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The effects of deposited sediments on temperate stream invertebrates

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A thesis submitted for the Degree of Doctorate of Philosophy

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September 2009

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Acknowledgements

Funding for the research was provided by the Wye and Usk Foundation, Wales, and I thank Dr Stephen Marsh-Smith and Simon Evans.

I also wish to thank:

My supervisor Prof. Steve Ormerod. After meeting him in Rome "by chance" I could not foresee such long and fructuous scientific relationship. Through his encouragement and advises he taught me how to transform ideas and data into papers.

Ian "*if you don't know how to do it ask Ian*" Vaughan for enlightening me on the infinite ways of looking at the data.

The Countryside Council for Wales and the Environment Agency for providing essential data.

Past and present members of the Catchment Research Group for their friendship, support and interesting conversations on how to survive a PhD. Special thank to Esther Clews for her help and company during my initial confused months in Cardiff.

Giorgio Pace and Lorenzo Lemme for their valuable field assistance and for rendering many long night shifts more bearable (and for sharing mosquitoes and caratopogonids bites).

My parents, obviously, for their tireless support, love and for sending lots of indispensable Italian food.

All the landowners for allowing access to study sites (even that one with the biting dog...).

Finally, the person that has been beside me and with whom I shared everything in the last wonderful decade. Thanks Federica for your existence.

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Chapter 1 - General Introduction

Aquatic ecosystems, in particular rivers and streams have been widely used and thus directly and indirectly modified by humans for centuries (Owens & Walling, 2002; Frings *et al*, 2009). Freshwaters have probably undergone faster degradation than most other ecosystems with extinction rates and population declines accelerating rapidly (Ricciardi & Rasmussen, 1999; Millennium Ecosystem Assessment, 2005). This is the consequence of multiple stressors with both direct effects, such as pollution, water abstraction, impoundment and introduced species, and indirect effects from extensive conversion of catchments for agriculture or other human uses (Allan, 2004). The latter gives rise to one of the most pervasive and widespread forms of running-water impairment in the form of altered sediment dynamics and excessive delivery of fine particles (Waters 1995).

Fine-grained sediments are naturally occurring in streams and rivers at all latitudes. The constant entrainment, transport and deposition of sediment are natural geomorphological processes that ultimately define channel-evolution through time. Increasingly, however, research based on long term monitoring is showing that fluxes of fine sediment are progressively increasing throughout the world as catchments are modified for agriculture, construction, deforestation or mining (Owens *et al*, 2005). It is estimated that human activity may be responsible (directly and indirectly) for c 80-90% of the fluvial sediments delivered to the coastal oceans (Owens *et al.*, 2005). On a long term perspective, global climate change may also influence precipitation patterns and soil erosion thereby altering river sediment regimes (Wilby, Dalgleish & Foster, 1997).

The ecological consequences of altered fine-grained sediment quantity and quality on lotic water organisms have been investigated increasingly for over 20 years, using diverse approaches from large-scale surveys to manipulative field and mesocosm experiments (Waters, 1995; Wood & Armitage, 1997).

Increased sediment loads can affect aquatic organisms across all trophic levels with both direct effects (e.g. on organisms' respiratory or feeding structures) and indirect effects (e.g. on habitat quality) generally resulting in lower productivity and diversity (see Chapter 2). However, basic understanding of i) the traits of organisms conferring sensitivity to sediments, ii) the wider ecosystem-level consequences and iii) the conservation implications is still relatively poor compared to other forms of stream impairment (organic pollution, acidification). This is because fine sediments in streams are often associated with other factors such as nutrients and pesticides, while their dynamics and quality are strongly determined by larger-scale catchment features that also influence aquatic organisms. Such covariation often precludes the straightforward assessment of the effects of sediment stress on natural systems. Moreover, as anthropogenic alterations of sediment dynamics can range from local habitat change to whole catchment modification, the exact source is rarely identified and the scale at which effects are evident could vary greatly (Imhof, Fitzgibbon & Annable, 1996).

