Baetidae) and *Ecdyonurus* spp. (Heptageniidae)), and stonefly larvae (*Leuctra hippopus* (Leuctridae: Kempny, 1899) and *Leuctra moselyi* (Morton, 1929: Leuctridae)).

Another factor to consider when assessing the impact of fine sediment on freshwater biota is the effect of prior exposure to elevated fine sediment amounts. A waterbody which has previously experienced elevated fine sediment may respond differently to fine sediment deposition compared to a waterbody which has not previously experienced fine sediment pressure. In situations where fine material begins to dominate the stream bed, surface sediments become clogged with silt, a process known as colmation (Boulton, 2007). The sealed interstices limit the refugial space available for invertebrates (Brunke, 1999), which can increase the impacts of anthropogenic and natural disturbances (Borchardt and Statzner, 1990). Although the evidence is not equivocal (Stubbington, 2011), the hyporheic zone has been found to act as a refuge under certain conditions, during both flooding and drying episodes (Marchant, 1988; Dole-Olivier *et al*., 1997; Delucchi, 1989; Clinton *et al*., 1996), so a colmated stream bed would limit this ability. The question of whether a colmated stream bed will affect the response of invertebrates to a fine sediment pulse has not yet been addressed in the literature. However, it is possible that in a stream which is not already colmated, invertebrates may be able to use hyporheic refugia to escape some of the negative effects caused by elevated fine sediment amounts, whereas in an already colmated stream this resource would not be available. Understanding how biota respond differently to fine sediment pressure depending upon previous sediment conditions is important for legislators and river managers as any legislation or management guidelines should be effective in different river types, such as those that experience chronic exposure to elevated fine sediment amounts and those which are only exposed to elevated fine sediment amounts intermittently.

1.6. Water quality legislation

In Europe, there is currently no legislation solely dedicated to the management of fine sediment. However, the control of fine sediment is a policy driver in water quality legislation at the local, national and international level (see summary Table 1.1; Collins *et al*., 2011). Although, the damage excessive amounts of fine sediment cause to freshwater ecosystems has been recognised, legislation to specifically control this problem has not yet been introduced.

Legislating for the control of fine sediment in freshwaters is difficult because, as discussed in the previous section, the impacts of fine sediment on water quality, physical habitat and aquatic biota are complex (Collins *et al*., 2011). Much of the current international water quality guidelines relating to thresholds in the

Table 1.1 Summary of legislation relating to fine sediment in the European Union, the United States, Canada, Australia and New Zealand (adapted from Bilotta and Brazier, 2008).

Organisation	Policy	Countries/States Involved	Guidelines	
European Union	EU Water Framework Directive (WFD) (European Commission 2000)	European Union	All surface and groundwater must meet a 'good ecological standard' (GES). Does not mention sediment explicitly, however its management is often necessary to meet a GES.	
US Environmental Protection Agency (EPA)	Clean Water Act (1972)	United States	Total Maximum Daily Load (TMDL) of sediment that a water body may receive, decided on a regional basis using a number of different methods. Technical guidance available for setting of TMDLs.	
Canadian Council of Ministers of the Environment (CCME)	Canadian Environmental Quality Guidelines (CEQG) for Protection of Freshwater Aquatic Life CCME (2007)	Canada	Low Flow Maximum increase of 25 mg/L from background levels for any short-term exposure (e.g., 24 h period). Maximum average increase of 5 mg/L from background levels for longer term exposures (e.g., inputs lasting between 24 h and 30 d). High Flow Maximum increase of 25 mg/L from background levels at any time when background levels are between 25 and 250 mg/L. Should not increase more than 10% of background levels when background is ≥ 250 mg/L.	
Australian and New Zealand Environment and Conservation Council (ANZECC)+Agriculture and Resource Management Council of Australia and New Zealand	Australian and New Zealand Guidelines for Fresh and Marine Water Quality ANZECC (2000)		Upland Rivers (>150m >1500m altitude)	Rivers
		South East Australia	2-25 NTU[1]	6-50 NTU[1]
		Tropical Australia	2-15 NTU[1]	2-15 NTU[1]
		South West Australia	10-20 NTU[1]	10-20 NTU[1]
		South Central Australia	10-20 NTU[1]	10-20NTU[1]
[1]NTU = Nephelometric T		New Zealand	4.1 NTU[1]	5.6 NTU[1]

concentration of fine sediment are based on the underlying assumption that the effects on aquatic biota generally increase with the concentration of fine sediment. This relationship has been found in many studies (e.g. Arruda *et al*., 1983; Broekhuizen *et al*., 2001; Kaller and Hartman, 2004; Bo *et al*., 2007), however, the response of aquatic biota to increasing concentrations of fine sediment is not straightforward.

1.6.1. The EU Water Framework Directive (WFD)

In Europe, the main piece of legislation to protect surface and groundwater is the EU Water Framework Directive (WFD) (European Commission, 2000). The Directive's aim is that all surface and groundwater within the EU reaches a 'good ecological status' (GES). To comply with the EU WFD, members are expected to characterise key pollutant pressures and impacts for each waterbody and to develop a River Basin Management Plan detailing the measures to control pollution impacts. The EU WFD does not legislate for the quality or quantity of fine sediment at the scale of the river basin, but its management is often necessary when seeking to reach a GES (Owens *et al*., 2005).

In terms of fine sediment management, the EU WFD recognises river basins are the principal unit of river systems, and that all of the environments found within a catchment are interconnected. This is important as the delivery of fine sediment to rivers and its retention and transport downstream depend on different processes occurring within a catchment. Therefore, a holistic catchment approach is crucial for effective management of fine sediment (Brills, 2008). Unfortunately, there is only a limited amount of information available at the catchment scale linking the magnitude of fine sediment concentrations with their potential impacts on the freshwater environment (Walling *et al*., 2007).

The future of water quality legislation in the UK is currently unclear, due its decision to leave the European Union. However, the Government have issued a White Paper which suggests that their intention is to transfer EU obligations into national law, meaning that it is likely that, at least for the present time, the EU WFD will be preserved and included within UK legislation (Howarth, 2017).

1.6.2. International legislation controlling fine sediment levels

The only country implementing statutory targets for sediment control is the United States. As part of the Clean Water Act (1972), the US Environmental Protection Agency (EPA) set guidelines relating to the Total Maximum Daily Load (TMDL) of specific pollutants that a waterbody may receive whilst still meeting water quality standards (Collins *et al*., 2011). The three pollutants for which there is technical guidance available are sediment, pathogens and nutrients. A percentage of the TMDL may then be allocated to the different pollutant sources within the catchment (Bash and Berman, 2001).

The US EPA has divided the country into different ecoregions. Each region has different water quality standards, which are derived from a comparison with relatively unpolluted waters in that region. The TMDLs for fine sediment are based on regression modelling, sediment rating curves and ‘professional judgement’ (Walling *et al*., 2007). For example, the TMDL for the Amite River Basin (covering an area of 5,700 km^2), located in South-eastern Louisiana and South-western Mississippi, US, is 281.219 tons/day. This catchment has been identified as suffering from sediment related issues caused by urbanisation, sand and gravel mining, forestry and agricultural practices over the last fifty years. To meet this standard requires a 55 % reduction in nonpoint sources of sediment (Mishra and Deng, 2009).

Sediment yield approaches, including the US EPAs approach, have been criticised due to the implicit uncertainty and wide variation found in sediment yield estimates (Hawkins, 2003). Furthermore, the majority of impacts of fine sediment on invertebrates are based on the amount of deposited material, which is partly related to local hydrological and hydraulic regimes, so targets not including these factors are difficult to justify (Jones *et al*., 2012). As there are considerable difficulties in applying threshold figures to uncertain and highly variable sediment yield data, it is better to use an indicator based approach, using the link between fine sediment and a measurable biotic response (Moore *et al*., 2001).

Walling *et al*. (2007) examined adopting the US approach in the UK, but concluded it was not feasible. The study found significant differences in fine sediment dynamics between US and UK catchments. As no uniform approach was utilised in the US, this was not deemed compatible with a UK approach, which aimed for a ‘standard’ methodology applicable either to clearly defined catchment types, or to all catchments. The data and resource requirements implicit in the successful implementation of the US approach were also not thought to be replicable in the UK (Walling *et al*., 2007).

1.6.3. European Protected Areas legislation

European member states need a method to control the amount of fine sediment in freshwater bodies and, thus, mitigate the damage it can cause. This is necessary to meet the requirements of legislation governing designated Protected Areas in Europe, such as the Habitats and Species Directives, which is the basis of Special Areas of Conservation (SACs), and the Urban and Wastewater Treatment Directive, which underpins the Sensitive Areas scheme. Although sediment is not mentioned explicitly in this legislation, there is an expectation that these environments are protected from a range of pollutants, including excess fine sediment (Collins *et al*., 2011).

The British Government has similar obligations in managing locations designated as Sites of Special Scientific Interest (SSSI), which are set out in the *Wildlife and Countryside Act 1981*. These are areas which Natural England has specified must be maintained in a ‘favourable condition’. This is achieved by designating targets for certain environmental and biological attributes, such as turbidity, water quality, habitat structure and flow. Natural England currently needs a more refined approach to manage suspended fine sediment and siltation (Cooper *et al*., 2008). However, this is a difficult task as currently there is not enough evidence linking fine sediment delivery from a catchment with specific negative ecological effects in the receiving habitats (Cooper *et al*., 2008; Walling *et al*., 2008).

1.7. Biomonitoring

Biomonitoring describes the use of biota to assess and track environmental change (Friberg *et al.*, 2011). The first objective of biomonitoring is to find the ideal bioindicator which by its presence, abundance and/or behaviour will reveal the effect of a stressor on biota (Friberg *et al*., 2011). This bioindicator may be at many different levels of organisation, ranging from molecules to entire ecosystems (Bonada *et al.*, 2006). In freshwater ecosystems, the most common biomonitoring protocols use invertebrates, algae and fish (Resh, 2008). Biota selected for use as a bioindicator will exhibit a broad range of ecological sensitivities/needs, spatial distributions and lifecycle durations/strategies which enable them to be used to indicate different stressors, and allow them to integrate a particular stressors effects both temporally and spatially (Friberg *et al.*, 2011). This makes this approach particularly effective in the aquatic environment where stressors are often intermittent, or have a high degree of temporal variability. Using a more traditional approach to monitor this type of stressor can be prohibitively costly, or difficult to achieve successfully, whereas biomonitoring can be done on a less frequent basis, making it a lower-cost option (Bonada *et al.*, 2006). Biomonitoring may also be more effective, as biological responses to stressors are evaluated directly, rather than using chemical data as a proxy for their response, making them a more direct assessment of ecological functioning (Friberg *et al.*, 2011). As biomonitoring is often used to support legislators and environmental managers it needs to be based on a foundation of strong scientific evidence, because if this is not the case it may lead to undetected environmental damage, or an undue burden on those that rely on water resources (Friberg *et al.*, 2011). This means that research examining the ecological effects of particular stressors are vital for the development of effective biomonitoring programmes.

1.7.1. Fine sediment indices

A variety of biological metrics have been developed to identify the impacts of environmental stressors, including nutrients, flow and habitat loss on invertebrates (Davy-Bowker *et al*., 2005; Dunbar *et al*., 2010). Until recently, few metrics had been developed to identify the impacts of fine sediment on invertebrates (Bryce *et al*., 2010). However, two new biomonitoring indices for fine sediment in the UK have been developed based on two different approaches: the Proportion of Sediment-sensitive Invertebrates (PSI) index and the Combined Fine Sediment Index (CoFSI). The PSI index used expert judgement to score taxa on their sensitivity/tolerance to fine sediment, based on existing information within the scientific literature (Extence *et al.*, 2011). The other approach was more data-driven and objective, relying on statistical analysis to place taxa along a gradient of fine sediment stress, this resulted in CoFSI (Murphy *et al.*, 2015). Although not discussed further in this thesis, there have also been recent efforts in other countries to develop fine sediment biomonitoring indices. One such example is the Biological Sediment Tolerance Index (BSTI), developed for use in Oregon, US, which uses weighted averaging to assign fine sediment tolerance scores to each taxa (Hubler *et al.*, 2016).

1.7.2. The Proportion of Sediment-sensitive Invertebrates (PSI) index

Extence *et al*. (2011) developed the PSI index based on an expert review of current literature to classify species and families of British benthic invertebrates on their sensitivity to fine sediment. Taxa were subjectively allocated into one of four Fine Sediment Sensitivity Ratings (FSSR) classes. The classification incorporates faunal traits, which were judged to allow the exploitation of fine sediment patches and deposits, such as morphological, physiological and behavioural adaptations. The approach also accounted for traits which were judged to prevent or exclude invertebrates from utilising fine sediment dominated habitats (Extence *et al*., 2011).

1.7.3. The Combined Fine Sediment Index (CoFSI)

Murphy *et al*. (2015) developed CoFSI using an empirical approach to define invertebrate fine sediment tolerance values. Fine sediment and biological data was collected from 179 streams throughout England and Wales during 2010 and 2011. The sites were selected to represent a broad range of different river types (e.g. upland streams, intermediate rivers, small steep streams and lowland streams), across a gradient of fine sediment pressures (using the sediment pressure categories detailed in Table 1.2). Multivariate ordination was then used to quantify the variation in invertebrate assemblages and to determine the environmental variables which explained the variation. Canonical correspondence analysis (CCA) then related the variations in the biotic data to a set of environmental variables (e.g. catchment area, discharge category, altitude, slope, surface velocity, distance from source and fine sediment inputs originating from local channel bank erosion). Following this step, the variables that had been identified in the CCA as co-variables were subjected to a partial CCA (pCCA). The co-variables were then factored out and the residual variation in the invertebrate assemblage samples were related to 27 modelled and measured fine sediment variables. A ranking of species sensitivity to fine sediment was then derived from the relative position of taxa in the pCCA ordination space, and formed the basis for deriving a new biotic index for the assessment of fine sediment pressures (Murphy *et al*., 2015). The CoFSI scores which were assigned to each taxa were developed on the basis of the response of species to two aspects of deposited sediment, described by two sub-indices, these were its response to the quantity of organic fine sediment (detailed by oFSI) and its response to total fine sediment quantity (detailed by ToFSI). The two sub-indices were combined to calculate CoFSI (Murphy *et al.,* 2015).

Table 1.2 Sediment pressure categories (based on specific yield) used in the development of CoFSI. From Murphy *et al*. (2015).

Fine-grained sediment pressure category	Range (kg ha^{-1} $year^{-1}$)
A	0-29.99
B	30-179.99
C	180-329.99
D	330-479.99
E	480-629.99
F	630+

1.7.4. Evaluation of current fine sediment indices

The PSI and CoFSI indexes have been recently developed and their effectiveness is still being examined. Glendell *et al*., (2013) tested the PSI metric by collecting 51 invertebrate samples from 13 locations within the Aller and Horner catchments in the southwest of the UK. Glendell *et al*., (2013) found that PSI and percentage fine sediment cover were more significantly related than the other metrics tested (LIFE, Average Score per Taxon [ASPT], Number of Taxa [NTAXA] and EPT % abundance). However, no significant relationship was found between PSI and suspended sediment concentrations. Glendell *et al*. (2013) hypothesised that fine sediment in suspension causes less direct impacts on aquatic biota than deposited sediment and is likely to only cause significant impacts if there are prolonged periods of high exposure (Glendell *et al*., 2013). Glendell *et al*. (2013) concluded that PSI does show promise as a tool to develop and monitor sediment targets, but that further testing is required under different environmental conditions.

In a larger study testing PSI, Turley *et al*. (2014) used data from 855 UK sites with information relating to deposited sediment and a further 451 sites which had data on suspended solids. Turley *et al*. (2014) found that PSI's correlation with fine sediment cover was comparable to the accuracy of other commonly used water quality indices (e.g. WHPT and LIFE). However, there was still considerable variance between PSI and fine sediment cover. This has led to a number of suggested refinements to the PSI metric. Turley *et al*. (2015) modified the FSSRs used to calculate PSI by incorporating empirical observations of percentage cover of fine sediment and invertebrate abundance, using data from a broad range of reference condition temperate lotic freshwater ecosystems. The result of this work is the Empirically-weighted PSI (E-PSI) index, which their study found to provide a strong correlation with fine sediment cover, and to have a higher median correlation coefficient when compared to other indices used to monitor the freshwater environment (e.g. WHPT and LIFE: Turley *et al*., 2015).

Murphy *et al*. (2015) tested the effectiveness of the CoFSI on an independent test data set. This dataset was composed of invertebrate and deposited fine sediment samples, comprising 26 samples retained from the original study, and an additional 101 samples taken between 2009 and 2011, as part of a separate study (Anthony *et al*., 2012). Murphy *et al*. (2015) found that CoFSI was significantly negatively correlated with a range of measures representing fine sediment stress (total reach-scale organic sediment mass, organic sediment mass in erosional areas and total reach-scale fine-grained sediment mass). Their independent testing led to the conclusion that CoFSI can be used as a robust indicator of benthic fine sediment. In particular, their testing found the correlation strength between CoFSI and the total fine sediment gradient was greater than that for PSI.

The proponents of both the CoFSI and PSI indices have highlighted the need for more testing to increase their accuracy. Murphy *et al*. (2015) advocate further experimental manipulations to extend the understanding of the exact factors which determine species distributions when subjected to fine sediment stress. A knowledge gap exists regarding the attributes of fine sediment that drive change in invertebrate assemblages.

1.8. Rationale for this research

Numerous studies have examined the effects of excessive fine sediment concentrations on freshwater ecosystems and their functioning (Bash *et al*., 2001; Bo *et al*., 2007; Jones *et al*., 2015; Elbrecht *et al.,* 2016; Bradley *et al*., 2017). However, due to the limitations of these studies (e.g. failure to control confounding factors, limited temporal nature and lack of consideration of the effects of prior exposure to fine sediment), and the highly complex nature of the relationship between fine sediment and aquatic biota, there is still a significant gap in our knowledge of this issue. Current research does not provide enough evidence to determine the cause-effect relationships between ecosystem responses and sediment pressures (Ramezani *et al*., 2014). Research into the effects of fine sediment is required to improve our understanding of the processes and mechanisms at work in these complex ecosystems. It is also vital from a practical perspective as river managers seek to control the amount of fine sediment entering freshwater ecosystems to mitigate some of the negative effects, and also to meet obligations from different water quality legislation (Bilotta and Brazier, 2008). Walling *et al*. (2007), Cooper *et al*. (2008) and Collins *et al*. (2012) have all produced reports for Natural England in the UK examining the idea of developing guideline sediment targets. However, all of these reports have concluded that further research is needed to elucidate the quantitative relationship between sediment loads and concentrations with their impacts on particular aquatic species. It is also vital that any guidelines take into account the variations in response to fine sediment dependent on prior exposure to elevated amounts of fine sediment. There is currently not enough evidence relating to this matter, so this potentially important factor cannot be considered when designing legislation or management advice.

1.9. Aims and research objectives

The primary aim of this thesis is to determine if substrate composition influences invertebrate response to a fine sediment pulse. This overarching aim has been split into four main objectives, which are associated with several hypotheses in each results chapter. The four main research objectives are:

1. To quantify how substrate composition influences invertebrate abundance, taxonomic richness and community composition.
2. To assess how a fine sediment pulse impacts benthic invertebrate community composition and the influence of substrate composition on the response.
3. To examine whether substrate differences influence invertebrate drift patterns during a fine sediment pulse.
4. To investigate whether invertebrates use the hyporheic zone during a fine sediment pulse, and assess its role as a refuge.

1.10. Thesis structure

This thesis consists of eight chapters, including this introductory chapter (Figure 1.2). Chapter 2 reviews the existing literature on fine sediment and its effects on aquatic biota. Chapter 3 describes the study site and methods used to conduct the experiments detailed in this thesis. Chapter 4 describes the response of invertebrates to differences in substrate composition. Chapter 5 examines the response of benthic invertebrates to a fine sediment pulse and the influence of substrate composition on this response. Chapter 6 investigates the drift behaviour of invertebrates in response to a fine sediment pulse. Chapter 7 examines how a fine sediment pulse influences the behaviour of invertebrates in the benthic sediments and hyporheic zone. Chapter 8 summarises the key findings of this PhD thesis and finishes with final conclusions and recommendations relating to the aims and hypotheses of the research.

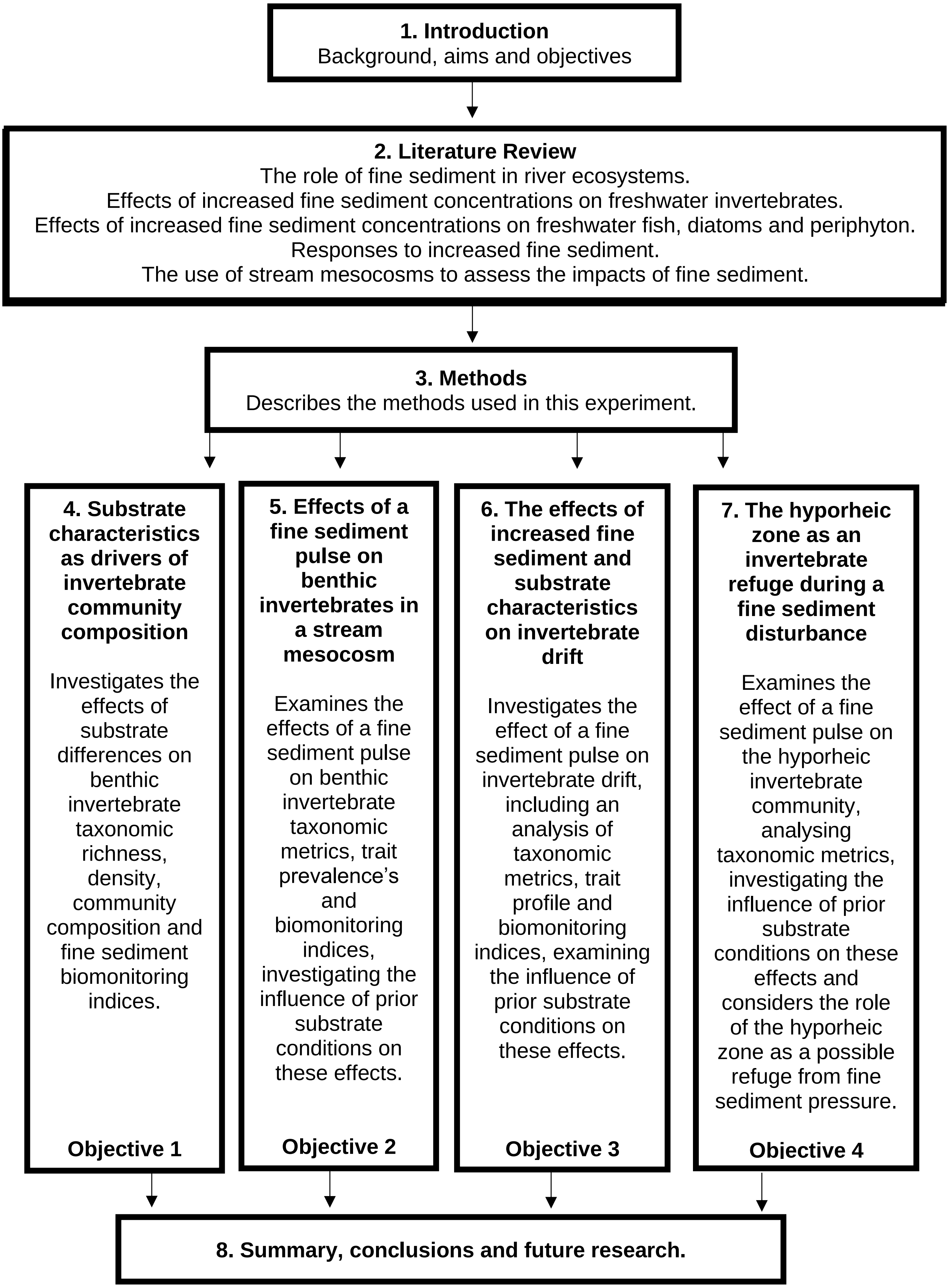

Figure 1.2 The structure of the thesis, the objectives relate to those detailed in section 1.8.

2. Literature review

2.1. Introduction

This chapter reviews the scientific literature that examines the effects of fine sediment on aquatic biota, with an emphasis on invertebrates. Chapter 1 discussed the role and value of fine sediment in freshwater ecosystems, and the problem of elevated fine sediment within freshwater ecosystems. This chapter discusses the physical, chemical and biotic effects of fine sediment on freshwater biota, and the effects of increased loading of fine sediment on community structure and composition. The use of species traits in recent studies of freshwater invertebrates is then discussed, examining how this approach differs from studies using traditional taxonomy. Finally, the chapter reviews the literature on different experimental approaches to measure the impact of fine sediment on invertebrates.

2.2. The role of fine sediment in river ecosystems

Sediment forms a vital, dynamic and essential part of river basins, and has a major role in the hydrological, ecological and geomorphological functioning of rivers (Owens *et al*., 2005). In a natural setting, sediment is produced by the erosion and weathering of soils, organic material and minerals in upstream areas and eroding river banks, and in-stream sources (Brills, 2008). In lowland areas, surface water flow rates decline, resulting in transported sediment being deposited on river banks and beds. At the catchment outlet, most of the remaining sediment is deposited in areas near the coast or within estuaries (Brills, 2008).

Transportation of fine sediment by rivers to oceans is an important part of the global geochemical cycle (Walling and Fang, 2003). Sediment-associated transport may account for >90% of the entire river-borne flux of the elements P, Mn, Ni, Pb, Cr, Fe and Al (Martin and Meybeck, 1979). In addition, Ludwig *et al*. (1996) has estimated that ca. 43% of the total load of organic carbon is carried from the land to oceans by sediment, in particulate form.

Influxes of organic matter and the transport of sediments are essential in the formation of freshwater habitats (Baron *et al*., 2003). Different rates of sediment supply and transport cause changes to substrate textures (Buffington and Montgomery, 1999; Lisle *et al*., 2000), whilst channel morphology is controlled by variations in sediment supply and discharge (Montgomery and Buffington, 1997, 1998; Massong and Montgomery, 2000). In streams with a relatively high sediment supply, where the transport capacity is less than sediment volume, the stream bed generally exhibits aggradation with simple channel morphologies, reduced scour depth and a stream bed dominated by unsorted, fine surface textures (Lisle, 1982; Lisle *et al*., 1993; Madej, 1999; Buffington *et al*., 2002; Yarnell *et al*., 2006). This type of stream results in habitats of reduced quality for aquatic biota (Pitlick and Van Steeter, 1998).

In contrast, stream reaches which receive relatively low sediment volumes may exhibit little sediment storage, as the majority of the sediment is transported, with only the least mobile particles remaining. This process creates bed degradation, resulting in simple channels, dominated by coarse sediment, with few surface features (Benda and Cundy, 1990; Lisle *et al*., 1993; Montgomery *et al*., 1996; Yarnell *et al*., 2006). Although, it should be noted, that these responses are reach-specific and that some reach types, such as step-pool, bedrock and cascade, are resilient to the majority of sediment supply or discharge disturbances (Montgomery and Buffington, 1997, 1998).

The reaches which exhibit the most diverse set of geomorphic features are those with a moderate relative sediment supply. These conditions produce channels with a range of geomorphic features (e.g. scour pools and depositional bars) and the resultant variable flows promote a diversity of sediment grain sizes, which produce a variety of surface textures (Yarnell *et al*., 2006).

2.3. Effects of increased fine sediment concentrations on freshwater invertebrates

There is considerable scientific evidence demonstrating that increased loads of fine sediment to river ecosystems impacts invertebrate communities (Hornig and Brusven, 1986; Richards and Bacon, 1994; Zuellig *et al*., 2002; Kaller and Hartman, 2004; Wood *et al*., 2005; Cover, 2006; Matthaei *et al*., 2006; Vasconcelos and Melo, 2008; Jones *et al*., 2012a; Collins *et al*., 2012; Mathers *et al*., 2014; Ramezani *et al*., 2014; Jones *et al*., 2015; Vadher *et al*., 2015), with the various different impacts potentially interacting with each other (Table 2.1, Table 2.2, and Figure 2.1). The volume of anthropogenic fine sediment delivery to rivers in many locations is now vastly greater than that which would be present through natural processes (Walling and Fang, 2003). Research by many different authors (e.g. Quinn and Hickey, 1990; Angradi, 1999; Herbst and Kane, 2006; Niyogi *et al*., 2007; Bryce *et al*., 2010) has highlighted that this may cause negative physical, chemical and biotic effects on invertebrate communities, which are reviewed below.

Table 2.1 Data from various studies regarding the effects of a range of fine sediment concentrations, and exposure durations, on invertebrates (adapted from Bilotta and Brazier, 2008).

Organism	**Fine Sediment Concentration (mgL^{-1} or NTU)**	**Duration of Exposure (h)**	**Effect on Organism**	**Country of Study**	**Reference**
Benthic invertebrates	8 mgL^{-1}	2.5	Increased rate of drift	Canada	Rosenberg and Wiens (1978)
Invertebrates	8-177 mgL^{-1}	1344	Reduced invertebrate density by 26%	New Zealand	Quinn *et al.* (1992)
Benthic invertebrates	62 mgL^{-1}	2400	77% reduction in population size	United States	Wagener and LaPerriere (1985)
Stream invertebrates	130 mgL^{-1}	8760	40% reduction in species diversity	England	Nuttall and Bielby (1973)
Macro-invertebrates	133 mgL^{-1}	1.5	Seven-fold increase in drifting invertebrates	Australia	Doeg and Milledge (1991)
Cladocera	82-392 mgL^{-1}	72	Survival and reproduction harmed	United States	Robertson (1957)
Invertebrates	Pulses	456	Reduced abundance and richness	Canada	Shaw and Richardson (2001)
Cladocera and Copepoda	300-500 mgL^{-1}	72	Gills and gut clogged	Germany	Alabaster and Lloyd (1982)
Chironomids	300 mgL^{-1}	2016	90% decrease in population size	United States	Gray and Ward (1982)
Benthic invertebrates	743 mgL^{-1}	2400	85% reduction in populaiton size	United States	Wagener and LaPerriere (1985)
Mayfly (leptophlebiid)	1000 NTU	336	No increased mortality	New Zealand	Suren *et al.*, (2005)
Invertebrates	20000 NTU	24	No increased mortality	New Zealand	Suren *et al.*, (2005)
Invertebrates	25,000 mgL^{-1}	8760	Reduction or elimination of populations	England	Nuttall and Bielby (1973)

2.3.1. Physical impacts

Abrasion

Fine sediment suspended in the water column and particles saltating along the river bed can damage the sensitive body parts of some invertebrate species by abrasion (Jones *et al*., 2012a). This process may cause behavioural responses in certain invertebrate species. Kurtak (1978) found that *Simuliidae* (Diptera; black fly larvae) typically retract their filter combs when faced with elevated fine sediment conditions. Although this behaviour will protect these vulnerable body parts, it will also result in a disruption to their normal functioning. Gallepp *et al*. (1974) observed that *Brachycentrus* (Trichoptera; caddis fly) exhibit a tendency to change their feeding behaviour in response to increased fine sediment concentrations, switching from a filter feeding method involving their limbs to a grazing approach. This behaviour is likely to protect limbs from abrasion (Kurtak, 1978), but it is noted by Jones *et al*. (2012a) that this may be a response to a reduction in food quality. In certain species of Trichoptera, individuals will avoid areas of high velocity to avoid abrasion by moving particles, choosing instead lower velocity areas of the river, or they may spend more time repairing damaged structures and cleaning (Eddington and Hildrew, 1995).

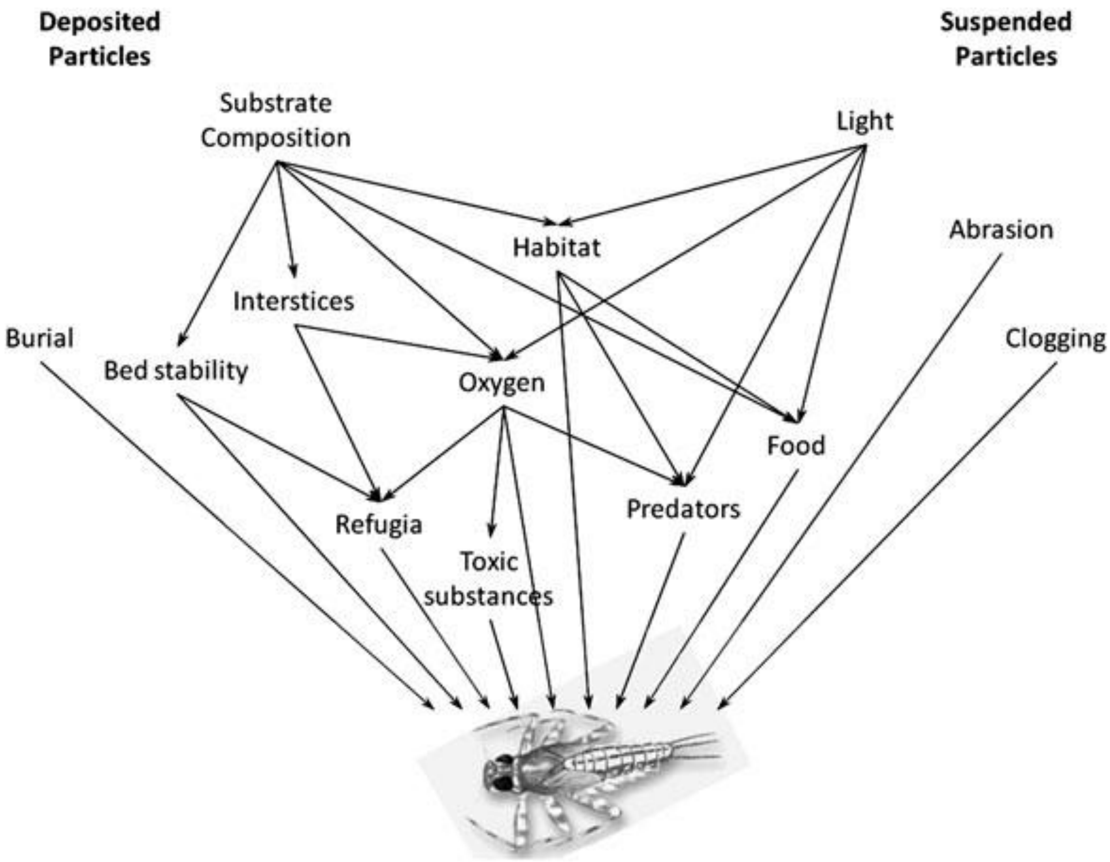

Figure 2.1 The direct and indirect effects of fine sediment (both suspended and deposited particles) on invertebrate communities (represented collectively by a mayfly larvae) and illustrating the interactions between them (from Jones *et al*., 2012a).

Effects of fine sediment on invertebrate drift

'Invertebrate drift' describes the passive or active downstream transport of aquatic organisms within the water column (Bilton *et al*., 2001). Drift is a fundamental colonisation process in rivers (Mackay, 1992; Bilton *et al*., 2001). The resilience of stream communities experiencing different environmental disturbances are thought to be partly attributable to drift, as it allows for the recolonization of denuded habitat patches with invertebrates from upstream locations (Bruno *et al*., 2012).

Excessive fine sediment loads may cause the number of invertebrates found in the drift to rise significantly (Gibbins *et al*., 2007a). This may be a voluntary behavioural response to increased fine sediment load, or it may be an involuntary process caused by the invertebrate being physically detached from the river substrate by either suspended, or saltating particles (Culp *et al*., 1986). Gibbins *et al*. (2007a) found that even low rates of sediment transport may cause catastrophic drift of invertebrates.

Larsen and Ormerod (2010b) used two second to third order streams, tributaries of the River Usk, in Wales to examine the effect of small increases in sediment transport and deposition on the drift response of the benthic invertebrate community. They carried out a replicated field-experiment, manipulating the fine sediment supply to one reach in each of their two replicate streams, using an un-manipulated reach upstream in each stream as a control. The results showed that even a relatively small amount of additional fine sediment (c. 4-5 kg m^{-2}) increased overall drift density by 45%. The increased fine sediment led to a decline in benthic density in their manipulated reaches of between 30 and 60 percent. Similar behavioural effects have occurred in other studies (e.g. Ciborowski *et al*., 1977; Rosenberg and Wiens 1978; Suren and Jowett, 2001; Matthaei *et al*., 2006). Increased invertebrate drift can deplete the benthic invertebrate standing stock, and change the composition and abundance of the community (Jones *et al*., 2012a). However, the behavioural response of drifting invertebrates can allow a quick recolonization of habitat patches after a fine sediment pulse, and may lead to less mortality among individual organisms (Jones *et al*., 2012a).

Effects of fine sediment on clogging in sensitive invertebrates

Filter feeding is common amongst many different invertebrate species. Excessive fine sediment concentrations clog delicate filter feeding structures, which hampers an invertebrate's feeding ability. Gaugler and Molloy (1980) found that exposure to high concentrations of suspended fine sediment inhibited the feeding of *Simulium vittatum* (Latreille, 1802; Simuliidae) larvae. Feeding inhibition was characterised by the larvae retracting either one or both of their cephalic fans (partially or completely; Gaugler and Molloy, 1980). Although the inhibited larvae could still feed occasionally, they were observed to be prevented from feeding for the majority of the time. This behaviour was also observed in other species of

Black fly larvae, such as *Simuliium pictipes* (Hagen, 1880: Simuliidae) and *Simuliium tuberosum* (Lundström, 1922: Simuliidae; Gaugler and Molloy, 1980). Gaugler and Molloy (1980) believed that the high particulate concentration meant that the animals ingested food at a quicker rate than it could be voided, resulting in their guts becoming filled with inert particles, thus causing the mechanoreceptors in their foregut to respond by terminating further ingestion. Kurtak (1978) found that feeding inhibition could occur with fine sediment particles <125 µm at concentrations greater than 50 mg $l^{-}1$.

In a study examining the effects of episodic sedimentation on net-spinning caddis flies, Strand and Merrit (1997) found that nets became clogged, prompting the invertebrates to either clean or replace them between sediment treatments. In the sediment-treated tanks, the caddis flies required a greater expenditure of energy to maintain their nets in working order. However, Strand and Merrit (1997) did find that sediment treatments made no overall difference to mortality rates, indicating that the extra energy required in net-maintenance was not detrimental to survival. Although this was the case, it was suggested that this type of effect may cause additional low-level, chronic stress on the benthos causing indirect effects on benthic invertebrate communities.

Effects of fine sediment on the burial of invertebrates

In stream reaches experiencing excessive amounts of deposited sediment, sedentary organisms may experience difficulties associated with burial, which may even extend to motile animals when deposition rates are high (Jones *et al*., 2012a). As sedentary animals, bivalve molluscs have been found to be particularly susceptible. A study by Ellis (1936) found many common species were unable to survive under deposits of silt 0.6-2.5 cm thick. However, many invertebrate species occupy depositional zones as they benefit from the influx of organic particles which they feed on. These animals are adapted to these conditions and they move to keep pace with accreting sediment (Jones *et al*., 2012a). When accretion rates increase, this can cause issues for some species as they become unable to excavate themselves. This ability varies between individual taxa and is dependent on the particle size of the deposited sediment (Wood *et al*., 2005).

The effects of burial by deposited sediments on many individual invertebrate taxa is still relatively unknown, but it is thought that behavioural avoidance strategies are common (Wood *et al*., 2005). Strategies may include drift, and seeking refuge in the hyporheic zone and/or the channel margins (Malard *et al*., 2002). Wood *et al*. (2001) investigated the response of the larvae of *Melampophylax mucoreus* (Hagen, 1861; Trichoptera: Limnephilidae) to burial under either 5 mm or 10 mm of sediment, and found that smaller individuals were less able to extricate themselves and that coarser sediment classes allowed individuals to extricate themselves more quickly than from finer fractions. Predicting how individual taxa will respond to burial is difficult, and research has shown a range of responses (Wallace *et al*., 1990; Dobson *et al*., 2000; Wood *et al*., 2001; Wood *et al*., 2005). It has been hypothesised that the main cause of mortality due to burial is not from the physical entrapment itself, but rather the changes to the chemical environment it may cause (Jones *et al*., 2012a).

Substrate composition

Fine sediment deposition changes the composition of river beds, by decreasing the average particle size and filling the interstices between larger particles (Jones *et al*., 2012a). Bed stability decreases if a surface drape of deposited sediment occurs (Kaufmann *et al*., 2009). The changes in physical bed structure affect many invertebrates, as most species have particular habitat requirements and will avoid areas that do not meet these requirements (Culp *et al*., 1983; Peckarsky, 1991; Sarriquet *et al*., 2007). This can mean a change in invertebrate community composition to favour species that are more tolerant of the new conditions. For instance, black fly larvae and several species of crawling mayfly larvae will actively avoid loose substrates (Bass, 1988; Ciborowski *et al*., 1977; Corkum *et al*., 1977), whereas some other invertebrates, such as certain species of Chironomidae and Ephemeridae favour finer sediments, as it enables them to construct tunnels (Jones *et al*., 2012a). However, research has found that where sand deposits are unstable abrasion and erosion cause difficulties for invertebrates to hold their position, meaning that relatively few taxa will be located there (Culp *et al*., 1986; Armitage and Cannan, 2000). In addition to changes to the environment on the surface of the river bed, fine sediment deposition also affects deeper layers of the substrate, which will be discussed in Section 2.5.

2.3.2. Chemical effects

Increased fine sediment may cause profound alterations to the chemical environment when deposited on river beds. Fine sediment can clog the interstitial space in substrates, which leads to a reduced percolation of water through the substrate, producing distinct gradients of oxygen and other dissolved substances, such as nitrate and ammonium (Pretty *et al*., 2006). Deposited sediments with a high organic content may benefit some invertebrate species, such as deposit feeders, as particulate organic matter may be a food source (Arruda *et al*., 1983; Hart, 1992; Jackson *et al*., 2007), however, for most species it can be detrimental. The increased microbial activity caused by the high organic content leads to oxygen depletion, which some invertebrate species are sensitive to, and also the build-up of substances which are potentially toxic to biota, such as ammonium (Jones *et al*., 2012a). For example, studies of hexagenid mayflies in lake environments by Rasmussen (1988) and Krieger *et al*. (2007) found that there was a strong correlation between the depths the mayflies burrow to in soft sediment and the depth of oxygen penetration. Krieger *et al*. (2007) noted that hexagenid nymphs are particularly sensitive to hypoxia, which would explain why they would avoid areas in the substrate with depleted dissolved oxygen levels. Deposited sediment may also harm invertebrate communities if it contains toxic levels of environmental pollutants, such as pesticides. For instance, a study by Phillips *et al*. (2004) found that sediments contaminated with organophosphate pesticides caused toxicity to daphnids, whilst contaminated sediments from mining areas have also been found to cause toxicity in freshwater ecosystems (Angelo *et al*., 2007; Méndez-Fernández *et al*., 2015).

2.3.3. Biotic impacts

The impact of fine sediment on aquatic macrophytes

Macrophytes influence the transportation and deposition of fine sediment, and are also impacted by sediment loading (Jones *et al.,* 2012b). The reduced grain size distribution found in river beds experiencing high levels of deposited fine sediment may increase erodibility and make plants more susceptible to being uprooted during high flows (Jones *et al*., 2012b). Macrophytes may also be affected by suspended particles in the water column. High turbidity caused by suspended particles decreases light penetration in the water column, reducing the light available for photosynthesis. The increased turbidity can result in reduced growth rates in submerged macrophytes (Henley *et al*., 2000; Parkhill and Gulliver, 2002). In extreme cases, Vermaat and De Bruyne (1993) found that constant high turbidity can prevent submerged macrophytes from existing in anything other than the shallowest areas, due to the reduction in light penetration.