These considerations show that current interpretation of ecological effects - especially if based on observational studies - could be limited by numerous confounding factors or inappropriately scaled approaches. In these circumstances experiments have the advantage of providing relatively controlled conditions with artificial sediment addition in flumes, mesocosms and experimental streams frequently employed in the past. Nonetheless, such experiments may have limited realism or lack true replication and caution is needed in extrapolating results to the field (Culp, Wrona & Davies, 1985; Fairchild *et al*, 1987; Suren & Jowett, 2001; Suren, Martin & Smith, 2005). Thus, there is a need to assess consistent patterns in the response of organisms to fine sediments unravelled by field surveys and experiments. This would help reveal possible causal relationships and underlying mechanisms. However, studies employing both surveys and manipulative in-stream experiments are surprisingly few (Angradi, 1999; Townsend, Uhlmann & Matthaei, 2008).

This thesis aims to investigate the extent and the biological effects of sediment deposition in the Usk Catchment in Wales. The Usk Catchment is an ideal location to investigate sedimentation effects on organisms for several reasons (See Chapter 3). Most of the river drains sandstones and mudstones (Old Red Sandstone Series) so there is little variation in underlying geology across locations, but these same sedimentary features create a potential for sediment mobilization (Sable & Wohl, 2006). Urbanization has a negligible impact since the catchment is scarcely populated, but dominant land-use varies from upland rough grazing land to improved grassland with possible implication for sediment delivery. Additionally, water chemistry is relatively uniform across the catchment, with flow well oxygenated and generally low in plant nutrients, so that major confounding variables should not mask apparent sediment effects (Clews & Ormerod, 2009; Larsen, Vaughan & Ormerod, 2009).

I used a blend of surveys over different spatial extents along with field experiments to assess how in-stream sediment character varied across locations in relation to land-use, and its effect on macroinvertebrates structure and function. Specifically, I attempted to test the following hypotheses:

1. Catchment and riparian land-use and associated processes (bank erosion) should explain most of the variability in the observed deposited sediments (Chapter 3)
2. At larger spatial resolution (catchment and reach scale), the composition of stream invertebrates should mostly reflect variation in dominant land-use and altitude, while the influence of sediments should be of secondary importance (Chapter 3).
3. At finer resolution (patch-scale) the influence of local substratum conditions (i.e. deposited fines) on invertebrates' assemblages should be increasingly apparent and I expected a decrease in EPT and overall richness and abundance with increasing fines (Chapter 3).
4. Specific invertebrates' life-history and behavioural traits should be disfavoured and thus relatively under-represented in sediment-rich locations; conversely, other traits reflecting a degree of adaptation to fine substrata should be relatively favoured (Chapter 4).
5. Short-term sediment release and transport should result in rapid invertebrate loss and redistribution through drift (Chapter 5).

6. Invertebrate responses to fine sediments should be consistent between surveys and experiments when a causal relation is involved. In particular, I expected consistency in how the representation of specific traits varied in relation to sediments gradient as observed in surveys and generated in experiments (Chapter 6).

These hypotheses are given specific background in each of the chapters in which they are tested. Additionally, to examine the possible conservation implications of sediment delivery in streams, I tested the hypothesis that sedimentation could promote the formation of nested subset patterns in species assemblages. Nested sub-set pattern occurs where species present in species-poor locations constitute a subset of the species in richer locations, so that in a perfectly nested system rare taxa only occur in the richest site and generalists at most sites. Nestedness has been examined in many biological systems, including stream invertebrates (Atmar & Patterson, 1993; Fernandez-Juricic, 2002; Hecnar *et al*, 2002; Heino, Mykra & Muotka, 2009), mostly to test biogeographical theories. Recent work suggest that not only large scale colonization-extinction processes could generate nestedness in communities, but also anthropogenic disturbance, habitat quality and behavioural effects on patch selection (Summerville, Veech & Crist, 2002; Hylander *et al*, 2005). For these reasons, nested subset analysis has been increasingly used to assess conservation effects in different ecosystem types. I therefore hypothised that, as species differ in their sensitivity to sedimentation, local selection through extinction or impaired colonization should generate nestedness as increased sediments would favour generalist over specialists.