Abrasion by suspended sediment particles in the water column may affect some susceptible macrophyte species, particularly those with submerged leaves (Jones *et al*., 2012b). As an adaptation to increased gas exchange and light harvesting underwater, the leaves of macrophytes are generally thinner when submerged and also lack a cuticle (Spence and Crystal, 1970; Sculthorpe, 1985). These adaptations mean that the submerged leaves are more susceptible to damage by fine sediment particles suspended in the water column. However, no such effect has yet been seen in the field (Waters, 1995), and it is hypothesised by Jones *et al*. (2012b) that only prolonged excessive concentrations of suspended fine sediment particles are likely to cause any significant damage, in which case submerged macrophytes are unlikely to survive due to other, indirect effects.

Macrophytes are also affected by deposited fine sediment. For example, deposited particles may attenuate the light reaching photosynthetic parts of plants, if they settle directly on them, affecting the plants ability to photosynthesise, resulting in reduced growth (Jones *et al*., 2012b). Fine sediment deposited directly on the leaves of plants may also hamper their ability to diffuse gases out of and into the plant, which will reduce the photosynthesis rate (Black *et al*., 1981; Jones *et al*., 2000). Excessive fine sediment deposition also smothers some macrophyte species; mosses and liverworts are particularly vulnerable due to their short stature and slow growth rate (Jones *et al*., 2012b).

The influx of bioavailable nutrients which fine sediment deposition may bring, depending upon its constituents, provides a more fertile rooting medium for macrophytes (Stutter *et al*., 2007; Jones *et al*., 2012b). The conditions which fine sediment deposition creates on the river bed also increases the nutrients available to macrophytes, which can result in increased primary production (Chambers and Kalff, 1985; Chambers *et al*., 1991, Heaney *et al*., 2001; Sagova-Mareckova *et al*., 2009). The balance between the costs of growing in anoxic, unstable substrates, and the benefits of increased nutrient availability means that the nature of the fine sediment material and the rate of deposition control the composition of the macrophyte community (Jones *et al*., 2012b).

Changes in macrophyte community composition may affect invertebrate communities, through a number of different mechanisms. Macrophytes have a significant impact on the transfer and conveyance of fine sediment in streams (Henley *et al*., 2000). Their physical presence in the water creates flow resistance and provides a physical block to the movement of water (Bal and Meire, 2009). This serves to retain sediment in river reaches, which may form habitat patches for invertebrate species. Habitat changes are one of the best descriptors of invertebrate community change (Petts *et al*.1993), this means that when macrophytes change habitat and flow conditions invertebrate community composition is altered (Henley *et al*., 2000; Jones *et al*., 2012a). Macrophytes have also been found to have a substantial effect on water chemistry and can cause significant changes to dissolved oxygen levels, so any alterations to macrophyte community composition may also affect the concentrations of dissolved oxygen available for invertebrate communities (Kaenel *et al.*, 2000).

Effects of fine sediment on food resources

Organic matter is a vital source of nutrients and energy for many aquatic organisms (Brills, 2008). Suspended particulate organic matter is a food resource used by filter-feeding invertebrates, so any increases in organic matter may allow populations to expand (Jones *et al*., 2012a). Increases in fine sediment deposition rich in particulate organic matter may also benefit deposit-feeders (Jones *et al*., 2012a). However, for both filter-feeders and deposit-feeders, if a large proportion of the increase in particulate matter is inorganic this may counteract the benefits of increases in quantity, as it can lead to problems with ingestion (Nuttall and Bielby, 1973; Gaugler and Molloy, 1980; Jones *et al*., 2012a).

Periphyton consists of algae, cyanobacteria, fungi, sedimented material and organic matter, and is found in a film on the surface of particles in aquatic environments, and is a common food source for scraper-feeding invertebrates (Jones *et al*. 2012a). Its nutritional quality may be affected by increased volumes of deposited fine sediment if the deposition increases the proportion of inorganic material in the periphyton assemblage. Increased turbidity caused by suspended fine sediment may also impact upon the periphyton assemblage, as the attenuation of light will reduce algal growth, consequently reducing the nutritional value of the periphyton (Quinn *et al*., 1992, 1997).

Fine sediment effects on food webs

Increased concentrations of fine sediment in freshwater ecosystems may also have a profound effect on fish populations, particularly in the early stages of their life cycle (Waters, 1995). Fine sediments can reduce the oxygen supply available to fish eggs, potentially resulting in their death (Wood and Armitage, 1997; Sear *et al*., 2008). In addition, Redding and Schreck (1982) found that suspended sediment may erode the mucus coating of gills, damaging them significantly.

Many fish species predate on invertebrates, so any declines in fish populations due to excessive fine sediment concentrations may release invertebrates from predation pressure (Jones *et al*., 2012a). Increases in turbidity caused by suspended fine sediment may also provide benefits for invertebrate communities as it hampers the ability of fish that use vision as their primary means of predation (Gardener, 1981; Zamor and Grossman, 2007). The scale of these effects on invertebrates is dependent upon the extent to which population growth is controlled by predation (Jones *et al*., 2012a). In a study on the predation of *Baetis* mayfly larvae by fish, Peckarsky *et al*. (2008) found population dynamics to be dependent upon the disturbance regime during periods of growth and development, and that predation increased during times of low disturbance. Fish exert less of a control on invertebrate populations in frequently disturbed conditions.

Fish species which are visual predators often favour larger invertebrates as their prey. These invertebrates are typically predators themselves, who prey on other invertebrate taxa. Therefore, if excessive fine sediment concentrations lead to a decline in fish populations, this will impact upon invertebrate community composition, favouring the larger predatory invertebrates, but exposing their prey to a greater risk from predation (Jones *et al*., 2012a). However, if excessive fine sediment concentrations lead to the loss of prey species, this means that those invertebrates which predate on them will suffer, and potentially be lost from the community, unless they have access to an alternative food source (Jones *et al*., 2012a).

Table 2.2 Summary of the effects of fine sediment on freshwater invertebrates.

Sediment effect	Implications for invertebrates
Abrasion by suspended sediment, or bedload movement.	Changes to feeding behaviour. Damage to vulnerable body parts (filter-feeding apparatus or gills) (Voelz and Ward, 1992).
Drift, caused by saltating particles and bed instability.	Removal of organisms from the substrate and their transport and deposition downstream (O'Hop and Wallace, 1983; Gibbins *et al*., 2005; Gibbins *et al*., 2010).
Clogging of organs (filter-feeding apparatus or gills) by increased suspended sediment concentrations.	Hampered ability to respire and feed (Hornig and Brusven, 1986).
Burial by deposition of suspended sediment.	Slow moving or sedentary organisms may become buried and unable to extricate themselves (Wood *et al*., 2005).
Changes to substrate composition resulting in colmation.	Organisms which use interstitial spaces as refugia, for feeding, or the incubation of eggs, may be adversely affected (Brusven and Rose, 1981; Dole-Olivier *et al*., 1997; Ward *et al*., 1998).
	Faunal movement, hydrological exchange and the exchange of nutrients or organic matter between the benthic and hyporheic zones becomes hampered (Pretty *et al*., 2006 ;Boulton, 2007).
Reduction in dissolved oxygen concentrations, due to microbial activity in sediments rich in organic matter.	May result in some sensitive species being unable to penetrate sediment past certain depths, dependent on their individual oxygen requirements (Nebeker *et al*., 1996; Krieger *et al*., 2007).
The accumulation of potentially toxic substances.	A multitude of adverse impacts to species sensitive to these toxic substances (Jones *et al*., 2012a).
Changes to habitat composition (macrophyte community composition and substrate grain size).	Strong correlation between invertebrate community composition and habitat patch composition, so any changes may be detrimental to a wide range of species (Kaller and Hartman, 2004; Matthaei *et al*., 2006).
Quantity and quality of food available may be affected by sediment effects on primary production. May also increase influx of organic matter.	May be beneficial to some species, especially those which feed on organic matter, however can also have detrimental effects on other species if their food supplies are adversely affected by changes in primary production (Graham, 1990; Thomson *et al*., 2005; Jones *et al*., 2012a; Descloux *et al*., 2014).

2.3.4. Effects of increased fine sediment concentrations on freshwater fish, diatoms and periphyton

Freshwater fish can be adversely affected by fine sediment, where its impact is complex, varying significantly depending on fish species and life stage. The majority of studies in to these effects have been carried out on salmonids, and it has been recognised that there is a lack of information regarding the effects of exposure to fine sediment on other freshwater fish species (Kemp *et al*., 2011).

Wood & Armitage (1997) identify a number of mechanisms by which high concentrations of fine sediment have been found to have an adverse effect on fish. The growth rates of fish can be reduced, as well as their disease tolerance. Extremely high sediment concentrations can lead to fish mortality, by clogging their gills (Bruton, 1985). Suitability of spawning habitat is reduced, adversely impacting the early development of fish (Chapman, 1988). Increased turbidity caused by high suspended sediment conditions can result in a reduction in primary production and can also be detrimental to the habitat availability of insectivore prey items, a consequence of which can be a reduction in the food available for fish (Bruton, 1985; Thomson *et al*., 2005). Fish species which rely on their vision for hunting also find their feeding ability adversely affected in conditions of high turbidity associated with elevated suspended sediment levels (Bruton, 1985; Ryan, 1991).

Diatoms and fine sediment have a reciprocal relationship, with diatoms affecting the retention and production of fine sediment within the catchment (Jones *et al*., 2014). The mechanisms by which diatoms increase the benthic load of fine sediments include changes to shear stresses, bed clogging and surface adhesion (Jones *et al*., 2014). High concentrations of fine sediments have been found to have a number of adverse effects on diatom assemblages, particularly via the mechanisms of scouring, burial and shading (Jones *et al*., 2014). The most acute effect of deposited fine sediment on diatom assemblages is due to the smothering of substrata usually used as an attachment point for the diatoms. This shifts the composition of diatom assemblages to favour more motile taxa, as they are better able to cope with the instability inherent in deposited fine sediments (Jones *et al*., 2014). The ability of raphid diatoms to migrate through deposited sediments have led to recent efforts to use diatoms as a bioindicator of fine sediment, an approach which is currently being tested (Jones *et al.*, 2017).

Elevated fine sediment levels have also been found to diminish the organic content of periphyton cells, hamper the ability of algal cells to attach to the substrate and in extreme cases completely smother and kill aquatic macrophytes and periphyton (Graham, 1990; Brookes, 1986).

2.4. Responses to increased fine sediment

The previous section detailed the impacts that fine sediment may have on freshwater biota. In the following section, the response of invertebrates to these impacts will be considered, both in terms of the prevalence of functional traits and in invertebrate dispersal behaviour.

2.4.1. Invertebrate traits

Excessive fine sediment concentrations can influence the taxonomic composition and the functional trait structure of invertebrate assemblages (Gayraud and Philippe, 2001; Growns *et al*., 2017; Wilkes *et al.*, 2017). 'Functional trait structure' refers to the combination of traits held by species within an invertebrate assemblage, but only considers traits which affect the performance of individual organisms and which may affect ecosystem functioning. Underpinning the traits-based approach is the habitat (templet) model proposed by Southwood (1977). The basis of this model is that in locations with similar environmental conditions, the trait composition of species assemblages should converge, even where species pools differ across biogeographic boundaries (Poff *et al*., 2006).

The traits-based approach has been proposed as a good method of disentangling the effects of multiple environmental stressors acting on freshwater ecosystems (Lange *et al*., 2014). Traits-based approaches have also been used as indirect functional indicators of stream ecosystem function (e.g. Townsend *et al*., 2008; Wagenhoff *et al*., 2012; Magbanua *et al*., 2013), and this mechanistic approach can have several advantages over the use of structural indices based on taxonomic lists of community composition (Lange *et al*., 2014). Trait responses are consistent across spatiotemporal scales (Poff, 1997; Bêche *et al*., 2006;

Menezes *et al*., 2010), and have been used to elucidate the mechanisms behind the effect of a variety of environmental pressures experienced by freshwater ecosystems (Townsend and Hildrew, 1994; Menezes *et al*., 2010; Statzner and Bêche, 2010). That trait-based approaches may be used across large spatial scales is an advantage in biomonitoring, as it enables a large number of regionally applied metrics to be supplemented by a more unified tool, which may be applied to lotic freshwater bodies across different biogeographical regions (Statzner and Bêche, 2010).

2.4.2. Fine sediment and the dispersal behaviour of freshwater invertebrates

The present study is the first to use the experimental manipulation of stream mesocosms to examine the effects of a fine sediment pulse on hyporheic, benthic and drifting invertebrates concurrently, whilst also identifying the influence of two different substrate types. Previous research has investigated these factors in isolation (e.g. Ciborowski *et al*., 1977; Mathers *et al*., 2014; Jones *et al*., 2015; Vadher *et al*., 2015). For instance, in a laboratory setting Vadher *et al*. (2015) examined the effects of fine sediment on the vertical movement of *Gammarus pulex* (Linnaeus, 1758: Gammaridae) within subsurface sediments. The study found a threshold at which fine sediment prohibits vertical migration. However, Vadher *et al*. (2015) noted that the results are only applicable to the substrate size and organisms used in their experiment. Although still producing very valuable results, this highlights the advantages of using a stream mesocosm approach for the research for this thesis, which assessed these effects on a range of taxa, not just a single species, and examined the influence of two different substrate types (coarse and fine), rather than the results only being applicable to one gravel matrix size range.

Culp *et al*., (1986) investigated the effect of fine sediment addition on drift in benthic invertebrates, finding that deposited sediment caused increased drift in one taxa, whilst saltation of suspended fine sediment was found to have a significant impact on benthic invertebrate densities and invertebrate community composition. They observed different drift responses between invertebrate taxa, which they theorised may be related to their vertical movement within the substrate. Larsen and Ormerod (2010b) studied the low level effects of fine sediment on invertebrates, noticing a decline in leuctrid stoneflies in the benthos following fine sediment exposure, but no corresponding increase in drift patterns. This led to the suggestion that movement into the hyporheos was a possible cause of this finding. However, as with the observation by Culp *et al*., (1986), this was not possible to investigate in their experiment, as only drift was sampled, rather than sampling the benthos, hyporheos and drift simultaneously as in the experimental design for this study. The lack of understanding regarding the effects of fine sediment on the hyporheos has also been noted more recently by Mathers *et al*. (2014), who highlight that the previous studies have been carried out only focussing on benthic habitats and biota.

The duration of exposure to fine sediment is a key factor in determining its effects on aquatic invertebrates (Bilotta and Brazier, 2008), which makes the temporal scale of research into this subject important. Suren *et al*., (2005) and Larsen and Ormerod (2010) have examined the effects of short term exposure (treatment periods 24 h, or less) to fine sediment on invertebrates, investigating its effect on mortality, drift and benthic composition. The studies both yielded important results. However, as noted by Larsen and Ormerod (2010b) difficulties arise when trying to scale-up the result. Newcombe and MacDonald (1991) examined the results of over 70 studies on the response of aquatic biota to fine sediment. As part of the research, it was found that the ranked severity of effect on aquatic biota was only poorly correlated with suspended sediment concentration (r^2 = 0.14, p>0.05), whereas, if duration of exposure was also included, in what they called a measure of suspended sediment intensity (duration of exposure multiplied by suspended sediment concentration), the correlation was stronger (r^2 = 0.64, p<0.01).

The research by Newcombe and MacDonald (1991) demonstrates that examining the effects of fine sediment on aquatic biota over a short time period will result in many of the negative effects being obscured. Also, in terms of providing useful information for environmental managers and legislators, it is important to try and provide information more easily relatable to the temporal scale in which they work, which is often measured in months and years, rather than hours (Wohl *et al*., 2015). This study aimed to avoid some of these pitfalls by examining the effects of fine sediment on aquatic invertebrates over a time period of 33 days.

Spatial scale is an important factor to consider when assessing how freshwater invertebrate communities are affected by excessive levels of fine sediment. Freshwater invertebrates are affected by deterministic processes operating at the local scale, and by processes and constraints operating at larger spatial scales (Mykra *et al*., 2007). The result of this means that it is not straightforward to extrapolate the results of investigations made at one scale to a different scale (Mykra *et al*., 2007). For instance, results derived from experiments at smaller scales may not be apparent at the scale relevant to river management and vice versa (DEFRA, 2012). It is for this reason that experiments undertaken using mesocosms, which approximate to the field scale, particularly those fed by river water which allow for natural colonisation by aquatic biota, may be more representative of natural conditions and provide a more realistic platform to examine the effects of fine sediment on aquatic invertebrates (Radwell and Brown, 2006; Connolly and Pearson, 2007).

2.5. Approaches to assess the impacts of fine sediment

There are four main approaches to assess the effects of fine sediment on aquatic biota:

1. Laboratory studies;
2. Experimental manipulations carried out at the field-scale (simulated events and stream mesocosm experiments);
3. Case studies based on pollution incidents and;
4. Correlation of data collected from field surveys.

The degree of control over possible confounding variables differs between each approach (generally decreasing from approach 1 to 4), whilst the scale, response type and the general applicability to real life conditions is also influenced (generally increasing from approach 1 to 4: Jones *et al*., 2012a). This means that when considering the effects of fine sediment on freshwater invertebrate communities, it can be useful to look at evidence stemming from a range of experimental approaches.

2.5.1. Laboratory studies

Laboratory experiments have been used to assess the sensitivity of certain aquatic invertebrate species to fine sediment pollution (e.g. Kurtak, 1978; Gaugler and Molloy, 1980; Hart, 1992; Wood *et al*., 2001; Donohue and Irvine, 2003). They have been used to assess the toxicity of fine sediment and to assess the concentrations required to cause mortality in various invertebrate species (Suren *et al*., 2005). However, this type of research has been criticised in relation to the toxicity of fine sediment to invertebrates, as in natural conditions the danger is not generally from direct toxicity, rather from associated effects, such as burial or changes to the physical habitat (Jones *et al*., 2012a).

However, some laboratory work has been conducted to assess the ability of different invertebrate taxa to resist burial by fine sediment and the effect which particle size may have on this process (Wood *et al*., 2001; Wood *et al*., 2005). Other laboratory studies have examined the effect of fine sediment on the feeding rate of a range of invertebrate taxa (Kurtak, 1978; Hornig and Brusven, 1986; Hart, 1992; Broekhuizen *et al*., 2001; Kent, 2008). These types of studies demonstrate the usefulness of laboratory experiments, as they benefit from being able to control many environmental variables in order to isolate the particular effects of fine sediment on the experimental question. It should be noted that due to the scale of these experiments, and the lack of other interacting variables which occur in a natural environment, care should be taken when relating their results to natural situations.

2.5.2. Experimental field manipulations

There has been a significant amount of research carried out using field-scale experimental manipulations, both in stream mesocosms and natural rivers (Vasconcelos and Melo, 2008; Mathers *et al*., 2014; Ramezani *et al*., 2014; Jones *et al*., 2015). Stream mesocosms enable the effects of fine sediment on invertebrates to be assessed under controlled experimental conditions. Flow-through stream mesocosm channels are usually linear channels which use water taken directly from a natural stream or river. This experimental setup can allow for natural colonisation, with invertebrates entering the mesocosm channels either in the drift from the natural stream or by aerial oviposition if the channels are uncovered. This has the benefit of reducing artificiality, and can provide an accurate representation of the physiochemical conditions and invertebrate assemblages found in a natural river.

In addition to flow-through stream mesocosm channels, there are also recirculating mesocosms which use tubes or cylindrical tanks. The mesocosms can either be closed systems which recirculate the same volume of water, or may be connected to a natural river or stream to allow a flow-through design. These types of mesocosm have also been used in research on the effects of fine sediment on invertebrates (Wagenhoff *et al*., 2012; Vadher *et al*., 2015). Although suitable for some types of experimental design, recirculating mesocosms have been criticised because they may develop divergent physiochemical conditions. Recirculating mesocosms may produce systems with unrealistic water column mixing, nutrient dynamics and air-water gaseous exchange (Schindler, 1998). There is also concern that in these types of system, when compared to natural standing water, an increased surface area to volume ratio may promote the inordinate dominance of attached algae (Schindler, 1998).

The results of research carried out using experimental manipulation of natural rivers (e.g. Suren and Jowett, 2001; Radwell and Brown, 2006; Connolly and Pearson, 2007; Kent and Stelzer, 2008; Molinos and Donahue, 2009) have been found to be extremely useful, and has proved to be an excellent source of information in analysing the impact of fine sediment pollution in rivers (Jones *et al*., 2012a). Experiments have been carried out involving the addition of fine sediment to river reaches, simulating the effect of a fine sediment pulse. Studies of this type have been used to investigate the impact of fine sediment on invertebrate drift and the taxon richness of invertebrate assemblages (Matthaei *et al*., 2006; Larsen and Ormerod, 2010a). Ramezani *et al*. (2014) have also carried out an experimental manipulation of a natural river, investigating not only sediment addition, but also the effects of sediment removal on invertebrates and fish.

Field studies can provide useful information about the effects of sediment pollution on river ecosystems. Field studies do not suffer from the same problems that other experimental setups can in the interpretation of their results, such as the difficulty of attempting to translate results carried out in very small scale laboratory studies to the reach scale that is more familiar to environmental managers (Jones *et al*., 2012a). The approach also enables the study of all of the different interactions between fine sediment and invertebrates, as laboratory experiments may not incorporate all of the elements found in a natural river.

However, in comparison to studies carried out using different experimental setups, the amount of research which has been carried out using reach-scale experimental manipulation is limited. This is due to the inherent practical difficulties in carrying out such field studies. The type of sites necessary, where it is permissible to add additional fine sediment to a river and not cause unacceptable consequences downstream, are very limited. As different rivers possess different types of invertebrate communities, and are subject to different environmental conditions, these types of experiment have only been carried out on a very small subset of the different river types around the world. Whilst the results are very useful, results from the experimental manipulation of one river type may not be easily transferable to rivers of a different type (Jones *et al*., 2012a).

2.5.3. Case studies

Case studies have also been used to study the response of invertebrate communities to increased fine sediment concentrations caused by episodic events (both anthropogenic and naturally occurring: e.g. Fritz and Dodds, 1999; Quist *et al*., 2003; Milner and Piorkowski, 2004; Blettler and Marchese, 2005; Bhat *et al*., 2006; Hedrick *et al*., 2007; Svendsen *et al*., 2009). Sediment pollution events are often of a diffuse nature, so this has meant that there are relatively few case studies which have examined their effects. As there is quite often no equipment in place to carry out continuous monitoring during these events, accurate quantification of sediment concentrations is not possible. This problem is often compounded by a lack of biological information from before and after the event (Jones *et al*., 2012a). This makes it extremely difficult to formulate accurate conclusions from such case studies (Angermeier *et al*., 2004; Jones *et al*., 2012a).

2.5.4. Correlation of data derived from field studies

Much of the existing research examining the impacts of excessive fine sediment concentrations on freshwater ecosystems is correlative, or observational in nature (e.g. Zweig and Rabeni, 2001; Richardson and Jowett, 2002; Kaller and Hartman, 2004). These types of studies rely on examining the relationships between large-scale chemical sampling and biological data. However, it is difficult to account for the natural variability between river reaches, which may differ in topography, geology and other environmental characteristics. These factors may influence fine sediment concentrations and freshwater invertebrate communities, so it becomes difficult to know if the results seen in the study are a result of fine sediment directly, or some co-varying factor (Jones *et al*., 2012a). Hence, it becomes difficult to identify the vital process linkages that exist between fine sediment stress and important environmental characteristics and parameters, and their effects on aquatic biota (Collins *et al*., 2011; Collins *et al*., 2012).

Often the study sites used for correlative, observational studies are subject to excessive amounts of fine sediment caused by intensive agricultural practices

(Jones *et al*., 2012a). This means that they may be also suffering from other physiochemical changes associated with intensive agriculture, such as biological contamination, organic pollution, increased nutrient and pesticide concentrations, increased light exposure and raised water temperature (Matthaei *et al*., 2006). These changes may all have an effect on invertebrate communities, so isolating the specific effects of fine sediment from these types of experiments is not always possible.

Each of these four approaches has advantages and disadvantages. However, the research carried out for this thesis was undertaken using twelve open air flow-through flume mesocosms, because they enable control of potential confounding factors and allow the measurement of different dispersal pathways (i.e. surface, hyporheic and drift). These mesocosms also have the advantage of being connected to a natural river, to allow for colonisation by invertebrates. Ledger *et al*. (2009) examined the artificiality of the same set of stream mesocosm channels used for this research and found that the physiochemistry of the mesocosms replicated that found in the connected river. It was found that the mesocosms also included representatives of all of the invertebrate families found in the source river. These factors make them ideal for the experimental setup required for this research.

2.6. Summary

Fine sediment is a vital component of freshwater ecosystems and is important for the hydrological, ecological and geomorphological functioning of rivers (Owens *et al.,* 2005). However, the negative effects of fine sediment on invertebrates are complex and wide-ranging. These effects can be physical (e.g. abrasion, drift, clogging, burial and habitat alteration), chemical (e.g. oxygen depletion and increased concentrations of toxic substances) and biotic (e.g. changes to food quality/quantity and alterations to predator-prey dynamics; Jones *et al*., 2012a).

This thesis will add to existing work by examining how fine sediment affects invertebrates. As the review by Jones *et al.* (2012a) makes clear, our understanding of the mechanisms by which fine sediment affects invertebrates is still limited. This thesis aims to fill some of the knowledge gaps highlighted in this literature review, particularly examining how a) differences in substrate composition influence the response of invertebrates to a fine sediment pulse and b) the dispersal pathways used by invertebrates in response to fine sediment disturbances.

3. Methods

3.1. Study area

The River Frome is situated in Dorset, UK (Figure 3.1). The catchment drains an area of 414 km^2 (Marsh and Hannaford, 2008). The upper part of the catchment is dominated by Cretaceous Chalk bedrock, whereas the lower catchment is underlain by clays, gravels and sands. Soils are characteristically well drained, shallow and chalky, although heavier, clay-influenced soils also occur (Marsh and Hannaford, 2008).

Figure 3.1 Location of the stream mesocosms at the Freshwater Biological Association's River Lab in Dorset, UK.

Agriculture is the primary land use within the catchment, consisting mainly of cereals and grazed pasture. Dorchester is the only large urban area in the catchment with a population of circa 19,000 in 2013 (Office of National Statistics, 2014). The mean annual rainfall at East Stoke was 1020 mm from the period 1965 to 2000, and the mean flow was 6.38 m^3s^{-1} at the East Stoke gauging station (Marsh and Hannaford, 2008).

The experiment was conducted using twelve open air flow-through stream mesocosms, 0.33 m width, 12.4 m length and 0.30 m depth, at the Freshwater Biological Association's (FBA) River Laboratory in Dorset, UK. Four blocks, containing three mesocosms, were situated perpendicular to, and fed from the Mill Stream, a tributary of the River Frome. The distance between each block was 2.5 m (Figure 3.2).

Figure 3.2 Arrangement of the stream mesocosms.

Unfiltered river water from the Mill Stream enters the mesocosms through a 110 mm upstream inflow pipe. The water arrives into a reservoir (*c.* 2 m long, 1 m wide and 0.35 m deep) at the upstream end of each block of mesocosms. The water then flows over a small weir in to the mesocosms. The height of the weir controls the rate of water flow in the channels, and was consistent across the experiment. The water exits the stream mesocosms over a small weir before flowing in to a ditch, which re-enters the Mill Stream.

3.2. Experimental setup

Prior to the experiment starting, the substrate in the twelve mesocosms was removed, and the steel lining of the mesocosms was cleaned. A ‘coarse’ and a ‘fine’ substrate composition treatment was prepared for the experiment. The ‘coarse’ substrate composition treatment consisted of sand (<2 mm, 6.6%), gravel (10 mm, 13.3%), pebble (20 mm, 66.6%) and cobble (>64 mm, 13.3%). The ‘fine’ substrate composition treatment comprised sand (25%), gravel (37.5%) and pebble (37.5%). The ‘fine’ substrate composition treatment was designed to represent a stream which had experienced elevated amounts of fine sediment and lacked interstitial space. The ‘coarse’ substrate composition treatment was chosen to represent a stream which had experienced relatively little fine sediment deposition. Both substrate composition treatments were chosen to represent the bed substrate in a typical lowland stream, and the amount of fine sediment in each treatment was tailored so that there was a clear difference in particle size between the two substrate types. The sediment was obtained from a local quarry and mixed using a cement mixer, to ensure consistency in the particle size distribution of each sediment mix.

Each mesocosm was divided into two 6.2 m sections at the halfway point along their length, which provided a total of 24 mesocosm sections. This arrangement has been used in previous work by Jones *et al*. (2015), where it was demonstrated that there was no effect related to whether samples were taken from an upstream or a downstream section. When conducting the experiment detailed here ‘upstream’ and ‘downstream’ were initially included as factors in the statistical analysis, but it was found that these factors had no impact on the results, so they were not included in subsequent analyses. Both substrate composition treatments were filled to a depth of 20 cm in each of the 24 mesocosm sections (Figure 3.3). In total, twelve of the mesocosm sections had a ‘fine’ substrate composition treatment, and twelve had a ‘coarse’ substrate composition treatment.

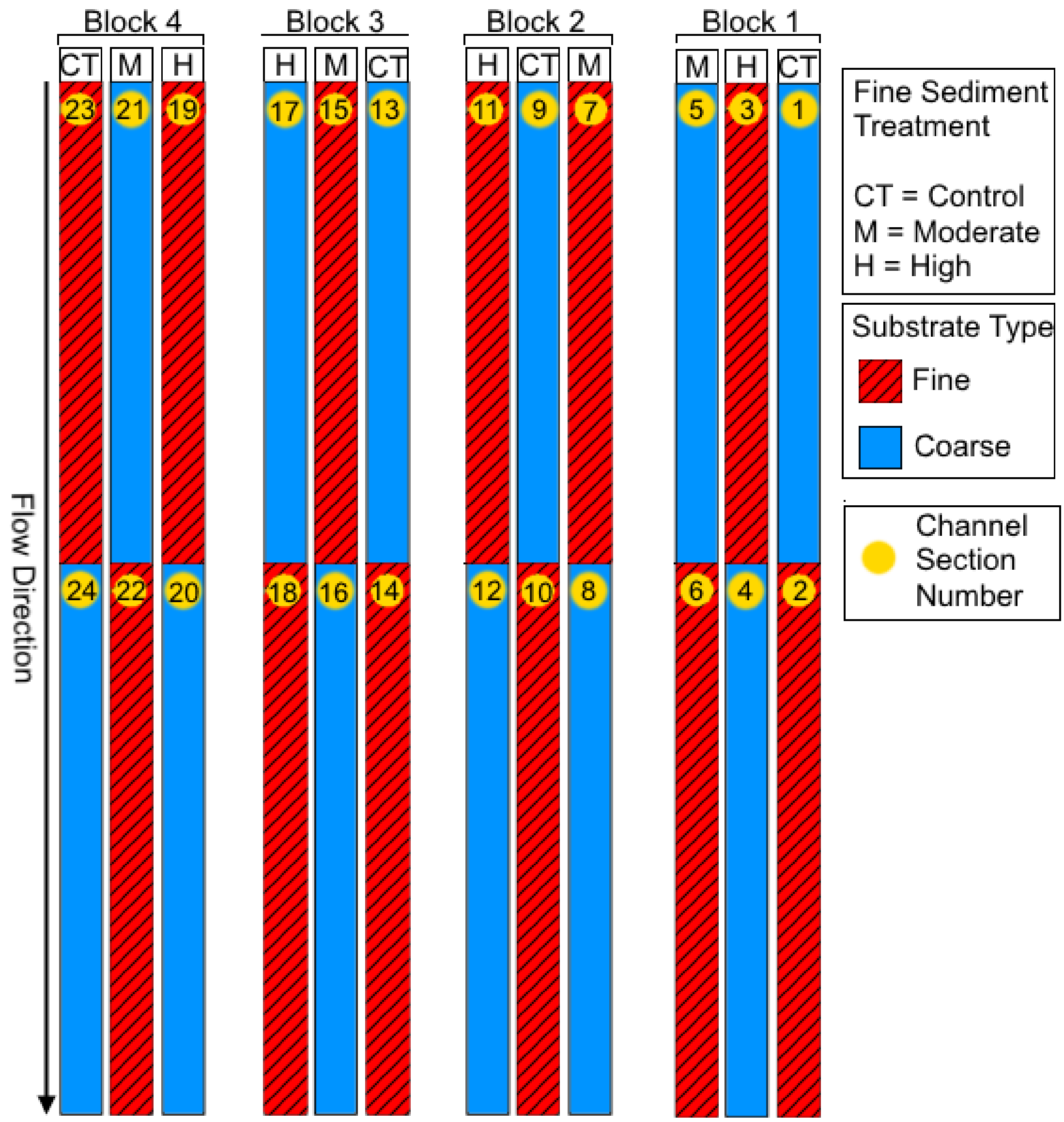

Figure 3.3 Arrangement of substrate composition and fine sediment treatments in the mesocosms.

Water was delivered to each mesocosm on 9th June 2015. Invertebrates colonised the mesocosms by drift from the Mill Stream and adult oviposition (Jones *et al*. 2015). The mesocosms were left for 69 days before the first sampling occasion to allow time for invertebrate colonisation. Although the length of time it takes for the invertebrate assemblage in the mesocosms to mimic a natural assemblage is unknown, this length of time compares favourably to previous experiments using the same set of mesocosms, which allowed a time period of 30 days (Jones *et al*., 2015) and 42 days (Harris, 2006). In order to ensure taxa not drifting, or reproducing, during this period were included, the colonisation process was aided by the addition of invertebrates from four kick samples in the River Frome. The samples were obtained at a location in the Mill Stream (i.e. adjacent to the mesocosms) that was not subject to substantial inputs of fine sediment. Aliquots (produced by dividing the kick samples into equal portions) were then added directly to the mesocosms. To prepare the aliquots, invertebrates were placed into a 10 l bucket filled with water, then a 0.25 l measuring jug was used to distribute the mix of water and invertebrates evenly between each mesocosm. To ensure that diatom mats did not colonise the mesocosms, which may encourage fine sediment settlement (Jones *et al*., 2014), shade clothes were used to cover the mesocosms throughout the period of colonisation.

3.3. Preparation and application of sediment treatments

Sediment for the treatments was sourced from a nearby reach in the River Frome, the Mill Stream and a pond connected to the Mill Stream. The sediment was sieved using a 2 mm mesh to exclude any larger particles from the treatments, and frozen for 48 hours to remove any invertebrate life.

The sediment treatments used in the experiment were:

- Control – no additional sediment and 30l of water from the Mill Stream.
- Moderate – 15 kg sediment and 30l of water from the Mill Stream.
- High – 30 kg sediment and 30l of water from the Mill Stream.

Before addition to the mesocosms, 30l of water from the Mill Stream was added to the sediment in a large plastic container, and then vigorously shaken to create a sediment slurry. The appropriate sediment slurry was then added to the head of each of the 24 mesocosm sections (see Figure 3.3), by pouring the sediment slurry directly in to the channel and letting it flow downstream and be deposited. This provided eight mesocosm sections in the ‘control’ group, eight mesocosm sections in the ‘moderate’ fine sediment treatment group, and eight mesocosm sections in the ‘high’ fine sediment treatment group. Half of the mesocosm sections in each group had the 'fine' substrate composition treatment and half had the 'coarse' substrate composition treatment.

3.4. Sampling regime

The schedule for the sampling regime is detailed in Table 3.2. All sampling was conducted in two stages, with mesocosm sections 1 – 12 always being sampled/treated the day before mesocosm sections 13 – 24. This was necessary as there were only enough drift nets to sample half of the mesocosm sections at one time. Sampling was always undertaken in a downstream to upstream direction and surber sampling was always completed prior to drift sampling, these measures were put in place to ensure that samples were not affected by the collection of other samples. This is why it was not possible to collect benthic surber samples in the 'during' phase of the experiment as they would have affected the drift samples being collected at that time. As hyporheic sampling was carried out using sampling tubes it was possible to take these samples without affecting the drift samples also being collected, meaning that it was possible to collect both drift and hyporheic samples in the 'during' phase of the experiment.

After the 'fine' and 'coarse' substrate composition treatments had been added to each mesocosm section, a five litre sample of the substrate from each mesocosm section was collected from a random location using a trowel, to ensure consistency in particle size between the mesocosm sections and to ensure the two substrate types were as intended upon installation. The substrate in each sample was dried and sieved into the following size fractions: <0.125, 0.25, 0.5, 1, 2, 4, 8, 16, 31.5, 45 and 63 mm or greater. Each size fraction was weighed to determine the particle size distribution within each substrate sample.

Three sampling tubes were inserted into the substrate of each mesocosm section in a triangular arrangement (Figure 3.4 and Figure 3.5). The sampling tubes were manufactured using PVC piping, with a diameter of 12 mm. Each pipe had four holes drilled 10 mm from the bottom, and each hole had a diameter of 5 mm. The tubes were sealed at the bottom using a foam bung. In order to keep the holes covered between sampling occasions, a foam plug was inserted into each tube, which was attached to a length of wire to enable its easy removal.

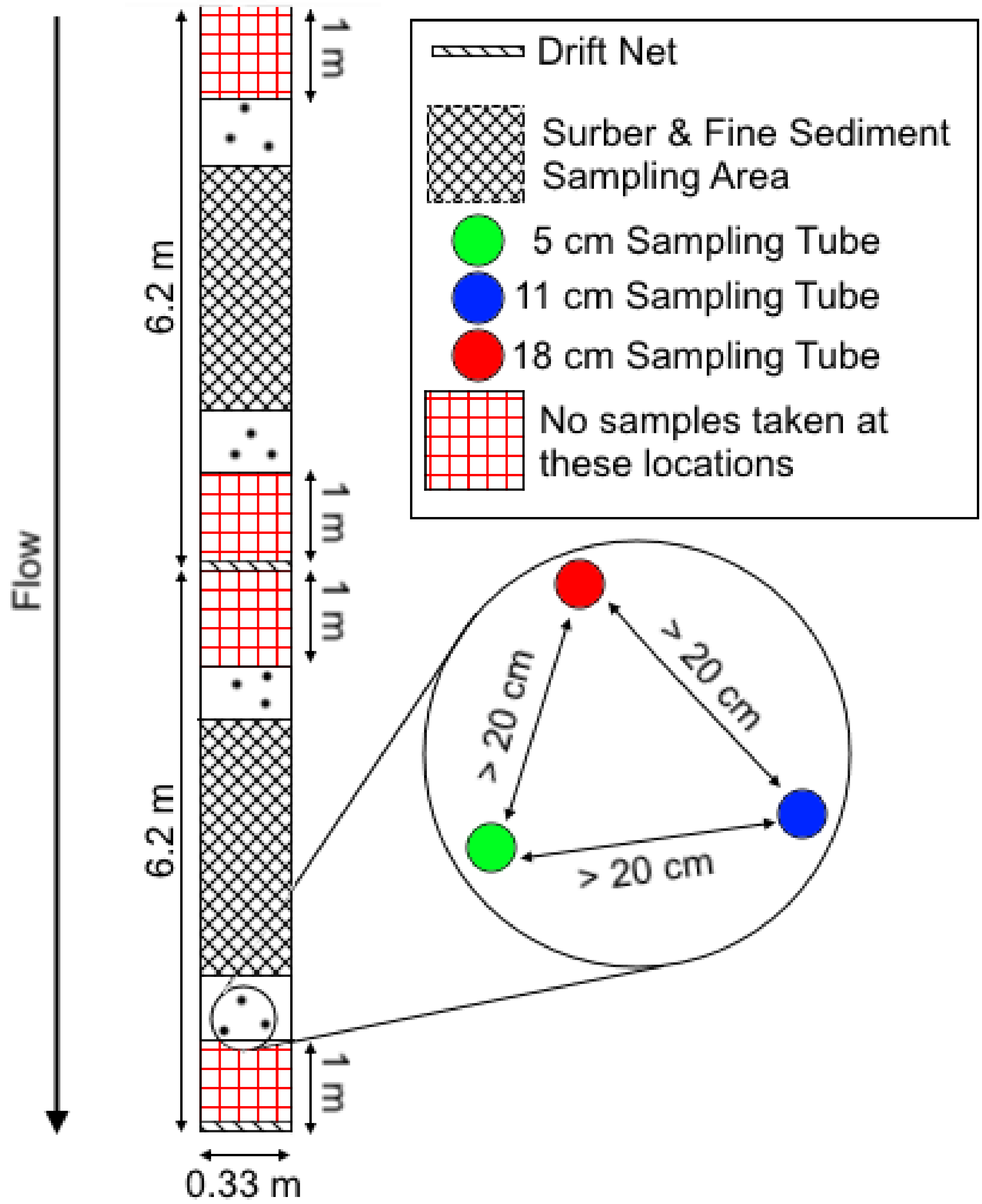

Figure 3.4 Locations of the hyporheic sampling tubes, drift nets and the area used for fine sediment and surber sampling within one mesocosm containing two experimental units. No samples were taken from areas cross-hatched in red.

The tubes were inserted in clusters of three, so that the holes of each tube were at three different depths within the substrate: 5, 11 and 18 cm. The arrangement of tubes within each cluster was such that there was always a distance of at least 20 cm between each tube. A cluster of sampling tubes were positioned at the downstream and upstream ends of each mesocosm section at a distance of 1 m from the beginning and end of each section.

Figure 3.5 Spatial arrangement of the hyporheic sampling tubes in the mesocosms.

Invertebrates were collected from the sampling tubes on the day prior to fine sediment addition, during, directly following, and 30 days after fine sediment addition. Prior to sampling, the foam bung was removed from the base of the sampling tube. This drew water from the zone in the substrate immediately adjacent to the four 5 mm holes which had been drilled near the base of each tube. This method ensured that the water originated from a depth of either 5, 11 or 18 cm respectively. Sampling of invertebrates was achieved by the collection of 500 mL of water from the sampling tube. After collection, water was sieved through a 250 µm mesh and the remaining sample preserved in 99% IMS. Invertebrates were identified to the lowest taxonomic level possible.

Benthic invertebrate samples were taken from each mesocosm section on the day prior to fine sediment addition, directly following, and 30 days after fine sediment addition. On each occasion, samples were taken from a random location at the upstream and downstream end of each mesocosm section using a surber sampler (sampling area 200 x 200mm, $0.04m^2$; net mesh size 250µm). The surface of the bed substrate was disturbed using a metal rod for 120s and the invertebrates disturbed flowed downstream into a net. The samples were preserved in 99% IMS. Invertebrates were then analysed to the lowest taxonomic level possible.

Invertebrate drift was sampled in each mesocosm section on the day prior to fine sediment addition, during, directly following, and 30 days after fine sediment addition. Drift nets (frame height 0.4 m, frame width 0.25 m; mesh size 1 mm) were installed at the downstream end of each mesocosm section. To ensure that the placement of drift nets at the bottom of the upstream mesocosm sections did not affect the downstream mesocosm sections they were emptied regularly, to make certain that the flow of water to the downstream sections was unaffected by their presence. Invertebrates drifted into the nets for a period of 24h, with the contents being emptied and preserved in 99% IMS every 6 h. Invertebrates were then separated from debris, identified to the lowest possible taxonomic level and counted.