All chapters are self-contained and intended as papers for publication with their own reference list.

1.1 References

Allan, J.D. (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics,* **35,** 257-284.

Angradi, T.R. (1999) Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications *Journal of the North American Benthological Society* **18,** 49-66

Atmar, W. & Patterson, B.D. (1993) The Measure of Order and Disorder in the Distribution of Species in Fragmented Habitat. *Oecologia,* **96,** 373-382.

Clews, E. & Ormerod, S.J. (2009) Improving bio-diagnostic monitoring using simple combinations of standard biotic indices. *River Research and Applications,* **25,** 348 - 361.

Culp, J.M., Wrona, F.J. & Davies, R.W. (1985) Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology,* **64,** 1345-1351.

Fairchild, J.F., Boyle, T., English, W.R. & Rabeni, C. (1987) Effects of sediment and contaminated sediment on structural and functional components of experimental stream ecosystems. *Water Air and Soil Pollution,* **36,** 271-293.

Fernandez-Juricic, E. (2002) Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia,* **131,** 269-278.

Frings, R.M., Berbee, B.M., Erkens, G., Kleinhans, M.G. & Gouw, M.J.P. (2009) Human-induced changes in bed shear stress and bed grain size in the River Waal (The Netherlands) during the past 900 years. *Earth Surface Processes and Landforms,* **34,** 503-514.

Hecnar, S.J., Casper, G.S., Russell, R.W., Hecnar, D.R. & Robinson, J.N. (2002) Nested species assemblages of amphibians and reptiles on islands in the Laurentian Great Lakes. *Journal of Biogeography,* **29,** 475-489.

Heino, J., Mykra, H. & Muotka, T. (2009) Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. *Diversity and Distributions,* **15,** 198-206.

Hylander, K., Nilsson, C., Jonsson, B.G. & Gothner, T. (2005) Differences in habitat quality explain nestedness in a land snail meta-community. *Oikos,* **108,** 351-361.

Imhof, J.G., Fitzgibbon, J. & Annable, W.K. (1996) A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences,* **53,** 312-326.

Larsen, S., Vaughan, I.P. & Ormerod, S.J. (2009) Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology,* **54,** 203-219.

Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: wetlands and water synthesis,* World Resources Institute, Washington, DC.

Owens, P.N., Batalla, R.J., A. J. Collins, B. Gomez, D. M. Hichs, A. J. Horowitz, Kondolf;, G.M., M. Marden, M. J. Page, D. H. Peacock, E. L. Petticrew, W. Salomons & N. A. Trustrumi (2005) Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications,* **21,** 693–717.

Owens, P.N. & Walling, D.E. (2002) Changes in sediment sources and floodplain deposition rates in the catchment of the river Tweed, Scotland, over the last 100 years: the impact of climate and land use change. *Earth Surface Processes and Landforms,* **27,** 403–423.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology,* **13,** 1220-1222.

Sable, K.A. & Wohl, E. (2006) The relationship of lithology and watershed characteristics to fine sediment deposition in streams of the Oregon Coast Range. *Environmental Management,* **37,** 659-670.

Summerville, K.S., Veech, J.A. & Crist, T.O. (2002) Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? *Oikos,* **97,** 195-204.

Suren, A.M. & Jowett, I.J. (2001) Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research,,* **35,** 725-737.

Suren, A.M., Martin, L.M. & Smith, B.J. (2005) Short-term effects of high suspended sediments on six common New Zealand stream invertebrates. *Hydrobiologia,* **548,** 67–74.

Townsend, C.R., Uhlmann, S.S. & Matthaei, C.D. (2008) Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology,* **45,** 1810-1819.

Waters, T.F. (1995) *Sediments in streams: sources, biological effects, and control,* AFS Monographs, Bethesda, Maryland.

Wilby, R.L., Dalgleish, H.Y. & Foster, I.D.L. (1997) The impact of weather patterns on historic and contemporary catchment sediment yields. *Earth Surface Processes and Landforms,* **22,** 353-363.

Wood, P.J. & Armitage, P.D. (1997) Biological Effects of Fine Sediment in the Lotic Environment
Environmental Management, **21,** 203-217.

Chapter 2 - Effect of suspended and deposited sediments on lotic organisms

Summary

1. A large array of anthropogenic activities in catchments and riparian habitats has altered sediment regimens resulting in excessive fine sediment delivery to streams and rivers worldwide. The consequent transport and deposition of fine sediments affect lotic organisms across all trophic levels with both direct and indirect effects. However, understanding the causes of altered sediment regimes and the mechanisms behind ecological effects is challenging. Fluvial sediment sources, and therefore their particle-size distribution, chemical properties and in-stream behaviour are extremely variable resulting in similarly variable biological responses. Also, in modified catchments, anthropogenic derived sediments are often associated with wider habitat modifications and in-stream stressors producing synergistic and antagonistic patterns in the biological response. Moreover temporal attributes of sediment releases, such as duration and frequency, can influence the severity of impact strongly, but appropriately designed studies are surprisingly few.

2. Many biological features influence sediment effects in lotic system. Recent studies have shown how certain life-history and behavioural traits can dictate organisms' sensitivity to sediments, but the majority of research has described gross community changes or species-specific tolerance. Studying changes in the representation of organisms' traits in impacted communities could aid a better understanding of the mechanisms involved but, in any given location, top-down hierarchical controls and selective pressures will ultimately select locally existing traits from the available pool. Consistent quantitative predictions of ecological impacts, even if based on more accurate mechanistic understanding, are therefore problematic.

3. In this review I critically summarise current knowledge on the ecological effects of increased fine sediments on primary producers, invertebrates and fish. Future research should aim to i) assess further the traits of organisms conferring sensitivity or tolerance, ii) understand better how sedimentation affects the transfer of energy among trophic levels and the influence of biotic interactions, iii) assess the individual and combined effect of sediment and the many associated stressors over a range of spatial scales.

4. Finally, the consequence of excessive sediment deposition on other semi- or non-aquatic taxa, such as amphibians, otters, river birds, but also riparian arthropods is largely unexplored. Even less is known about the effects of increasing sedimentation on microbial metabolism and nutrient cycling.

2.1 Introduction

"Erosion is the most insidious threat, for it is often unspectacular and goes unnoticed from one year to the next". The opening paragraph of Cordone and Kelley's (1961) classic review on the influence of inorganic sediment on aquatic life is today even more appropriate. Although the effects of land erosion and associated siltation have long been recognized as major factors in river ecology (Aitken, 1936; Ellis, 1936), the advent of quantitative studies is still relatively recent, mostly stemming from assessments of industrial and mining operations (Nuttall & Bielby, 1973; Extence, 1978; Scullion & Edward, 1980; Turnpenny & Williams, 1980; Cline, Short & Ward, 1982). Fine sediment deposition is now considered one of the greatest hazards to the biological integrity of streams and rivers worldwide (Waters, 1995).