Due to the design of the mesocosm sections, the flow rate was maintained at a consistent velocity in each channel. Therefore, the density of drifting invertebrates could be calculated. The flow rate was measured once using an Electromagnetic Current Meter 30 days after the fine sediment pulse.

3.5. Summary of sample regime

Table 3.1 Number of samples of each type resulting from experimental fieldwork using stream mesocosms.

Sample type	Number of samples
Invertebrate – Drift	384
Invertebrate – Benthic	144
Invertebrate – Hyporheic	384

Table 3.2 Sampling schedule for stream mesocosm experiment, boxes detail type of samples taken on each sampling occasion. 'Before', 'During', 'After' and '30 days' refer to the different phases of the experiment.

		Before		During		After			30 days	
09/06/2015		16/08/2015	17/08/2015	19/08/2015	20/08/2015	21/08/2015	22/08/2015		17/09/2015	18/09/2015
AM - Substrate samples taken.	69 day colonisation period	Drift sections 1 - 12	Drift sections 13 - 24	Sediment treatments applied to sections 1 - 12	Sediment treatments applied to sections 13 - 24	Drift sections 1 - 12	Drift sections 13 - 24	Channels left for 30 days	Drift sections 1 - 12	Drift sections 13 - 24
PM - Water delivered to channels		Benthic sections 1 - 12	Benthic sections 13 - 24	Drift sections 1 - 12	Drift sections 13 - 24	Benthic sections 1 -12	Benthic sections 13 - 24		Benthic sections 1 - 12	Benthic sections 13 - 24
		Hyporheic sections 1 - 12	Hyporheic sections 13 - 24	Hyporheic sections 1 - 12	Hyporheic sections 13 - 24	Hyporheic sections 1 - 12	Hyporheic sections 13 - 24		Hyporheic sections 1 - 12	Hyporheic sections 13 - 24

4. Substrate characteristics as drivers of invertebrate community composition

4.1. Introduction

High habitat heterogeneity is important for healthy, functioning river ecosystems (Collier *et al*., 1998; Kaiser *et al*., 1999; Palmer *et al*., 2000). A range of sediment sizes, including coarse and fine particles, contribute to substrate diversity and support a variety of aquatic organisms. However, increases in suspended and deposited fine sediment can alter physical habitats and their aquatic biota. A better understanding of the impacts of increased fine sediment deposition on physical habitats and aquatic organisms is needed for effective intervention and management strategies (Walling *et al*., 2007; Mathers *et al*., 2017).

Excessive deposition of fine sediment may change the composition of river substrates by reducing average particle size, filling interstices between coarser particles and reducing bed stability (Wood and Armitage, 1997). Increased mass of deposited fine sediment can also lead to decreased habitat heterogeneity as the micro-topography of the river bed becomes homogenised (Buendia *et al*., 2013). Most invertebrate species exhibit a preference for the type of habitat which they occupy. On the Maple River in Michigan, U.S., Fairchild and Holomuzki (2002) demonstrated that substrate size strongly influences the micro-distribution of hydropsychid caddis flies. For instance, *Hydropsyche betteni* (Ross, 1938: Hydropsychidae) and *Ceratopsyche sparna* (Ross, 1938: Hydropsychidae) were found to favour coarse substrates, such as boulders and logs over finer substrates, such as cobbles and gravels. A change to substrate composition may cause changes in the invertebrate assemblage (Culp *et al*., 1983; Sarriquet *et al*., 2007). As average particle size decreases, previous studies (e.g. Angradi, 1999; Matthaei *et al.*, 2006) have found that invertebrate assemblages transition from those dominated by Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa to assemblages with a greater prevalence of invertebrates which are better adapted to burrowing, such as oligochaetes, amphipods and gastropods (Hall *et al*., 1984; Larsen *et al*., 2009). Changes in community composition are often accompanied by reductions in taxonomic richness and invertebrate density, as substrates consisting of a large proportion of fine sediment are suitable habitat for a smaller range of organisms than substrates showing greater heterogeneity in particle size (Zweig and Rabeni, 2001; Buendia *et al*., 2013). If fine sediment deposition reduces bed stability, the unstable substrate will only be able to harbour a very limited number of taxa as it will offer limited protection from erosion and abrasion (Armitage and Cannan, 2000). As well as restricting the habitat available to benthic invertebrates, reductions to the interstitial space within river substrates caused by fine sediment deposition or other disturbances, such as drought and high flows, may negatively impact benthic invertebrate assemblages by reducing the availability of refuges to escape predation, (Lancaster and Hildrew, 1993).

Fine sediment deposition may also indirectly affect benthic invertebrate assemblages by causing changes to the quantity and quality of their food supply, and by changing the water chemistry (Eriksen, 1966; Nuttall and Bielby, 1973; Graham, 1990; Jones *et al*., 2012a). These changes are dependent on the composition of the deposited fine sediment. Fine sediment rich in particulate organic matter may benefit some invertebrate species (e.g. filter feeders) that are able to use it as a source of food. However, this effect may be negated by reductions in nutritional quality if the fine sediment contains a high proportion of inorganic matter (Jones *et al*., 2012a). Water chemistry can also be affected by the deposition of fine sediment rich in organic matter, which causes reductions in dissolved oxygen due to microbial activity (Eriksen, 1966). As many invertebrate species (including many EPT species) are sensitive to dissolved oxygen levels, this may lead to substantial changes in the invertebrate assemblage. Microbial activity in fine sediments rich in organic matter may also lead to an increase in substances which are toxic to invertebrates, such as ammonium, manganous and ferrous ions (Jones *et al*., 2012a). Periphyton, an important source of food for many invertebrate species, is also affected by fine sediment deposition, as excessive amounts may impact its quality and abundance (through the processes of abrasion, increased shading and burial – see section 2.4 for further details). If deposited fine sediments contain a large proportion of inorganic matter, the nutritional quality of periphyton is reduced, which may impact grazing invertebrates (Nuttall and Bielby, 1973).

There have recently been efforts to develop a biomonitoring index which uses invertebrates to assess the stress caused to rivers by fine sediment. As discussed in Chapter 1, Section 1.6.1, the PSI index (Extence *et al*., 2011) and CoFSI (Murphy *et al*., 2015) assess the impact of fine sediment on invertebrate communities. In the development of these indices, different invertebrate species were given a score relating to their sensitivity to fine sediment. Subsequently, these sensitivity scores for each PSI taxon were assigned a weighting, derived from extensive monitoring data. These new scores, known as Empirically-weighted PSI (E-PSI), were still constrained by the original PSI scores, but now had a more empirical basis (Turley *et al*., 2015).

CoFSI was developed based on an empirical approach. Murphy *et al*., (2015) used partial canonical correspondence analysis on data from an extensive, targeted field survey to derive scores describing the sensitivity of species to total deposited fine sediment [Total Fine Sediment Index (ToFSI)] and deposited organic matter [Organic Fine Sediment Index (OFSI)], which were then combined into an overall CoFSI score. As these indices are sensitive to different aspects of fine sediment pressure (Wilkes *et al.,* 2017), it will be interesting to see how they respond to the two substrate types in this experiment. In contrast with a natural scenario, this experiment isolates the invertebrates from the effects of suspended fine sediment and organic matter, which usually accompany fine sediment pressure, solely focussing on the effect of different levels of deposited fine sediment within the substrate.

4.2. Research aims

In this chapter, the influence of substrate on invertebrate taxonomic richness, invertebrate density and community composition was investigated. In addition, the performance of the PSI and CoFSI index was investigated to determine whether substrate differences could be detected. This differed from other studies as the effects of deposited inorganic fine sediment were examined in isolation from the effects of organic fine sediment and suspended fine sediment. In particular, we tested the following hypotheses:

- Benthic invertebrate taxonomic richness and density will be lower in the 'fine' substrate composition treatment.
- Differences in substrate characteristics (i.e. coarse and fine sediment) will influence community composition.
- Fine sediment biomonitoring indices will detect differences in substrate composition.

4.3. Method

Chapter 3, Section 3.1. contains a detailed description of the study area. Please see Chapter 3, Section 3.2. for further information regarding the method used for this work. Benthic invertebrates were sampled from a random location at the upstream and downstream ends of each mesocosm section. These samples were obtained using a surber sampler (sampling area 200 x 200mm, $0.04m^2$; net mesh size 250µm). The sampling method entailed disturbing the substrate with a metal rod for 120 s, within the confines of the surber sampling area, the disturbed invertebrates then flowed downstream to be collected in the sampling net. The samples were immediately preserved in 99% IMS, before their subsequent identification to the lowest taxonomic level possible, given their size, condition and the available identification keys.

4.3.1. Data analysis

Substrate composition

The percentage of fine sediment (<2 mm in size) by mass in each of the substrate samples ($n = 24$) was calculated. An independent-samples t-test was used to identify a difference in the mean substrate size between the 'coarse' and 'fine' substrate composition treatments.

Benthic invertebrate data

Invertebrate densities and taxonomic richness were square root transformed prior to analysis to achieve a normal probability distribution. A General Linear Model (GLM) was used to identify any differences in invertebrate densities and taxonomic richness between substrate types, with 'mesocosm block' included in the GLM as a blocking factor (randomised complete block design). This blocking factor was used to account for any potential effect of the mesocosm block. Substrate composition treatment was included as a fixed factor and the interaction between mesocosm block and substrate type was not included in the analysis. Invertebrate samples were grouped within each replicate.

The taxa found in each sample were assigned a fine sediment sensitivity rating based on the E-PSI index (Turley *et al*., 2015), and the scores in CoFSI (Murphy *et al*., 2015). Total scores according to these indices were then calculated for each sample by summing the sensitivity ratings for all of the taxa present in the sample (on a presence/absence basis). Average fine sediment sensitivity scores for each sample were subsequently calculated by dividing the sum of the sensitivity ratings for each taxon by the number of scoring taxa present (some taxa found in the samples have not been assigned scores in the E-PSI and CoFSI indices).

To test for any differences in the average fine sediment sensitivity scores for each sample (E-PSI, OFSI, ToFSI and CoFSI) between the two substrate types, a GLM was performed, with mesocosm block included as a blocking variable (randomised complete block design). The independent-samples t-test and the GLM analyses were carried out in IBM SPSS Statistics (version 24).

Benthic invertebrate community composition

To examine differences in benthic invertebrate community composition between the two substrate types, permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used. This analysis was performed on a matrix of similarities between samples, calculated using Bray-Curtis distances.

Invertebrate data were square root transformed prior to analysis to account for the potential effects of skewed invertebrate abundance distributions.

Non-metric multidimensional scaling (NMDS), with 50 randomised starts, was used to visually show the PERMANOVA results. All of the multivariate data analysis was carried out using the PRIMER 6 software package, with the PERMANOVA+ add-on (Anderson *et al.*, 2008).

4.4. Results

4.4.1. Substrate composition

There was a significant difference in the percentage of fine sediment (<2 mm in size) by mass between the 'coarse' and 'fine' substrate composition treatments (t (22) = 9.019, p = 0.001). The 'fine' substrate composition treatment contained a greater mean total percentage mass of fine particles (18%) than the 'coarse' substrate composition treatment (3.79%; Figure 4.1).

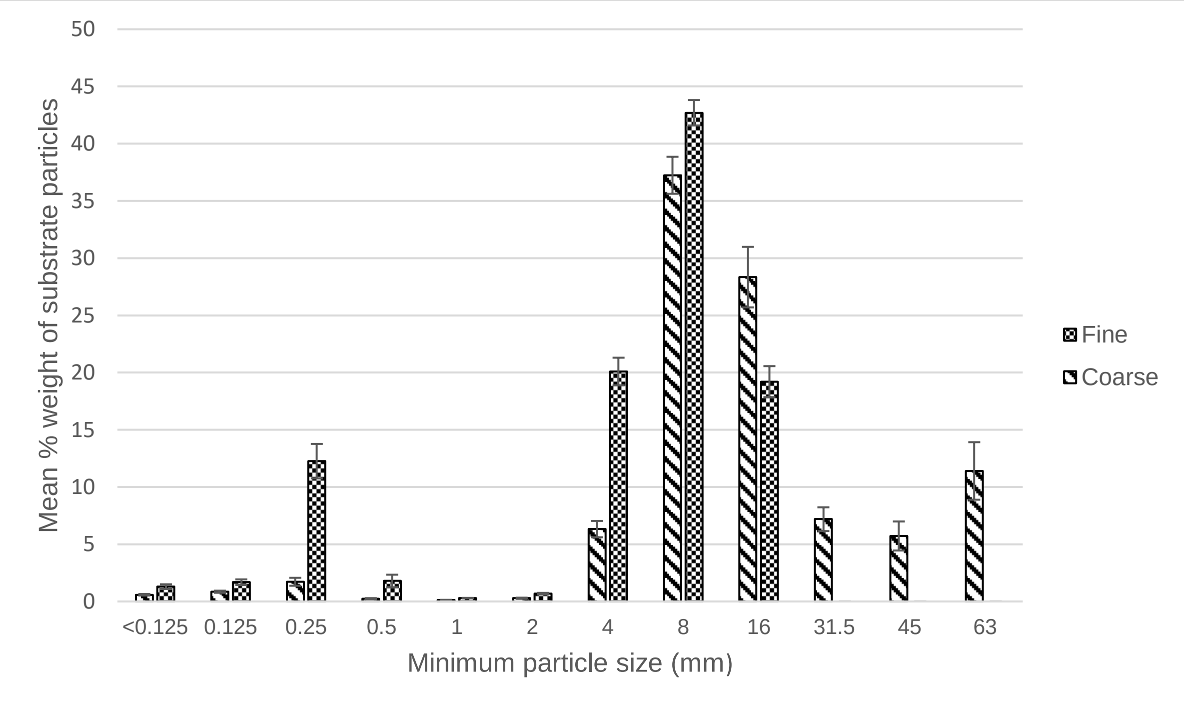

Figure 4.1 Mean (±1 SE) percentage weight of substrate particles among size classes at the start of the experiment (i.e. before water was delivered to the channels).

4.4.2. Benthic invertebrates

In total, 1311 invertebrates from 35 families were recorded from the benthic samples (Table 4.1). Tanypodinae were the most abundant taxa, followed by Tanytarsini, both of which are from the Chironomidae family.

Table 4.1 Invertebrates recorded from the investigation and the percentage they comprise of the total invertebrate abundance. Invertebrate taxa which comprised <1% of the total invertebrate abundance are not detailed.

Taxon	Percentage of total invertebrate abundance
Tanypodinae (Chironomidae)	28
Tanytarsini (Chironomidae)	21
Oligochaeta	13
Asellus aquaticus (Asellidae; Linnaeus, 1758)	7
Hydropsyche pellucidula (Hydropsychidae; Curtis, 1834)	5
Baetidae	5
Gammarus pulex (Gammaridae; Linnaeus, 1758)	4
Chironomini (Chironomidae)	3
Radix balthica (Lymnaeidae; Linnaeus, 1758)	2
Hydroptila spp.	2
Ephemera danica (Ephemeridae; Müller, 1764)	1
Polycentropus flavomaculatus (Polycentropodidae; Pictet, 1834)	1

Invertebrate density varied between 25-2075 ind m^{-2}. No difference occurred in the mean density of invertebrates between the ‘fine’ and the ‘coarse’ substrate (GLM: $F_{(4, 43)} = 3.013$, $p = 0.09$; Figure 4.2).

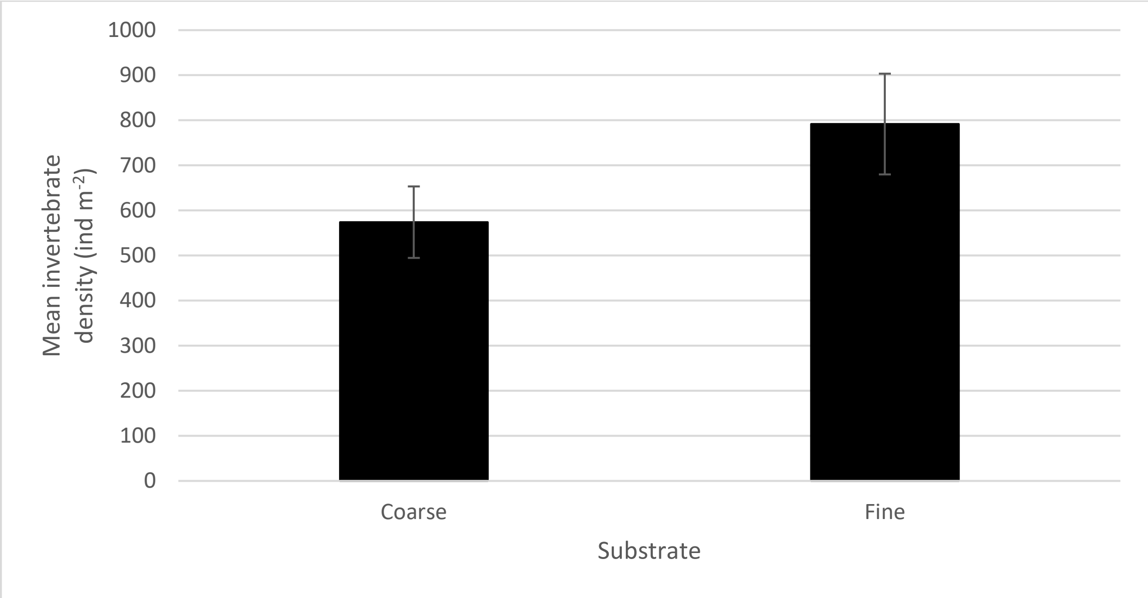

Figure 4.2 Influence of substrate type on mean (±1 SE) density of invertebrates.

Taxonomic richness varied between 1 and 14 and was significantly higher in the 'fine' than the 'coarse' substrate composition treatment (GLM: $F_{(4, 43)} = 4.059$, $p = 0.05$; Figure 4.3).

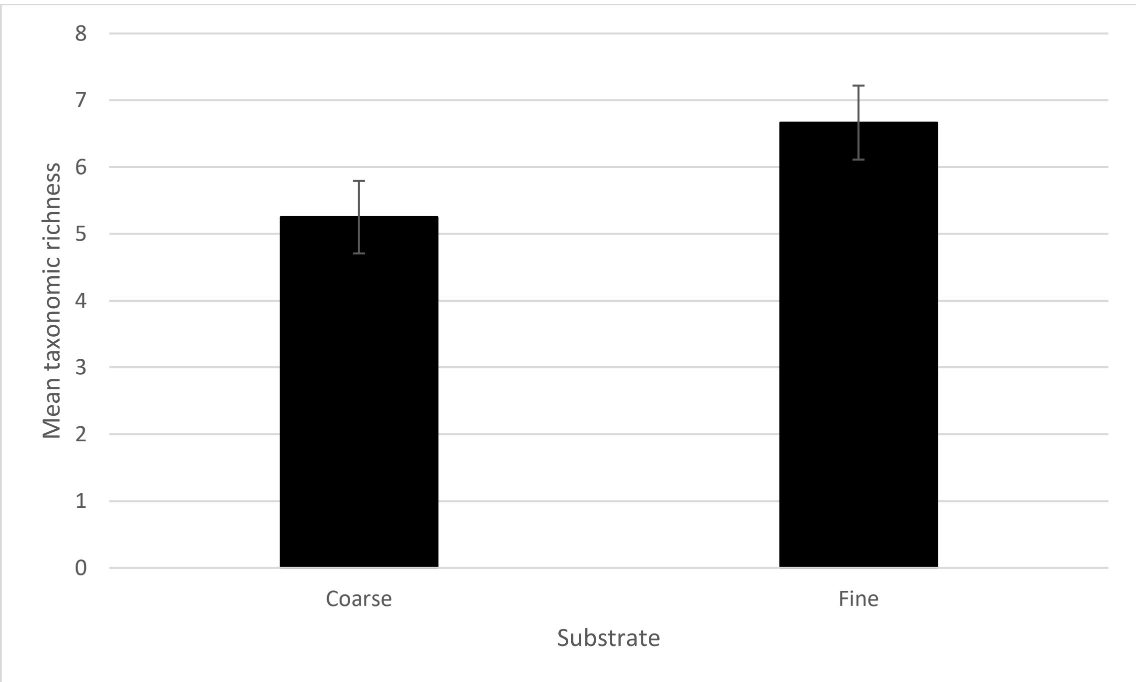

Figure 4.3 Influence of substrate type on mean (±1 SE) taxonomic richness.

4.4.3. Benthic invertebrate community composition

PERMANOVA indicated that there was no significant difference in invertebrate community composition between the ‘coarse’ and ‘fine’ substrate composition treatments (Table 4.2). This result was supported visually in the NMDS plot (Figure 4.4), which showed overlap in the invertebrate community composition between substrate types.

Table 4.2 Results of PERMANOVA comparing benthic invertebrate communities occurring on ‘fine’ and ‘coarse’ substrate composition treatments.

Treatment	degrees of freedom (*df*)	sums of squares (*SS*)	mean squares (*MS*)	pseudo-*F* ratio	permutation *p* (P(perm)) value	number of unique permutations (Perms)
Substrate	1	2925.8	2925.8	1.9273	0.1767	425
Block	3	21775	7258.3	4.8778	0.0001	9906
Substrate x Block	3	4554.3	1518.1	1.0202	0.4455	9889
RES	40	59521	1488			
Total	47	88776				

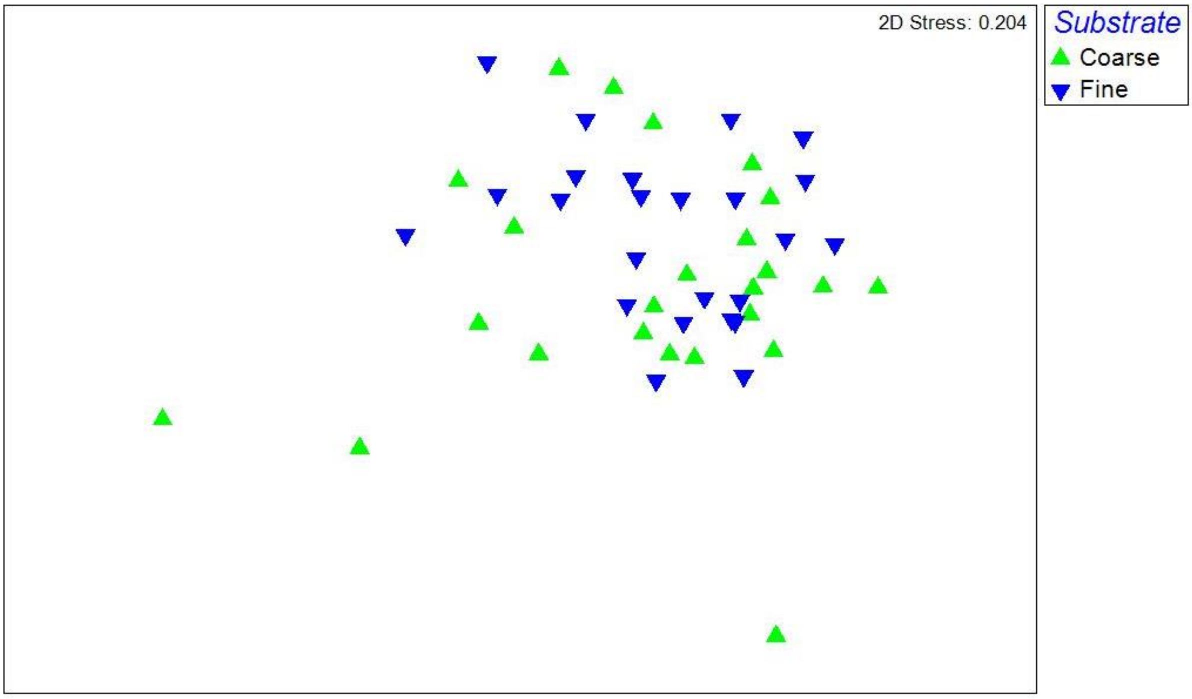

Figure 4.4 NMDS ordination of invertebrate community composition from the 'coarse' and 'fine' substrate types. No significant difference was detected between substrate composition treatments.

4.4.4. Performance of biomonitoring indices

Scores for E-PSI, ToFSI, OFSI and CoFSI were calculated for each sample in this study and then divided by the number of scoring taxa present in the sample (Table 4.3). When tested, the only significant association with substrate composition treatment was found to be with ToFSI/No. Taxa (GLM: $F_{(1,43)}$ = 4.623, p = 0.037): ToFSI/No. Taxa was significantly higher in the 'coarse' than the 'fine' substrate composition treatment.

Table 4.3 Mean E-PSI/No. Taxa, OFSI/No. Taxa, ToFSI/ No. Taxa and CoFSI/No. Taxa for each substrate type . Significant results ($p < 0.05$) are indicated in bold.

	Coarse	Fine
E-PSI/No. Taxa	0.48	0.46
OFSI / No. Taxa	5.30	5.25
ToFSI / No. Taxa	**4.74**	**4.35**
CoFSI / No. Taxa	4.55	4.31

4.4.5. Individual taxa responses

Figure 4.5 shows the response of individual invertebrate taxa to the two different substrate types. *Radix balthica* (Linnaeus, 1758: Lymnaeidae) and Tanytarsini were more abundant in samples from the ‘coarse’ substrate composition treatment, whereas *Cordulegaster boltonii* (Donovan, 1807: Cordulegastridae), *Ephemera danica* (Müller, 1764: Ephemeridae), *G. pulex, Hydropsyche pellucidula* (Curtis, 1835: Hydropsychidae) and Oligochaeta were more abundant in samples from the ‘fine’ substrate composition treatment.

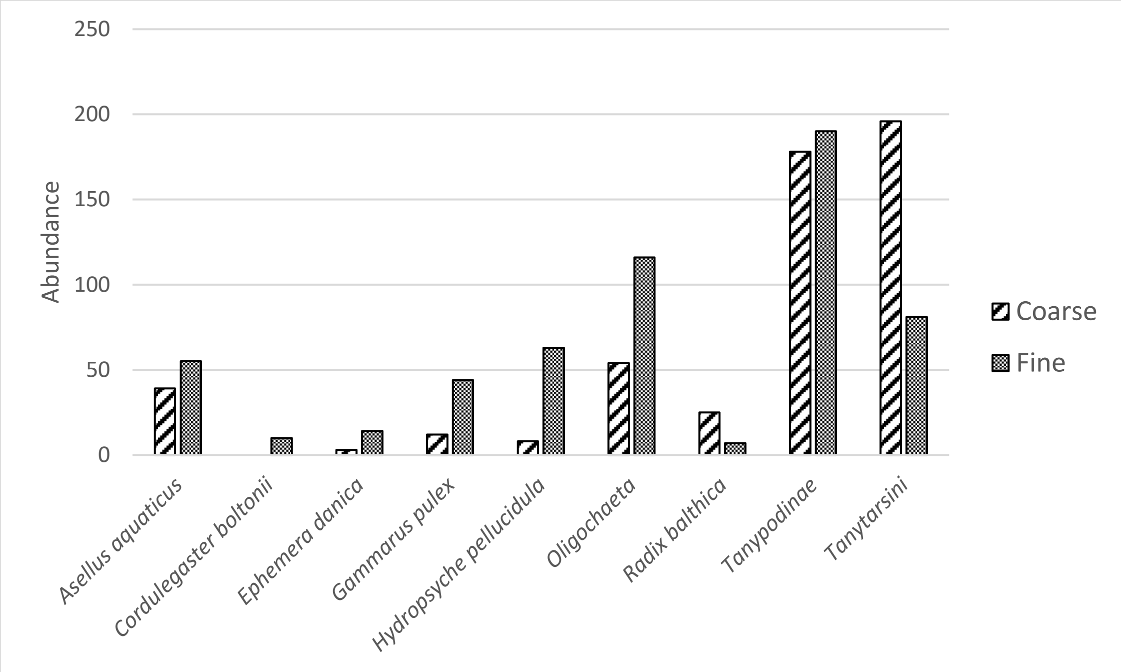

Figure 4.5 Total abundance of taxa in each substrate type for the nine taxa where the difference between total abundances is greater than ten

4.5. Discussion

4.5.1. Influence of substrate on taxonomic richness and invertebrate density

Mean taxonomic richness was found to be significantly higher in the 'fine' than the 'coarse' substrate composition treatment. This finding contradicts the first hypothesis of this study. Earlier work has found that coarse substrates provide a favourable habitat for colonisation by invertebrates because of the heterogeneous mix of particle sizes and the greater interstitial space than fine substrates (Erman and Erman, 1984). For the same reasons, it was also originally hypothesised that the 'coarse' substrate composition treatment would harbour a greater density of invertebrates than the 'fine' substrate composition treatment. However, no difference in invertebrate density occurred between the 'coarse' and the 'fine' substrate composition treatment. Therefore, the hypothesis that benthic invertebrate density would be lower in the 'fine' substrate composition treatment was not supported.

The results from the present study are in contrast to some previous studies, such as Erman and Erman (1984) and Williams and Mundie (1978), that found that invertebrate density and/or taxonomic richness was significantly correlated with substrate type. Erman and Erman (1984) conducted an experiment examining the effect of median particle size on invertebrate taxonomic richness and total abundance. In their experiment, artificial substrate trays containing a range of median particle sizes (2, 8 and 32 mm) were left in a natural stream to be colonised by invertebrates for seven days. The results of their experiment revealed that taxonomic richness and total abundance of invertebrates increased significantly with an increase in median particle size from 2 to 32 mm. Williams and Mundie (1978) conducted a similar experiment in an artificial side channel, constructed adjacent to the Big Qualicum River, in Canada. In their experiment, they used wooden colonisation troughs, which were similar to the artificial substrate trays used by Erman and Erman (1984), but contained considerably larger particles sizes (4620cm^2 compared to 693.25cm^2). The troughs contained three different sizes of gravels (11.5, 24.2 and 40.8mm mean diameter), and invertebrates were left to colonise for 28 days. A significant difference in invertebrate abundance was found in the medium gravel (24.2mm mean diameter), compared to the other two particle sizes. Invertebrate abundance in the troughs containing the small gravel (11.5mm mean diameter) and large gravel (40.8mm in diameter) was not significantly different.

The results from the present study are not totally unexpected, as many other studies have found that an increase in substrate particle size does not result in increased invertebrate abundance and/or taxonomic richness (e.g. Minshall and Minshall, 1977; Culp *et al.*, 1983; Darrow and Pruess, 1989; Parker, 1989; Williams and Smith, 1996 and Rae, 2004). For example, Parker (1989) examined the effect of substrate composition on the distribution of invertebrates in a desert stream in Nevada, U.S. Mesh colonisation baskets containing either gravel (mean particle diameter 11.5 mm), pebble (mean particle diameter 32.9 mm) or cobble (mean particle diameter 67.9 mm) were left in the stream to colonise for 32 days. Although, the study showed a significant difference in invertebrate abundances between the substrate types, the highest abundances were found in the gravel substrate, followed by the pebble substrate, with the lowest abundances in the cobble substrate.

In addition to examining invertebrate distribution, the study also investigated the effect that substrate particle size had on the retention of particulate organic matter. Interestingly, the study found that the gravel substrate retained the greatest amount of fine particulate organic matter (<1 mm), followed by the pebble substrate, with the cobble substrate retaining the least. As part of their study, Parker (1989) examined the link between fine particulate organic matter and invertebrate abundance, and found a significant positive correlation between the two variables. Parker (1989) concluded that the abundance of fine particulate organic matter was an important factor in determining benthic invertebrate abundance. The study by Parker (1989) suggest that rather than having a direct effect on invertebrate abundance, substrate particle size may be indirectly related to invertebrate abundance through its influence on fine particulate organic matter retention.

This potential explanation for the results in this study is also supported by the work of Rabeni and Minshall (1977), who note that the colonisation of the substrate by invertebrates is strongly influenced by the availability of detritus rather than particle size. Detritus is a mixture of small pieces of particulate organic matter that form the food supply of many invertebrate species. Rabeni and Minshall (1977) examined factors affecting the microdistribution of benthic stream insects. As part of their study, trays containing different substrate sizes were placed in a stream and left for a period of between 7 days and 1 month to allow for colonisation by invertebrates. In agreement with the current experiment, Rabeni and Minshall (1977) did not find particle size had a significant effect on invertebrate densities, but did find greater mean invertebrate densities on the fine substrate. In agreement with the study by Parker (1989), Rabeni and Minshall's (1977) research revealed that fine substrate particles tend to trap and store small particles of detritus, compared with coarse substrate particles which typically trap larger detritus, such as small sticks and twigs. As many invertebrate species feed on smaller detrital particles, they will favour the finer substrate where concentrations of this resource are maybe higher. The spatial distribution of detritus may explain the results in the present study, however, this explanation is speculative and more research would be needed to investigate this potential explanation further.

Another possible explanation for the taxonomic richness and the density results reported in this study is that the invertebrate community available to colonise the mesocosm channels may already prefer a substrate characterised by fine sediments. The pool of colonising invertebrates in this experiment were drawn from the River Frome, which is situated in a lowland agricultural catchment and has been identified as being impacted by excess fine sediment (Grabowski and Gurnell, 2015). The high fine sediment levels in the Frome catchment may have had a filtering effect on the invertebrate taxa in the colonising species pool, and excluded taxa who are sensitive to fine sediment, leaving only invertebrates who are able to tolerate high fine sediment amounts. The overall invertebrate assemblage in this experiment was dominated by Tanypodinae, Tanytarsini, Oligochaeta and *Asellus aquaticus* (Linnaeus, 1758: Asellidae), which accounted for 69% of the total invertebrate abundance (Table 4.1). These taxa are not known as being sensitive to fine sediment stress (Murphy *et al.,* 2015; Turley *et al*., 2015), and it has been reported that in response to fine sediment pressure invertebrate assemblages transition from those comprising a range of EPT taxa to ones which are adapted to burrowing such as Oligochaeta, Bivalva and Chironomidae (Wood and Armitage, 1997). So, it may be conceivable that enough of the colonising taxa actually preferred the habitat provided by the ‘fine’ substrate composition treatment to explain the results seen in this study.

Bed stability is another issue to consider when contrasting the taxonomic richness and invertebrate density results of the present study with others. Coarser substrates are typically more stable than fine substrates, as they are less likely to be affected by erosional processes (Effenberger *et al.*, 2006). In a natural environment, abrupt changes to velocity, such as after a heavy period of rainfall, can lead to unstable substrate patches being denuded of invertebrates, as the fine particles are transported easily (by current velocities not sufficient to transport coarser particles) and invertebrate communities may experience catastrophic drift (Gibbins *et al*., 2007a). This process means that in a natural environment, in locations which experience regular flow disturbances, coarser, stable substrates, have been found to support a greater density and taxonomic richness of invertebrates than fine substrates (Matthaei and Townsend, 2000). However, bed stability, which, in a natural environment would limit the range of species able to colonise fine substrates, has been excluded from this mesocosm experiment as flow velocities were maintained at a constant, relatively slow rate of 0.106 m s^{-1}. Slow velocities allow invertebrate species to colonise areas of fine substrate and persist at these locations, where otherwise it may not have been possible if the substrate was subject to natural variations in flow velocity (Gibbins *et al*., 2007b).

4.5.2. Influence of substrate on fine sediment biomonitoring indices

The mean ToFSI/No. Taxa was significantly higher in the ‘coarse’ than the ‘fine’ substrate composition treatment (Figure 4.4), indicating that these samples contained a greater proportion of invertebrates sensitive to the total mass of deposited fine sediment. As total mass of deposited fine sediment is determined by the inorganic component, this finding is in agreement with the experimental design, where the mass of inorganic fine material in the substrate was manipulated. Finding a significant difference in the ToFSI/No. Taxa between the two substrate types, but not in the OFSI/No. Taxa scores, indicates that the invertebrate communities in the mesocosm channels have been influenced by the difference in substrate types as would be expected, and that the CoFSI index is sophisticated enough to detect this response. However, E-PSI does not distinguish between the organic component of fine sediment and the total fine sediment amount, so it may be that differences in organic matter between the two substrate types may have confounded its ability to detect the substrate differences.

4.5.3. Influence of substrate on invertebrate community composition

The results of this experiment also did not support the second hypothesis, as PERMANOVA revealed no significant differences in invertebrate community composition between substrate types. There are a number of factors which may have resulted in this outcome, such as the potential effect of organic matter, the composition of the colonising invertebrate community, or the influence of substrate stability.

Individual taxa show differing responses to substrate composition (Figure 4.5). *A. aquaticus* is relatively insensitive to fine sediment stress (Murphy *et al.,* 2015; Turley *et al*., 2015) (E-PSI = 0.37, CoFSI = 3.323 [E-PSI is scored from 0 - 1 and CoFSI is usually with the range of 3.0 – 6.5, with higher values indicating greater sensitivity in both indices]), and show increased abundance in the 'fine' substrate, as expected. However, the abundance of *H. pellucidula* was greater in the 'fine' than in the 'coarse' substrate composition treatment, which is not expected, as they are particularly sensitive to fine sediment stress (Murphy *et al.,* 2015; Turley *et al*., 2015) (E-PSI = 1, CoFSI = 5.857). *H. pellucidula* are classified as more sensitive to the organic component of fine sediment (oFSI = 7, ToFSI = 6) than the total fine sediment amount, so this may partly explain why they have not responded in this experiment as expected.

Further examination of *H. pellucidula* abundances in individual samples shows that over half (58.73%) of the individuals responsible for the increased abundance in the 'fine' substrate composition treatment originate from one sample. This finding highlights a problem in using stream mesocosms. Downes *et al*. (1993) investigated the distribution of benthic invertebrates over small spatial scales and found variation in species' abundances within closely spaced samples. In this experiment, an attempt was made to overcome this problem by replicating each substrate type 12 times, but these natural variations in abundance over small spatial scales may have impacted the results. The findings of this study are useful in showing the response of individual taxa to different aspects of fine sediment stress, particularly inorganic deposited fine sediment, and suggest that it may be worthwhile to study the response of *H. pellucidula* further. As highlighted by Wood *et al*. (2005), the responses of individual invertebrate species may be highly variable, but investigating them is important to reach an understanding of how fine sediment affects the entire invertebrate community.

Differing dispersal abilities of freshwater organisms may also influence the responses of invertebrates to different substrate characteristics. A study by Williams and Hynes (1977) found that the number of taxa colonising a new channel in a Canadian stream did not reach an equilibrium until 100 days. In contrast, Malmqvist *et al*. (1991) found the species recruitment rate was still significant after 500 days for invertebrates colonising an artificial stream in southern Sweden, and Minshall *et al*. (1983) found that species richness took longer than 400 days to plateau in invertebrates recolonising the Teton River, Idaho, U.S. When compared with the 69-day colonisation period in this study, the colonisation dynamics (e.g. differing dispersal abilities, biotic interactions and pioneer effects) present in a natural stream may not have been present in the stream mesocosms. However, 69 days is still significantly longer than many other such studies in this field (such as Culp *et al*, 1983; Williams and Smith, 1996 and Rae, 2004), and the results can still provide an insight into some of the processes occurring, such as the response of invertebrates to deposited fine inorganic sediment, in isolation from suspended sediment. It should also be noted that Harris *et al.* (2007) investigated the mesocosm channels used in the present experiment, concluding that if left to colonise naturally, as they were in this experiment, they contain a representative invertebrate community. In fact, their analysis estimated that the channels housed an estimated 87% of the richness in the Mill Stream (to which the mesocosm channels are connected, see section 3.1 for further explanation).

4.6. Summary

It was hypothesised that increasing the amount of fine sediment within the substrate would negatively affect invertebrate density and taxonomic richness. However, no difference in invertebrate density occurred between the ‘coarse’ and the ‘fine’ substrate composition treatments, and taxonomic richness was higher in the latter substrate. These findings demonstrate that invertebrate responses to increased fine sediment within different substrate types are complex, a finding supported by the contradictory evidence found in other studies. The results from this study demonstrate that other factors also have a strong influence on the colonisation behaviour of invertebrates, in addition to fine sediment pressures. These factors include food availability, the composition of the colonising species pool, and substrate stability. Additional research is required to further elucidate some of these complex interactions.

5. Effects of a fine sediment pulse on benthic invertebrates in a stream mesocosm

5.1. Introduction

5.1.1. Pulse and press disturbances

Disturbances have been recognised as an important factor in the structuring of invertebrate assemblages in freshwater ecosystems (Palmer *et al.*, 1995). The temporal aspect of their intensity and their duration may be used to separate disturbances into two groups, pulse and press disturbances (Collier and Quinn, 2003). Press disturbances may arise quickly, before reaching a constant level which persists over substantial time periods potentially causing chronic damage to aquatic communities or ecosystems. This category includes many anthropogenic disturbances, such as flow regulation, channelisation and land-use change (Bender *et al.*, 1984; Collier and Quinn, 2003). Pulse disturbances are characterised by their short-term nature, causing a sudden change in the system after which it returns to its previous equilibrium state (Bender *et al.*, 1984). Pulse disturbances are typically the result of point source inputs, or intense hydrologic events occurring over a short time scale, such as flooding, and may cause acute damage to the system (e.g. changes to abundance, taxonomic composition, or the prevalence of functional traits) followed by subsequent recovery (Madej and Ozaki, 1996; Lisle *et al.*, 2001; Collier and Quinn, 2003). Fine sediment is often delivered to rivers in an episodic manner, in the form of a fine sediment pulse, potentially resulting from anthropogenic activities within the catchment, or through natural geomorphic processes, such as landslides (Venditti *et al.*, 2010). This results in the discrete input of significant quantities of fine sediment to the aquatic ecosystem, which can have detrimental effects on the biota at all trophic levels (Jones *et al.*, 2012a; Mathers *et al.*, 2017a).

Molinos and Donohue (2009) demonstrated that the concentration and exposure time of a fine sediment pulse influences the response of benthic invertebrates. Their experiment was conducted using laboratory-based artificial streams, in which they subjected individuals of *A. aquaticus* (Asellidae), *Glossosoma boltonii* (Curtis, 1834: Glossosomatidae), *Rhithrogena semicolorata* (Curtis, 1834: Heptageniidae) and *B. rhodani* (Baetidae) to sediment disturbances, which varied in magnitude (maximum suspended sediment concentrations of either 0, 250, 600 or 2000 mg/l) and exposure time (either 1, 3, 5 or 7 days). The results of their experiment showed that the response of invertebrates to fine sediment disturbances cannot be considered in terms of the exposure time, or the concentration of fine sediment individually, as the effects on invertebrates come from the interaction of these two factors.

5.1.2. Effects of a fine sediment pulse on abundance and taxonomic richness

Exposure to a fine sediment pulse has been found to affect invertebrate abundance and taxonomic richness (Shaw and Richardson, 2001; Vasconcelos and Melo, 2008). Gomi *et al*. (2010) examined the response of invertebrates to a pulse of sediment released from behind a dam, in central Japan. The dam release subjected the invertebrate community to a peak bedload transport rate of 0.232 kg s^{-1}, which resulted in substantial deposition of fine sediment (to a maximum depth of 0.5 m immediately below the dam). Invertebrate samples were taken before and after the sediment release from two reaches, one 30 m reach which began 10 m downstream of the dam and one 30 m reach 200 m downstream of the dam. Analysis of these samples showed that the fine sediment pulse reduced invertebrate abundances in the upstream and downstream reaches to 6.7 and 25.1 % of the pre-pulse means respectively. As part of the experiment Gomi *et al.* (2010) also sampled suspended sediment, discharge, bed load sediment and invertebrate drift. By analysing the time when the abundance of drifting invertebrates began to increase, the authors concluded that the invertebrates responded to increases in bed load sediment and its deposition, rather than increases in discharge or suspended sediment. The findings of Gomi *et al*. (2010) support the view that deposited fine sediment prompts benthic invertebrates to escape benthic and interstitial habitats.

As well as finding a decrease in invertebrate abundance following the sediment pulse, Gomi *et al*. (2010) also found a decrease in taxonomic richness. These changes were thought to arise due to the structural changes in the substrate brought about by sediment deposition, such as the infilling of interstitial space by fine sediment particles, which causes sediment-sensitive species to lose their favoured habitat. The experiment by Gomi *et al.* (2010) examined the response of invertebrates to a concentration of fine sediment that exceeded natural conditions. However, similar results have also been found in other studies which have investigated the effects of lower concentrations of fine sediment (e.g. Kaller and Hartman, 2004; Bo *et al.*, 2007; Elbrecht *et al.*, 2016; Beermann *et al*., 2018).

5.1.3. Effects of a fine sediment pulse on functional trait composition

The composition of an invertebrate assemblage under varying environmental constraints is governed by the composition of the functional traits possessed by that assemblage (Townsend and Hildrew, 1994). This has led to efforts to use species traits to produce a framework linking environmental stressors, such as excess fine sediment, with responses in biological communities (Menezes *et al.*, 2010). This approach has been identified as a good way of disentangling the effects of multiple stressors on freshwater invertebrate communities and, because of its mechanistic nature, it has several advantages over taxonomic methods, such as its applicability over large spatial scales and its ability to identify causal relationships with particular stressors (Menezes *et al.*, 2010; Statzner and Bêche, 2010; Lange *et al.*, 2014). However, there is currently some conflicting information regarding trait-fine sediment relationships, so further work is needed to study these relationships in greater detail, and under controlled conditions, to enable the further refinement of traits-based biomonitoring indices (Wilkes *et al.* 2017).

It may be expected that a theoretical approach can be employed to decide how the prevalence of certain invertebrate traits is likely to be altered in response to increasing amounts of deposited fine sediment. For instance, it would appear logical to hypothesise that small-bodied taxa would be excluded by increased amounts of deposited fine sediment as they would be more susceptible to smothering and would have a reduced dispersal ability as fine sediment infills the interstitial space within the substrate (Wood *et al*., 2001; Wagenhoff *et al*., 2012; Descloux *et al*., 2014; Wilkes *et al*., 2017). The literature would also suggest that the prevalence of taxa exhibiting the perennial, univoltine, or semivoltine trait modalities would reduce with increased amounts of deposited fine sediment, whilst the prevalence of taxa exhibiting multivoltine and ephemeral trait modalities would be increased, as this allows invertebrates to quickly colonise unstable substrates, such as deposited fine sediment patches (Larsen *et al*., 2011; Buendia *et al*., 2013; Wilkes *et al*., 2017). Traits related to diet and feeding strategy would also be expected to be affected by increased amounts of deposited fine sediment, with decreases expected in the prevalence of shredders, filter feeders and scrapers due to a dilution of food resources, burial, clogging of feeding apparatus and a reduction in food quality (Jones *et al*., 2012a; Wilkes *et al*., 2017). It may also be expected that the prevalence of traits related to locomotion would be impacted by rising amounts of deposited fine sediment (Wilkes *et al*., 2017). For instance, the prevalence of invertebrates with the burrowing trait modality may be expected to increase as this would allow an animal to move within fine sediment deposits, whereas the prevalence of invertebrates with the interstitial trait modality may be expected to decrease as the interstices become filled with deposited fine sediment (Larsen *et al*., 2011; Buendia *et al*., 2013). However, as much as these hypotheses might appear to be logical, it quickly becomes apparent when examining experimental data that the picture is not quite so clear, with many inconsistencies being reported in the response of these traits between studies.

Buendia *et al*. (2013) carried out a study on the river Isábena catchment, in Spain. This catchment contains small areas of badlands, comprised of miocene continental sediments, which are highly erodible, resulting in rivers with highly variable suspended sediment concentrations (varying over five orders of magnitude, to a maximum of 300 g l^{-1}). The study set out to examine the effect of fine sediment on the trait structure of invertebrate assemblages and to assess the effectiveness of a set of trait-based and taxonomic metrics, which may be useful in detecting the influence of fine sediment on invertebrate assemblages. Buendia *et al.* (2013) found that fine sediment levels affected the prevalence of certain invertebrate traits. The trait most evidently associated with fine sediment was life history, with multivoltinism (the ability to have more than two generations per year) being selected for in locations with high levels of fine sediment. Other trait modalities found to increase in representation with increasing amounts of deposited fine sediment were short life cycle, deposit feeding, small size and tegumental respiration. Buendia *et al.* (2013) note that invertebrates with short life cycles and multivoltinism may be better suited to quickly colonise and adapt to unstable substrates with high concentrations of fine particles, which are easily mobilised (Kaufmann *et al.*, 2009). As deposited fine sediment fills interstices within the substrate and reduces porosity, this is likely to affect larger-sized invertebrates to a greater extent than small-sized invertebrates. This may explain the association between the small size trait modality and high concentrations of deposited fine sediment found in the study by Buendia *et al.* (2013).

It should be noted that studies similar to that of Buendia *et al*. (2013) have produced a range of findings regarding the association between fine sediment and different invertebrate traits, many of which are not replicated between experiments (e.g. Rabeni *et al.*, 2005; Logan, 2007; Larsen *et al*., 2011; Mondy and Usseglio-Polatera*,* 2013; Descloux *et al.*, 2014; Mathers *et al.,* 2017b and Murphy *et al.*, 2017). For instance, Larsen *et al.* (2011) conducted a study using colonisation trays, placed in the river Usk, in Wales, to examine the effect of fine sediment deposition on the structure and function of invertebrate assemblages. The experiment subjected invertebrate assemblages to different amounts of deposited fine sediment (either 0, 1, or 2 kg of additional sand per tray) and monitored them over a period of 19 days. In contrast to the results reported by Buendia *et al.* (2013), Larsen *et al*. (2011) found no link between fine sediment and either body size, or voltinism traits.

Research in this area has also produced several other conflicting results regarding the response of individual invertebrate traits to fine sediment induced pressure. Studies by Rabeni *et al.* (2005) and Buendia *et al.* (2013) examined the functional responses of the invertebrate community to fine sediment and found that the prevalence of the filter feeding trait modality was reduced as fine sediment increased. This result conflicts with the outcome of a study by Mondy and Usseglio-Polatera (2013), who examined the prevalence of invertebrate traits in response to substrate clogging, finding that increased fine sediment led to an increase in the prevalence of invertebrates with the filter feeding trait modality. There are numerous mechanisms by which fine sediment may affect the ability of different feeding strategies to be successful (for a full review please see Section 2.3 of this thesis), therefore, it is reasonable to expect that fine sediment will influence the prevalence of certain feeding strategies within an invertebrate assemblage. However, a number of studies have only found a weak correlation (or an inconsistent response across different studies) between functional feeding group and fine sediment amounts (e.g. Culp and Davis, 1983; Duncan and Brusven, 1985; Buendia *et al.* 2013).

Studies examining the influence of fine sediment on the ovoviviparity trait modality have revealed different outcomes. Larsen *et al.* (2011), Descloux *et al*. (2014) and Mathers *et al.* (2017) all found that increasing fine sediment amounts led to a decrease in the prevalence of invertebrates with the ovoviviparity trait modality, whereas Mondy *et al.* (2013) and Murphy *et al.* (2017) found the opposite result; an increase in the prevalence of the ovoviviparity trait modality with increasing amounts of fine sediment. In contrast to these results, Buendia *et al.* (2013) found no significant connection. As Murphy *et al.* (2017) noted, it is easy to understand how ovoviviparity may benefit invertebrates in locations with high amounts of deposited fine sediment. In these conditions, not having to deposit eggs onto an unstable substrate where they may be buried by fine sediment deposition, or easily washed away due to substrate instability is an advantage, so it is unexpected that some studies have found a negative correlation between the prevalence of this trait modality and fine sediment.

However, further exploration of the results of these studies reveals a potential explanation. As explained by Larsen *et al*. (2011), in their study, the only taxon with the ovoviviparity trait modality was *Gammarus* spp. (Gammaridae), so declines in the prevalence of ovoviviparity simply represented declines in the abundance of *Gammarus* spp., which may have occurred for reasons independent of the ovoviviparity trait modality.

These contrasting findings may provide a greater understanding of the causal mechanisms which result in the prevalence of particular trait modalities in response to particular environmental conditions (Murphy *et al.* 2017). For instance, Buendia *et al.* (2013) found that the prevalence of small-sized invertebrates increased with rising amounts of deposited sediment. However, Descloux *et al.* (2014) investigated the trait structure of invertebrate communities along a gradient of sediment colmation, using three reaches in the catchment of the Rhône river, and found the opposite association in terms of body size. Descloux *et al.* (2014) found that increasing colmation led to a decrease in the prevalence of small-sized invertebrates. Although this result is in opposition to their original hypothesis, Descloux *et al.* (2014) explained that colmation may have increased the temporal stability of the benthic habitat, favouring larger-sized invertebrates.

The study by Buendia *et al*. (2013) also identified a link between method of locomotion and fine sediment deposition. Sites with high levels of fine sediment deposition appeared to favour swimmers, whilst invertebrates with the crawler and burrower trait modality declined in response to increasing fine sediment deposition. This contrasts with the findings of Rabeni *et al.* (2005), Larsen *et al.* (2011) and Mondy *et al.* (2013) who note404d that increasing fine sediment deposition led to an increase in the prevalence of invertebrates with the burrowing trait modality. The results of Buendia *et al*. (2013) are surprising, not only as they differ from similar studies, but because they appear counterintuitive. As detailed by Larsen *et al.* (2011), invertebrates with the burrowing trait would be expected to be favoured in substrates dominated by fine sediment as it would allow them to travel within the substrate, rather than being left immobile due to fine sediment deposition. However, there are possible explanations for the findings of Buendia *et al.* (2013) related to the environmental conditions of their study. For instance, the high densities of deposited fine sediment found in their study may have led to a reduction in dissolved oxygen, causing the fine sediment deposits to be unfavourable to burrowers (Jones *et al.*, 2012a). Differences in flow rates between the various studies may also be responsible for the differing response of locomotion traits to increased deposited fine sediment. If sites with high amounts of deposited fine sediment were also slow flowing this may favour swimmers, a response mediated by flow rather than fine sediment amounts (Naman *et al.*, 2016). Many of the contradictions seen in the literature regarding trait-fine sediment relationships may be the result of confounding environmental factors, such as flow rate or dissolved oxygen levels. This highlights a research need for more controlled experiments which can limit some of these confounding factors and highlights how mesocosm experiments, such as the present study, are important in furthering our understanding of these complex relationships, without some of the confounding factors seen in field experiments.

One other possible explanation for the findings of Buendia *et al.* (2013) is that the invertebrate community in the Isábena continued to be dominated by EPT taxa, even in areas with greater deposited fine sediment. In other studies, increasing fine sediment deposition has been responsible for a transition from invertebrate assemblages dominated by EPT taxa to one dominated by animals with burrowing adaptations, such as diptera and oligochaetes (Ryan, 1991). In the Isábena, sites with increased amounts of deposited fine sediment often did not contain many individuals, but were dominated by Ephemeroptera and Trichoptera, particularly *Baetis* spp. (Baetidae) and *Hydropsyche* spp. (Hydropsychidae). To survive in these conditions, the invertebrate species have traits, other than burrowing, which confer resilience (such as generalist feeding strategies, short generation times and high fecundities) (Buendia *et al.,* 2013). The prevalence of these trait modalities at a particular location are not simply a result of different environmental pressures (such as an increase in fine sediment deposition), but also depend on the pool of trait modalities present in the existing invertebrate assemblage, or the invertebrate assemblage from which new colonisers are drawn from. If the original inhabitants have traits which allow them to survive in the new environmental conditions, then a change in the trait composition of the invertebrate assemblage may not be witnessed. Also, as noted by Mathers *et al.* (2017), the magnitude of the effects of fine sediment on the trait composition of the invertebrate assemblage is affected by the complexity of the habitat prior to sedimentation. Increasingly complex habitats are more likely to exhibit greater changes to the trait composition of their invertebrate assemblages than simpler, more homogeneous ones. This makes it reasonable to hypothesise that the invertebrate community in a stream which has previously been subject to elevated amounts of deposited fine sediment will respond differently to a fine sediment pulse than one which has not previously been subjected to these conditions. This is an important question, which has not previously received much attention, and one which the present study intends to answer.

Understanding the effect that fine sediment may have on the prevalence of certain invertebrate traits has become important in recent years, as a trait-based approach to biomonitoring is increasingly used (Mathers *et al.*, 2017a). As can be seen from some of the examples detailed above (e.g. Larsen *et al.*, 2011; Buendia *et al.*, 2013; Mondy *et al.*, 2013), there are still many inconsistencies within the literature regarding significant associations between fine sediment and specific invertebrate traits, and even contradictions regarding the direction of these associations (Murphy *et al.* 2017). The present study tested these associations, as with the increasing use of a traits-based approach to biomonitoring the more these theories are tested in a controlled environment, such as the stream mesocosm setup in this experiment, the more they can be relied upon to form the basis of biomonitoring approaches. One of the unique aspects of the present study is that, as well as examining the response of invertebrates to a fine sediment pulse, it also investigated how this response is mediated by prior substrate conditions. This provides useful information in understanding how the effects of a fine sediment pulse may change across different stream types, assessing how the response to a fine sediment pulse differs depending upon the historic fine sediment deposition regime.

5.2. Research aims

This chapter examines the effect of a fine sediment pulse and the influence of prior substrate conditions on benthic invertebrate community composition and the trait-profile of the invertebrate community. In addition, the performance of the fine sediment biomonitoring indices CoFSI and E-PSI was examined, in terms of their ability to detect the effects of the fine sediment pulse. This study is not confounded by covarying factors and is unique in that it investigated the effect of prior substrate conditions on the response of benthic invertebrates to a fine sediment pulse. The following hypotheses were tested:

- Benthic invertebrate density and taxonomic richness will decline with increasing fine sediment loading.
- The density and taxonomic richness of EPT taxa will decline with increased fine sediment loading.
- The influence of prior substrate conditions will affect community response to fine sediment loading.
- Fine sediment biomonitoring indices will detect the effect of the fine sediment pulse.
- The prevalence of certain invertebrate traits will be correlated with fine sediment and substrate composition treatments.

5.3. Method

Please see Chapter 3, Section 3.1. for a description of the study area. For a detailed explanation of the sampling method, please see Chapter 3, Section 3.4. Benthic invertebrate samples were collected from an upstream and downstream location within each mesocosm section before, directly following, and 30 days post the fine sediment pulse. Benthic invertebrates were obtained by using a surber sampler (sampling area 200 x 200mm, 0.04m^2; net mesh size 250µm). Bed substrate was disturbed using a metal rod for 120s and the invertebrates flowed downstream into the surber net. Invertebrate samples were preserved in

99% IMS, and identified to the lowest taxonomic level possible, typically genus and species.

5.4. Data analysis

5.4.1. Invertebrate density and taxonomic richness

Invertebrate density and taxonomic richness were analysed using repeated-measures ANOVA, incorporating ‘block’ (used as a blocking factor, to factor out any possible effect caused by the mesocosm block the sample originated from), ‘sediment treatment’ and ‘substrate type’ as the three between-subject factors and ‘time’ (before, directly following and 30 days after the sediment pulse) as the within-subjects factor. The GLM employed for this analysis was used to identify any interactions between these effects also. This analysis was performed using the GLM procedure in the SAS 9.4 statistics package (SAS Institute, 2013).

5.4.2. Taxonomic community composition

Permutational analysis of variance (PERMANOVA; Anderson, 2001) was used to identify differences in invertebrate taxonomic community composition between sediment treatments, substrate types and between the three sampling occasions (before, directly following and 30 days after the fine sediment pulse). Bray-Curtis distances were used to calculate a matrix of similarities between samples. Prior to analysis, invertebrate density data was square root transformed to ensure homoscedasticity. NMDS was used to provide a visual display of the PERMANOVA results. This procedure was completed using 50 randomised starts. Multivariate analysis of invertebrate taxonomic community composition was completed in the PRIMER 6 software package, utilising the PERMANOVA+ add-on (Anderson *et al.*, 2008).

5.4.3. Biomonitoring indices

Each sample was scored according to the presence or absence of different invertebrate taxa. Samples were scored according to the E-PSI, ToFSI, OFSI and CoFSI indices (Turley *et al.*, 2015; Murphy *et al.*, 2015), then the total of each score for every sample was divided by the number of scoring taxa in that sample. Not all of the taxa in the experiment were assigned a scored due to no information being present, so these taxa were excluded from the calculations. This data was then analysed using the same procedure as that outlined in Section 5.4.1 relating to invertebrate density and taxonomic richness.

5.4.4. Invertebrate trait analysis

Analysis of the effects of fine sediment and substrate type on the prevalence of particular invertebrate traits was performed using an approach combining the RLQ and Fourth-corner methods. The trait data assigned to species in this analysis was derived from a combination of three freshwater invertebrate species trait resources:

- French Genus Trait Database (Tachet *et al.,* 2000)
- www.freshwaterecology.info (Schmidt-Kloiber and Hering, 2015)
- Data on hyporheic invertebrate traits (Descloux *et al.*, 2014)

The majority of the trait data used in this study originated from the French Genus Trait Database, which was gathered by French biologists and features information on those taxa which are found in French freshwater ecosystems. Many of these taxa also occupy freshwater sites in the UK, making this a useful resource for British ecologists. Taxa and traits present in the study, but not found in the French database, were imported from the other two resources. There were also some taxa in the present study which either have no trait information listed in any of these resources, or were sampled at such a taxonomic resolution that trait data was not applicable. These taxa only make up 28 % of the total invertebrate taxa recorded in this study and were excluded from the trait analysis.

Data describing eleven invertebrate traits were used in this study. Each of these traits incorporated a varying number of trait-classes. The affinity of each individual taxon to a particular trait-class was described by a number ranging from 0 to 5, with 5 representing the greatest affinity and 0 representing the least affinity. Affinities in the freshwaterecology.info dataset were originally scored on a range from 0 to 10, so these numbers were converted by halving their value and rounding up to the nearest integer, thus changing 5's to 3's and 10's to 5's, with 1's remaining as 1's.

RLQ is a form of ordination incorporating three tables (as opposed to the typical two tables) which enables analysis of the relationship between species traits and different environmental variables. Data from this study were arranged into three different tables. Data regarding the blocking factors, substrate and sediment treatments, arranged by sample, formed the 'R' table, describing the environment. Species abundances, arranged by sample, formed the 'L' table. Trait data, arranged by species, formed the 'Q' table.

The first step of the analysis was to perform separate ordinations on each of the three different tables. A correspondence analysis was performed on the species abundance data (L table); a principle component analysis was used on the trait data (Q table), as all of the variables are quantitative; and a Hill and Smith (1976) analysis was used on the environmental data (R table), as it allows for the analysis of categorical and quantitative variables. RLQ analysis was then used to combine the three discrete ordinations of the R, L and Q tables to identify the main associations between trait-classes and environmental gradients, taking into account the weighting provided by species abundances.

Fourth-corner analysis (Dray and Legendre, 2008; Dray *et al.*, 2014) was then employed to test the bivariate relationships between environmental variables and individual traits. This analysis was chosen because, unlike in the RLQ analysis, a statistical test of significance is performed on the correlation between environmental and trait data at the individual trait level (rather than testing the overall pattern across all traits). Although fourth-corner analysis is able to test the significance of any correlations between trait and environmental data, it should be noted that it is unable to account for any potential covariance between environmental variables or between traits. The significance of any relationships was examined by performing 4999 permutations of species and 4999 permutations of sites. Due to the large number of comparisons being made in this test *p*-values were adjusted by means of the false discovery rate method (FDR; Benjamini and Hochberg, 1995). Both the RLQ and fourth-corner analyses were performed in R 3.4.4 (R Core Team, 2014), using the ade4 package (Dray and Dufour, 2007).

5.5. Results

5.5.1. The response of benthic invertebrate density and taxonomic richness to different sediment pulse and substrate composition treatments

A total of 5415 invertebrates were recorded in the samples taken for this analysis. These invertebrates included representatives from 54 separate invertebrate taxa, across 144 samples (Table 5.1).

Table 5.1 The most abundant invertebrate taxa recorded from the experiment. The remaining 42 taxa not included in this table accounted for <8% of the total invertebrate abundance.

Taxon	Percentage of total invertebrate abundance
Tanypodinae (Chironomidae)	24
Tanytarsini (Chironomidae)	22
Asellus aquaticus (Asellidae)	12
Gammarus pulex (Gammaridae)	8
Oligochaeta	7
Hydropsyche pellucidula (Hydropsychidae)	5
Baetis spp. (Baetidae)	4
Radix balthica (Lymnaeidae)	3
Crangonyx pseudogracilis (Crangonyctidae)	2
Hydroptila spp.(Hydroptilidae)	2
Ephemera danica (Ephemeridae)	2
Diamesinae (Chironomidae)	1

Mean invertebrate density varied between 715 – 1728 ind m^{-2} (Figure 5.1). On the sampling occasions immediately following the fine sediment pulse, and 30 days after the fine sediment pulse, the effects of the sediment pulse and substrate composition treatments, or their interaction, were found not to have a significant effect on mean invertebrate density (Table 5.2, Table 5.3).

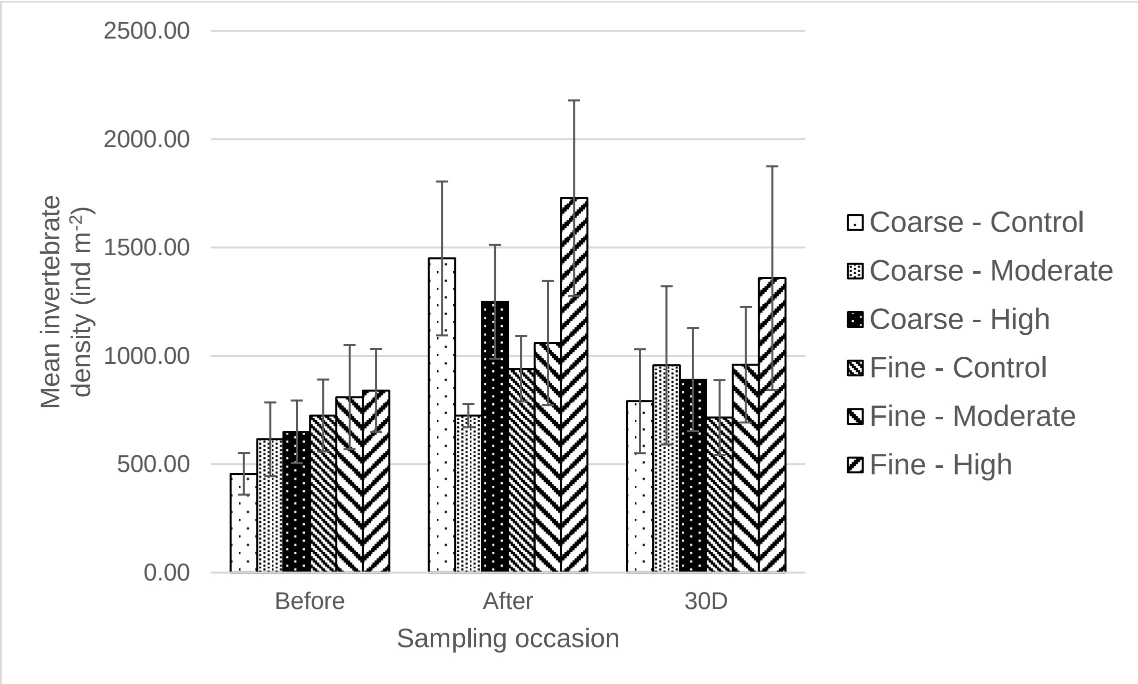

Figure 5.1 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) invertebrate density (ind m^{-2}).

Table 5.2 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on invertebrate density on the sampling occasion following the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	1.60	0.2148
Substrate	1, 39	0.00	0.9663
Sediment x Substrate	2, 39	0.45	0.6400

Table 5.3 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on invertebrate density on the sampling occasion 30 days after the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	0.14	0.8724
Substrate	1, 39	0.33	0.5713
Sediment x Substrate	2, 39	0.30	0.7411

Repeated-measures analysis of variance (ANOVA) revealed no significant effect of either the sediment pulse or the substrate composition treatments on invertebrate density. The effect of time was found to be significant (Table 5.4). However, the interaction of time with either the sediment pulse or substrate composition treatments was not significant (Table 5.4).

Table 5.4 Results of repeated measures ANOVA examining the effect of sediment pulse and substrate composition treatments, time, and their interaction, on invertebrate density. Significant results ($p < 0.05$) are indicated in bold.

	degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	7.68	**0.0009**
Time x Sediment	4, 78	0.23	0.9194
Time x Substrate	2, 78	0.99	0.3754
Time x Sediment x Substrate	4, 78	0.20	0.9353

Mean taxonomic richness varied between 4.75 and 9.75 (Figure 5.2). On the sampling occasion immediately after the fine sediment pulse, no significant effect of the sediment pulse, or substrate composition treatments, or their interaction, were found on taxonomic richness (Table 5.5).

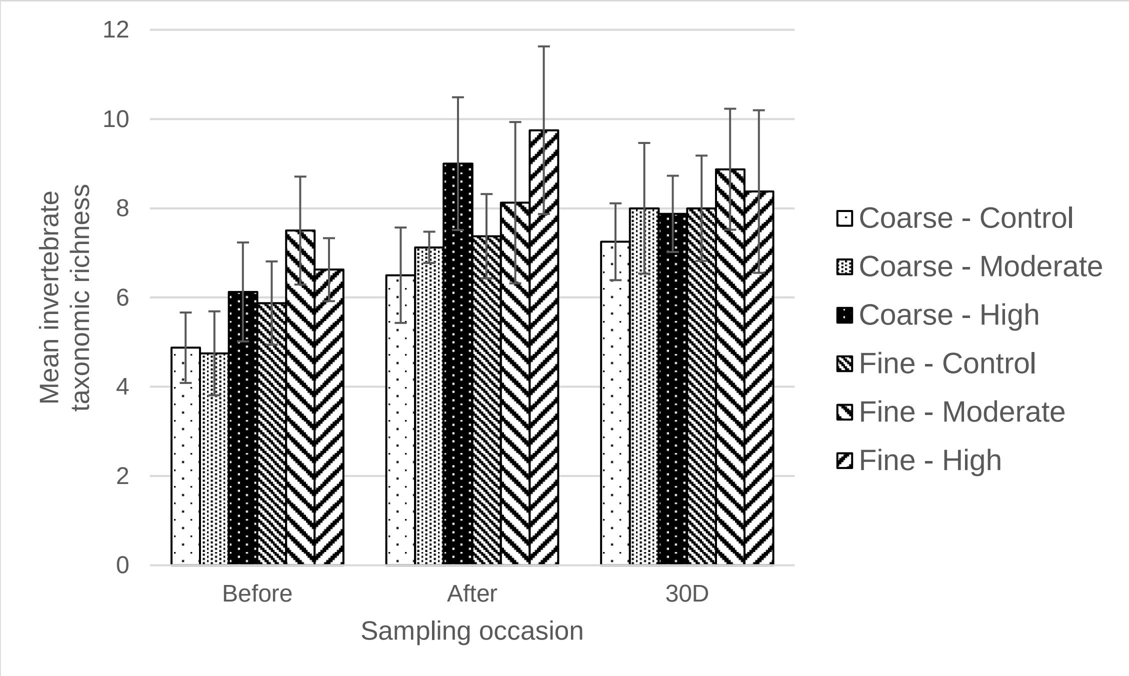

Figure 5.2 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) invertebrate taxonomic richness.

Table 5.5 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on invertebrate taxonomic richness on the sampling occasion following the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	2.79	0.0736
Substrate	1, 39	1.01	0.3199
Sediment x Substrate	2, 39	0.01	0.9931

On the sampling occasion 30 days after fine sediment addition, no significant effect of the sediment pulse, or substrate composition treatments, or the interaction of these two factors, was found on invertebrate taxonomic richness (Table 5.6).

Table 5.6 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on invertebrate taxonomic richness on the sampling occasion 30 days after the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	0.31	0.7343
Substrate	1, 39	0.70	0.4088
Sediment x Substrate	2, 39	0.02	0.9833

The repeated-measures ANOVA did reveal that time had a significant effect on invertebrate taxonomic richness, but no significant effect of the interaction of time with the sediment pulse, or substrate composition treatments, was found (Table 5.7).

Table 5.7 Results of repeated measures ANOVA examining the effect of sediment pulse and substrate composition treatments, time, and their interaction, on invertebrate density. Significant results ($p < 0.05$) are indicated in bold.

	degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	10.90	**0.0001**
Time x Sediment	4, 78	0.92	0.4580
Time x Substrate	2, 78	0.26	0.7693
Time x Sediment x Substrate	4, 78	0.23	0.9199

5.5.2. The density and taxonomic richness of EPT taxa in response to different sediment pulse and substrate composition treatments

When testing for between-subjects effects, the repeated-measures ANOVA found no significant influence of the sediment pulse, substrate composition treatments, or their interaction, on EPT density (Tables 5.8 and 5.9; Figure 5.3). The interaction of sediment pulse and substrate composition treatments on EPT density was close to significance on the sampling occasion after the fine sediment pulse (Table 5.8). Further testing of between-subjects effects and within-subjects effects found no significant associations (Table 5.10).

Table 5.8 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on EPT density on the sampling occasion after the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	1.37	0.2656
Substrate	1, 39	0.31	0.5805
Sediment x Substrate	2, 39	3.15	0.0540

Table 5.9 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on EPT density on the sampling occasion 30 days after the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	0.64	0.5310
Substrate	1, 39	0.69	0.4120
Sediment x Substrate	2, 39	0.06	0.9401

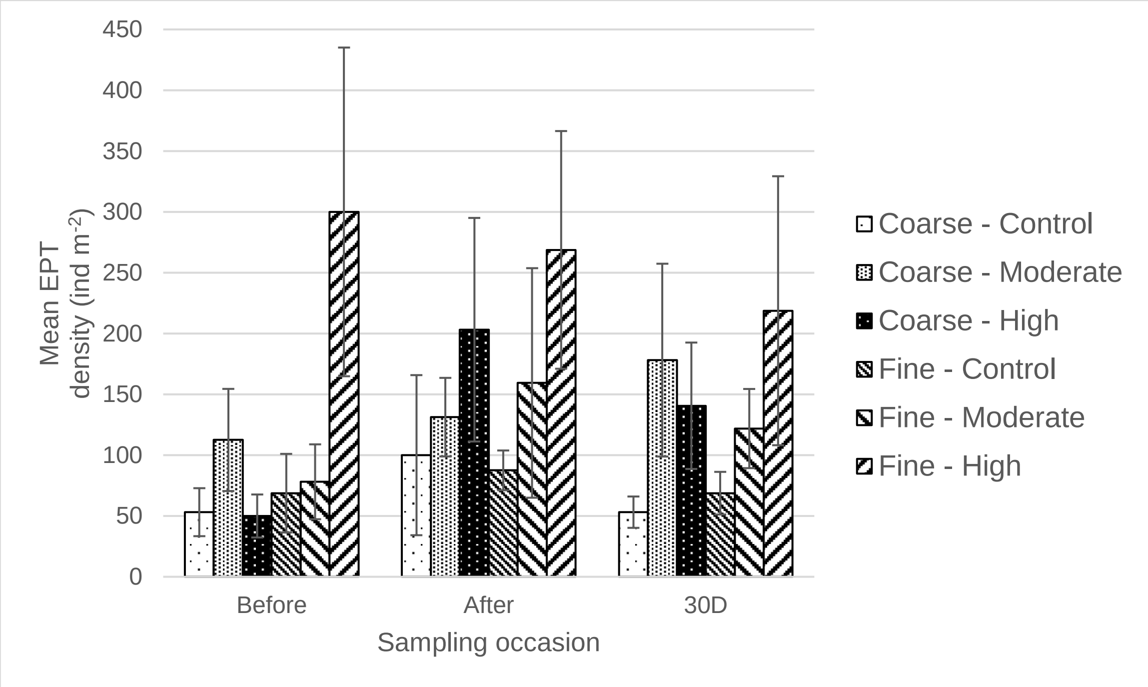

Figure 5.3 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) EPT density (ind m^{-2}).

Table 5.10 Results of repeated measures ANOVA examining the effect of sediment pulse and substrate composition treatments, time, and their interaction, on EPT density.

	degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	2.14	0.1241
Time x Sediment	4, 78	0.54	0.7096
Time x Substrate	2, 78	0.05	0.9489
Time x Sediment x Substrate	4, 78	1.62	0.1785

Between-subjects testing found no significant influence of the sediment pulse, substrate composition treatments, or their interaction, on the taxonomic richness of EPT, on the sampling occasion after the fine sediment pulse and 30 days after the fine sediment pulse (Tables 5.11 and 5.12; Figure 5.4). The effect of the sediment pulse on EPT taxonomic richness was close to significance on the sampling occasion after the fine sediment pulse (Table 5.11). Within-subjects testing found that time had a significant influence on the taxonomic richness of EPT, but no other significant effects were found (Table 5.13).

Table 5.11 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on EPT taxonomic richness on the sampling occasion after the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	2.87	0.0685
Substrate	1, 39	1.70	0.2005
Sediment x Substrate	2, 39	0.57	0.5728

Table 5.12 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on EPT taxonomic richness on the sampling occasion 30 days after the fine sediment pulse.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	1.81	0.1769
Substrate	1, 39	0.05	0.8310
Sediment x Substrate	2, 39	0.22	0.8041

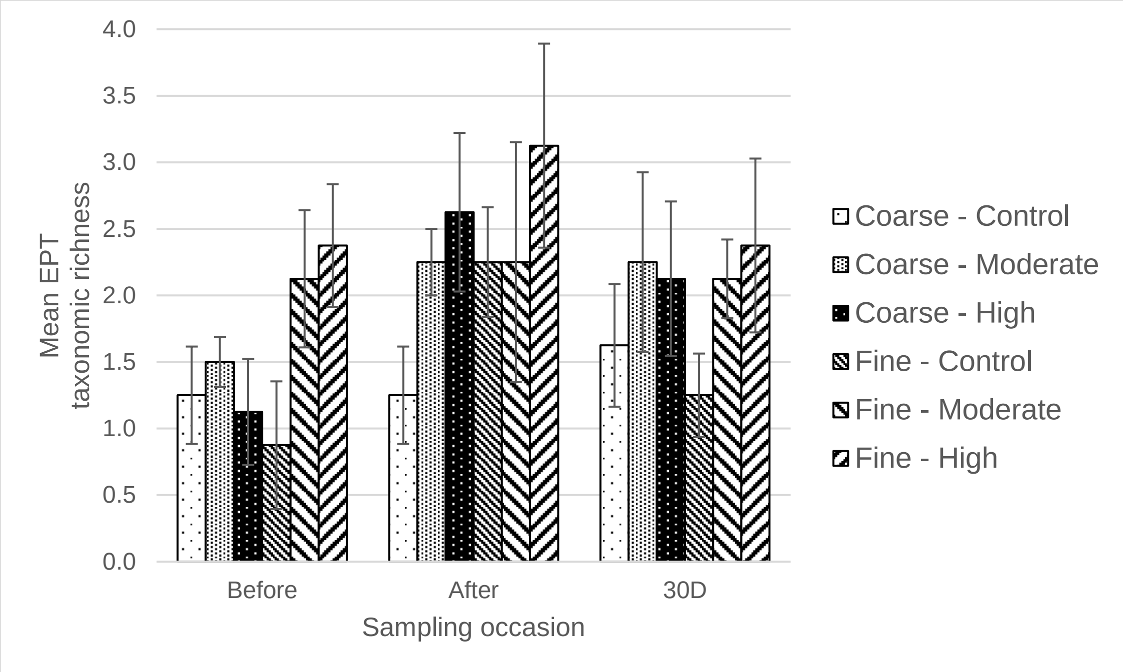

Figure 5.4 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) EPT taxonomic richness.

Table 5.13 Results of repeated measures ANOVA examining the effect of sediment pulse and substrate composition treatments, time, and their interaction, on EPT taxonomic richness. Significant effects are highlighted in bold ($p < 0.05$).

	degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	4.31	**0.0168**
Time x Sediment	4, 78	0.35	0.8440
Time x Substrate	2, 78	0.87	0.4248
Time x Sediment x Substrate	4, 78	0.92	0.4574

5.5.3. Benthic invertebrate community composition

PERMANOVA showed no significant effect of either the sediment pulse or substrate composition treatments on invertebrate community composition (Table 5.14; Figures 5.5 and 5.6). Time was found to have a significant effect on invertebrate community composition (Figure 5.7; Table 5.14). The interaction between the sediment pulse and substrate composition treatments was also found to have a significant effect on invertebrate community composition (Table

5.14). The interaction between time, sediment and substrate also had a significant effect on invertebrate community composition (Table 5.14).

Table 5.14 Results of a PERMANOVA examining the effect of sediment pulse and substrate composition treatments on the benthic invertebrate community. Significant results are indicated in bold.

Source	Degrees of freedom (*df*)	Sums of squares (SS)	Mean squares	Pseudo-*F* ratio	*p*(Pperm)	Unique permutations
Time	2	19317	9658	7.8169	**0.0001**	9921
Block	3	49889	16630	13.4590	**0.0001**	9907
Sediment Pulse	2	3082	1541	1.2471	0.2197	9915
Substrate Composition	1	2015	2015	1.6309	0.1074	9937
Time x Block	6	17397	2900	2.3467	**0.0001**	9855
Time x Sediment	4	4405	1101	0.8913	0.6536	9876
Time x Substrate	2	3905	1953	1.5803	0.0624	9920
Block x Sediment	6	9864	1644	1.3306	0.0678	9856
Block x Substrate	3	5353	1784	1.4442	0.0793	9897
Sediment x Substrate	2	4220	2110	1.7076	**0.0376**	9926
Time x Block x Sediment	12	12239	1020	0.8255	0.8814	9820
Time x Block x Substrate	6	7207	1201	0.9721	0.5398	9851
Time x Sediment x Substrate	4	7597	1899	1.5371	**0.0268**	9885
Block x Sediment x Substrate	6	18943	3157	2.5552	**0.0001**	9846
Section(Block x Sediment x Substrate)	0	0	No test			
Time x Block x Sediment x Substrate	12	14054	1171	0.9478	0.6205	9831
Res	72	88962	1236			
Total	143	268450				

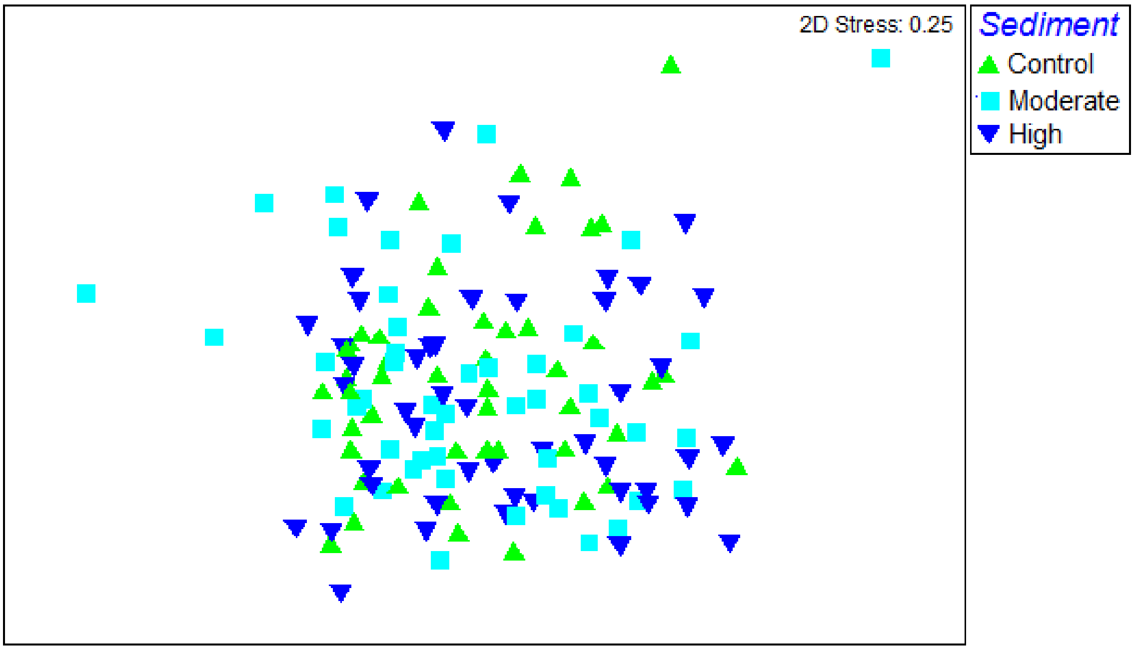

Figure 5.5 Results of NMDS ordination of invertebrate community composition on the three sediment pulse treatments used in this experiment. No significant difference was detected between sediment pulse treatments.

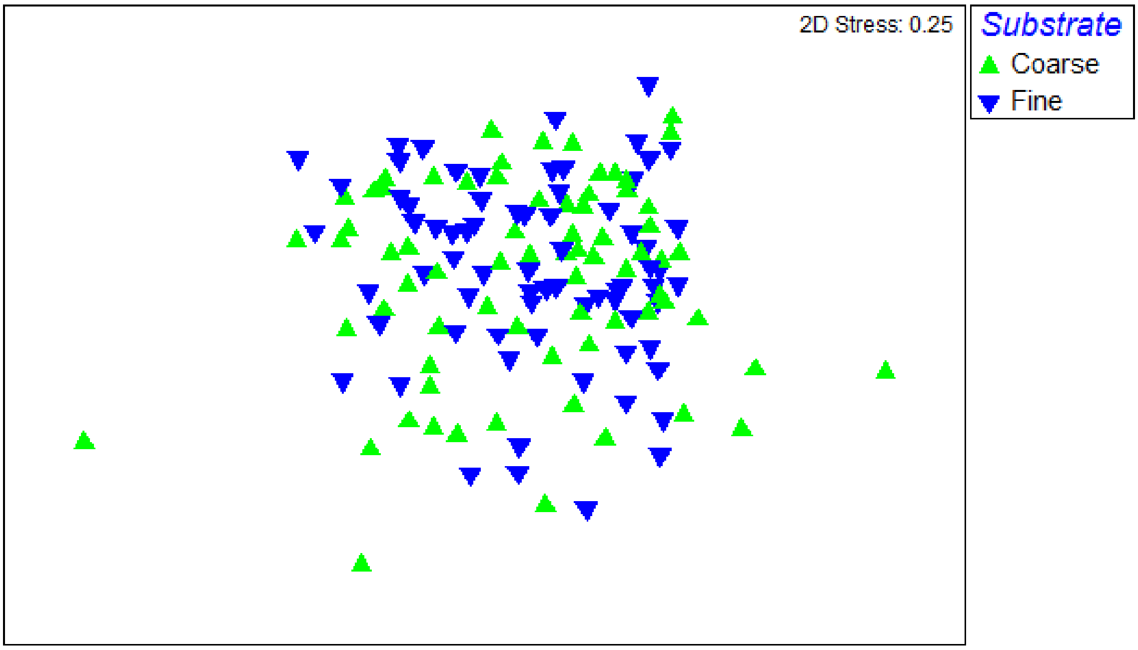

Figure 5.6 Results of NMDS ordination of invertebrate community composition on the two different substrate types used in this experiment. No significant difference was detected between substrate composition treatments.