While sedimentation is a natural geomorphologic process in rivers, fine sediment fluxes and sediment transport are increasing in catchments impacted by a range of human activities (Table 2.1; Olley & Wasson, 2003; Owens *et al*, 2005) including agriculture (Lenat, 1984; Walling, 1990; Larsen, Vaughan & Ormerod, 2009), mining (Nuttall & Bielby, 1973; Scullion & Edward, 1980), deforestation and forestry (Kreutzweiser & Capell, 2001; Kreutzweiser, Capell & Good, 2005), construction (Extence, 1978; Cline *et al.*, 1982; Davies & Nelson, 1993), groundwater abstraction (Bickerton *et al*, 1993) and livestock grazing (Olley & Wasson, 2003; Braccia & Voshell, 2006). Global climate change is also likely to modify precipitation, hydrologic regimes and temperature, therefore altering soil erosion rates, channel morphology and sediment transport (Wilby, Dalgleish & Foster, 1997). Although natural river water is never sediment free, excessive sediments from anthropogenic activities are considered to overwhelm the "assimilative capacity" of a stream – i.e. the ability of a natural system to absorb anthropogenic wastes and other materials without being degraded. Detrimental effects on habitats and biota then result (Cairns, 1977).

Physical - habitat effects

Sediment transport and deposition modify the physical-chemical properties of aquatic habitats and affect hydrological processes (Fig. 2.1) in ways that include (i) increased turbidity (Davies-Colley *et al*, 1992; Davies-Colley & Smith, 2001); (ii) changing substratum structure and porosity (Schalchli, 1992; Rehg, Packman & Ren, 2005); (iii) decreasing bed heterogeneity and pool-riffle patterns (Rathburn & Whol, 2001; Gayraud, Herouin & Philippe, 2002); (iv) filling interstices, thus reducing hydrological exchange between surface and groundwater while decreasing nutrient and oxygen supply to the hyporheos (Turnpenny & Williams, 1980; Richards & Bacon, 1994). Sandy substrata are believed to store large amount of fine detritus (Metzler & Smock, 1990), potentially altering organic matter budgets in the impacted location.

Inorganic sediment deposition has little effects on the chemical properties of the water (Ellis, 1936; Fossati *et al*, 2001), but small, charged particles such as clays can transport adsorbed contaminants. In that case, consequences for organisms and ecosystems are many and are reviewed elsewhere (Warren *et al*, 2003)

Despite growing research effort on the ecological implications of fine sediment delivery to streams, understanding of the factors determining organisms' sensitivity and the consequences for ecological processes is still scarce.

Here, I review the current knowledge on the effects of fine sediments on aquatic life across all trophic levels; aiming to identify sediment characteristics and biological aspects that influence not only the ecological effects, but also our ability to detect and manage them. I thus recognize gaps in knowledge and suggest possible future research directions.

2.2 Fine sediment properties

Material transported in flowing waters is either solid or in solution, organic or inorganic. Particles > 2mm are considered gravels, whereas sand (2 to 0.063 mm), silt (0.063 to 0.004 mm) and clay (<0.004 mm) constitute what is normally referred to as the fine fraction.

The entrainment and behaviour of sediments in lotic waters is mainly dependent on water flow velocity, particle grain size and shape, although grain size distribution, which controls the degree of packing and cohesion, also determines the behaviour of particles in the water column (Pye, 1994). Particle density, sphericity, roundness (sharpness of edges) and surface texture also influence sediment behaviour and ecological impact (see below).

Natural, but also anthropogenically derived sediments in any stream section have three major origins: surface (hill slope) erosion, upstream / tributary inputs and channel bed / bank erosion. Channel-derived particles are normally coarser then particles from hill slopes, and are generally associated with the bed material load. In contrast, surface sources usually provide fine sediments constituting the suspended / wash load (Knighton, 1998).

Once entrained, coarse particles tend to remain in contact with the stream bed (bedload) by rolling and sliding and their volume is generally higher in sandy beds than in gravels. Particles whose settling velocity is slower than the upward components of flow and turbulence constitute suspended load, which is transported virtually without bed contact.

Suspended load can account for up to 90% of the total sediment transported by a stream or river (Allan, 1995), However, while much suspended sediment is transported during floods, baseflow transport can be constantly high even at base flows and represents an important disturbance to organisms (Culp, Wrona & Davies, 1985; Bond, 2004; Gibbins *et al*, 2007)

Deposition occurs when the flow or shear velocity falls below the settling velocity of a particle, which is normally less than that required for entrainment (Knighton, 1998). Settling velocity is dependent upon particle size, and therefore very small particles (silt and clay size) will be transported further downstream than coarser particles. River deposits can form within the channel, in the channel margins, in the floodplain and mouth. Deposition mainly occurs in low flow areas such as margins, backwaters, pools and downstream of obstructions, but macrophytes stands and periphyton can enhance local deposition.

2.3 Sediment characteristics influencing ecological effects

Sources and associated stressors

Sources of fluvial sediment, their particles' characteristics and behaviour are highly diverse and variable, therefore understanding and predicting associated ecological effects on stream organisms is particularly challenging. Not only physical-chemical properties and particle size distribution of sediments change according to variable sources, but anthropogenic derived sediments are often associated with wider habitat modifications and in-stream stressors that result in complex ecological responses. Catchment modifications from agriculture, urbanization and forestry, for example, not only alter natural sediment dynamics and quantity in streams, but represent major ecological influences *per se* (Table 2.1).

In cultivated catchments sediment deposition and nutrient enrichment are often associated and, as sediment particles in agricultural landscapes tend to be finer (e.g. Matthaei *et al*, 2006), contaminants such as pesticides could also be absorbed and delivered to the water (Stone & Droppo, 1994; Owens *et al.*, 2005). Moreover, other stressors affect streams in developed catchments such as loss of riparian habitat, altered hydrology, light and temperature (Manel, Buckton & Ormerod, 2000; Allan, 2004). Similarly, timber harvest, besides increasing sources of organic sediment, can modify flow regime where the soil is wetter as a result of reducing interception and evapotranpiration (Allan, 1995). Biological responses to sediment-associated stressors can therefore show synergistic and antagonistic patterns so that sediments' effects are exacerbated in the first case and masked in the latter. For example, higher nutrients can increase algal productivity to the benefit of grazer organisms, but associated sediment inputs would outweigh such positive effects (Townsend, Uhlmann & Matthaei, 2008). Conversely, the biggest negative effects could be apparent only when high nutrient and sediments coincide. These kind of subsidy-stress responses have been observed frequently and, despite evidence that different nutrient conditions can alter the response of benthic organisms to disturbance (Gafner & Robinson, 2007; Niyogi *et al*, 2007b), interaction between land-use, sediments and biological response has been poorly explored (Matthaei *et al.*, 2006; Larsen *et al.*, 2009).

Different sediment sources will also influence the spatial scale of ecological impact and, in turn, our ability to detect them. Large scale catchment modification, for example for agriculture or forestry, will result in diffuse release of fines over broad areas, whereas sediment delivery from local bank erosion or livestock poaching is likely to be a localized phenomenon. In these circumstances appropriately scaled investigations may be necessary (Larsen *et al.*, 2009).

Particle size

Sediment effects not only are influenced by larger scale covariables, but obviously depend on particles' physical and chemical characteristics, which vary according to dominant catchment geology, soil type and available sources (Walling & Amos, 1999; Sable & Wohl, 2006). Streams draining erodible rock-type such as sandstone, for example, have greater rates of fine sediment transport than streams in slower weathering lithology (Bond, 2004; Sable & Wohl, 2006). Catchment geology can also determine mean sediment particle size and thus their in-stream behaviour. The supply of relatively coarse sediments and their constant in-stream redistribution, even at base flows, represent a major ecological disturbance that could denude stream patches of benthic organisms through displacement or behavioural avoidance (Gibbins, 2007). Few studies, however, have specifically assessed the effects of different particle sizes within the fine (<2 mm) fraction. For example, hydropsychid larvae exposed to sediment loads drifted when buried by particles <1 μm, whereas bigger particles induced a buried-alive behaviour (Runde & Hellenthal, 2000). Dobson et al. (2000) showed that particles <1mm are detrimental to buried individual *Potamophylax cingulatus* to the extent that they will abandon their cases in order to escape, thus increasing the risk of predation, whilst very few of those buried by larger particles were forced to leave their case. Similarly, the time needed by buried Trichoptera larvae (*Melampophylax mucoreus*) to escape, significantly increased with finer sediments (Wood, Vannn & Wanless, 2001). Not only size *per se*, but also sediment sorting (grain-size distribution) and textural properties (e.g. roughness) will affect transport thresholds and thus biological responses (Holomuzki & Biggs, 2003). These few examples, although based on *ex-situ* experiments, show how the ecological effects of sediments depend on their size and distribution that, however, are difficult to quantify in the field.