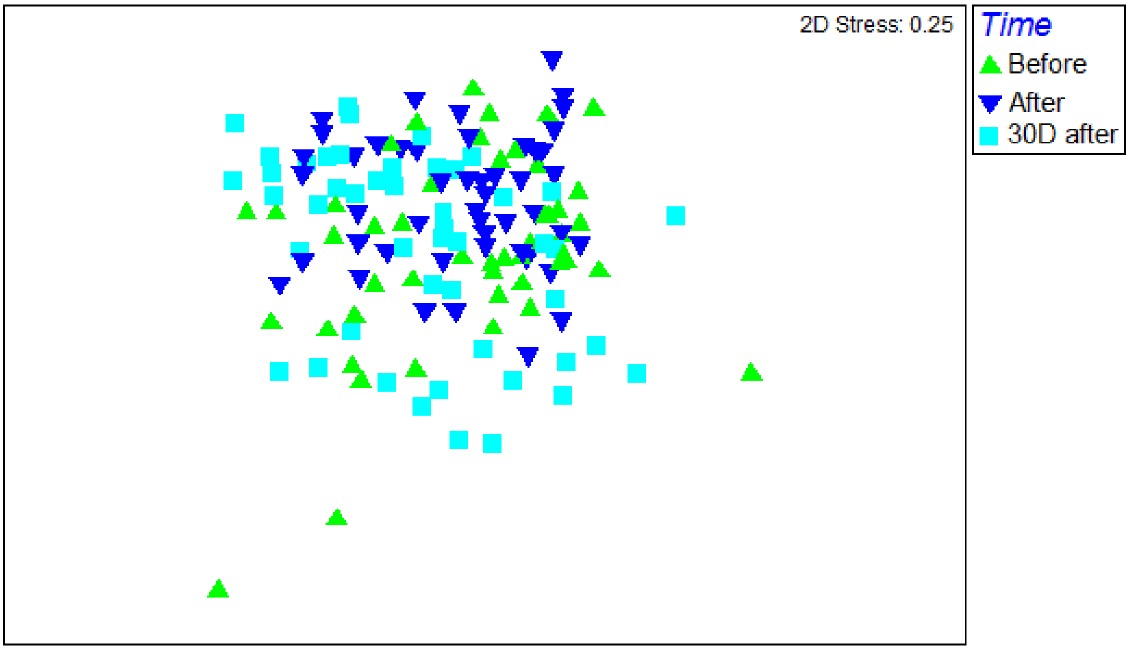

Figure 5.7 Results of NMDS ordination of invertebrate community composition on the three sampling occasions used in this experiment. A significant difference ($p < 0.05$) was detected between sampling occasions.

5.5.4. EPT community composition

PERMANOVA found a significant influence of time (Figure 5.8), sediment pulse (Figure 5.9), substrate composition (Figure 5.10) and the interaction of time with sediment pulse and substrate composition on community composition of EPT (Table 5.15).

Table 5.15 Results of PERMANOVA examining the effect of sediment pulse and substrate composition treatments on the EPT community. Significant results are indicated in bold ($p < 0.05$).

Source	Degrees of freedom (*df*)	Sums of squares (SS)	Mean squares	Pseudo-*F* ratio	*p*(Pperm)	Unique permutations
Time	2	9899.4	4949.7	4.5749	**0.0002**	9945
Block	3	36257	12086	11.17	**0.0001**	9929
Sediment	2	6571.9	3285.9	3.0371	**0.0031**	9940
Substrate	1	2962	2962	2.7377	**0.0304**	9963
Time x Block	6	9846.6	1641.1	1.5168	0.0695	9905
Time x Sediment	4	5878.7	1469.7	1.3584	0.1757	9923
Time x Substrate	2	1783.8	891.92	0.82438	0.5705	9921
Block x Sediment	6	10911	1818.5	1.6808	**0.0326**	9902
Block x Substrate	3	6880.6	2293.5	2.1199	**0.0216**	9940
Sediment x Substrate	2	3463.8	1731.9	1.6007	0.1409	9930
Time x Block x Sediment	12	11647	970.61	0.89711	0.654	9890
Time x Block x Substrate	6	7685.6	1280.9	1.1839	0.2701	9915
Time x Sediment x Substrate	4	8313.2	2078.3	1.9209	**0.0232**	9945
Block x Sediment x Substrate	6	17236	2872.7	2.6552	**0.0001**	9919
Section(Block x Sediment x Substrate)	0	0	No test			
Time x Block x Sediment x Substrate	12	13691	1140.9	1.0545	0.391	9887
Res	72	77899	1081.9			
Total	143	2.31E+05				

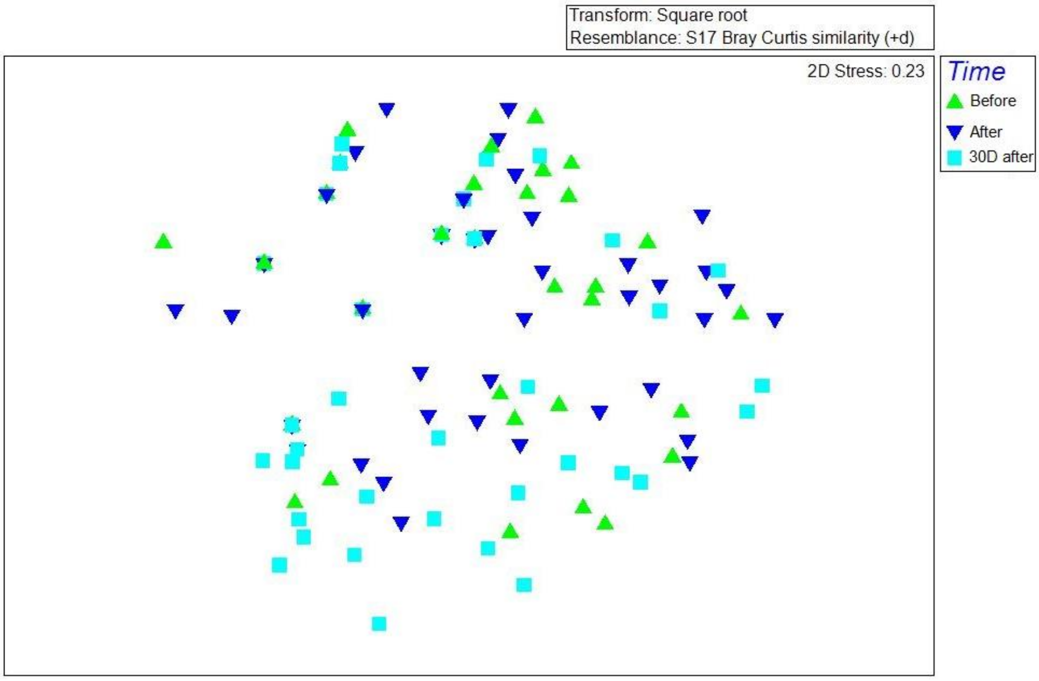

Figure 5.8 Results of NMDS ordination of EPT community composition on the three sampling occasions used in this experiment. A significant difference (p < 0.05) was detected between sampling occasions.

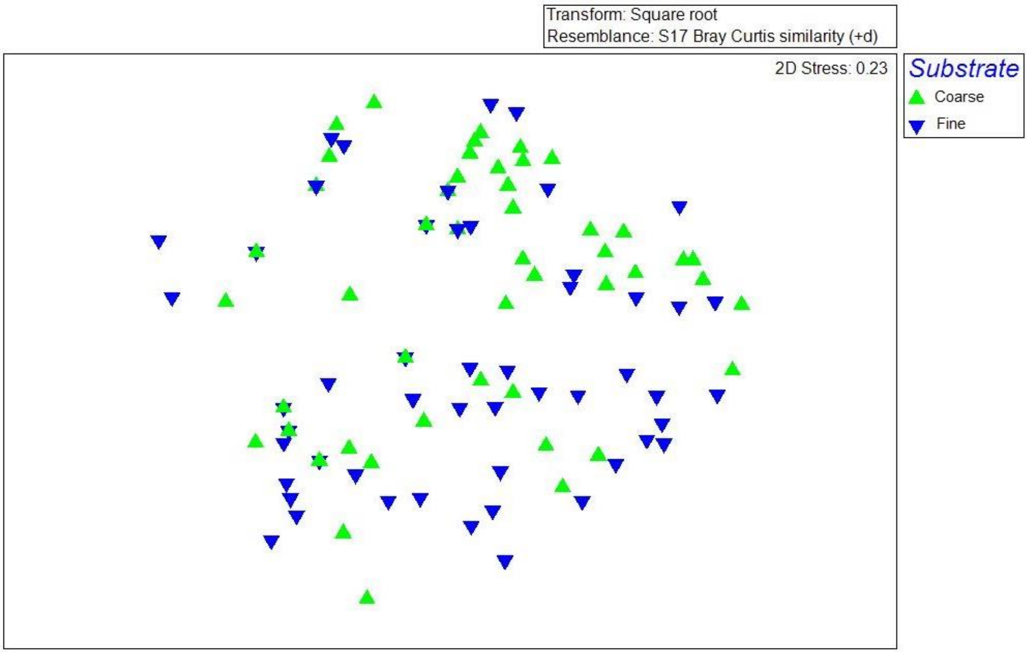

Figure 5.9 Results of NMDS ordination of EPT community composition on the two different substrate types used in this experiment. A significant difference (p < 0.05) was detected between substrate composition treatments.

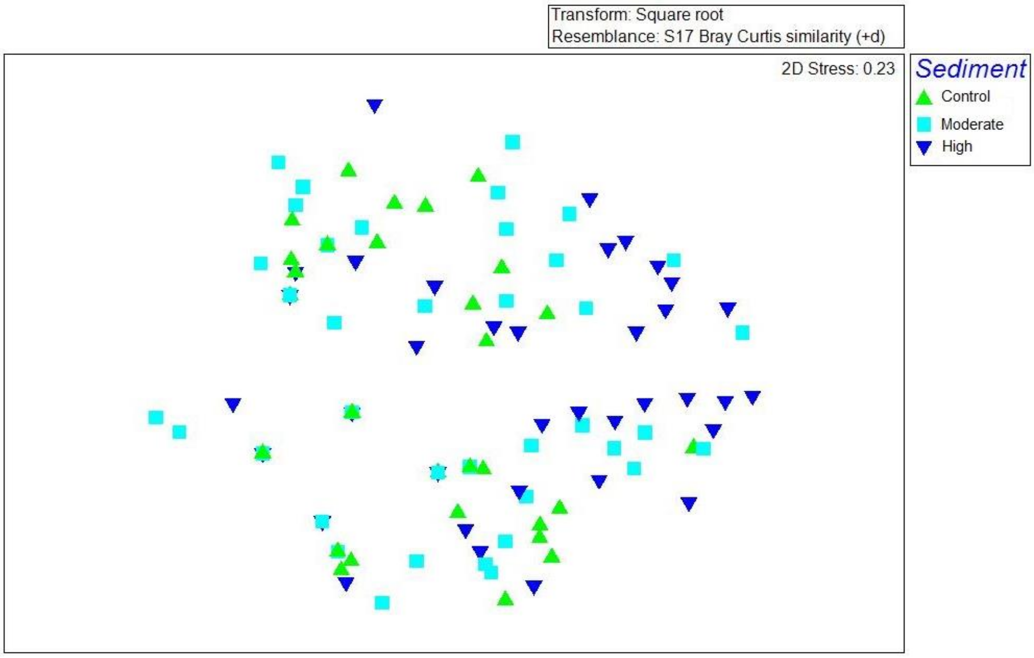

Figure 5.10 Results of NMDS ordination of EPT community composition on the three sediment treatments used in this experiment. A significant difference (p < 0.05) was detected between sediment pulse treatments.

5.5.5. Response of fine sediment biomonitoring indices to a fine sediment pulse

Testing for between-subjects effects revealed that mean E-PSI/No. Taxa was significantly associated with the interaction between sediment pulse and substrate composition treatments on the sampling occasion after the fine sediment pulse (Table 5.16). On this occasion, in the sediment treated channels, invertebrates recorded from the 'coarse' substrate composition treatment were found to have higher mean E-PSI/No. Taxa than invertebrates recorded from the 'fine' substrate composition treatment, indicating that they are more sensitive to fine sediment (Figure 5.11). Also, testing for within-subjects effects, revealed that the effect of time alone and the interaction between time, substrate and sediment were significantly associated with E-PSI/No. Taxa (Table 5.17). No other significant associations between either substrate, sediment, time, or their interactions, and E-PSI/No. Taxa were found.

Table 5.16 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on mean E-PSI/No. Taxa on the sampling occasion after the fine sediment pulse. Significant results (p < 0.05) are highlighted in bold.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	0.16	0.8537
Substrate	1, 39	1.58	0.2163
Sediment x Substrate	2, 39	4.26	**0.0213**

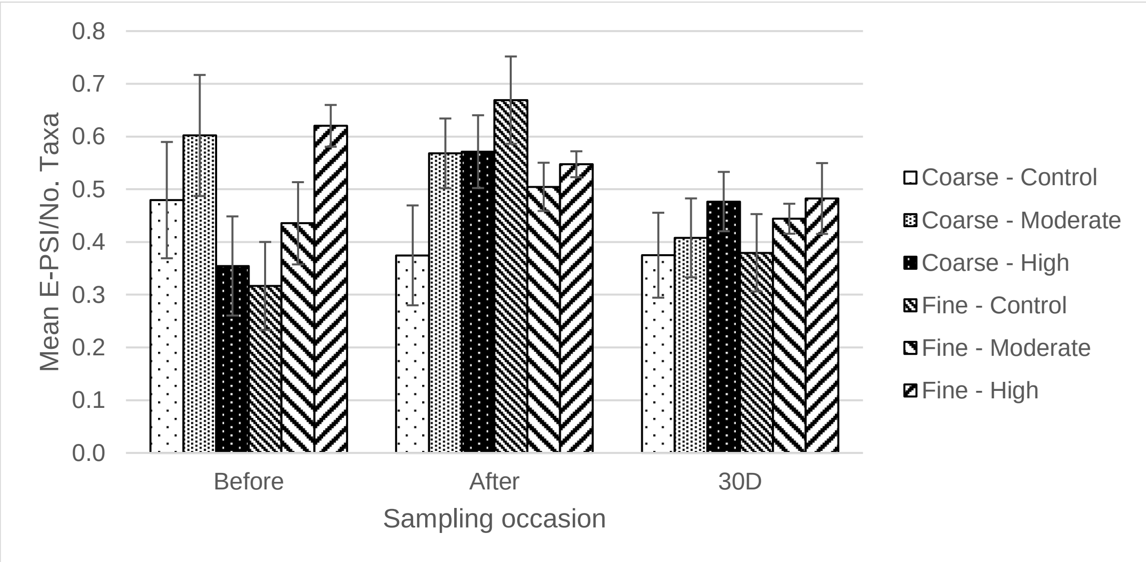

Figure 5.11 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) E-PSI/No. Taxa.

Table 5.17 Results of repeated measures ANOVA examining the effect of sediment pulse and substrate composition treatments, time, and their interaction, on E-PSI/No. Taxa. Significant effects are highlighted in bold (p < 0.05).

	degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	4.64	**0.0125**
Time x Sediment	4, 78	0.30	0.8795
Time x Substrate	2, 78	0.61	0.5484
Time x Sediment x Substrate	4, 78	4.03	**0.0051**

Analysis of between-subjects effects revealed a significant association between OFSI/No. Taxa and the sediment pulse treatments on the sampling occasion 30 days after the fine sediment pulse (Table 5.18). On this occasion mean OFSI/No. Taxa was lower in the samples taken from the 'control' channels when compared to the sediment treated channels, of the same substrate type, indicating that these channels contained a greater number of invertebrate taxa sensitive to fine sediment (Figure 5.12). No further significant associations were found when testing other between-subjects effects and when testing within-subjects effects.

Table 5.18 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on mean OFSI/No. Taxa on the sampling occasion 30 days after the fine sediment pulse. Significant results ($p < 0.05$) are highlighted in bold.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	4.52	**0.0172**
Substrate	1, 39	0.52	0.4735
Sediment x Substrate	2, 39	2.49	0.0961

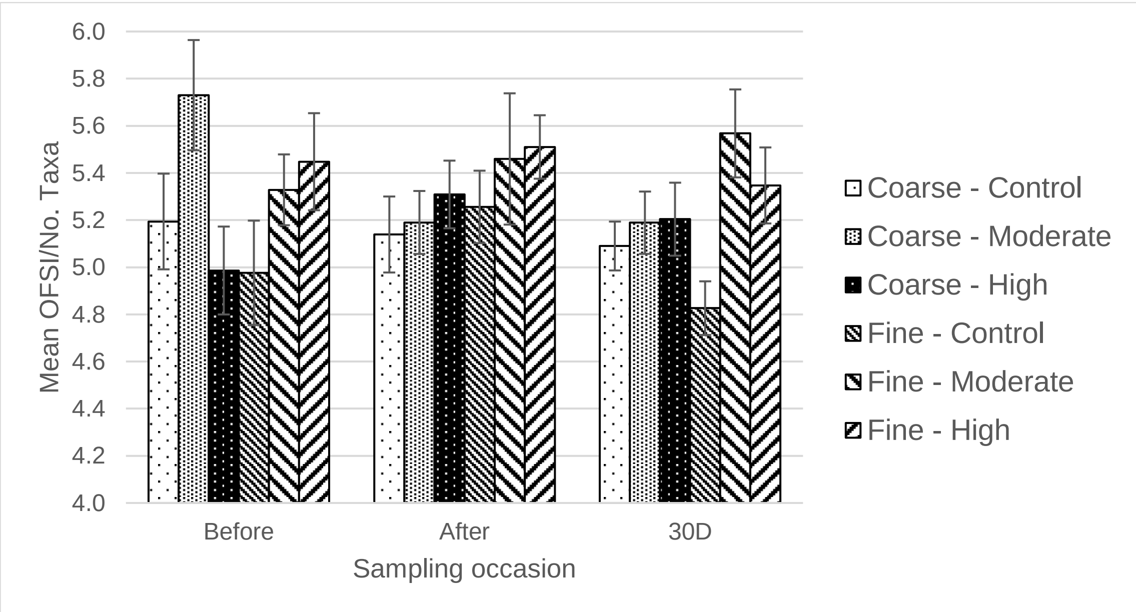

Figure 5.12 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) OFSI/No. Taxa.

Testing of between-subject effects found a significant effect of the interaction between the sediment pulse and substrate composition treatments on ToFSI/No.Taxa, on the sampling occasion after the fine sediment pulse (Table 5.19). The effect of sediment pulse treatment on this occasion was also found to be close to significance (Table 5.19). On this occasion, in the samples taken from the fine sediment treated channels, mean ToFSI/No.Taxa were higher from the ‘coarse’ substrate composition treatment than the ‘fine’ substrate composition treatment, indicating that the ‘coarse’ substrate composition treatment contained a greater number of sediment sensitive invertebrate taxa (Figure 5.13). Also on this occasion, mean ToFSI/No.Taxa were greater from the ‘moderate’ sediment pulse treatment than the ‘high’ sediment pulse treatment, indicating that the samples taken from the ‘high’ sediment pulse treatment contained a greater number of invertebrate taxa tolerant of fine sediment when compared to samples taken from the ‘moderate’ sediment pulse treatment (Figure 5.13). Within-subjects effects testing found a significant effect of the interaction between time and the sediment pulse treatments on ToFSI/No.Taxa (Table 5.20). No other significant associations were found between ToFSI/No.Taxa and either, sediment, substrate, or time, when tested with either between-subjects testing, or within-subjects testing.

Table 5.19 Results of the GLM examining the effect of sediment pulse and substrate composition treatments, and their interaction, on mean ToFSI/No. Taxa on the sampling occasion immediately after the fine sediment pulse. Significant results ($p < 0.05$) are highlighted in bold.

	degrees of freedom (*df*)	*F* value	*p* value
Sediment	2, 39	3.01	0.0609
Substrate	1, 39	2.72	0.1074
Sediment x Substrate	2, 39	4.62	**0.0158**

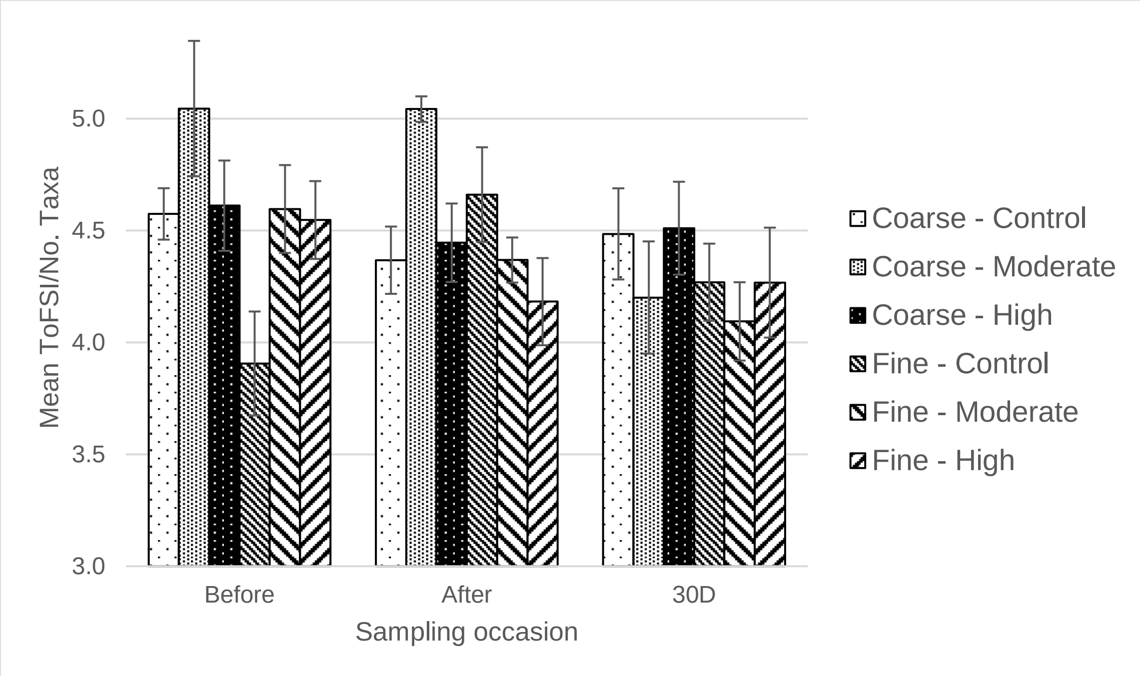

Figure 5.13 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) ToFSI/No. Taxa.

Table 5.20 Results of repeated measures ANOVA examining the effect of sediment pulse and substrate composition treatments, time, and their interaction, on ToFSI/No. Taxa. Significant effects are highlighted in bold ($p < 0.05$).

	degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	2.90	0.0610
Time x Sediment	4, 78	3.27	**0.0156**
Time x Substrate	2, 78	0.53	0.5919
Time x Sediment x Substrate	4, 78	2.03	0.0981

Tests of between-subjects effects found no significant associations between the sediment pulse, or substrate composition treatments, or the interaction between these two factors, and CoFSI/No. taxa following the fine sediment pulse. Tests of within-subjects effects did find a significant association between time and CoFSI/No. taxa (Table 5.21). This testing also found a significant effect of the interaction between time and the sediment pulse treatment on CoFSI/No. taxa, and also the combined interaction of time, sediment pulse and substrate composition treatments (Table 5.21). On the sampling occasion immediately following the fine sediment pulse, in the channels subject to the ‘moderate’ and ‘high’ sediment pulse treatments, mean CoFSI/No. Taxa was greatest from the ‘coarse’ substrate composition treatment, when comparing equivalent fine sediment pulse treatments, indicating that the invertebrate taxa subject to this treatment have a greater sensitivity to fine sediment than those subject to the ‘fine’ substrate composition treatment (Figure 5.14). Also on this sampling occasion, samples taken from channels subject to the ‘high’ sediment pulse treatment had lower mean CoFSI/No. taxa than samples taken from the channels subject to the ‘moderate’ sediment pulse treatment, when comparing with samples taken from the same substrate composition treatment, indicating taxa with a greater tolerance of fine sediment (Figure 5.14).

Table 5.21 Results of repeated measures ANOVA examining the effect of sediment pulse and substrate composition treatments, time, and their interaction, on CoFSI/No. Taxa. Significant effects are highlighted in bold ($p < 0.05$).

	degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	3.54	**0.0336**
Time x Sediment	4, 78	2.63	**0.0405**
Time x Substrate	2, 78	1.11	0.3357
Time x Sediment x Substrate	4, 78	2.72	**0.0354**

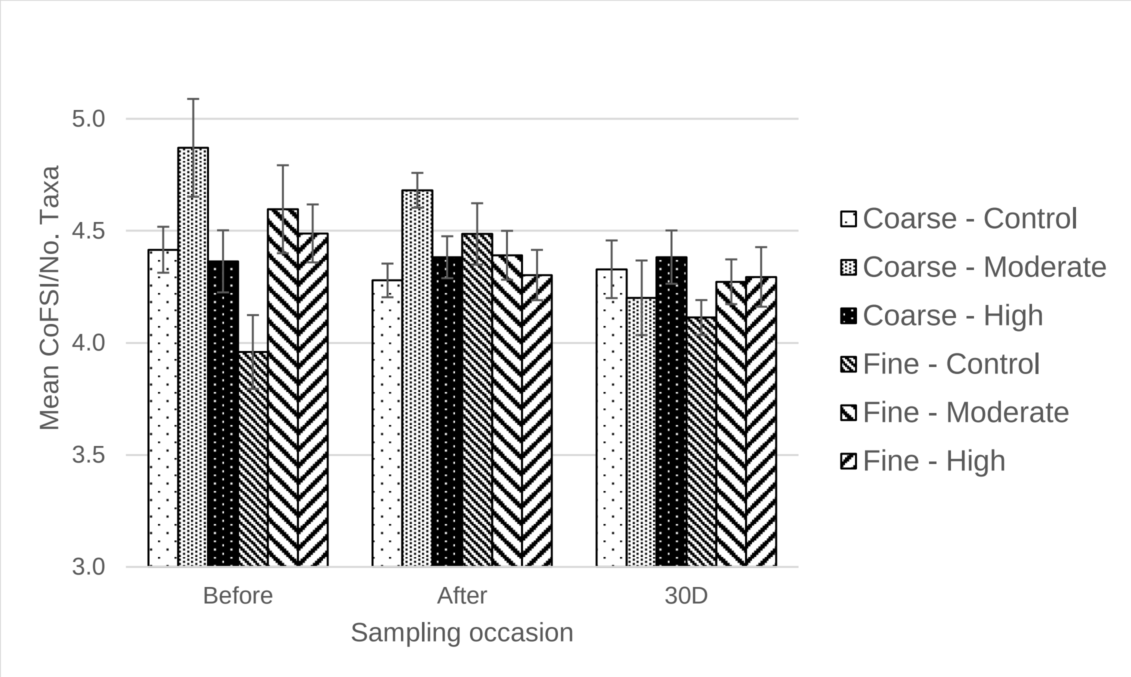

Figure 5.14 Influence of sediment pulse and substrate composition treatments on mean (±1 SE) CoFSI/No. Taxa.

5.5.6. Invertebrate trait analysis

The global testing procedure undertaken as part of the RLQ analysis was significant, indicating a global relationship between species traits and environmental variables (p = 0.0002 for permutation Model 2 and p = 0.0034 for permutation Model 4). However, further analysis using the fourth-corner method found no significant associations between any particular traits and environmental variables. The first axis of the RLQ had a significantly negatively correlated association with the phase after the fine sediment pulse and a significantly positively correlation with the phase 30 days after fine sediment addition (Figure 5.15). Analysis found a significant negative association between the trait modality 'Reproduction – clutches, free' and the first axis of the RLQ and a significant negative association between the trait modality 'Dispersal – aquatic active' and the second axis of the RLQ (Figure 5.16).

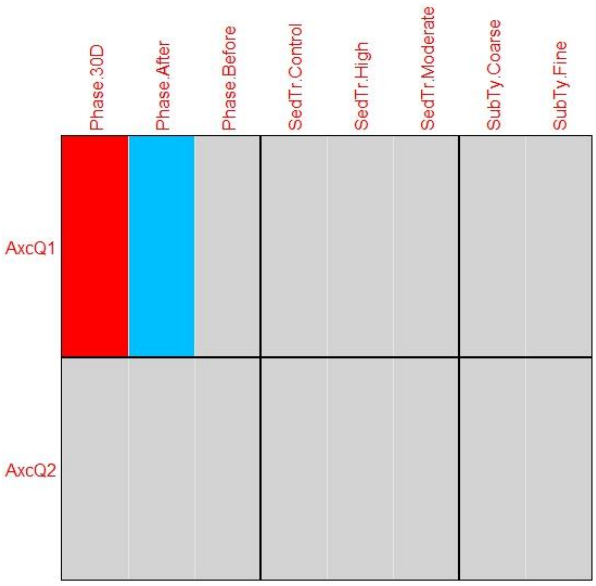

Figure 5.15 Results of RLQ and fourth-corner tests showing associations between the first two RLQ axes for environmental variables and traits (AxcQ1/Q2). If they were significant ($p<0.05$) the negative and positive associations are shown in the figure by blue and red cells respectively. Grey cells detail non-significant associations. The false discovery rate procedure (FDR) was used to adjust p values for multiple comparisons

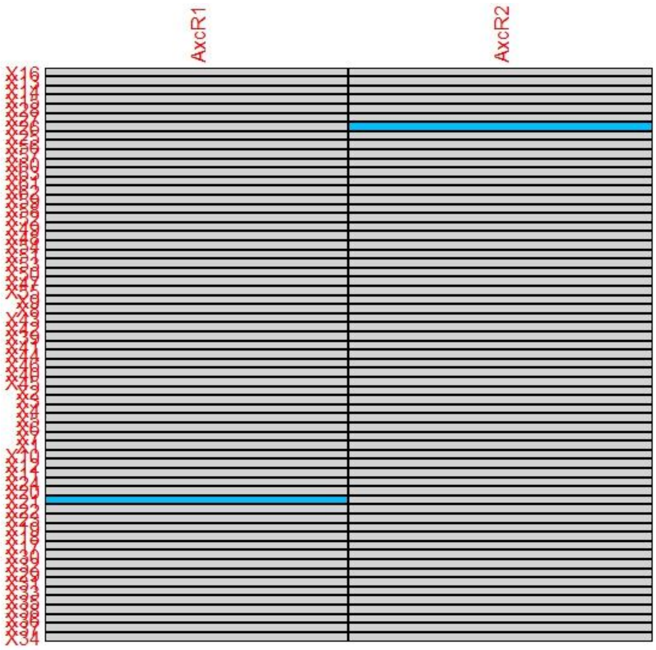

Figure 5.16 Fourth-corner tests relating the first two RLQ axes for environmental variables (AxcR1/R2) with traits.

5.6. Discussion

5.6.1. Influence of prior substrate conditions on the response of invertebrates to a fine sediment pulse

The results of this study indicate that the particle size of the substrate influences how the invertebrate community responds to a fine sediment pulse. Multivariate analysis did not detect a significant association between benthic invertebrate community composition and either sediment or substrate independently, but there was a significant influence of the interaction of substrate composition and sediment pulse treatment, and of the interaction between time, substrate composition and sediment pulse treatment (Table 5.1). Further evidence of the important role that substrate characteristics may have in altering the response of invertebrates to a fine sediment pulse are provided by the significant effect of the interaction between substrate composition and sediment pulse treatments on E-PSI/No. Taxa and ToFSI/No. Taxa. These results indicate that in order to understand and predict the effects of fine sediment on benthic invertebrates it is important to also consider the substrate characteristics of their benthic habitat. Particularly, these results indicate that a stream which has already been subject to elevated fine sediment pressure, resulting in a substrate dominated by small particles, may respond differently to a fine sediment pulse when compared to a stream with a coarser substrate profile. Previous results gleaned from field studies of the effects of fine sediment on benthic invertebrates may not be universally applicable across stream types due to the influence of the underlying substrate. Unless this is accounted for when interpreting results from these studies they may not present a true picture of the mechanisms at work.

Understanding how the effects of fine sediment are influenced by other factors is increasingly important considering the development of biomonitoring indices specifically to identify fine sediment stress, which to be effective will have to work across different stream types (Murphy *et al.,* 2017). In this study the combined effects of an experimental fine sediment pulse and manipulation of substrate composition were significantly associated with ToFSI/No. Taxa on the sampling occasion after the fine sediment pulse. Following the fine sediment pulse mean ToFSI/No.Taxa declined in the channels receiving the ‘moderate’ and ‘high’ fine sediment treatments, whilst within these two sediment treatments, mean scores were consistently higher for the samples taken from the ‘coarse’ substrate composition treatment when compared to the ‘fine’ substrate composition treatment. High ToFSI values are indicative of taxa that are classed as being more sensitive to the total amount of fine sediment, so it would be expected to see a decline in these scores following sediment addition, as was the case in this study.

The fact that a response was seen in ToFSI/No. Taxa and not in oFSI/No. Taxa could possibly be explained by the fact that the total amount of fine sediment is more closely related to physical changes in the habitat of benthic invertebrates, which are directly related to substrate characteristics, such as the amount of interstitial space available to invertebrates. Therefore, the effects of these two factors on the invertebrate community are intertwined. It is conceivable to think that a fine substrate, lacking in interstitial space, may be affected to a greater degree by the infilling of deposited fine sediment than a coarser substrate with a greater amount of interstitial habitat available for invertebrates. This relationship has been seen in this study. The organic component of fine sediment is more closely associated with chemical changes to the environment, which has subsequent effects on invertebrates, which, although this response may still be affected by substrate characteristics, is not related directly to the physical effects of fine sediment deposition, so substrate characteristics may not have such an interactive effect on the invertebrate community.

An association was also found between CoFSI/No.Taxa, ToFSI/No. Taxa and the interaction of time with sediment (Tables 5.20 and 5.21). The means of both of these scores showed a general decreasing trend between the ‘before’ sampling occasion and the ‘after’ sampling occasion, in response to increased fine sediment levels (Figures 5.13 and 5.14). The statistically significant decreases through time (indicating a change to more taxa insensitive to fine sediment) in response to fine sediment increases demonstrate that these indices are able to identify the effects of a fine sediment pulse. This is particularly interesting to see when considering that traditional metrics (e.g. invertebrate density, taxonomic richness, EPT density and EPT taxonomic richness) either did not have a significant association with sediment treatment, or responded positively, contrary to expectations. These results support the idea that biomonitoring indices can be developed to identify specific stressors in the freshwater environment, discriminating between them and other stressors which may be acting upon the invertebrate community at the same time, and that their continued development is a worthwhile aim. Such stressor specific diagnostic indices provide regulatory agencies with a useful tool to aid them in their task of improving and protecting the freshwater environment.

5.6.2. Effects of a fine sediment pulse on the trait profile of the invertebrate community

The results of the RLQ fourth-corner analysis of the trait data recorded in this study are largely inconclusive. No significant associations between any particular traits and environmental variables were found. Two isolated, significant associations, were found between traits and each of the first two RLQ axes, but it is unwise to consider traits in isolation, as they do not respond in isolation to changes in the environment (Murphy *et al.*, 2017). As highlighted by Verberk *et al.* (2013), from an evolutionary perspective single traits are not acted upon by the forces of natural selection, rather selection acts upon species. The success of a species in a particular environment is enabled by the interaction of many different traits. This means that the value of a particular trait and the contribution it makes to the ability of a species to thrive in a particular environment are dependent upon the other traits possessed by the species and the constraints on the species provided by its morphology. Due to the importance of the interactions of traits within a species, traits-based approaches to ecological studies, such as this one, should not consider single traits in isolation, they should instead focus on the way in which combinations of traits interact with each other and are restricted by its morphology (Verberk *et al.* 2013).

One other issue to consider when explaining the lack of a response in the trait profile of the invertebrates in this study is the lack of trait data available for some of the taxa present in this study. This results in the trait analysis missing potentially key information regarding the trait response of the taxa for which trait data was not available. Unfortunately, the incomplete nature of existing information regarding invertebrate traits has also been highlighted in other studies (e.g. Murphy *et al.,* 2017; Mathers *et al.,* 2017) and it is something which should be addressed by freshwater ecologists in the near future, considering the increasing use of trait-based approaches.

5.6.3. Influence of fine sediment pulse and substrate composition treatments on the taxonomic composition of the invertebrate community

In response to the fine sediment pulse this study has identified either a lack of response in invertebrate community metrics (e.g. invertebrate density and taxonomic richness), or a result which is contrary to that which was hypothesised. For example, multivariate PERMANOVA analysis found a significant association between the composition of the EPT community and both the sediment pulse and the manipulation of substrate composition, as was hypothesised. However, both EPT density and taxonomic richness did not respond in response to rising amounts of fine sediment, contrary to the original hypothesis. This is in contrast to a number of different studies (e.g. Gray and Ward, 1992; Angradi, 1999; Waters, 1995; Rabeni *et al.*, 2005; Larsen *et al.*, 2011; Wagenhoff *et al.* 2012; Piggott *et al*., 2015) which found either reductions in EPT abundance, EPT taxonomic richness, or reductions in both of these metrics in response to increases in fine sediment. This response is logical, as many EPT taxa are known to be sensitive to fine sediment, so reductions in the number of species, or in their individual abundance, would be expected in relation to increases in fine sediment.

This is not the only study to find that EPT metrics do not respond as expected to increasing amounts of fine sediment. Some studies have found no change in these metrics (e.g. Lenat *et al.*, 1981; Kaller and Hartman, 2004; Downes *et al,* 2006), whereas Matthaei *et al*. (2006) found an increase in the abundance of EPT taxa, similarly to the present study. One of the possible explanations for this finding is that although EPT taxa are generally considered to be sediment sensitive, there is in fact a range of sediment sensitivities within this group and also the sediment sensitivity of some species may not yet be truly understood. The two EPT taxa which were most abundant in the present study were *Baetis* spp. (Baetidae) and *H. pellucidula* (Hydropsychidae). They are both described as being relatively sensitive to fine sediment in the E-PSI and CoFSI indices, but a study by Buendia *et al.* (2013) found *Baetis* spp*.* (Baetidae) and *Hydropsyche* spp*.* (Hydropsychidae) to be the dominant taxa in sedimented reaches in their study and other studies have also found these taxa to be relatively tolerant of fine sediment (e.g. Nuttall, 1972; Nuttall and Bielby, 1973; Wallace and Gurtz, 1986; Reylea *et al.* 2000). These findings indicate that EPT metrics may not be the most suitable method to detect the effects of fine sediment on invertebrates, due to the variability of sediment sensitivities within this group, and highlights the fact that although fine sediment biomonitoring indices may be more effective than other, traditional, metrics, they still require some refinement to make sure they accurately reflect mechanisms in the real world and are able to deal with the complexity of interactions found in natural situations.

A further possible explanation for the lack of an effect, or a counterintuitive effect, of the fine sediment pulse on certain invertebrate metrics in this study is that the invertebrate community may have already been relatively insensitive to the effects of fine sediment. As noted by Mathers *et al*. (2017), streams which are relatively free from anthropogenic alterations, contain low levels of fine sediment, and are home to many sediment sensitive taxa will exhibit a greater response to increasing fine sediment concentrations than a stream which has been already been experiencing high levels of fine sediment and contains a greater proportion of sediment tolerant taxa. Examining mean E-PSI and CoFSI scores in the benthic invertebrate samples taken in the period before any fine sediment addition in this experiment reveals an invertebrate community which is already relatively insensitive to fine sediment (mean E-PSI/No.Taxa = 0.56, mean CoFSI/No. Taxa = 4.48). This is not surprising given that the River Frome, from which the invertebrates colonised the mesocosm channels, is in a lowland agricultural catchment so the colonisation pool available is likely to contain a greater proportion of invertebrates which are relatively insensitive to fine sediment pressure.

5.7. Summary

The results from this analysis demonstrate that the response of benthic invertebrates to a fine sediment pulse is influenced by prior fine sediment deposition. This is an important finding which clearly shows that to fully understand the impacts of fine sediment on invertebrates it is important to also consider substrate characteristics. Fine sediment biomonitoring indices have also been demonstrated, in this study, to be more effective than traditional metrics (e.g. abundance, taxonomic richness, EPT abundance and taxonomic richness) at identifying fine sediment stress. The testing and evaluation of fine sediment biomonitoring tools under different conditions can aid in their refinement and will lead to them becoming increasingly more important for those seeking to monitor and manage fine sediment in the lotic freshwater environment.

6. The effects of increased fine sediment and substrate characteristics on invertebrate drift

6.1. Introduction

Invertebrate drift describes the downstream transport, either active or passive, of aquatic invertebrates when they are carried within the water column (Waters, 1972). It is an important process in the lotic freshwater environment, playing a role in the colonisation, dispersal and stressor-avoidance behaviour of invertebrate communities (Larsen and Ormerod, 2010; Ríos-Touma *et al.*, 2012; Naman *et al.*, 2016). The importance of drift as a mechanism for both colonisation and dispersal varies by taxa. Taxa which are more sedentary and less motile, such as bivalves and gastropods, have been found to be more reliant on drifting behaviour when colonising new habitats, as opposed to more motile taxa, such as trichoptera and plecoptera, which are also able to use their crawling and swimming abilities (Mackay, 1992).

6.1.1. Passive and active invertebrate drift

Invertebrate drift may be split into two categories, i.e. passive drift or active drift. Passive drift describes invertebrates experiencing hydraulic stress, such as increased near-bed shear stress resulting from changes in turbulence or discharge, and accidentally becoming detached from the substrate (Gibbins *et al.*, 2009). Active drift describes invertebrates intentionally leaving the substrate to join the current (Naman *et al.*, 2016). Naman *et al.* (2016) described three flow-related thresholds which govern passive drift in stream invertebrates. The first threshold is when discharge is great enough to reach the critical level of shear stress necessary for the entrainment of organic matter, such as detritus or algal mats. Once this threshold has been reached, invertebrates using this material as substrate will become entrained (Allan, 1995; Vinson, 2001). The second threshold is reached once discharge is great enough to saltate fine organic matter and sand-sized particles, which may scour benthic invertebrates from the bed and cause them to enter the drift (Gibbins *et al*., 2007b). The third threshold is reached when discharge becomes great enough to mobilise all particles on the stream bed, forcing the entrainment of benthic invertebrates which had been utilising this habitat (Anderson and Lemkuhl, 1968). However, as noted by Naman *et al.* (2016), if critical shear stress is sufficient to dislodge and entrain invertebrates, but not sufficient to mobilise substrate, then a large abundance of invertebrates may still be subject to passive drift, even in the absence of significant substrate mobilisation. Crossing any of these flow related thresholds may result in 'catastrophic drift', defined by Gibbins *et al.*, (2007b) as a significant increase in drifting invertebrates caused by disturbances such as pollution events or floods.

Active drifting behaviour may be initiated by invertebrates to avoid benthic predators (Kratz, 1996; Huhta *et al.*, 2000; Hammock *et al.* 2012; Sullivan and Johnson, 2016), to aid patch selection whilst foraging (Hildebrand, 1974; Kohler, 1985), during emergence (Neale *et al.*, 2008), and to find new habitat if local invertebrate densities are too high, or local food resources are limited (Corkum, 1978; Hildrew and Townsend, 1980; Kohler, 1992; Fonseca and Hart 1996; Rowe and Richardson, 2001; Siler *et al*., 2001). Invertebrates may also actively enter the drift in response to stressors in their local environment, such as exposure to insecticides (Lauridsen and Friberg, 2005), acid (Courtney and Clements, 1998), reduced discharge (Minshall and Winger, 1968), salinity (Beermann *et al.*, 2018) and increased amounts of fine sediment (Béjar *et al.*, 2017). In reality, for many species, the distinction between passive and active drift is blurred, as it is not possible to determine if sheer stress or entrained particles dislodges invertebrates or they actively "let go" to avoid damage or seek refuge.

6.1.2. Fine sediment effects on invertebrate drift

A number of studies have examined the effects of increased fine sediment on invertebrate drift, with some examining the effects of deposited fine sediment (Angradi, 1999; Suren and Jowett, 2001; Ramezani *et al.*, 2014; Beermann *et al.*, 2018), some examining the effects of suspended fine sediment (O'Hop and Wallace, 1983; Bond and Downes, 2003; Béjar *et al.*, 2017) and some examining a combination of both factors (Ciborowski *et al.*, 1977; Shaw and Richardson, 2001; Connolly and Pearson, 2007; Molinos and Donohue, 2009; Gomi *et al.*, 2010). It is important to make the distinction between the effects of suspended fine sediment and those of deposited fine sediment, as the mechanisms by which they may affect invertebrate drift are different (Jones *et al.*, 2012a).

Suspended fine sediment in the water column, or fine sediment partially in suspension (taking the form of particles moving by saltation), may abrade benthic invertebrates, potentially damaging any vulnerable body parts, whilst also possibly causing them to be dislodged from the substrate and either actively or passively enter the drift. This process has been observed in a study by Culp *et al.* (1986), who found increased fine sediment resulted in saltating sand particles causing catastrophic drift in the artificial channels of their experiment. Suspended sediment may affect invertebrate drift through its impact upon the amount of light reaching the benthic environment. Drifting behaviour in invertebrates has been found to fluctuate in relation to a diel pattern, with more invertebrates entering the drift during the hours of darkness (Waters, 1972; Flecker, 1992). This is thought to be due to the decreased risk of predation from animals which rely on their vision to hunt. Increased turbidity and reduced light availability on the stream bed associated with increased suspended sediment may encourage this type of behavioural drift, as the environment is viewed as being safer in which to drift (Béjar *et al.*, 2017). Deposited fine sediment is thought to have an effect on invertebrate drift due to the direct and indirect negative effects it may have upon the animals themselves and their environment (reviewed in Chapter 2). If an invertebrate is subject to these negative impacts, and is able to initiate drifting behaviour, it may utilise drift to escape these unfavourable conditions.

In addition to initiating drifting behaviour in response to environmental stressors, invertebrates have been found to utilise the hyporheic zone as a refuge (Marchant, 1988; Delucchi, 1989; Clinton *et al*., 1996; Dole Olivier *et al.*, 1997; Stubbington, 2012; Maazouzi *et al.*, 2017). Recent research has found that in some rivers this process may be even more important than drift in promoting the resilience of invertebrate communities (Vander Vorste *et al.*, 2015). However, the extent to which the hyporheic zone can act as a refuge may be constrained by fine sediment deposition, as an influx of fine particles reduces interstitial space within the substrate, limiting the vertical connectivity of the streambed and making it harder for benthic invertebrates to access deeper layers (Descloux *et al.*, 2014; Vadher *et al.*, 2015; Vadher *et al.*, 2017). Therefore, it is possible to hypothesise that if a stream has already experienced an increased load of fine sediment, resulting in a colmated substrate, the hyporheic zone may have limited potential to provide a refugium for invertebrates escaping a fine sediment pulse. Subsequently, there is a higher probability of invertebrates entering the drift in response to a fine sediment pulse in a colmated stream compared with a stream with a coarser substrate, as without access to the interstitial space within the substrate, a greater number of invertebrates may utilise drifting behaviour. The experiment detailed in this chapter is one of the first to examine the effect of initial substrate characteristics on the drift response of invertebrates to a fine sediment pulse. It aimed to provide useful information for freshwater ecologists considering how the drift response of invertebrates may differ in a stream which has been subject to high levels of fine sediment over an extended period when compared with a stream not subject to these conditions.

6.1.3. Effects of flow and previous exposure to elevated fine sediment amounts on invertebrate drift

In the past, researchers have struggled to disentangle the effects of increased flow and increased fine sediment on invertebrate drift in a natural setting, as these two factors often in occur in conjunction during floods (O'Hop and Wallace, 1983). This means that manipulative, controlled experiments such as the present study are necessary to identify the separate effects of each of these factors. It is important to separate these two factors from a management perspective because they differ in the type of pressure they apply to the freshwater ecosystem. Sudden increases in flow may have an acute effect on invertebrate drift as the increased hydraulic forces mobilise sediment, increase scour, and often also mobilise benthic invertebrates, which may lead to large decreases in benthic invertebrate abundance (Gibbins *et al*., 2007). However, the effects of increased fine sediment on invertebrate drift are often of a more chronic nature, with gradual increases in deposited sediment changing the benthic habitat and potentially resulting in increased drift as invertebrates seek a more favourable habitat (Larsen and Ormerod, 2010). The legacy effects of sediment pulse events are also important to consider as they may require a different management response depending upon the duration of their effects. This is why the present study not only considers the immediate effects of a fine sediment pulse, it also investigates how prior increased sediment deposition affects the response of invertebrates, in addition to assessing whether the effects are still felt 30 days after the sediment pulse.

6.2. Research aims

This study aimed to investigate the drifting behaviour of invertebrates in response to a fine sediment pulse, and to assess whether this behaviour is influenced by prior conditions (in relation to deposited fine sediment). The use of stream mesocosms for this experiment allowed the investigation to be performed without many of the confounding factors often seen in studies of this type, and it is unique in its consideration of prior substrate conditions and their potential effect on drifting behaviour. Tests of the following hypotheses were made:

- Increased fine sediment will lead to increased density and taxonomic richness of drifting invertebrates.
- Increased fine sediment will result in increased density and taxonomic richness of the EPT taxa.
- Differences in substrate characteristics will results in a higher density of invertebrates drifting from the ‘fine’ substrate composition treatment when compared with the ‘coarse’ substrate composition treatment.
- The taxonomic composition of the drifting invertebrate assemblage will be affected by increased fine sediment and differences in substrate composition.
- Increased fine sediment and differences in substrate composition will have an effect on the prevalence of certain invertebrate traits within the drift community.

6.3. Method

The study area is described in Chapter 3, Section 3.1. A more detailed explanation of the sampling methods used may be found in Chapter 3. Drift samples were taken in the 24h directly before the fine sediment pulse, during the fine sediment pulse, after the fine sediment pulse and 30 days after the fine sediment pulse. On each sampling occasion drift nets were left in place for 24h and were emptied every 6h. The 'during' sampling occasion began at the same time as the application of the fine sediment pulse, with the 'after' sampling occasion beginning immediately after (exactly 24h after the application of the sediment pulse treatments). Sampling was completed using drift nets (frame height 0.4 m, frame width 0.25 m, mesh size 1 mm) located at the bottom of each mesocosm section (resulting in one net half way down and one net at the end of each mesocosm channel). Invertebrates were then preserved and identified to the lowest possible taxonomic level, usually genus, or species.

6.4. Data analysis

6.4.1. Drift density, EPT drift density, taxonomic richness and EPT taxonomic richness

Drift density (number of drifting invertebrates/ 100 m^3) was calculated by first estimating the volume of water filtered by each net. This estimate was achieved by multiplying the area of the submerged section of the drift net by the length of the water column that passed through each drift net (derived by multiplying the average water velocity (m s^{-1}) by the amount of time each net was in place). The density of drifting invertebrates was then obtained by dividing the number of drifting invertebrates caught in the net by the volume of water filtered by the net. Following initial exploratory analysis, drift densities were log_{10} transformed to homogenise variances among treatments.

A repeated-measures ANOVA was used to determine the effects of an experimental sediment pulse and substrate composition on invertebrate drift density, the taxonomic richness of drifting invertebrates and the taxonomic richness of EPT. The between-subjects factors used for this analysis were ‘block’ (which was used to factor out any potential effects caused by differences between the mesocosm blocks), ‘sediment treatment’ and ‘substrate type’. The within-subjects factor in this model was ‘time’ (consisting of four levels: ‘before’, ‘during’, ‘after’ and ’30 days after’). The GLM used for this analysis was chosen as it allows for the examination of any interactions between these effects. The GLM procedure in SAS 9.4 was used to perform this analysis (SAS Institute, 2013).

6.4.2. Taxonomic community composition

To examine the influence of the sediment pulse and substrate composition treatments on the taxonomic composition of the drifting invertebrate assemblage and their interaction with time, a PERMANOVA was employed (Anderson, 2001). This analysis was performed on a matrix of similarities derived from the Bray-Curtis distances between each sample. A dummy variable of one was used to construct the similarity matrix as within the analysis there were a significant number of samples which contained zero invertebrates. Invertebrate abundances were $\log_{10}(x+1)$ transformed prior to analysis to ensure homoscedasticity. To visually illustrate the PERMANOVA results, NMDS was used, employing 50 randomised starts. If any significant treatment effects were found, a similarity percentages (SIMPER) routine was used to identify the taxa responsible for the observed differences. This multivariate analysis was completed in the PRIMER 6 software package, using the PERMANOVA+ add-on (Anderson *et al.*, 2008).

6.4.3. Invertebrate trait analysis

A combination of the RLQ and Fourth-corner methods was carried out to examine the effect of the sediment pulse and substrate composition treatments on the prevalence of invertebrate traits within the population of drifting invertebrates. Trait data used in this analysis was derived from three sources:

- www.freshwaterecology.info ((Schmidt-Kloiber and Hering, 2015)
- French Genus Trait Database (Tachet *et al.,* 2000)
- Data on hyporheic invertebrate traits (Descloux *et al.*, 2014)

The French Genus Trait Database (Tachet *et al.,* 2000) provided the majority of the trait information used in this study. However, information for some of the taxa found in this study was not available from this resource, so this data was imported from the other two sources detailed above. Out of a total of 62 taxa identified in this study, trait information was available for 44 of them (constituting 71% of the total number of taxa). This disparity exists because trait data was either not available for a particular taxon, or the trait information was not at a taxonomic level which matched that of the present analysis. The analysis was undertaken following the same procedure outlined in Chapter 5, Section 4.3.

6.5. Results

6.5.1. Invertebrate drift density and taxonomic richness

A total of 2,190 invertebrates comprising 62 taxa were identified from the drift samples (Table 6.1). There was a considerable amount of variability between these samples, as has been identified before in other studies of invertebrate drift (Neale *et al.*, 2008).

Table 6.1 The 17 most abundant taxa identified in the drift samples. These taxa account for 90 % of the total abundance of drifting invertebrates. This table does not include taxa which individually accounted for < 1% of the total abundance of drifting invertebrates identified (45 taxa, which as a whole accounted for 10 % of the total abundance of drifting invertebrates).

Taxa	Percentage of total invertebrates sampled	Cumulative percentage	Trait information available
Radix balthica (Lymnaeidae)	19.04	19.04	Yes
Gammarus pulex (Gammaridae)	15.39	34.43	Yes
Baetidae	11.00	45.43	Yes
Limnius volckmari (Elmidae)	6.39	51.82	Yes
Brachycentrus subnubilus (Brachycentridae)	6.12	57.94	Yes
Hydropsyche pellucidula (Hydropsychidae)	5.34	63.28	Yes
Tanytarsini (Chironomidae)	5.21	68.49	Yes
Hydroptila spp.(Hydroptilidae)	3.79	72.28	Yes
Tanypodinae (Chironomidae)	3.52	75.8	Yes
Asellus aquaticus (Asellidae)	3.42	79.22	Yes
Crangonyx pseudogracilis (Crangonyctidae)	3.01	82.23	Yes
Hydrophilidae	1.55	83.78	No
Hydropsyche contubernalis (Hydropsychidae)	1.42	85.2	Yes
Corixidae	1.23	86.43	No
Psychodidae	1.14	87.57	Yes
Simuliidae	1.10	88.67	No
Elmis aenea (Elmidae)	1.00	89.67	Yes

Mean drift density was not significantly different between the ‘fine’ and the ‘coarse’ substrate composition treatments before the addition of fine sediment (Figure 6.1; GLM: $F_{(2, 15)} = 1.21$, $p = 0.2882$). On the sampling occasion during fine sediment addition, significant differences in mean drift densities were observed between fine sediment pulse treatments (GLM: $F_{(2, 15)} = 10.81$, $p = 0.0012$). On this sampling occasion, in both substrate composition treatments, mean drift density was greatest from the 'high' fine sediment pulse treatment, followed by the 'moderate' fine sediment pulse treatment, with the 'control' sediment pulse treatment having the lowest mean density of drifting invertebrates (Figure 6.1). This pattern was repeated on the sampling occasion directly after fine sediment addition, although these differences were not found to be significant (GLM: $F_{(2, 15)} = 1.8$, $p = 0.1992$).

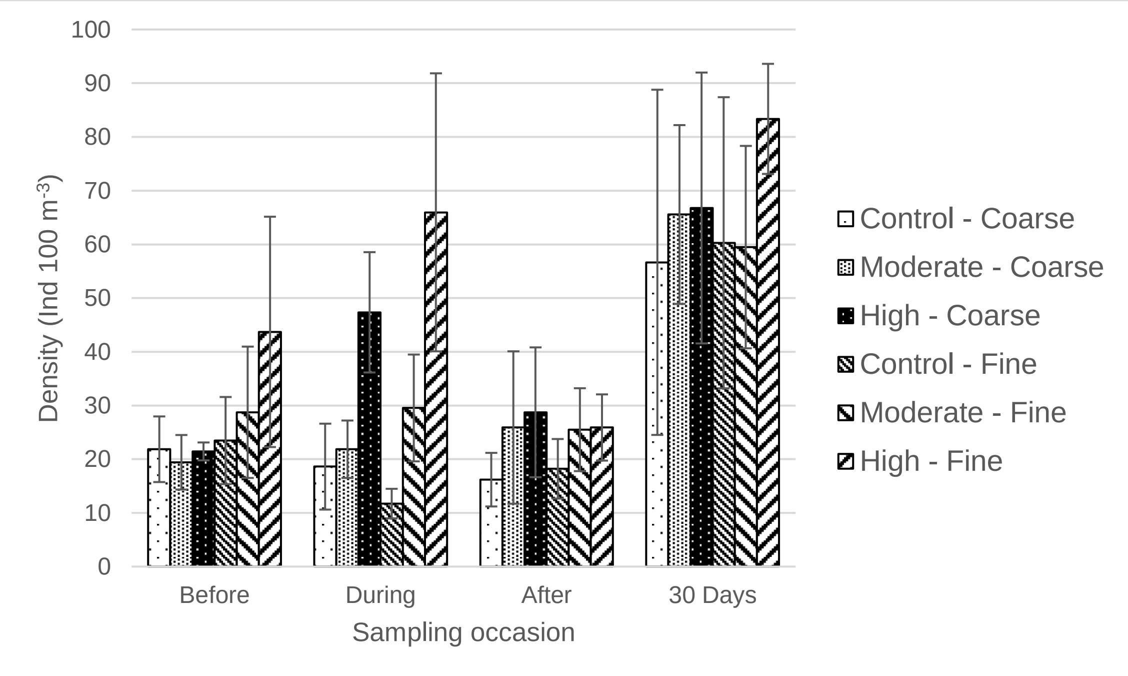

Figure 6.1 Influence of sediment pulse and substrate composition treatments on mean density (Ind $100m^{-3}$; ±1 SE) of drifting invertebrates.

Repeated measures ANOVA revealed no significant effect of the interaction of time with either sediment pulse or substrate composition treatments on drift densities, the interaction of time with sediment pulse treatment is close to significance (Table 6.2).

Table 6.2 Results of repeated measures ANOVA examining the effects of substrate composition and sediment pulse treatments on drift density over four sampling occasions. Significant results (p < 0.05) are highlighted in bold.

Source	Degrees freedom (*df*)	*F* value	*p* value
Time	3, 45	22.43	**<0.0001**
Time x Block	9, 45	4.5	**0.0003**
Time x Sediment Pulse	6, 45	2.2	0.0601
Time x Substrate Composition	3, 45	0.17	0.9179
Time x Sediment Pulse x Substrate Composition	6, 45	0.5	0.8069

Mean taxonomic richness of the drifting invertebrate assemblage varied between a low of 5.5 to a high of 13.25 (Figure 6.2). On the sampling occasion during the fine sediment pulse, the sediment pulse treatment was found to have a significant effect on taxonomic richness (GLM: $F_{(2, 15)} = 4.24$, $p = 0.0347$). On this occasion, taxonomic richness was greatest for invertebrates drifting in the 'high' sediment pulse treatment, in both the 'coarse' and 'fine' substrate composition treatments (Figure 6.2). However, repeated measures ANOVA found no significant effect of the interaction of time with either sediment pulse, or substrate composition, treatments on taxonomic richness (Table 6.3).

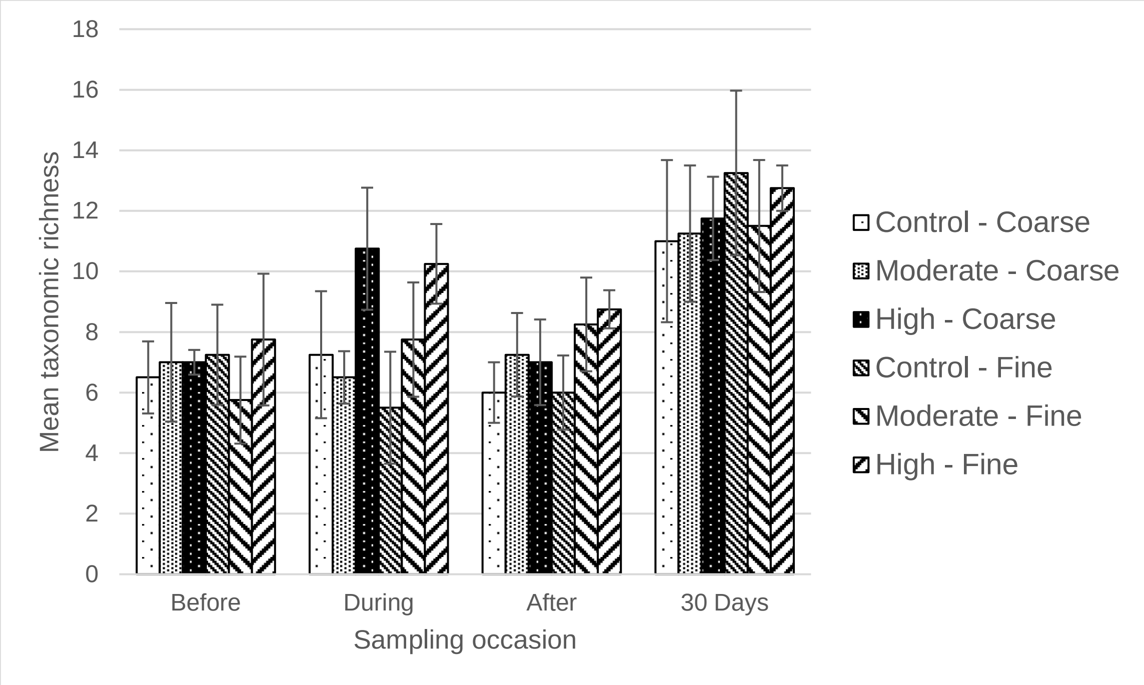

Figure 6.2 Influence of sediment pulse and substrate composition treatments on the mean taxonomic richness (±1 SE) of drifting invertebrates.

Table 6.3 Results of repeated measures ANOVA examining the effects of substrate composition and sediment pulse treatments on the taxonomic richness of drifting invertebrates over four sampling occasions. Significant results (p < 0.05) are highlighted in bold.

Source	Degrees of freedom (*df*)	*F* value	*p* value
Time	3, 45	15.16	**<0.0001**
Time x Block	9, 45	2.13	**0.0466**
Time x Sediment Pulse	6, 45	1.03	0.4196
Time x Substrate Composition	3, 45	0.35	0.7927
Time x Sediment Pulse x Substrate Composition	6, 45	0.4	0.8751

6.5.2. EPT drift density and taxonomic richness

There was a statistically significant difference in the mean EPT drift density between substrate composition treatments on the sampling occasion before the application of the sediment pulse treatments (GLM: $F_{(1, 15)} = 6.55$, $p = 0.0218$).

On this occasion, the mean EPT drift density was greater from the ‘fine’ substrate composition treatment than the ‘coarse’ substrate composition treatment (Figure 6.3). There was also an increase of 27 % in the mean drift density of EPT taxa from the ‘fine’ substrate composition treatment when compared with the ‘coarse’ substrate composition treatment over the course of the experiment. Analysis of between-subjects effects found a statistically significant effect of the sediment pulse treatment on mean EPT drift density on the sampling occasion during the sediment pulse (GLM: $F_{(2,15)} = 16.78$, $p = 0.0001$). At this time, in both substrate composition treatments, mean EPT drift density was greatest from the channels sections subject to the ‘high’ sediment pulse treatment, followed by the ‘moderate’ sediment pulse treatment. The channel sections subject to the ‘control’ sediment pulse treatment were found to have the lowest mean EPT drift densities on this occasion (Figures 6.3). Between-subjects testing also revealed a statistically significant interactive effect of the combination of sediment pulse and substrate composition treatments on mean EPT drift density on the sampling occasion ‘after’ the sediment pulse ($F_{(2, 15)} = 4.19$, $p = 0.0358$). The results of the analysis of within-subjects show a statistically significant effect of the interaction of time with substrate composition treatment on mean EPT drift density, whilst the effect of the interaction of time with sediment pulse treatment was close to significant (Table 6.4).

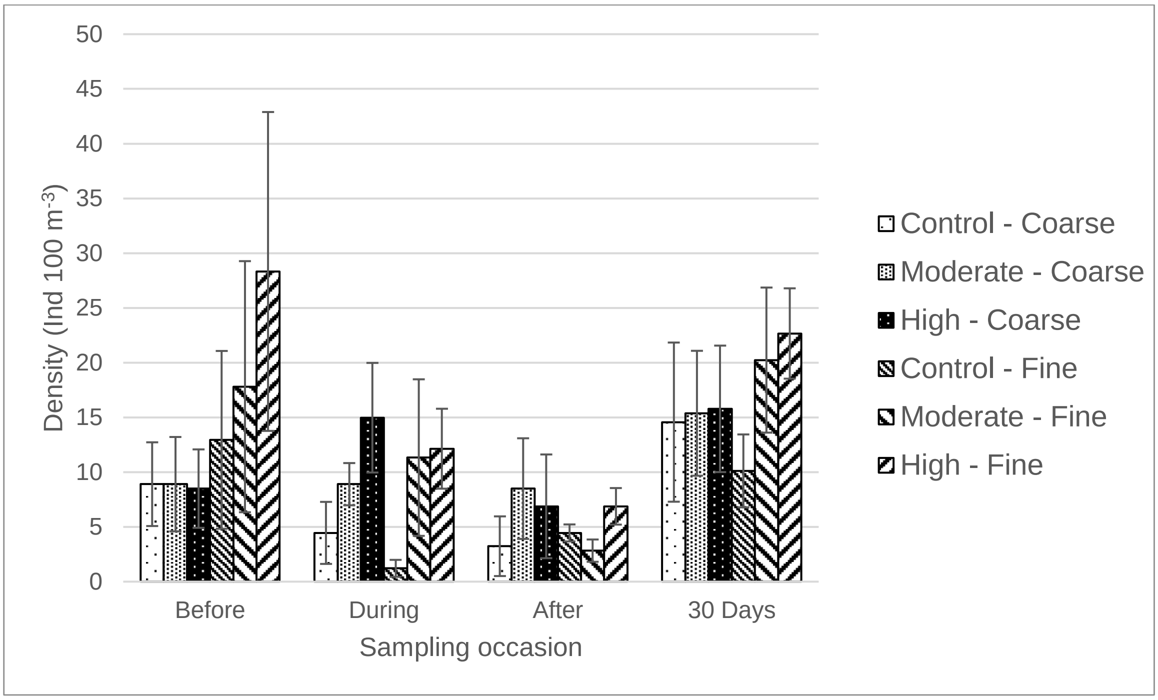

Figure 6.3 Influence of sediment pulse and substrate composition treatments on mean density (Ind 100m^{-3}; ±1 SE) of drifting EPT.

Table 6.4 Results of repeated measures ANOVA investigating the effects of substrate composition and sediment pulse treatments on mean EPT drift density across four sampling occasions. Significant results (p < 0.05) are indicated in bold.

Source	Degrees of freedom (*df*)	*F* value	*p* value
Time	3, 45	14.83	**<0.0001**
Time x Block	9, 45	2.71	**0.0129**
Time x Sediment Pulse	6, 45	2	0.0858
Time x Substrate Composition	3, 45	2.98	**0.0411**
Time x Sediment Pulse x Substrate Composition	6, 45	1.7	0.1442

Between-subjects analysis found that mean EPT drift taxonomic richness was significantly influenced by the sediment pulse treatment on the sampling occasion 'during' the fine sediment pulse (GLM: $F_{(2,\ 15)} = 4.54$, $p = 0.0287$). On this occasion, in both substrate composition treatments, mean EPT drift taxonomic richness was greatest in the channel sections subject to the 'high' sediment pulse treatment, followed by the 'moderate' sediment pulse treatment. The lowest mean

EPT drift taxonomic richness on this occasion was recorded from the channel sections subject to the ‘control’ sediment pulse treatment (Figure 6.4). Results of the repeated measures ANOVA analysing within-subjects effects on mean EPT drift taxonomic richness found no significant interaction of time with either sediment pulse or substrate composition treatments (Table 6.5).

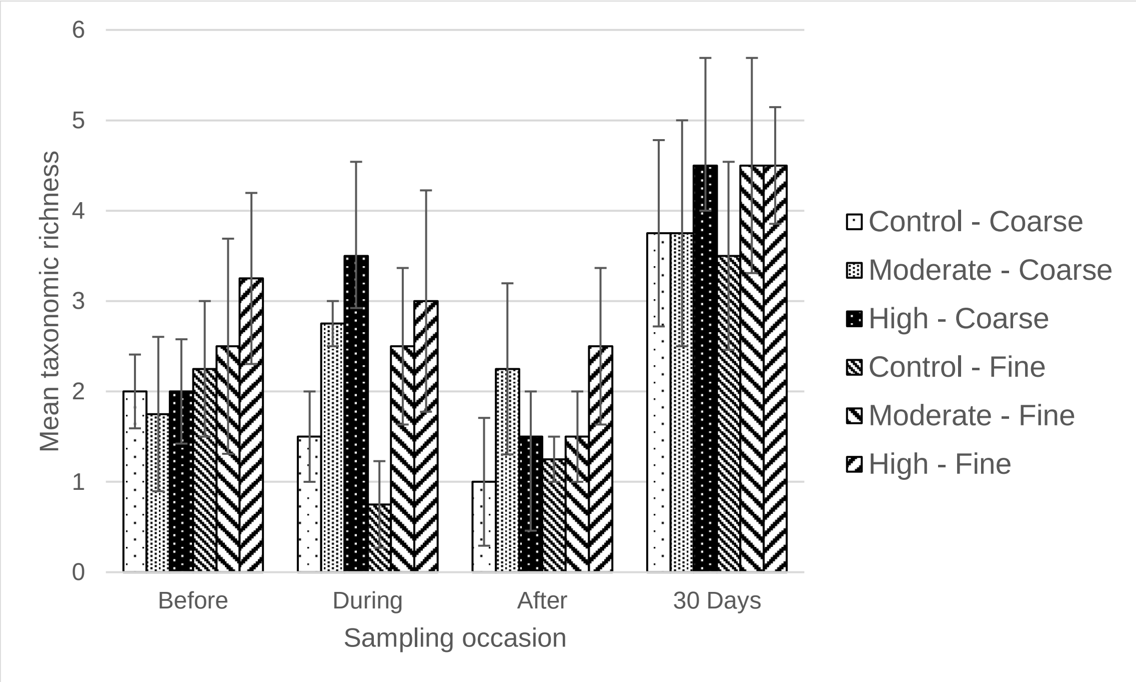

Figure 6.4 Influence of sediment pulse and substrate composition treatments on the mean taxonomic richness (±1 SE) of drifting EPT

Table 6.5 Results of repeated measures ANOVA investigating the effects of substrate composition and sediment pulse treatments on mean EPT taxonomic richness across four sampling occasions. Significant results (p < 0.05) are indicated in bold.

Source	Degrees of freedom (df)	F value	p value
Time	3, 45	13.37	**<0.0001**
Time x Block	9, 45	1.32	0.2538
Time x Sediment Pulse	6, 45	0.65	0.6921
Time x Substrate Composition	3, 45	0.81	0.4959
Time x Sediment Pulse x Substrate Composition	6, 45	0.36	0.9022

6.5.3. Taxonomic composition

The sediment pulse treatment was found to have a significant influence on the taxonomic composition of the drifting invertebrate assemblage (Table 6.6: Figure 6.5). No other statistically significant effects of any other factors of interest, or their interactions were detected (Figure 6.6). Further pair-wise tests found a significant difference in the taxonomic composition of the drifting invertebrate assemblage between the ‘control’ and ‘high’ sediment pulse treatments (p = 0.0188), but no significant differences between the ‘control’ and ‘moderate’ groups (p = 0.2863), or the ‘high’ and ‘moderate’ groups (p = 0.1432). SIMPER analysis showed that six drifting invertebrate taxa contributed up to 45 % of the significant difference between the ‘control’ and ‘high’ sediment pulse treatments. These taxa were: *G. pulex* (Gammaridae), Baetidae, *R. balthica* (Lymnaeidae), *Limnius volckmari* (Panzer, 1793: Elmidae), *Brachycentrus subnubilus* (Curtis, 1834: Brachycentridae) and *H. pellucidula* (Hydropsychidae). The mean abundances of these six taxa, on the sampling occasion ‘during’ the sediment pulse, were all higher in samples taken from the ‘high’ sediment pulse treatment than from the ‘control’ sediment pulse treatment.

Table 6.6 Results of a PERMANOVA examining the influence of sediment pulse and substrate composition treatments on the taxonomic composition of the drifting invertebrate community. Statistically significant results are highlighted in bold ($p < 0.05$).

Source	Degrees of freedom (*df*)	Sums of squares (*SS*)	Mean squares (*MS*)	Pseudo-*F* ratio	Permutation *p* (P(perm))	Unique permutations
Time	3	21864	7288.1	6.5159	**0.0001**	9897
Block	3	22490	7496.8	6.7025	**0.0001**	9906
Sediment pulse	2	3691.8	1845.9	1.6503	**0.0357**	9910
Substrate composition	1	450.96	450.96	0.40318	0.9369	9938
Time x Sediment pulse	6	5044.7	840.79	0.7517	0.9169	9838
Time x Substrate composition	3	3547.1	1182.4	1.0571	0.3988	9891
Sediment pulse x Substrate composition	2	1455	727.48	0.6504	0.8739	9913
Time x Sediment pulse x Substrate composition	6	5243.8	873.97	0.78137	0.8889	9849
Res	69	77177	1118.5			
Total	95	140970				

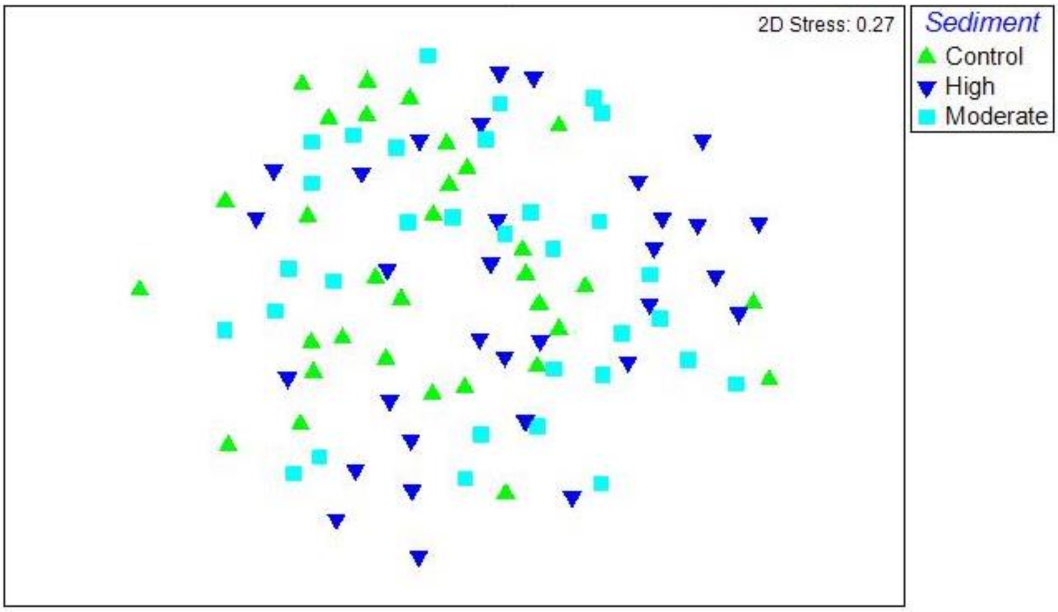

Figure 6.5 Results of the NMDS ordination of the taxonomic composition of the drift community delineated by sediment pulse treatment. A significant difference ($p < 0.05$) was detected between sediment pulse treatments.

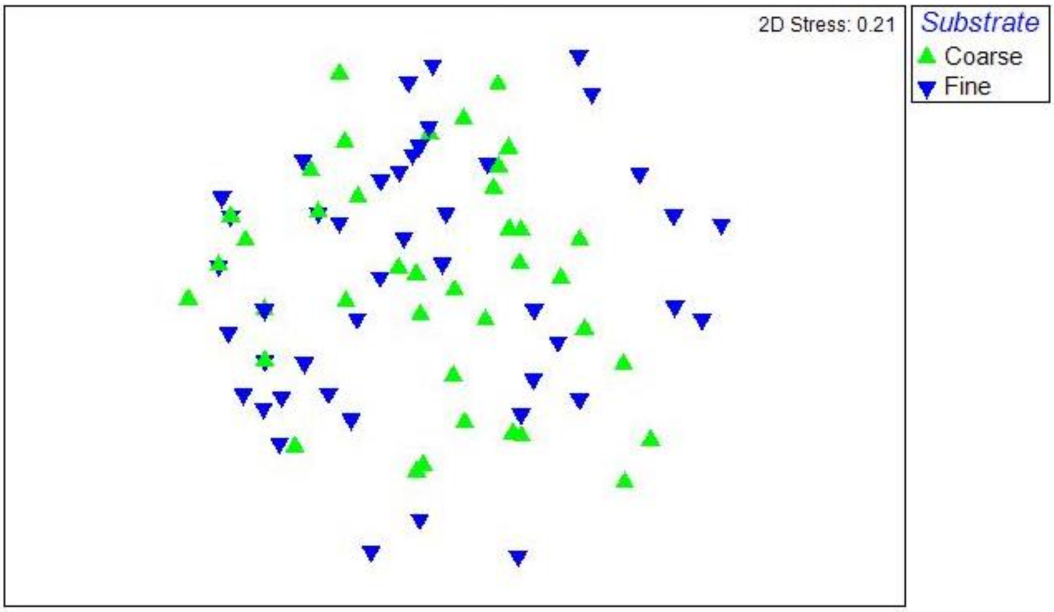

Figure 6.6 Results of the NMDS ordination of the taxonomic composition of the drift community delineated by substrate composition treatment. No significant difference was detected between substrate composition treatments.

Results of the PERMANOVA investigating the effects of a sediment pulse (Figure 6.7) and substrate composition treatments (Figure 6.8) on the taxonomic composition of the EPT drift community mirror the findings from the PERMANOVA analysis that investigated the entire invertebrate drift assemblage. The sediment pulse treatment was found to be the only statistically significant influence on taxonomic composition (Table 6.7).

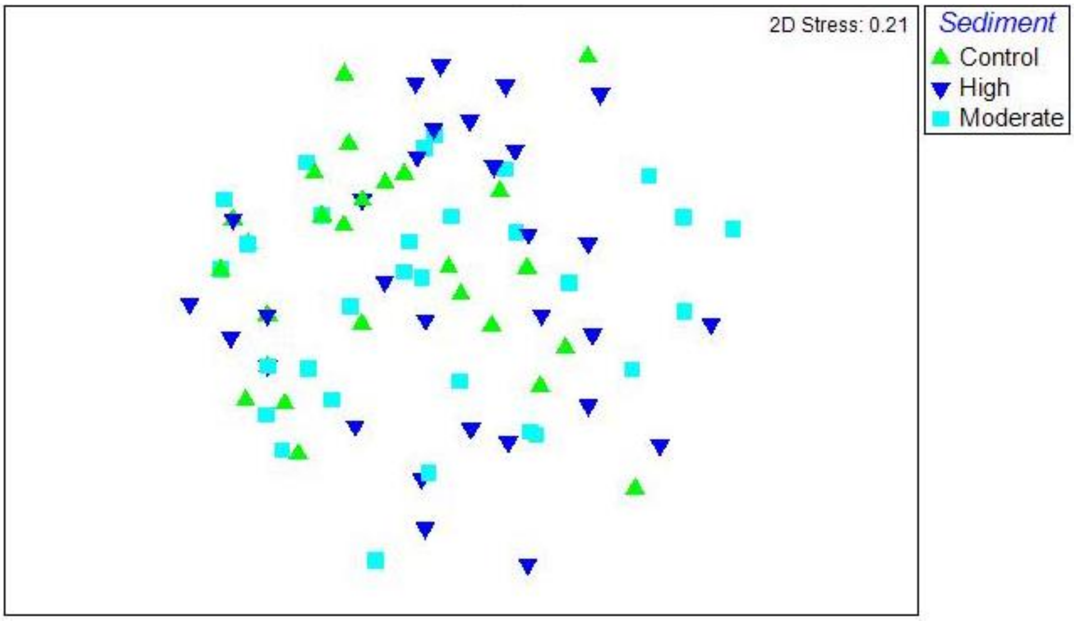

Figure 6.7 Results of NMDS ordination of the taxonomic composition of the EPT drift community delineated by sediment pulse treatment. A significant difference ($p < 0.05$) was detected between sediment pulse treatments.

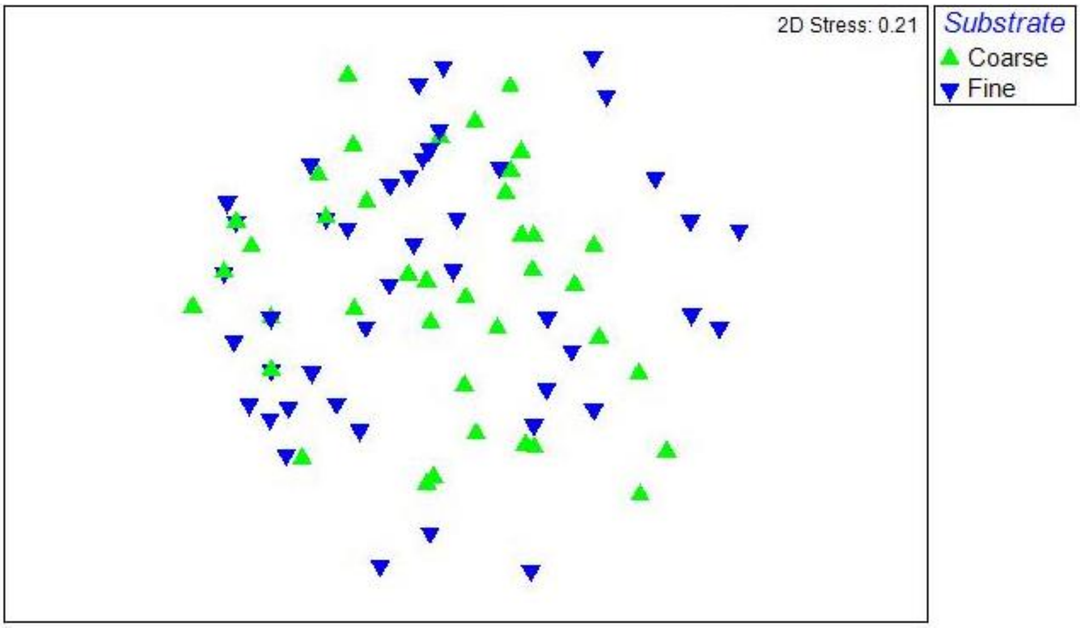

Figure 6.8 Results of NMDS ordination of the taxonomic composition of the EPT drift community delineated by substrate composition treatment. No significant difference was detected between substrate composition treatments.

Table 6.7 Results of PERMANOVA investigating the effect of sediment pulse and substrate composition treatments on the taxonomic composition of the EPT drift community. Statistically significant results have been highlighted in bold (p < 0.05).

Source	Degrees of freedom (*df*)	Sums of squares (*SS*)	Mean squares (*MS*)	Pseudo-*F* ratio	Permutation *p* (P(perm))	Unique permutations
Time	3	11211	3737.1	7.7097	**0.0001**	9934
Block	3	17066	5688.5	11.736	**0.0001**	9925
Sediment pulse	2	2419.3	1209.7	2.4956	**0.0156**	9947
Substrate composition	1	136.01	136.01	0.28059	0.8391	9969
Time x Sediment pulse	6	1536.4	256.07	0.52829	0.9417	9911
Time x Substrate composition	3	1503.2	501.07	1.0337	0.4202	9935
Sediment pulse x Substrate composition	2	557.93	278.97	0.57552	0.772	9948
Time x Sediment pulse x Substrate composition	6	2295.9	382.65	0.78942	0.7353	9889
Res	69	33446	484.72			
Total	95	70172				

6.5.4. Invertebrate trait analysis

RLQ axis 1 accounted for 51 % of the total co-inertia (describing the relationship between species traits and environmental variables), whilst RLQ axis 2 accounted for 32 %. The global test conducted as part of the fourth-corner analysis showed a significant influence of the environmental variables on species distribution (model 2; p = 0.0004), but found no significant relationship between functional traits and species distribution (model 4; p = 0.9506). Combined RLQ and fourth corner analysis did not find any significant associations between the RLQ axes and particular trait classes. No significant associations were found between RLQ axes and either sediment pulse or substrate composition treatments. No significant correlations between particular trait classes and environmental variables were found.

6.6. Discussion

6.6.1. Effect of sediment pulse on drift density, taxonomic richness and taxonomic community composition

The results of this experiment demonstrate that the fine sediment pulse significantly influenced the density, taxonomic richness and community composition of invertebrates drifting in the mesocosm channels. Also, the results suggest that the magnitude of the fine sediment pulse was related to the density of drifting invertebrates, as the 'high' sediment pulse treatment resulted in a greater mean density of drifting invertebrates than the 'moderate' sediment pulse treatment (Figure 6.1). As well as being consistent across the two substrate composition treatments investigated in this experiment, this result was also seen in the EPT taxa (although this would be expected as EPT are included in the data covering the whole assemblage). These findings support the hypothesis that a fine sediment pulse causes an increase in invertebrate drift and changes its taxonomic composition.