On the same theme, the existing substratum structure in a given location will influence ecological effects of sedimentation. The composition of benthic invertebrates, in particular, is mostly dictated by substratum characteristics, so that fine-sediment-rich areas would likely support pre-adapted taxa that may even benefit from increased sediment delivery.

Temporal components

Only relatively recently, and led by a toxicological approach, research has progressively focused on temporal attributes of sedimentation events; individual and combined effects of concentration, exposure time and frequency were assessed.

Newcombe and collaborators (Newcombe & MacDonald, 1991; Newcombe & Jensen, 1996) were among the first to develop a dose-response model predicting the severity of impact based on suspended sediment concentration and exposure time. However, their calibration was mostly based on meta-analysis of available data and only focused on fish populations. Shaw and Richardson (2001), exposing artificial channels to sediment pulses of constant concentration but variable duration, observed that both invertebrate metrics and trout growth were negatively correlated with pulse duration. Gard (2002) on the other hand, attributed the lack of any significant effect of sediment loading on fish survival and macroinvertebrates to the relatively low sediment concentration and limited duration of loadings. Recently, Molinos & Donohue (2009) showed that the biological response to sediment concentration, exposure time and their interaction can be variable specific; in other words, the relative weight of concentration and time strongly depended on the biological component under exam. Besides concentration and duration, however, the severity of effect is also related to the frequency of exposure. For example, freshwater mussels exposed to suspended solid every 3 hours reduced their metabolic rate, but did not shift to alternative catabolic substrates, whereas they shifted to complete reliance on non-protein body stores when exposed every 0,5 hours, giving signs of evident starvation (Aldridge, 1987).

Despite the evidence that research will certainly benefit from integrating temporal components in assessing sedimentation impacts and developing a dose-response model, specific studies are surprisingly few.

2.4 Biological aspects influencing sediment effects

Organisms' traits

The literature on the effects of deposited and suspended sediments on aquatic organisms is huge and thoroughly reviewed (Ryan, 1991; Waters, 1995; Wood & Armitage, 1997). The majority of studies, however, described gross community changes or individual tolerance and survival, while the functional characteristics of sensitive taxa or the consequences for ecosystem-wide processes are largely unexplored. This is despite relatively recent research showing how certain life-history traits make some organisms more vulnerable than others. In particular, organisms with external gills (Lemly 1982; Townsend 2008); filter feeders (Strand & Merritt, 1997; Runde & Hellenthal, 2000; Fossati *et al.*, 2001); grazers (Graham, 1990; Rabeni, Doisy & Zweig, 2005) and swimmers (Fossati *et al.* 2001; Rabeni 2005) all appeared to be negatively affected by increasing fines. Additionally, hyporheic invertebrates and amphibionts (Richards & Bacon, 1994; Gayraud & Philippe, 2003; Olsen & Townsend, 2003), clingers (Pollard & Yuan, 2009), organisms laying unprotected eggs (Doledec *et al*, 2006) and visual predators (Rowe & Dean, 1998) are also likely to be affected by reduced interstitial space and increased turbidity. In this view, sediment effects could then be associated with changes in the representation of specific life-history traits in impacted communities. Use of such functional measure to assess ecological effects has clear advantages over strictly taxonomic approaches; most notably, the potential to link observed patterns to underlying processes and the increased predictability and transportability. The relative stability of trait measures across ecoregions (Gayraud & Philippe, 2003) and over time (Bêche, McElravy & Resh, 2006), makes this approach ideal for biomonitoring. Further, use of functional measures such as feeding guilds could be a valuable proxy of major ecosystem attributes like nutrient cycling and longitudinal material transport (Yoshimura *et al*, 2006).