The results in this study are comparable with previous investigations, such as a study by Larsen and Ormerod (2010). Their study involved the experimental addition of fine sand to two replicate headwater streams (located in Wales, U.K.), in a before-after-control-impact design. Sediment addition was found to have a significant impact on drift density and drift propensity. The sediment addition treatment used by Larsen and Ormerod (2010) was 4-5 kg m^{-2}, whereas the 'moderate' treatment in the present study was higher, equating to 7.33 kg m^{-2} and the 'high' treatment equating to 14.66 kg m^{-2}. A further difference in the sediment treatments between the Larsen and Ormerod (2010) study and the present study were the types of fine sediment used; Larsen and Ormerod (2010) used children's play-sand, whereas the present study used fine sediment sourced from the Frome catchment. It may be that the differences in the physical characteristics of the fine sediment treatments influenced their effects on the invertebrates (e.g. if one fine sediment treatment was more abrasive than the other). The Usk catchment differs from the Frome catchment, which provided the pool of potential invertebrate colonisers in this study, in a number of ways: the Usk is an upland catchment which drains semi-natural rough pasture, whereas the Frome is a lowland catchment mostly draining agricultural land, consisting of cereal crops and grazed pasture. Despite these differences, the response of drift density to the addition of fine sediment was broadly similar. Larsen and Ormerod (2010) recorded an average increase of 15 individuals drifting per 100 m^3, following sediment addition. This compares with the present study which identified an average of 16 extra individuals drifting per 100 m^3 from the 'coarse' substrate composition treatment and an average of 36 extra individuals drifting per 100 m^3 from the 'fine' substrate composition treatment.

In a natural setting, increases in discharge often lead to the increased mobilisation and subsequent transport of fine sediment, so field studies investigating the effects of increased concentrations of fine sediment on invertebrate drift may be confounded by the accompanying increases in discharge, which may have an effect on invertebrate drift in their own right (Gibbins *et al*., 2007). This mesocosm study allowed a constant rate of discharge to be maintained throughout the experiment, which allows for the conclusion that the increases in drift density and taxonomic richness which were recorded were caused by the fine sediment pulse rather than any change in discharge.

The sediment pulse treatment significantly influenced the taxonomic richness of drifting invertebrates on the sampling occasion 'during' the sediment pulse. As hypothesised, taxonomic richness was significantly higher in drift samples subject to the 'high' sediment pulse treatment across both substrate composition types. It appears that the sediment pulse changed benthic conditions enough to make them intolerable for some taxa. Amongst these taxa are some which are capable of using drift to escape this localised pressure. As conditions deteriorated, less individuals of these taxa may no longer have been present in benthic samples, leading to a decrease in benthic taxonomic richness, rather appearing in drift samples, increasing their taxonomic richness. In samples taken from the ‘fine’ substrate composition treatment, there appeared to be a clear relationship between sediment pulse magnitude and taxonomic richness, with the ‘high’ sediment pulse treatment resulting in the greatest taxonomic richness of drift samples, followed by the ‘moderate’ sediment pulse treatment and then the ‘control’ sediment pulse treatment. This pattern was not repeated in the drift samples taken from the ‘coarse’ substrate composition treatment where the lowest taxonomic richness was instead recorded from the ‘moderate’ sediment pulse treatment. These differences in results obtained from the two substrate composition treatments may reflect the fact that the ‘coarse’ substrate composition treatment was able to ameliorate some of the negative effects of the sediment pulse, to some degree, possibly by absorbing more of the deposited sediment into the substrate, or possibly by offering a better refugium. This may have meant that the ‘moderate’ sediment pulse in the ‘coarse’ substrate composition treatment did not have the same magnitude of effect on taxonomic richness as the same level of sediment pulse in the ‘fine’ substrate composition treatment.

The effect of the fine sediment pulse on the density and taxonomic richness of drifting invertebrates appears to have been short-lived. Although an effect was detected in the drift samples taken in the 24 h immediately following the fine sediment pulse, no significant effect was detected in the next 24 h period, or 30 days after the pulse. This finding means that whichever mechanism, or mechanisms, are responsible for the increases in drift and taxonomic richness following a fine sediment pulse, they must begin relatively quickly (within the first 24 h of exposure) and end with equal rapidity. Due to the nature of the sediment pulse simulated in this experiment, and the relatively low flow rate maintained in the mesocosm channels, much of the fine particles constituting the sediment pulse were deposited on the channel bed as the sediment pulse travelled downstream in the mesocosm channels. Hence, the invertebrates may have been responding to a number of different potential aspects of the fine sediment pulse, aspects either associated with increased suspended sediment, or increased sediment deposition, or a combination of the two. In their 2010 study, Larsen and Ormerod found that drift responses to fine sediment addition were not immediate, beginning in the first period of darkness following sediment addition; a finding also reported in other, similar experiments (e.g. Rosenberg and Wiens, 1978; Fairchild *et al*., 1987) and a finding which is in keeping with the knowledge that invertebrate drift behaviour usually follows a crepuscular pattern (Neale *et al.*, 2008). This led them to the conclusion that the invertebrates were avoiding the fine sediment induced changes to their habitat, rather than responding immediately in a form of behavioural displacement. In addition to a response to changed habitat conditions, invertebrates have also been seen to enter the drift immediately in response to saltating sand particles (Culp *et al.*, 1986), something which may have also occurred in the present study. The results from the present study suggest that these responses peaks in the first 24 h period following increases in fine sediment. This may indicate that during this 24 h period, any sediment sensitive invertebrates which have the ability, will initiate drifting behaviour leaving behind only invertebrates which are either tolerant of the new habitat or incapable of extricating themselves.

The PERMANOVA analysis showed a statistically significant difference in the taxonomic composition of the drifting invertebrate assemblage between sediment pulse treatments. This reflects the differing sensitivities and behavioural responses of particular invertebrate taxa in response to increases in fine sediment. Of the six taxa identified by SIMPER analysis as being most responsible for differences in the composition of the drifting invertebrate assemblage between the ‘control’ and ‘high’ sediment pulse groups, some taxa are known as being sensitive to fine sensitive stress, such as Baetidae, *B. subnubilus* (Brachycentridae) and *H. pellucidula* (Hydropsychidae), so their presence in the drift would be expected to increase in response to the fine sediment pulse. However, some of the other taxa identified by SIMPER, such as *G. pulex* (Gammaridae), *R. balthica* (Lymnaeidae) and *L. volckmari* (Elmidae) have previously been identified as being relatively tolerant to fine sediment stress, so their increased numbers in the drift from the ‘high’ sediment pulse treatment when compared with the 'control' sediment pulse treatment requires some further explanation. One plausible reason for the increased drift of *G. pulex* (Gammaridae) and *L. volckmari* (Elmidae) in response to the fine sediment pulse is that they are relatively mobile taxa. Although they are able to tolerate fine sediment, and are often common in rivers with high amounts of fine sediment, once the habitat quality begins to decrease due to the fine sediment pulse their mobility allows them to enter the drift to find a more optimal habitat. The increased drift responses of *G. pulex* (Gammaridae) and *L. volckmari* (Elmidae) in response to experimental fine sediment additions have also been recorded in studies by Suren and Jowett (2001) and Larsen and Ormerod (2010).

6.6.2. Effect of substrate composition treatment on drift density, taxonomic richness and taxonomic community composition

The influence of substrate composition treatment on drift density and taxonomic richness was not as clear as that of the sediment pulse treatment, with the analysis detecting no significant influence on either the density, taxonomic richness, or the taxonomic composition of the drift assemblage. However, when looking only at the EPT taxa, which may be thought of as being generally more sensitive to fine sediment stress than other taxa (Kaller and Hartman, 2004), the influence of substrate composition treatment becomes more influential. Before the sediment pulse treatment was applied, EPT drift density was significantly greater in the 'fine' substrate composition treatment than the 'coarse'. This may reflect the differences in interstitial space between the two substrate composition treatments. As the 'coarse' substrate offered a greater amount of interstitial habitat this may have reduced the need for invertebrates to initiate drifting behaviour to find new habitat to colonise, whereas the 'fine' substrate had only a limited amount of interstitial habitat available, making it more likely that invertebrates would need to drift to reach a new habitat to colonise.

The interaction of substrate composition treatment with sediment pulse treatment significantly influenced EPT drift density on the sampling occasion 'after' the sediment pulse had been applied. On this occasion, no individual effects of either sediment pulse or substrate composition treatments were detected, only their interaction. The interactive effect of these two treatments on this occasion are hard to interpret and no obvious pattern was discernible from looking at the mean EPT drift densities (Figure 6.3).

Repeated-measures ANOVA detected a significant influence of the interaction of time with substrate composition treatment on EPT drift density over the course of the experiment. This indicates that substrate composition differences did have a significant effect on EPT drift density over the course of the experiment. The increase of 27 % in the mean drift density of EPT taxa from the 'fine' substrate composition treatment when compared with the 'coarse' substrate composition treatment over the course of the experiment provides evidence for the view that the general drift response of EPT taxa is affected by substrate composition (Holomuzki, 1996) and it may be likely that it was the differences in interstitial space between 'coarse' and 'fine' substrates which was driving this difference, as discussed earlier. However, this study did not find any direct evidence to show that the particular drifting behaviour seen in response to the sediment pulse was affected by differences in substrate composition.

6.6.3. Influence of sediment pulse treatment and substrate composition on invertebrate traits

The trait analysis detected no influence of either sediment pulse or substrate composition treatment on the prevalence of certain invertebrate traits within the drifting invertebrate assemblage. There are a number of potential explanations for this finding which may merit further study. One of the problems experienced when conducting the trait analysis as part of this investigation relates to the scope of information on invertebrate traits which is currently available. Although information was gleaned from three different trait databases for this analysis, out of the 62 drift taxa identified there was only trait information available for 44 of them, resulting in 29 % of the total number of recorded taxa not being represented in the trait analysis. Furthermore, there are some doubts regarding the accuracy of some of the trait information contained in the trait databases, so some researchers have advised caution when relying on them for analyses and have called for more work to be put in to the production of these resources (Buendia *et al.*, 2013; Descloux *et al.*, 2014; Mathers *et al*., 2017). A further potential reason for the lack of a detectable trait-mediated response to either of the two treatments examined in this study may be due to the method of analysis used. Although a combined RLQ and Fourth-corner analysis has been used successfully in a number of trait studies (e.g. Wesuls *et al.*, 2011; Lindo *et al.*, 2012; Oldeland *et al.*, 2012; Dray *et al.*, 2014; Murphy *et al.*, 2017), it is unable to consider interactions between treatments in its analysis, so it may have missed some potential interactive effects between treatments which may have been expected to have an influence on trait prevalence within this study.

6.7. Summary

The results detailed in this chapter show a clear increase in invertebrate drift in response to increased fine sediment amounts. This demonstrates that some invertebrate taxa enter the drift in response to a fine sediment pulse, but it is not clear from this study whether this is active or passive behaviour. Prior fine sediment deposition, and its effect on the substrate, has also been shown to influence the drift response of EPT taxa. In addition, the data clearly shows that the increased drift of invertebrates in response to a fine sediment pulse peaks in the first 24 h following exposure and is not detectable 30 days later. These are important findings and highlight the fact that the drift response of invertebrates to increased fine sediment should not be considered in isolation from the other factors identified in this chapter (e.g. substrate characteristics and fine sediment-sensitivities). This study also supports the idea that it is important to consider the taxon-specific drift response of individual invertebrate taxa when assessing the effects of fine sediment on the invertebrate assemblage as a whole.

7. The hyporheic zone as an invertebrate refuge during a fine sediment disturbance

7.1. Introduction

The hyporheic zone is the region of saturated sediments which form the direct interface between groundwater and surface water in rivers and streams (Environment Agency, 2009). The boundaries of this zone are governed by local sediment structure and hydrological dynamics, so may vary spatially and temporally (Jones *et al*., 2015). Complex hydrological exchanges occur at this interface, facilitating the transfer of nutrients, organic matter and invertebrates between surface water and ground water environments (Williams *et al.*, 2010). This leads to a dynamic environment, which is often distinct from both groundwater and surface water in terms of its physiochemical properties, and may be characterised by significant physicochemical gradients (Triska *et al*., 1993). The hyporheic zone is also a location of redox reactions, where dissolved oxygen, dissolved organic carbon and nutrients, supplied by downwelling water, enable high rates of transformation and biogeochemical activity (Boulton *et al*., 1998; Krause *et al*., 2008).

The hyporheic zone provides a number of ecosystem services in freshwater environments, such as aiding the retention and processing of organic matter (Drummond *et al.,* 2014), thermoregulation (Hester and Gooseff, 2010), pollutant attenuation (Hester and Gooseff, 2010; Drummond *et al.*, 2014), and housing the microbial community which performs many of the biogeochemical processes (e.g. methanogenesis, nitrification, denitrification etc.) necessary for a functioning freshwater ecosystem (Mendoza-Lera and Datry, 2017). The microbial community found in the hyporheic zone represents the majority of activity and biomass in lotic ecosystems, and may constitute up to 96 % of the total respiration (Naegeli and Uehlinger, 1997; Pusch *et al.*, 1998; Fischer and Pusch, 2001). Aquatic plants use the hyporheic environment as a rooting zone (Madsen *et al.*, 2001), many salmonid fish species use it for spawning (DeVries, 1997) and it is inhabited by both hypogean and benthic invertebrate species (Richards and Bacon, 1994; Stubbington, 2012).

The organisms present in the hyporheic zone have been classified into three different groups (Gilbert *et al.,* 1994). Stygoxenes have no affinity for groundwater habitats and are only present accidentally due to passive dispersal processes. Stygophiles actively utilise the available habitat and exploit its resources, showing a greater affinity for the hyporheic environment than Stygoxenes. Stygophiles may themselves be broadly divided into three groups, those that make only occasional use of the hyporheos (typically early instars of invertebrates which transition to benthic habitats later in their development cycle), those which require access to both surface water and hyporheic habitats during their development, and permanent members of the hyporheos (invertebrates found in the hyporheic zone during all stages of their life, although they may be also capable of living in benthic habitats for some of these life stages). The final classification is for organisms which are typically restricted to, and adapted for, life in subterranean ground water. They are known as Stygobites and are permanent residents of the hyporheic zone, as well as deeper subterranean aquatic habitats such as caves and aquifers. The invertebrate communities in the majority of lotic hyporheic environments are dominated by meiofauna (defined operationally as organisms in the 50–500 μm size range: Fenchel, 1978), a group which includes tardigrades, rotifers, nematodes, microcrustaceans and small oligochaetes (Hakenkamp and Palmer, 2000). Invertebrates are typically less abundant than the meiofauna in hyporheic environments, with communities being dominated by Crustacea (such as Isopoda and Amphipoda), mayfly and stonefly nymphs, and other insects (Boulton, 2008).

Research has been carried out into the use of the hyporheic zone as a refuge for benthic invertebrates during flood events (e.g. Clifford, 1966; Williams and Hynes, 1974; Dole Olivier *et al*., 1997; Gayraud *et al*., 2000; Holomuzki and Biggs, 2000; Boulton *et al*., 2004), surface freezing (Orghidan, 1959), to escape rising water temperatures (e.g. Evans and Petts, 1997; Wood *et al.*, 2010; Vander

Vorste *et al.*, 2017), to shelter from pollution (e.g. Jeffrey *et al.*, 1986; Belaidi *et al.*, 2004), following streambed drying (e.g. Imhof and Harrison, 1981; Delucchi, 1989; Clinton *et al*., 1996; Maazouzi *et al*., 2017; Vadher *et al.*, 2017; Vadher *et al.*, 2018a), and during low flows (e.g. James *et al*., 2008; Wood *et al*., 2010; Stubbington *et al*., 2011). Stubbington (2012) and Dole-Olivier (2011) have each reviewed the available research examining the ability of the hyporheic zone to act as a refuge for benthic invertebrates during disturbances in the surface stream (the 'hyporheic refuge hypothesis'), with both authors finding that evidence to support the hypothesis is equivocal. Although the hypothesis is supported in a number of studies, this result is not consistent across the literature. This led both authors to the conclusion that the hyporheic zone may indeed act as a refuge, but not for all taxa and only if the habitat meets their needs. Also, Stubbbington (2012) concluded that the ability of the hyporheic zone to form a refuge is dependent upon the characteristics of the disturbance. At present, there is limited knowledge on the ability of the hyporheic zone to form a refuge from pressure caused by excessive suspended fine sediment concentrations and this is a research gap which the present study has addressed.

One of the largest influences on the ability of the hyporheic zone to function as either a permanent habitat or a temporary refuge for invertebrates is the composition of the sediment. This characteristic affects the interstitial architecture, porosity and permeability of the substrate (Stubbington, 2012). These factors determine the volume of interstitial space inhabitable by invertebrates, and the spatial arrangement and size of the networks available to move within the substrate (Stubbington, 2012). In situations where fine material begins to dominate the stream bed, surface sediments become clogged with silt, a process known as colmation (Boulton, 2007). The sealed interstices limit access to the hyporheic zone and also limit the refugial space available for invertebrates (Brunke, 1999; Descloux *et al.*, 2013), which can increase the impacts of anthropogenic and natural disturbances (Borchardt and Statzner, 1990). This indicates that the capability of the hyporheic zone to function as a refuge for invertebrates from the impacts of a pulse of fine sediment may be hampered if it has previously been subject to a high loading of fine sediment, resulting in a colmated substrate. This issue has recently been studied in work by Vadher *et al.* (2015, 2018b) who used a series of mesocosm experiments to examine whether the vertical migration of *G. pulex* (Gammaridae) was impeded by fine sediment. In their experiments, the authors found that increasing the volume of fine sediment within the substrate resulted in a significant decrease in animals migrating downwards and a significant increase in animals becoming stranded on the substrate surface, unable to escape the disturbance.

7.2. Research aims

The present study investigated the effects of initial stream bed sediment conditions on the use of the hyporheic zone by invertebrates whilst experiencing pressure caused by excessive fine sediment concentrations. This information will be useful in furthering the understanding of how invertebrate communities respond to fine sediment pressures in different stream types and to help to distinguish between the effects of chronic and acute fine sediment stress. Information on these responses will be vital for environmental managers and legislators when considering how to tailor fine sediment control strategies for different lotic freshwater environments. This study is unique in that the response of the hyporheic and drifting invertebrate assemblages to a fine sediment pulse were assessed in tandem. The following hypotheses were tested:

- Increased suspended fine sediment concentration will result in increased abundance and taxonomic richness of hyporheic invertebrates.
- Invertebrate abundance and taxonomic richness in the hyporheos will increase in response to the fine sediment pulse to a greater extent in the ‘coarse’ than the ‘fine’ substrate composition treatment.
- Increased suspended fine sediment concentration and differences in substrate characteristics will influence the taxonomic composition of the hyporheic invertebrate assemblage.

7.3. Method

A description of the study area is located in Chapter 3, Section 3.1. The methods used in this investigation are given in further detail in Chapter 3, Section 3.2. Hyporheic sampling was carried out on the day prior (‘before’), ‘during’, 24 h ‘after’ and ‘30 days’ after the fine sediment pulse. Hyporheic samples were taken from depths of 5 and 18 cm. Sampling was achieved through the collection of 500 mL of water from the sampling tube, which was then sieved through a 250 µm mesh. Invertebrates were then preserved in 99 % IMS, prior to their identification to the lowest taxonomic level possible.

Data analysis

7.3.1. Hyporheic abundance and taxonomic richness

The abundance and taxonomic richness of hyporheic invertebrate assemblages were analysed to determine if they had been influenced by the sediment pulse and substrate composition treatments. Prior to analysis, invertebrate abundances were $\log_{10}(x+1)$ transformed to ensure homoscedasticity and to account for the samples with zero recorded invertebrates. Abundance and taxonomic richness data from the samples taken at a depth of 5 cm and 18 cm were analysed separately. Repeated-measures ANOVA was then employed on the four separate data sets (abundance data recorded from depths of 5 cm and 18 cm and taxonomic richness data recorded from depths of 5 cm and 18 cm), incorporating ‘block’ (a blocking factor employed to account for any possible effect caused by differences between blocks of mesocosm channels), ‘sediment pulse’ and ‘substrate composition’ as between-subjects factors and ‘time’ (consisting of three levels: ‘before, ‘during’ and ‘after’) as the within-subjects factor. The general linear (GLM) model employed for this analysis had the ability to also examine any interactive effects caused by a combination of these factors. The GLM procedure in the SAS 9.4 statistics package was used for this analysis.

7.3.2. Taxonomic composition of the hyporheic invertebrate community

To investigate any differences in the taxonomic composition of the hyporheic invertebrate community caused by either sediment pulse or substrate composition treatments, or their interaction, a PERMANOVA was used. The hyporheic invertebrate communities at 5 cm and 18 cm depths were examined separately as part of this analysis, with the same PERMANOVA model used for both analyses. The model used for the PERMANOVA incorporated 'time', 'sediment pulse' and 'substrate composition' as fixed factors. 'Block' was treated as a random factor and was included to factor out any differences due to the particular mesocosm block from which a sample was taken. Each mesocosm section was assigned a 'Section' number, which was also included as a random factor, nested within 'block', 'sediment' and 'substrate'. Prior to analysis, invertebrate abundances were $\log_{10}(x + 1)$ transformed to account for samples which contained zero invertebrates and to ensure homoscedasticity. The PERMANOVA was performed, using 9999 permutations, on a matrix of similarities derived from the Bray-Curtis distance between samples. A dummy variable of one was added to all samples when computing Bray-Curtis distances to account for any samples where zero invertebrates of any taxonomic group had been recorded. Following this analysis NMDS, utilising 50 random starts and based on the Bray-Curtis resemblance matrix, provided a visual display of the PERMANOVA results. If any significant treatment effects were found, a similarity percentages (SIMPER) routine was used to identify the taxa responsible for the observed differences between treatments. This multivariate analysis was completed using PRIMER 6 and the PERMANOVA+ add-on (Anderson *et al.*, 2008).

7.4. Results

7.4.1. Hyporheic abundance and taxonomic richness

A total of 1,126 invertebrates were identified from the hyporheic samples, from 29 taxonomic groups (Table 7.1).

Table 7.1 The 22 most abundant taxa recorded from the hyporheic samples taken in this study. The remaining 8 taxa recorded from samples, but not listed here, account for <1 % of the total hyporheic invertebrates recorded.

Taxa	Percentage of total hyporheic invertebrates recorded
Crangonyx pseudogracilis (Crangonyctidae)	25.67
Cyclopoida	21.49
Asellus aquaticus (Asellidae)	9.68
Tanypodinae (Chironomidae)	8.97
Ostracoda	7.02
Tanytarsini (Chironomidae)	5.51
Gammarus pulex (Gammaridae)	4.97
Oligochaeta	4.80
Daphniidae	4.71
Diamesinae (Chironomidae)	1.42
Leptophlebiidae	0.89
Sericostoma personatum (Sericostomatidae)	0.89
Ephemera danica (Ephemeridae)	0.62
Hydracarina	0.44
Leuctra inermis (Leuctridae)	0.36
Oribatida	0.36
Polycelis nigra/tenuis (Planariidae)	0.36
Helophoridae	0.27
Leuctra hippopus/mosleyi (Leuctridae)	0.27
Limnius volckmari (Elmidae)	0.27
Hydraenidae	0.18
Stratiomyidae	0.18

7.4.2. Abundance and taxonomic richness at 5 cm depth

The mean abundance of hyporheic invertebrates at 5 cm depth was significantly influenced by the sediment pulse treatment during the fine sediment pulse (GLM: $F_{(2, 39)} = 3.25$, $p = 0.0494$). On this occasion, samples taken from the 'coarse' substrate composition treatment had a greater mean abundance of invertebrates from channel sections subject to the ‘high’ sediment pulse treatment, followed by the ‘control’ sediment pulse treatment, with the ‘moderate’ sediment pulse treatment yielding the lowest mean invertebrate abundance (Figure 7.1). Samples taken from the ‘fine’ substrate composition treatment on this sampling occasion showed the greatest mean abundance of invertebrates from the ‘high’ sediment pulse treatment, followed by the ‘moderate’ sediment pulse treatment. Samples taken from the channel sections subject to the ‘control’ sediment pulse treatment contained the lowest mean abundance of invertebrates on this sampling occasion (Figure 7.1).

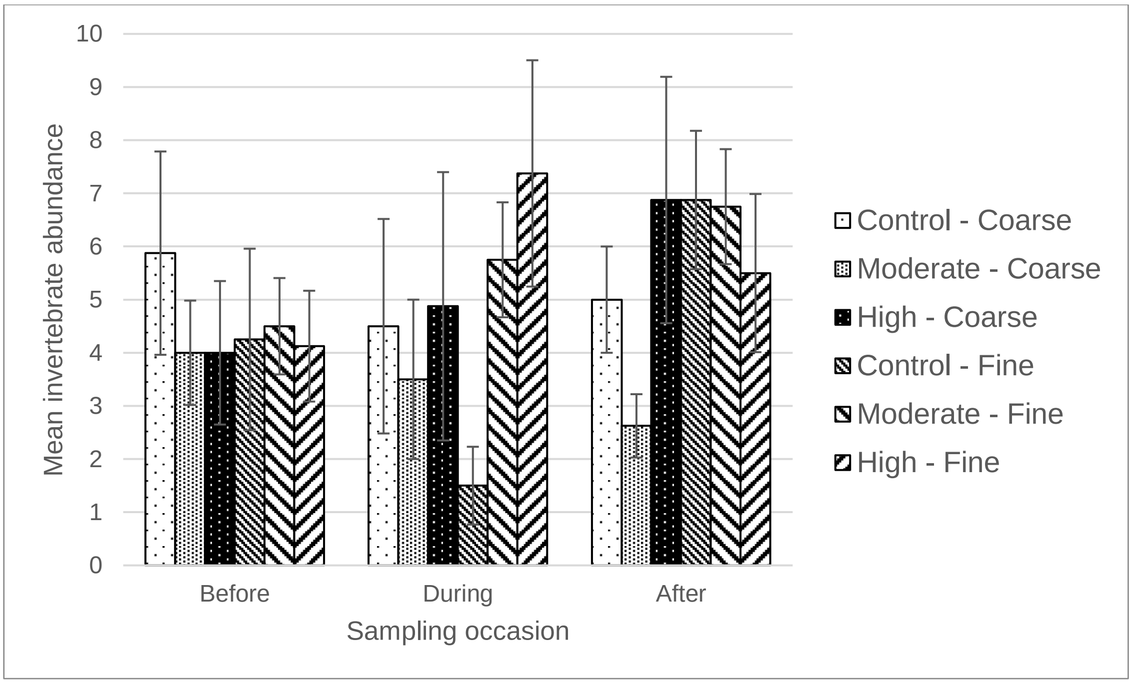

Figure 7.1 Influence of sediment pulse and substrate composition treatments on mean abundance (±1 SE) of hyporheic invertebrates at a depth of 5 cm.

Results from the repeated measures ANOVA examining within-subjects effects found no significant influence of sediment pulse or substrate composition treatments, or their interaction with time, on mean invertebrate abundance (Table 7.2). The effect of the interaction of time with sediment pulse is near to significant (Table 7.2).

Table 7.2 Results of the repeated measures ANOVA examining the effect of substrate composition and sediment pulse treatments on mean hyporheic invertebrate abundance at a depth of 5 cm across three sampling occasions.

Source	Degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	3.03	0.054
Time x Block	6, 78	1.5	0.1894
Time x Sediment Pulse	4, 78	2.06	0.0937
Time x Substrate Composition	2, 78	1.1	0.3374
Time x Sediment Pulse x Substrate Composition	4, 78	1.05	0.3864

The mean taxonomic richness of hyporheic invertebrates at 5 cm depth was found to be significantly influenced by the interaction of sediment pulse treatment and substrate composition treatment during the fine sediment pulse (GLM: $F_{(2, 39)} = 3.65$, $p = 0.0353$). On this occasion, mean taxonomic richness in the samples taken from the 'coarse' substrate composition treatment was highest in samples subject to the 'control' sediment pulse treatment (Figure 7.2), whereas in the samples taken from the 'fine' substrate composition treatment, taxonomic richness was joint highest in samples taken from both 'high' and 'control' sediment pulse treatments (Figure 7.2).

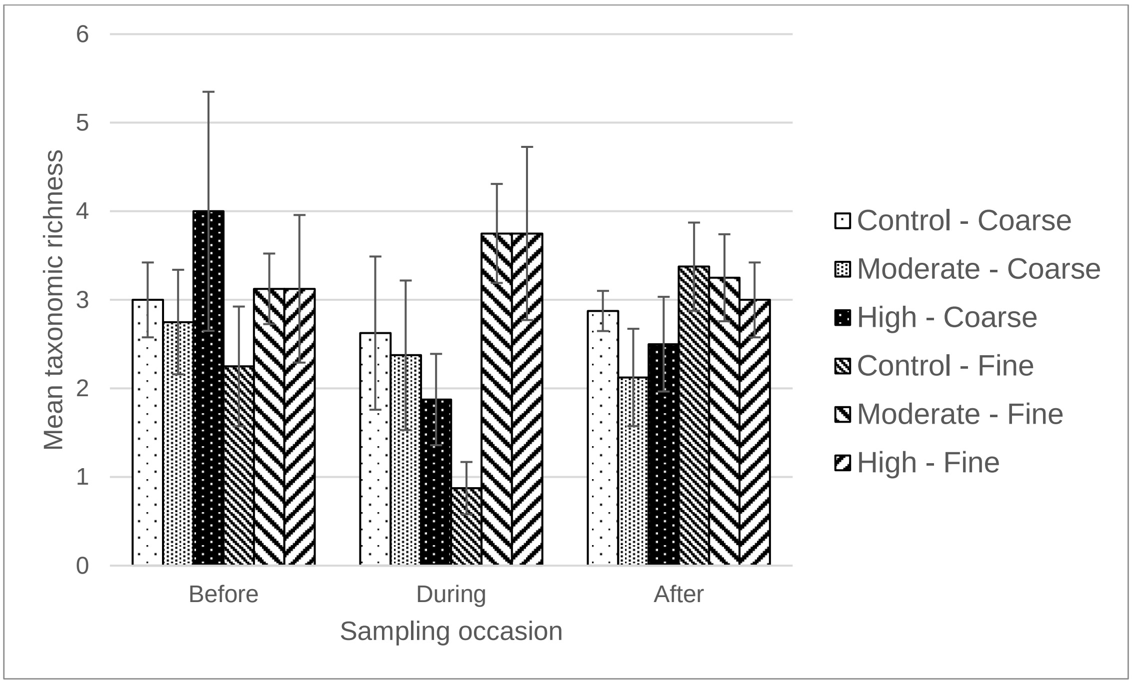

Figure 7.2 Influence of sediment pulse and substrate composition treatments on mean taxonomic richness (±1 SE) at a depth of 5 cm.

Analysis of within-subjects effects did not find any significant influence of time in interaction with either sediment pulse or substrate composition treatments on mean hyporheic taxonomic richness at 5 cm depth; these results are detailed in Table 7.3.

Table 7.3 Results of the repeated-measures ANOVA investigating the effect of sediment pulse and substrate composition treatments on hyporheic taxonomic richness, at a depth of 5 cm.

Source	Degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	0.43	0.6505
Time x Block	6, 78	1	0.4296
Time x Sediment Pulse	4, 78	1.16	0.335
Time x Substrate Composition	2, 78	0.4	0.6714
Time x Sediment Pulse x Substrate Composition	4, 78	1.2	0.319

7.4.3. Abundance and taxonomic richness at 18 cm depth

Analysis of between-subjects effects found a significant influence of substrate composition treatment on mean hyporheic invertebrate abundance at 18 cm depth, on the sampling occasion 'before' the sediment pulse (GLM: $F_{(1, 39)} = 4.68$; $p = 0.0367$). On this occasion, mean invertebrate abundance at 18 cm depth was greater in the samples taken from channel sections subject to the 'coarse' substrate composition treatment (Figure 7.3) than channel sections subject to the 'fine' substrate composition treatment (Figure 7.3).

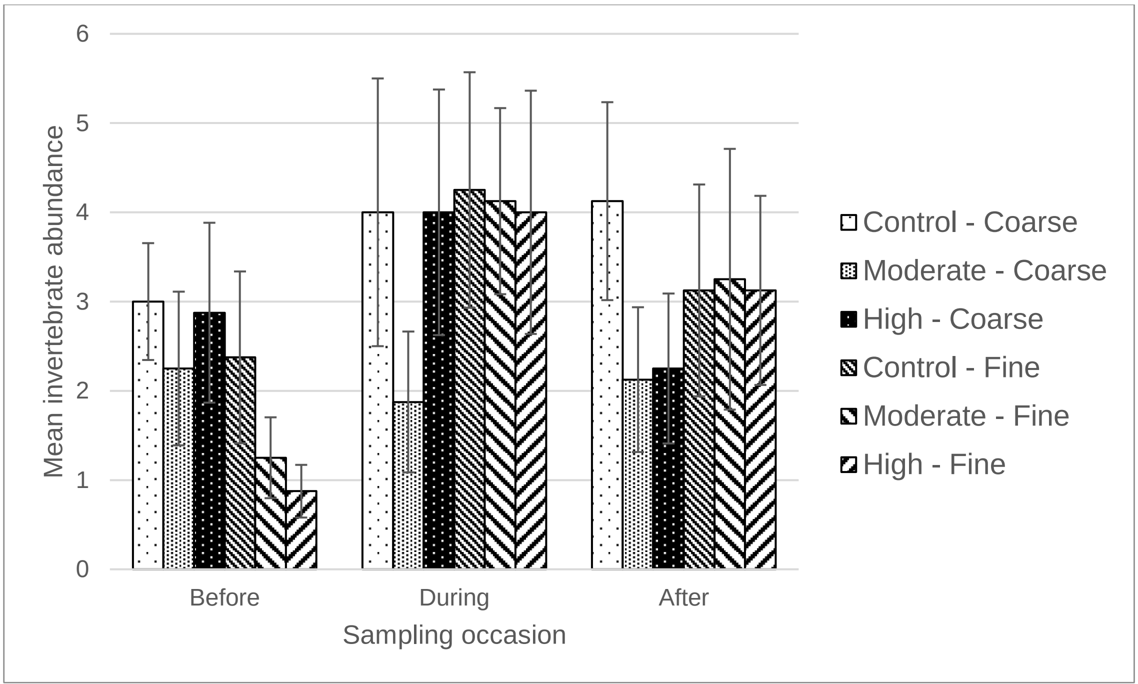

Figure 7.3 Influence of sediment pulse and substrate composition treatments on mean abundance (±1 SE) of hyporheic invertebrates at a depth of 18 cm.

Analysis of within-subjects effects using a repeated-measures ANOVA found no significant influence of the interaction of time with either sediment pulse, or substrate composition treatments, on mean hyporheic invertebrate abundance at 18 cm depth (Table 7.4).

Table 7.4 Results of the repeated-measures ANOVA examining the effect of substrate composition and sediment pulse treatments on mean hyporheic invertebrate abundance across three sampling occasions, at a depth of 18 cm. Significant results (p < 0.05) are indicated in bold.

Source	Degrees of freedom (df)	F value	p value
Time	2, 78	3.51	**0.0346**
Time x Block	6, 78	1.97	0.0803
Time x Sediment Pulse	4, 78	0.21	0.9306
Time x Substrate Composition	2, 78	3.05	0.0528
Time x Sediment Pulse x Substrate Composition	4, 78	1.01	0.4077

Analysis of within-subjects effects found no significant influence of either sediment pulse or substrate composition treatments, or their interaction, on the mean taxonomic richness of the hyporheic invertebrate assemblage at a depth of 18 cm. There was no discernible pattern in hyporheic taxonomic richness at a depth of 18 cm (Figure 7.4). Within-subjects testing, using a repeated-measures ANOVA, also found no significant influence of the interaction of time with either sediment pulse or substrate composition treatments, or their interaction, on hyporheic taxonomic richness at a depth of 18 cm (Table 7.5). Repeated-measures ANOVA did find that the interactive effect of time and substrate composition treatment on taxonomic richness was near to significant (Table 7.5).

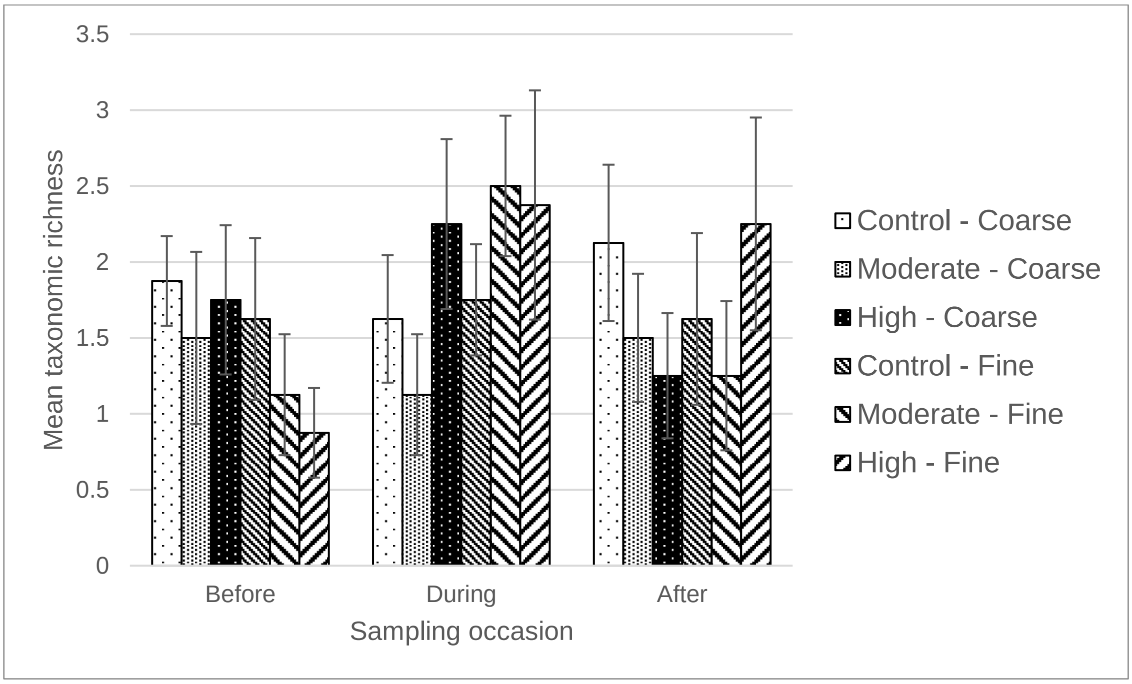

Figure 7.4 Influence of sediment pulse and substrate composition treatments on mean taxonomic richness (±1 SE) at a depth of 18 cm.

Table 7.5 Results of the repeated-measures ANOVA examining the effect of substrate composition and sediment pulse treatments on mean hyporheic invertebrate taxonomic richness at a depth of 18 cm across three sampling occasions.

Source	Degrees of freedom (*df*)	*F* value	*p* value
Time	2, 78	2.26	0.1115
Time x Block	6, 78	1.55	0.1738
Time x Sediment Pulse	4, 78	1.05	0.386
Time x Substrate Composition	2, 78	2.66	0.076
Time x Sediment Pulse x Substrate Composition	4, 78	1.82	0.1342

7.4.4. Taxonomic composition of the hyporheic invertebrate assemblage

Taxonomic composition of the hyporheic assemblage at a depth of 5 cm

PERMANOVA was used to examine the influence of sediment pulse and substrate composition treatments on the taxonomic composition of the hyporheic invertebrate assemblage at a depth of 5 cm (Table 7.6). This analysis found that although the sediment pulse treatment did not have a significant effect (Figure 7.5), substrate composition treatment did have a significant effect on the taxonomic composition of the hyporheic invertebrate assemblage at a depth of 5 cm (Figure 7.6). The PERMANOVA results are supported visually by the NMDS ordination (Figures 7.5 and 7.6). Analysis using the SIMPER routine identified three taxa which were responsible for up to 43 % of the differences observed between substrate types. These taxa were: Cyclopoida, *Crangonyx pseudogracilis* (Bousfield, 1958: Crangonyctidae) and Tanypodinae (Chironomidae). Cyclopoida and *C. pseudogracilis* (Crangonyctidae) were both more abundant in the 'fine' substrate composition treatment, whilst Tanypodinae (Chironomidae) was more abundant in the 'coarse' substrate composition treatment.

Table 7.6 Results of a PERMANOVA examining the influence of sediment pulse and substrate composition treatments on the taxonomic composition of the hyporheic invertebrate assemblage at a depth of 5 cm. Statistically significant results are highlighted in bold ($p < 0.05$).

Source	Degrees of freedom (*df*)	Sums of squares (*SS*)	Mean squares (MS)	Pseudo-F ratio	Permutation *p* (P(perm))	Unique permutations
Time	2	3563.3	1781.6	2.3185	**0.0109**	9918
Block	3	12587	4195.5	5.4978	**0.0001**	9920
Sediment pulse	2	1640.4	820.19	1.0748	0.3844	9943
Substrate composition	1	1948.4	1948.4	2.5531	**0.028**	9948
Time x Sediment pulse	4	1834.5	458.62	0.60097	0.9005	9932
Time x Substrate composition	2	1014.2	507.11	0.66451	0.7525	9924
Sediment pulse x Substrate composition	2	1767.4	883.71	1.158	0.3236	9922
Time x Sediment pulse x Substrate composition	4	1820	455	0.59623	0.9047	9929
Res	123	93866	763.13			
Total	143	120040				

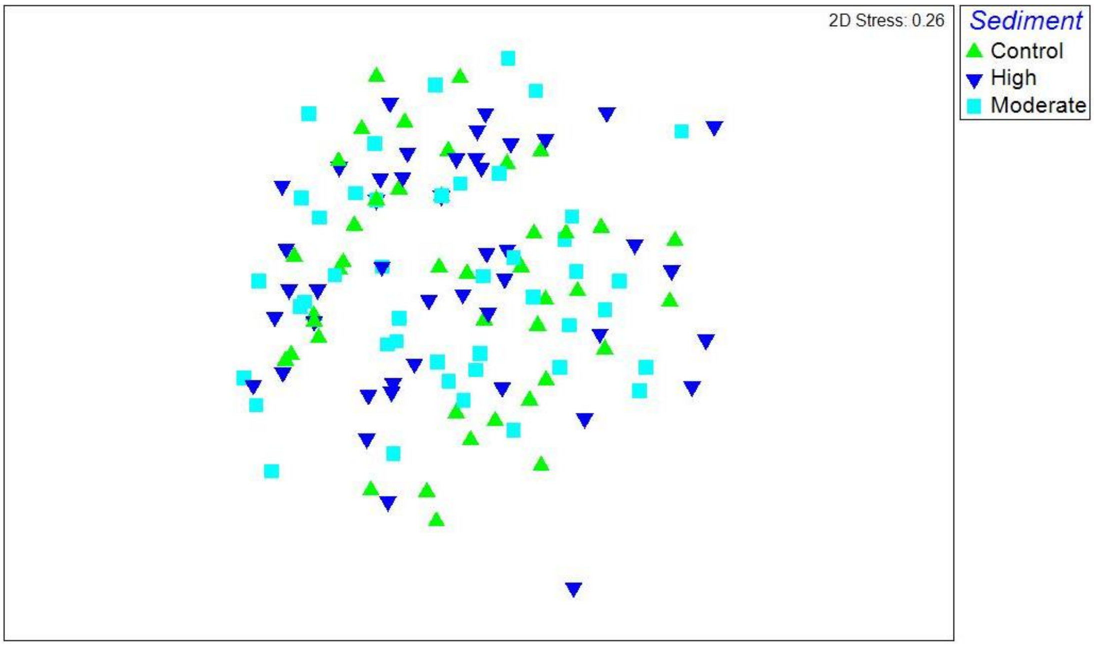

Figure 7.5 NMDS ordination of the taxonomic composition of the hyporheic assemblage at a depth of 5 cm, delineated by sediment pulse treatment. No significant difference was detected between sediment pulse treatments.

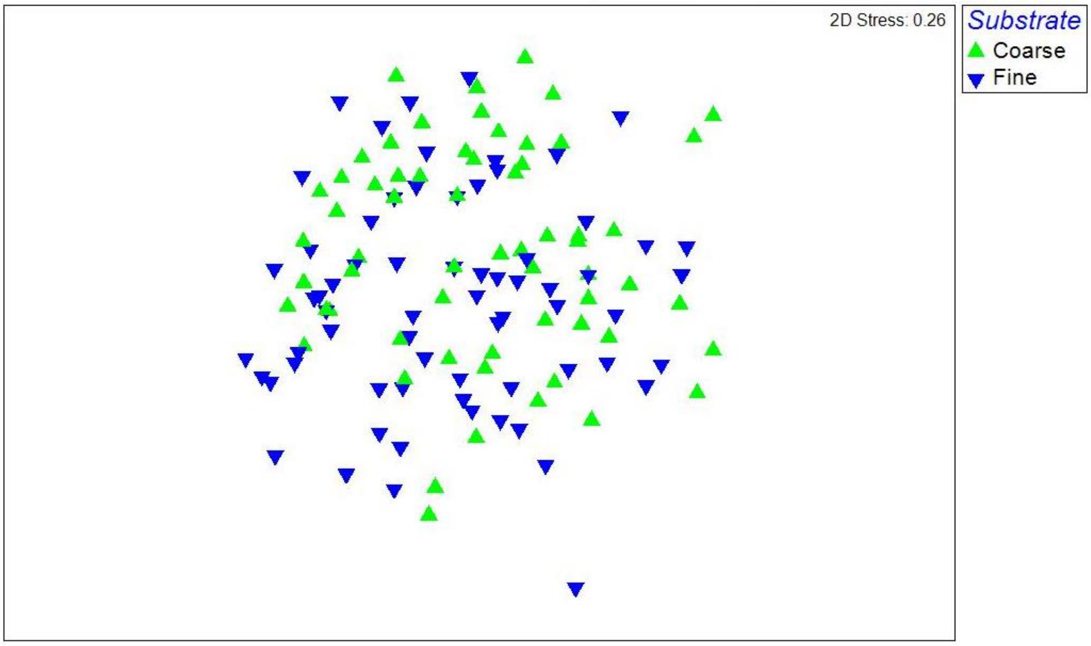

Figure 7.6 NMDS ordination of the taxonomic composition of the hyporheic assemblage at a depth of 5 cm, delineated by substrate composition treatment. A significant difference ($p < 0.05$) was detected between substrate composition treatments.

Taxonomic composition of the hyporheic assemblage at a depth of 18 cm

A PERMANOVA was conducted to investigate the influence of sediment pulse and substrate composition treatments on the taxonomic composition of the hyporheic invertebrate assemblage at a depth of 18 cm. PERMANOVA indicated that the sediment pulse treatment had a significant effect on the taxonomic composition of the hyporheic invertebrate community at a depth of 18 cm (Table 7.7; Figure 7.7). Further pairwise testing found a significant difference between the ‘control’ and the ‘moderate’ sediment pulse treatments ($p = 0.0033$), but not between the ‘control’ and the ‘high’ ($p = 0.4444$) or the ‘moderate’ and ‘high’ ($p = 0.2201$) sediment pulse treatment. SIMPER analysis showed that *C. pseudogracilis* (Crangonyctidae) were responsible for up to 30 % of the significant difference between the ‘control’ and ‘moderate’ sediment pulse treatments and were recorded in greater numbers from the ‘control’ sediment pulse treatment. In contrast with the hyporheic invertebrate assemblage at 5 cm depth, there was no effect of substrate composition on the assemblage at 18 cm depth (Figure 7.8).

Table 7.7 Results of a PERMANOVA examining the influence of sediment pulse and substrate composition treatments on the taxonomic composition of the hyporheic invertebrate assemblage at a depth of 18 cm. Statistically significant results are highlighted in bold (p < 0.05).

Source	Degrees of freedom (*df*)	Sums of squares (*SS*)	Mean squares (*MS*)	Pseudo-*F* ratio	Permutation *p* (P(perm))	Unique permutations
Time	2	4094	2047	4.7743	**0.0001**	9957
Block	3	9712.7	3237.6	7.5511	**0.0001**	9918
Sediment pulse	2	1874.2	937.11	2.1856	**0.0342**	9946
Substrate composition	1	186.05	186.05	0.43393	0.7522	9950
Time x Sediment pulse	4	1452.8	363.21	0.84712	0.6211	9914
Time x Substrate composition	2	1351.9	675.95	1.5765	0.1429	9931
Sediment pulse x Substrate composition	2	1122.4	561.22	1.309	0.2536	9939
Time x Sediment pulse x Substrate composition	4	669.66	167.41	0.39047	0.9622	9934
Res	123	52737	428.76			
Total	143	73415				

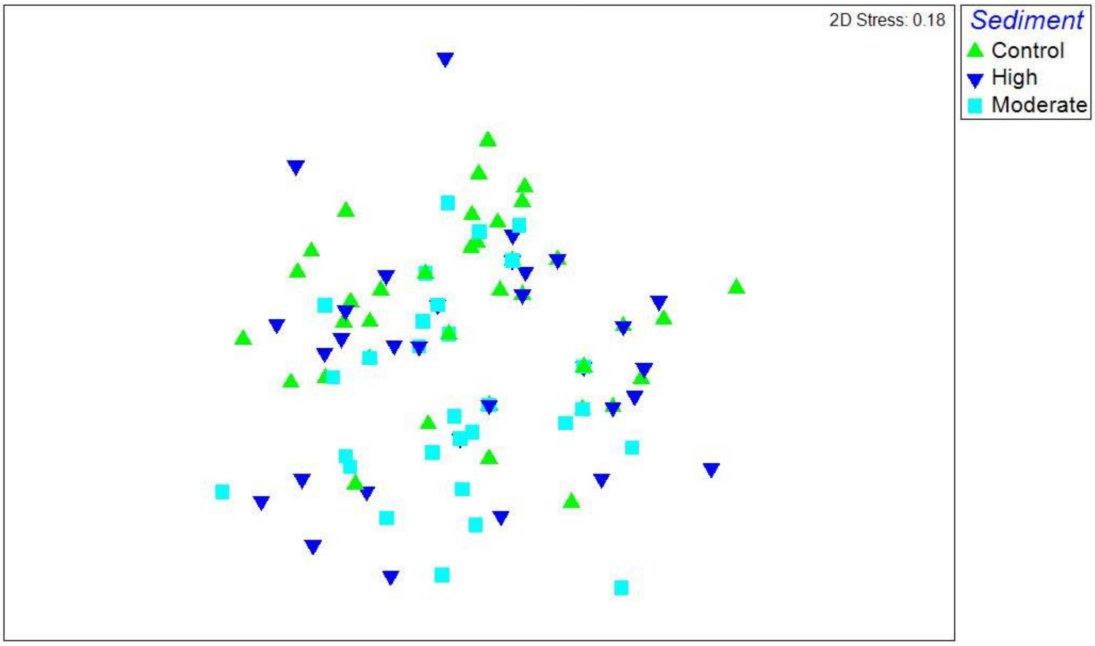

Figure 7.7 NMDS ordination of the taxonomic composition of the hyporheic assemblage at a depth of 18 cm, delineated by sediment pulse treatment. A significant difference (p < 0.05) was detected between sediment pulse treatments.

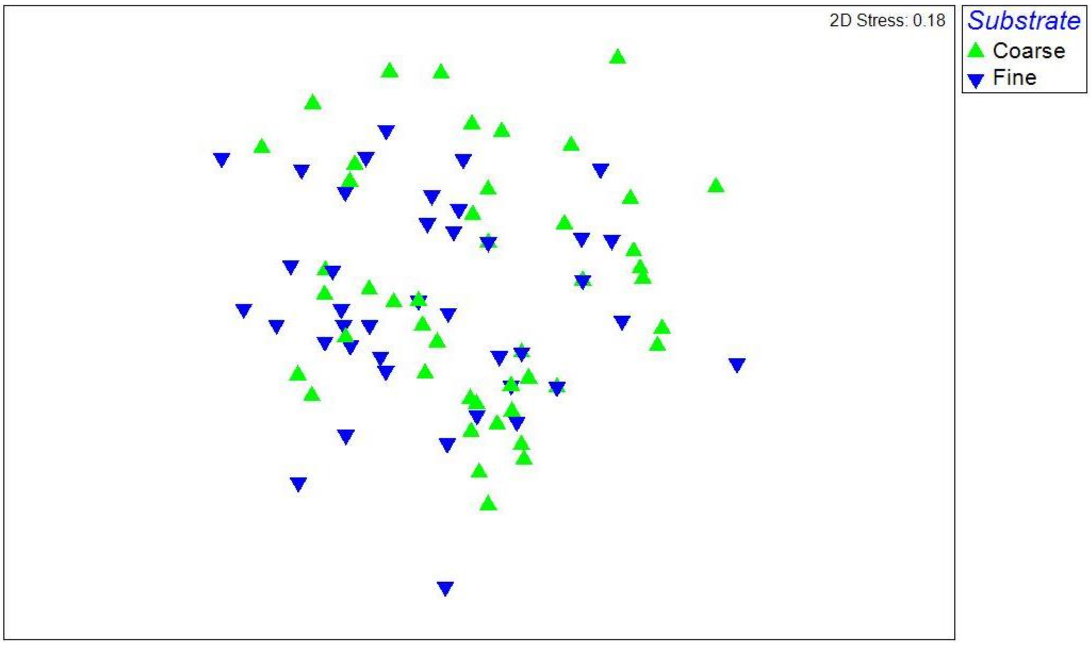

Figure 7.8 NMDS ordination of the taxonomic composition of the hyporheic assemblage at a depth of 18 cm, delineated by substrate composition treatment. No significant difference was detected between substrate composition treatments.

7.5. Discussion

7.5.1. Effect of sediment pulse treatment on hyporheic invertebrate abundance, taxonomic richness and taxonomic community composition

The fine sediment pulse had a significant influence on the abundance of hyporheic invertebrates at a depth of 5 cm ‘during’ the sediment pulse treatment (Figure 7.1; GLM: $F_{(2, 39)} = 3.25$, $p = 0.0494$). This finding supports the hypothesis that invertebrates may use the hyporheic substrate as a refuge in response to fine sediment pressure. The sediment pulse treatment had a proportional effect on mean hyporheic invertebrate abundance, with the greatest abundances recorded in samples subject to the ‘high’ sediment pulse treatment followed by the ‘moderate’ and the ‘control’ sediment pulse treatment. However, when examining the mean hyporheic invertebrate abundance recorded from the ‘coarse’ substrate composition treatment, the effects of the sediment pulse treatment became less clear (Figure 7.3). Although the greatest mean hyporheic abundance was recorded from the ‘high’ sediment pulse treatment, the next greatest mean abundance was recorded from the ‘control’ rather than from the ‘moderate’ sediment pulse treatment. This was contrary to the hypothesis that increased suspended fine sediment concentration would result in increased abundance of hyporheic invertebrates. There are several possible explanations for these findings. Potentially the ‘coarse’ substrate composition treatment, which provided increased interstitial space, was able to absorb more of the fine sediment deposited by the pulse. This may have lessened the impact of the pulse on benthic invertebrates. This effect may have been enough to assuage some of the impact from the ‘moderate’ sediment pulse treatment and reduce the refuge-seeking response of benthic invertebrates, but not enough to ameliorate the effect of the ‘high’ sediment pulse treatment. An alternative explanation is that the sediment pulse resulted in the addition of organic matter to the mesocosm channels, an important food resource for freshwater invertebrates (Rabeni and Minshall, 1977). The ‘coarse’ substrate composition treatment may have stored more of this resource than the ‘fine’ substrate composition treatment due to the increased interstitial space (Parker, 1989). Invertebrates may then have been attracted to the upper layer of the hyporheic zone, at a depth of 5 cm, by the additional organic matter (Williams and Smith, 1996). If invertebrates had to migrate vertically through the substrate to reach this organic matter (Vadher *et al.*, 2015) the ‘coarse’ substrate composition treatment would be easier for invertebrates to travel through than the ‘fine’ substrate composition treatment due to the increased interstitial space. This phenomenon may not have occurred with the ‘high’ sediment pulse treatment as the negative effects of the increased amount of fine sediment may have outweighed the positive effects of increased amounts of organic matter.

The interaction of sediment pulse and substrate composition treatment significantly influenced the mean taxonomic richness of the hyporheic invertebrate assemblage at a depth of 5 cm on the sampling occasion during the sediment pulse. However, the direction of the effect seen was not as hypothesised. It was thought that the interaction of the sediment pulse and substrate composition treatments would have led to an increase in mean hyporheic taxonomic richness, as invertebrates sought refuge from the sediment induced pressure in benthic sediments, and that this increase would be greatest in the ‘coarse’ substrate composition treatment as this treatment would afford easier access to the hyporheic zone. However, a more complicated picture emerged from the experimental data (Figure 7.2). In the ‘fine’ substrate composition treatment taxonomic richness was lowest in the hyporheic samples subject to the ‘control’ sediment pulse treatment, with the samples subject to the ‘moderate’ and ‘high’ sediment pulse treatments recording the joint highest mean taxonomic richness. The pattern in the ‘coarse’ substrate composition treatment was the reverse of what was hypothesised, with the samples from the ‘control’ sediment pulse treatment recording the greatest mean taxonomic richness, followed by the ‘moderate’ sediment pulse treatment, with the ‘high’ sediment pulse treatment recording the lowest taxonomic richness. These results may provide further tentative evidence that the effects of the sediment pulse were not as severe in the ‘coarse’ substrate composition treatment due to some characteristics of the substrate (such as being able to absorb greater quantities of fine sediment), and that this may explain some of the counterintuitive results in this study.

The taxonomic composition of the hyporheic invertebrate assemblage at a depth of 18 cm was found to be significantly influenced by the sediment pulse, with further pair-wise testing revealing that it was the difference between the 'control' and 'moderate' sediment pulse treatments which were responsible for this significant difference. It is interesting that the effects of the sediment pulse were detected at 18 cm depth, but not at 5 cm depth as would be expected. It is also interesting that a difference was detected between the 'control' and 'moderate' sediment pulse treatments, but not the 'control' and 'high', or 'high' and 'moderate' treatments. These anomalies are hard to explain, but the very low abundances and paucity of taxa in the samples taken at 18 cm depth may have had an effect. Many samples were lacking invertebrates, so it may be the case that an increase in the number of samples taken from this depth would help to provide greater clarity on the response of hyporheic invertebrates to a sediment pulse and substrate composition treatments. For instance, *C. pseudogracilis* (Crangonyctidae), which were identified as the taxa responsible for the largest difference between the 'control' and 'moderate' sediment pulse treatments, only showed a difference in abundance of 10 individuals over the duration of the experiment.

7.5.2. Effect of substrate composition treatment on hyporheic invertebrate abundance, taxonomic richness and taxonomic community composition

Prior to the sediment pulse the mean hyporheic invertebrate abundance at a depth of 18 cm was significantly higher in the 'coarse' than the 'fine' substrate composition treatment. This result supports the findings of other studies in this field which have found that coarse substrates were able to support greater populations of hyporheic invertebrates than finer substrates, as their increased interstitial space provides additional habitat and their increased permeability allows for a greater exchange of oxygen, organic matter and nutrients (Strommer and Smock, 1989; Dole-Olivier *et al.*, 1997; Strayer *et al.*, 1997; Stubbington *et al.*, 2012; Jones *et al.* 2015). Following the application of the sediment pulse treatment the significant difference between the abundances of hyporheic invertebrates recorded from the two substrate composition treatments was no longer detected. The reason for this could be due to the fact that invertebrate abundance increased consistently in the 'fine' substrate composition treatment (Figure 7.3), possibly indicating that invertebrates which do not usually use the hyporheos in the 'fine' substrate composition treatment were forced to migrate downwards by the fine sediment pulse. This finding highlights the impact that a fine sediment pulse may have on the ability of the substrate to function as an invertebrate habitat (Descloux *et al.*, 2013).

The substrate composition treatment was also found to have a significant influence on the taxonomic composition of the hyporheic invertebrate assemblage at a depth of 5 cm. *C. pseudogracilis* (Crangonyctidae), one of the three taxa identified as being responsible for up to 43 % of the difference in taxonomic composition between the two substrate composition treatments, have been identified previously as being tolerant to fine sediment (Extence *et al.*, 2013), so it is expected that they would occur at higher abundance in the 'fine' substrate composition treatment. The abundance of Cyclopoida was highest in the 'fine' substrate composition treatment, a result which appears to contradict the findings of other studies. For instance, both Angradi (1999), Descloux *et al.* (2013) and Jones *et al.* (2015) recorded decreased abundance of Cyclopoida in response to rising fine sediment amounts. Due to the differences in methods used by these studies it is difficult to compare the degree of colmation at which Cyclopoida responded, but further investigation may be useful in assessing which aspects of colmation the Cyclopoida were responding to and to explain why their response may have been different in the present study when compared to previous studies. Tanypodinae (Chironomidae), the third taxa identified as being responsible for a considerable proportion of the difference in taxonomic composition between the two substrate treatments, were recorded from the ‘coarse’ substrate composition treatment in greater numbers than the ‘fine’ substrate composition treatment. This taxon has previously been identified as having an intermediate tolerance to fine sediment (Murphy *et al.*, 2015), so its increased abundance in the ‘coarse’ substrate composition treatment may simply reflect an increase in suitable interstitial habitat leading to increased abundance. Although these results did not show a significant effect between the interaction of sediment pulse and substrate composition treatments, as may have been expected, they do provide further evidence that the particle size distribution of the substrate may exert a significant effect on the hyporheic invertebrate assemblage.

7.6. Summary

The evidence presented in this chapter demonstrated that a fine sediment pulse had an influence on invertebrate use of the hyporheic zone, with increased fine sediment amounts resulting in increased invertebrate abundance in the top layer of this zone. An effect of prior substrate conditions was also identified in the use of the hyporheic zone by invertebrates in response to a fine sediment pulse. This effect warrants further investigation to identify the causal mechanisms behind the responses seen in this study. The results found in this investigation support the idea that invertebrates in the hyporheic zone may be good candidates to investigate in terms of their biomonitoring potential, as the fine sediment pulse was found to exert a clear influence on their taxonomic composition.

8. Synopsis, management implications and future research

8.1. Introduction

The amount of fine sediment entering watercourses has increased substantially over the last century, with most UK catchments seeing increases ranging from a factor of 2 to 10 (Foster and Lees, 1999; Evans, 2006), putting pressure on freshwater ecosystems (Jones *et al.,* 2012a, 2012b; Jones *et al.*, 2014). This is highlighted by the fact that fine sediment has been identified as the fifth most common stressor in English water bodies and can be held responsible for 12 % of WFD failures (Grabowski and Gurnell, 2016). Managing and legislating for excess fine sediment depends upon a full understanding of the physical, biological and anthropogenic factors controlling its delivery to the river, its storage and transport (Wilkes *et al*., 2018). Excess fine sediment has implications for aquatic habitats and ecology (Mathers *et al*., 2017). This thesis focussed on determining the effects of a fine sediment pulse on the invertebrate community and assesses whether these effects were influenced by prior sediment deposition. The research was unique in examining the effects of fine sediment pulse and substrate composition treatments on benthic, hyporheic and drifting invertebrates concurrently over a 30-day period. In particular, this research addressed the following objectives:

- To quantify how substrate composition influences invertebrate abundance, taxonomic richness and community composition (Chapter 4).
- To assess how a fine sediment pulse impacts benthic invertebrate community structure and community composition, and the influence of substrate composition on the response (Chapter 5).
- To examine whether substrate differences influence invertebrate drift patterns during a fine sediment pulse (Chapter 6).
- To investigate whether invertebrates use the hyporheic zone during a fine sediment pulse and assess its role as a refuge (Chapter 7).

The results of the mesocosm experiment described in this thesis have provided an examination of the effect of a fine sediment pulse on the invertebrate community investigating whether these effects are influenced by prior substrate conditions. The work described in these chapters has successfully addressed each of the four objectives. In this chapter the main findings related to each objective have been reviewed in addition to an assessment of their implications. Key themes arising from the research are also discussed in this chapter. Recommendations are also given on how these findings may inform the future regulation and management of fine sediment. Finally, this chapter discusses how fine sediment research may evolve in the future.

8.2. Attainment of thesis objectives

Chapter 4 investigated the effect of two different substrate composition treatments on the invertebrate community. This investigation examined the impact of different levels of deposited fine sediment within the substrate, which addressed the first objective of the thesis.

- To quantify how substrate condition influences invertebrate abundance, taxonomic richness and community composition.

One of the principal hypotheses for this chapter was that increased amounts of fine sediment in the substrate would result in decreases in invertebrate density and taxonomic richness. This hypothesis was not supported by the results. These results, although unexpected, offer valuable insights into the role of substrate particle size in shaping invertebrate communities. The 'fine' substrate composition treatment resulted in significantly greater taxonomic richness, a direct contradiction of the hypothesis. These results demonstrate that although increased amounts of fine sediment in the substrate have previously been shown to negatively impact the invertebrate community, with decreases in density and taxonomic richness (Williams and Mundie, 1978; Erman and Erman, 1984; Williams and Smith, 1996), this outcome is not universal.

The potential reasons behind the results found in this study are interesting to consider as they may have implications for river managers. As the mesocosm channels used for this study were directly connected to the Mill Stream, which is a tributary of the River Frome, the potential pool of colonising invertebrates was mainly drawn from the Frome catchment (Harris et al., 2007). The Frome is a lowland river, in an agricultural catchment, which has previously been impacted by excess fine sediment (Grabowski and Gurnell, 2016). High amounts of fine sediment deposition in the River Frome may have filtered out fine sediment sensitive taxa from the pool of colonising invertebrates available to populate the mesocosm channels. Consequently, these taxa may preferentially utilise the habitat provided by the 'fine' substrate composition treatment, resulting in the increased taxonomic richness in this habitat.

The results in this chapter demonstrate that the effects of fine sediment deposition on invertebrate communities vary depending upon the range of sensitivities to fine sediment present in the invertebrate community (Larsen et al., 2009). This finding is supported in work by Matthaei et al. (2006) who found that fine sediment had the greatest effect on rivers with the highest invertebrate diversity, and which had not previously been subject to elevated amounts of fine sediment. The work of Larsen et al. (2009) supports this finding, as they found the effects of fine sediment to be greatest in upland reaches where invertebrate diversity was highest, compared to lowland reaches where invertebrate diversity is lower. If this experiment had been conducted in a location where the colonising population of invertebrates had not experienced any exposure to elevated fine sediment amounts the 'coarse' substrate composition treatment may have been the favoured habitat of a greater number of invertebrate taxa than that seen in the present study. This information may be of use to those working on river rehabilitation projects, as it demonstrates that simply removing fine sediment particles from the river substrate may not result in increased taxonomic richness and abundance if there is not a pool of colonising invertebrates available which will benefit from the change in substrate conditions. This highlights the fact that rehabilitating a river which has been subject to fine sediment pressure over a substantial time period may not lead to immediate changes to the invertebrate community, and is dependent upon other factors, in addition to those solely related to physical habitat or environmental conditions.

Chapter 4 also examined the ability of fine sediment biomonitoring indices to detect differences in substrate composition in terms of the mass of deposited fine sediment present within the substrate. There was a significant difference in the ToFSI scores between the 'fine' and 'coarse' substrate composition treatments, with the 'coarse' substrate composition treatment recording significantly higher ToFSI scores, indicating that the 'coarse' substrate composition treatment was favoured by more sediment-sensitive taxa. This finding is expected as the experimental design manipulated the total amount of non-organic fine sediment within the substrate, and ToFSI was designed to detect such differences (Murphy *et al.*, 2015). This is an encouraging indication of the usefulness of biomonitoring indices in the detection of fine sediment induced pressure, particularly as more traditional metrics such as taxonomic richness, or abundance, did not respond to an increased mass of deposited fine sediment within the substrate as expected in this experiment.

Chapter 5 identified the effects of a fine sediment pulse on the benthic invertebrate community and assessed how these effects were mediated by substrate composition treatment. This chapter addressed the second objective of the thesis.

- To assess how a fine sediment pulse impacts benthic invertebrate community structure and community composition and the influence of substrate composition on the response.

The invertebrate community did not respond as hypothesised following the fine sediment pulse. The sediment pulse treatment had no significant effect on the density, taxonomic richness or taxonomic composition of the invertebrate community. However, the experiment showed a significant influence of the combined effects of sediment pulse and substrate composition treatments on invertebrate community composition, and also of the combined effects of sediment pulse and substrate composition treatments and time. Therefore, although no inherent differences in invertebrate community composition were detected between the two substrate composition treatments, they did promote a significantly different response to the fine sediment pulse treatments.

The experiment also identified a significant effect of the interaction between sediment pulse and substrate composition treatments on the ToFSI and CoFSI biomonitoring indices. ToFSI and CoFSI results show that on the sampling occasion immediately after the fine sediment pulse the taxa inhabiting the channels subject to the ‘coarse’ substrate composition treatment were on average more sensitive to fine sediment than taxa occupying the channels subject to the ‘fine’ substrate composition treatment. These results confirm the original hypothesis that differences in substrate characteristics would affect invertebrate community response to sediment loading. This demonstrates that invertebrate communities in rivers which experienced increased fine sediment deposition in the past would respond differently to a fine sediment pulse compared to rivers with a coarser bed substrate. This indicates the importance of considering the frequency of sediment pulse events when assessing their effects on invertebrate communities.

Findings from this study also supported the results of other investigations which have concluded that the effects of fine sediment should not be considered in isolation, as the interaction with other stressors may lead to unpredictable effects (Bond and Downes, 2003; Matthaei et al., 2010; Beermann et al., 2018). For instance, research by Matthaei et al. (2010) found that the negative impact of fine sediment on aquatic biota was greater at reduced flow rates. This finding led the authors to conclude that water abstraction from streams already experiencing elevated fine sediment inputs may cause greater negative consequences for the invertebrate fauna than abstraction from similar sized streams experiencing lower levels of fine sediment deposition. The results of the present study indicate a possible mechanism behind the additional negative effects of fine sediment under low flow conditions. Low flows increase fine sediment deposition, whereas high flows may flush fine material from the substrate (Jones *et al.*, 2015). If a stream has already been subject to low flows it is therefore likely that this has led to increased fine sediment deposition and consequently a substrate dominated by finer particles. This problem is compounded if flows are never sufficient to flush this excess of fine particles from the bed (Jones *et al.*, 2015). Results from the present study demonstrated that a fine substrate would promote a different response from the invertebrate community when compared to a coarser substrate not subject to previously elevated fine sediment deposition.

Chapter 5 further demonstrated the potential of biomonitoring indices to detect fine sediment pressure. Although invertebrate density, taxonomic richness, EPT density and EPT taxonomic richness were not significantly influenced by the fine sediment pulse, a response was seen in the biomonitoring indices. Mean CoFSI and ToFSI scores per taxon declined significantly in the mesocosm channels subject to the high fine sediment pulse treatment. This indicated a change from more sediment-sensitive taxa to more sediment-tolerant taxa. Mean ToFSI and CoFSI scores per taxon were also significantly higher in the channels subject to the 'coarse' substrate composition treatment, indicating that this was the favoured habitat of more sediment-sensitive taxa. This finding was promising as it demonstrated that biomonitoring indices could discern the effects of the sediment pulse treatment and differences in fine sediment amounts within the substrate, whereas simply examining taxonomic richness and abundance would have shown no difference. Metrics such as taxonomic richness and abundance have traditionally been used when examining the effect of stressors on freshwater ecosystems, but the results of this study and others demonstrate using these metrics may obscure the underlying processes at work. This issue has been identified before (e.g. Brooks et al., 2002; Mouillot et al. 2006), but the research carried out for this thesis provides good evidence from a carefully-controlled experiment, without the potentially confounding factors which are often found in this type of study.

Taxonomic richness was not significantly affected by the fine sediment pulse treatment in this study, a result which, although unexpected, has also been seen in other studies of the effect of fine sediment on aquatic invertebrates (e.g. Lenat et al., 1981; Sarriquet et al. 2007; Descloux *et al.*, 2013). Other studies have also found EPT taxonomic richness and abundance to be negatively affected by fine sediment pressure (e.g. Gomi *et al.,* 2010; Larsen *et al.*, 2011; Buendia *et al.*, 2013). However, this finding was not reproduced in the present study. Given the fact abundance and taxonomic richness metrics do not respond to fine sediment in the same manner across studies, there may be other influential factors at work. In relation to the present study it is important to consider the impact of sediment-tolerant taxa on these metrics. As already discussed in this chapter, the invertebrates that colonised the mesocosm channels in the study mostly originated from the Frome catchment, which is characterised by large amounts of deposited fine sediment. Therefore, there was a pool of relatively sediment tolerant taxa which were able to exist in the 'fine' substrate in the mesocosm channels subject to the sediment pulse treatments. The relatively low flow rate in the mesocosms channels also made the fine substrate reasonably stable, when compared to a natural river with a varying flow rate, which would have increased its ability to form a habitat for certain taxa. So, although the fine sediment pulse may have excluded some sediment-sensitive taxa completely, or diminished their abundance, it may have also promoted an increase in sediment-tolerant taxa and increased their individual abundances. If the influx of sediment-tolerant taxa balances out the loss of sediment-intolerant taxa, both in terms of the number of taxa and their individual abundances, then no change will be seen in taxonomic richness or the abundance of individual taxa.

Examining the taxonomic richness and abundance of EPT taxa has been suggested as a solution to this problem (Angradi, 1999; Conroy *et al.*, 2016). EPT taxa are typically more sensitive to fine sediment and would be expected to exhibit a greater response to fine sediment than the invertebrate community as a whole (Kaller and Hartman, 2004; Larsen *et al.*, 2009; Wagenhoff *et al.*, 2012). However, there are a range of sediment sensitivities present within EPT taxa, therefore in certain conditions some EPT may respond positively to fine sediment whilst some respond negatively, leading to a balancing-out effect which in turn limits the discrimination ability of EPT metrics. This may be the reason why, although a significant effect of the sediment pulse was detected on EPT community composition, no effect was detected on EPT taxonomic richness or abundance. Results from the present study demonstrate that the effects of fine sediment on abundance and taxonomic richness may be subtle or obscured by increases in sediment-tolerant taxa. Biomonitoring indices specifically focussed on the impacts of fine sediment do not have these drawbacks and have been shown in the present study to be a more accurate way to identify the effects of fine sediment on invertebrate communities. Their continued development and application will provide river managers with a better set of tools to identify fine sediment pressure than more traditional metrics.

Chapter 6 examined the response of invertebrate drift to a fine sediment pulse and investigated how this response was influenced by prior substrate conditions. This chapter focused on the third objective of the thesis, which was:

- To examine whether substrate differences influence invertebrate drift patterns during a fine sediment pulse (Chapter 6).

The results in Chapter 6 supported the hypothesis that a fine sediment pulse would influence the drifting behaviour of invertebrates. Increased mean density and taxonomic richness of invertebrates was recorded in the drift in response to increasing fine sediment amounts. This key finding is in agreement with other studies (e.g. Doeg and Milledge, 1991; Larsen and Ormerod, 2010b; Béjar et al. 2017), and supports the view that the fine sediment pulse either directly caused more invertebrates to involuntarily enter the drift through dislodgement by saltating particles, or that the change in habitat caused by increased deposited fine sediment caused more invertebrates to voluntarily enter the drift as the habitat became unfavourable for them.

One of the unique aspects of the experiment detailed in this thesis was that it investigated the legacy of the fine sediment pulse by examining whether any effects were still apparent 30 days after the event. The results showed that the effects of the fine sediment pulse on invertebrate drift occurred within a 24 h period immediately following the sediment pulse treatment, but did not persist past this time. This is an important finding which has implications for the management of fine sediment in the natural environment. The effects of fine sediment on invertebrate communities are felt most acutely in the 24 h immediately following exposure. During this time period sediment-intolerant invertebrates which have the ability to disperse via drift appear to do so. As invertebrates responded so rapidly to the fine sediment pulse, this suggests that preventing excesses of fine sediment from entering watercourses is particularly important because it may have an immediate effect on invertebrate populations.

Chapter 7 investigated the use of the hyporheic zone by invertebrates in response to a fine sediment pulse and examined whether this response was influenced by substrate composition. This answered the fourth objective of the thesis.

- To investigate whether invertebrates use the hyporheic zone during a fine sediment pulse, and assess its role as a refuge (Chapter 7).

Many studies have investigated the influence of increased fine sediment on the benthic invertebrate community (e.g. Angradi, 1999; Buendia *et al.*, 2013; Béjar *et al.*, 2017; Beermann *et al.*, 2018), however there is a paucity of studies which have investigated its effects on the benthos and hyporheos in tandem (Descloux *et al.* 2013). This is unfortunate, as it has been stated that in order to fully understand the influence of excess fine sediment on lotic freshwater invertebrates we must investigate the benthic and hyporheic environments simultaneously (Descloux *et al.*, 2013). This was one of the first studies to adopt this approach while also concurrently investigating the effects on invertebrate drift. It is difficult to compare the results from this study with others given the lack of research which has examined all of these factors, so only tentative conclusions may be drawn. It would be beneficial to further test these questions in other environments, such as tightly controlled laboratory studies, or manipulative field experiments in a variety of river types.

The hypothesis that invertebrates use the hyporheic zone to escape pressure induced by a fine sediment pulse was partially supported. Invertebrates in the ‘fine’ substrate composition treatment responded to the fine sediment pulse as hypothesised with significantly increased invertebrate abundances recorded from the top 5 cm of the hyporheic zone during the sediment pulse. This increased abundance was greatest in the channels subject to the ‘high’ sediment pulse treatment, followed by the ‘moderate’ sediment pulse treatment. However, as no significant effect of the fine sediment pulse on benthic invertebrate abundance was detected (Chapter 5), it is not clear whether or not the increased abundance of invertebrates at a depth of 5 cm was due to them escaping fine sediment induced stress in the benthic habitat.

The results of the drift study reported in Chapter 6 support the view that certain invertebrate taxa used drift as a mechanism to escape the effects of the fine sediment pulse, so it is feasible that certain invertebrate taxa may have also migrated downwards to escape the sediment pulse effects, with this loss being too small to be detected in the benthic results presented in Chapter 5. An alternative hypothesis may be that the fine sediment pulse delivered increased amounts of organic matter to the top 5 cm of the hyporheic zone, which may have attracted invertebrates from deeper within the substrate who could utilise it as a food resource (Rabeni and Minshall, 1977). Using the data collected in this study it was not possible to rule out either explanation, but the results do indicate that this is an issue which would warrant further investigation.

The difference between the two substrate composition treatments had some effect on the response of invertebrates to the fine sediment pulse, but not always in the manner hypothesised. It was initially thought that the ‘coarse’ substrate composition treatment would promote greater use of the hyporheic zone by invertebrates in response to the fine sediment pulse due to the increased interstitial space available (Descloux *et al.,* 2013), but this was not borne out by the results of the study. Substrate differences did result in significantly increased invertebrate abundance in the ‘coarse’ substrate composition at 18 cm depth before the addition of fine sediment, which supports the findings of previous studies that increased clogging within the hyporheic substrate leads to reductions in invertebrate density (Boulton *et al.*, 1988; Descloux *et al*., 2013). However, instead of promoting greater use of the hyporheic zone, there is tentative evidence to suggest that the ‘coarse’ substrate composition treatment appeared to ameliorate some of the effects of the fine sediment pulse, possibly by allowing more fine sediment to infiltrate the bed than in the fine substrate composition treatment, thereby reducing its impact on the benthic environment. It is also possible that the effect of the fine sediment pulse on hyporheic invertebrates was confounded by the differing particulate organic matter storage capacities of the two substrate composition treatments used in this study (Rabeni and Minshall, 1977; Parker, 1989). These findings warrant further experimental studies to identify exactly which mechanism, or combination of mechanisms, may explain the findings in the present study.

Although the exact mechanisms are unclear, it can be seen from the results of the present study that the fine sediment pulse did impact the hyporheic invertebrate assemblage, with an effect on the taxonomic composition of the hyporheic invertebrate assemblage being affected at 18 cm depth. This is an important finding and supports the idea, proposed by Descloux *et al.*, (2013), that the hyporheic invertebrate community may be used as bioindicators of fine sediment stress. It is an approach which has a number of advantages over the use of benthic invertebrates. Descloux *et al.* (2013) similarly observed that the effects of excess fine sediment were experienced to a greater extent in the hyporheic environment. The hyporheic zone is also disturbed less than the benthic environment by short duration flow pulses which can result in the removal of fines from the substrate (Lenat *et al.*, 1979), and as it stores fine sediment it may more accurately reflect the longer term fine sediment dynamics at a particular location and provide a good indication of chronic fine sediment stress. However, for this approach to be developed further more experimental work, such as the present study, is required to identify taxa which may be able to function as indicators.

8.3. Key findings

This research has clearly demonstrated that how the invertebrate community responds to a fine sediment pulse is affected by the particle size distribution of the substrate. Evidence discussed in the preceding chapters has demonstrated that this is true for both the benthic and hyporheic invertebrate community. Although the manner of the effect was not always as hypothesised, it has been shown that when considering the effects of fine sediment on the invertebrate community the role of substrate composition should be considered.

In this study, traditional metrics for assessing the invertebrate community (e.g. richness, abundance, or EPT metrics) have consistently not performed as well at detecting the influence of the fine sediment pulse, or greater amounts of fine sediment in the substrate, as biomonitoring indices designed specifically for this task. Although to be expected, these results are useful as they further demonstrate the potential of biomonitoring indices to improve our monitoring capability in the freshwater environment. Their further refinement and development is to be encouraged as an improved monitoring ability makes it more likely that management interventions may be designed to positively impact freshwater ecosystems.

The final key finding from this study has been that predicting the effects of a fine sediment pulse on the freshwater invertebrate community is not possible without some knowledge of the prevailing fine sediment conditions and the range of sediment sensitivities present within that community. Some of the hypothesised effects of fine sediment on the invertebrate community were not realised in this study due to the effects of high levels of fine sediment within the River Frome. This worked to mask some of the effects of the fine sediment pulse, by ensuring that the invertebrate community available to colonise the mesocosm channels were already relatively insensitive to the effects of fine sediment. Findings such as this have wider implications, as they emphasise the need to recognise that the effects of excessive amounts of fine sediment will not be universal across all lotic freshwater communities, they will need to be assessed with a sound understanding of the characteristics of each community.

8.4. Future directions for fine sediment research

This thesis has delivered one of the first examinations of the effect of prior sediment deposition on the response of invertebrates to a fine sediment pulse and is unique in investigating its effect on benthic, hyporheic and drifting invertebrates concurrently, over a substantial time period under carefully controlled conditions. As well as providing important evidence to improve the monitoring and management of fine sediment in the freshwater environment, it has also identified a number of areas which warrant further research, which are discussed in the following section.

8.4.1. Further exploration of invertebrate trait-fine sediment relationships to improve biomonitoring approaches

Biomonitoring using a functional traits-based approach has the potential to improve our ability to monitor the impacts of excess fine sediment in lotic freshwater environments (Mathers *et al.*, 2017). As has been seen in the present study, the use of biomonitoring indices already enables better discrimination of fine sediment pressure than more traditional metrics. However, these indices may be further improved if we are able to develop our knowledge of the often complex mechanistic relationships between invertebrate traits and fine sediment (Wilkes *et al.*, 2018). Evidence from the present study demonstrates that our current knowledge of these relationships is incomplete. This lack of understanding has also been highlighted in other studies, with reports of conflicting responses of invertebrate traits to excess fine sediment (Buendia *et al.*, 2013; Descloux *et al.*, 2014; Mathers *et al.,* 2017; Murphy *et al.*, 2017). In addition to furthering our understanding of the mechanistic response of invertebrates to excess fine sediment, it is also necessary to refine and improve the information in our trait databases, so that they include more taxa (a problematic issue identified in the present study) and also include more trait information relevant to the response of invertebrates to fine sediment (Wilkes *et al.* 2017).

8.4.2. An improved understanding of the differing responses of individual taxa to excess fine sediment

Evidence from this study, and many others, has shown that the response of individual invertebrate taxa to excess fine sediment is highly variable (Culp *et al.*, 1986; Gomi *et al.*, 2010; Buendia *et al.*, 2013; Beermann *et al.*, 2018). As can be seen from the results detailed in this study some invertebrate taxa are very tolerant of increased amounts of deposited fine sediment, whilst some are known to be sensitive to even small increases (Larsen and Ormerod, 2010b). However, our knowledge of these different responses is currently lacking, as evidenced by the contradictory fine sediment sensitivity ratings applied to the same invertebrate taxa in two of the leading fine sediment biomonitoring indices (Extence *et al.*, 2011; Murphy *et al*., 2015). If we can improve upon this knowledge it will enable us to better manage and legislate for the detrimental effects increased fine sediment amounts can have on lotic freshwater environments.

8.4.3. Increased knowledge regarding the effects of fine sediment on invertebrates within the hyporheic environment

This was one of the first studies to examine the effects of a fine sediment pulse on benthic and hyporheic invertebrates in tandem. It identified significant effects of the fine sediment pulse on the taxonomic composition of the hyporheic invertebrate assemblage. However further research in this area is required, both to improve our understanding of the response of benthic invertebrates to fine sediment in the hyporheic environment, and to investigate the possible use of hyporheic invertebrates in fine sediment biomonitoring (Descloux *et al.*, 2013). This research should encompass different river types as substrate differences have been shown to have a highly influential effect upon the ability of the hyporheic environment to function as a habitat for invertebrates and it should include rivers with varying organic matter inputs, as this has also been demonstrated to exert significant control on hyporheic invertebrate assemblages (Descloux *et al.*, 2013).

8.5. Final conclusions

Excesses of fine sediment have been identified as having significant negative effects on lotic freshwater invertebrate communities. However, there is currently a lack of knowledge regarding the mechanistic links between increased fine sediment amounts and invertebrate assemblages. The aim of this thesis was to address some of these knowledge gaps, so that the monitoring and management strategies addressing the fine sediment problem can be further refined and developed. This thesis has produced some important results which will be particularly useful for those trying to manage this problem. The study was unique in considering the effects of prior fine sediment deposition on the response of invertebrates to a fine sediment pulse, finding that it may indeed exert a significant influence on their behaviour. As a result, it can be said that this is an important factor for environmental managers to consider when they attempt to monitor and control fine sediment in different river types and to differentiate between the effects of chronic and acute fine sediment pressure. Another important finding of this research is that biomonitoring indices focussed on fine sediment, although still in a period of development and refinement, are useful tools in identifying fine sediment induced stress. Finally, this thesis has demonstrated that the drift behaviour, and the use of the hyporheic zone, in response to a fine sediment pulse is taxon-specific and has provided further useful information regarding their responses. This information may aid the refinement of trait databases, with the hope that traits-based approaches to fine sediment monitoring may fulfil their potential.

9. References

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