However, in a given location the overall biological response to sedimentation would obviously depend on the relative representation of such sensitive traits within the community. Top-down hierarchical controls will ultimately determine local assemblages as regional and catchment filters would select locally available life-history traits (Cardinale *et al*, 2002; Schweiger *et al*, 2007).

Quantitative predictions of ecological impacts, even if based on more accurate mechanistic understanding, are therefore problematic.

Recovery time

In line with the previous section, the ability of a population to recover from an episodic event is dictated by its resilient traits, such as polivoltinism or asexual reproduction (Doledec *et al.* 2006; Townsend *et al.* 2008). Also, insects with flying adult stages are better re-colonisers than non-flying forms (Waters, 1995). However, the recovery time of impacted biota will also depend on an available source of colonisers (e.g. unimpacted tributaries), as well as current velocity and flood intervals (Osmundson *et al*, 2002). It follows that the season and timing of episodic sediment delivery will influence the severity of impact. Complete recovery within a year, for instance, has been observed by both Cline *et al.*(1982) and Barton (1977), studying the effect of a road construction on small streams; high discharge and the short-term sediment supply contributed to the fast recovery. Conversely, Zuellig *et al.* (2002) after sediment flushing from a reservoir, attributed the fast recolonization of some stream taxa to their rapid reproduction cycles. The extent of deposition and the rate of sediment re-supply are also crucial. For example, 20 years after large-scale logging in an Idaho river, fine sediments were still stored in salmon spawning areas, as muddy tributaries prevented any amelioration (Platts *et al*, 1989).

Surveys and experiments studying long-term sediment effects and recovery rate may be more expensive and logistically demanding, but not necessarily less important.

As siltation has been associated with declining primary production, for example by reducing light penetration or abrading benthic growth, some authors (e.g. Ryan, 1991) argued that streams relying on allochthonous energy sources (e.g. litter from riparian zone) may be less sensitive. This hypothesis has not been tested yet, but, most of the streams where primary energy sources come from detritus inputs drain the headwater section (Vannote *et al*, 1980) and could therefore be intrinsically more sensitive (Matthaei *et al.*, 2006; Connolly & Pearson, 2007; Larsen *et al.*, 2009).

Biotic interactions

One aspect that has been unduly neglected is the relation between sediment stress and species interactions. Even the functional approach of matching life-history traits with habitat templet is ultimately auto-ecological. That is, interspecific interactions are not accounted for despite the evidence that communities are strongly structured by competition, facilitation and predation (Schoener, 1983; Englund *et al*, 2009).

For example, larval hydropsychids are notorious ecosystem engineers, whose silk retreats can enhance stream bed stability and favour suitable habitats for other species (Cardinale, Gelmann & Plamer, 2004; Nakano, Yamamoto & Okino, 2005); their reported sensitivity to fine sediments and their premature loss from silted locations could result in lower bed stability with unpredictable consequences for other organisms. Additionally, stoneflies and shrimps have been shown to reduce significantly the rate of fine sediment accumulation in stream bed interstices (Pringle *et al*, 1993; Zanetell & Peckarsky, 1996). Top-down and bottom-up controls are also likely to mediate sediment effects. Insectivorous and drift-feeding fish would be indirectly affected by lower densities of benthic invertebrates or by a shift in the community towards burrowing and thus unavailable taxa (Suttle *et al*, 2004). Also, even a small increase in bedload has been associated with altered macroconsumer effects on benthic biomass, organic matter and fungal accumulation on leaf debris (Schofield, Pringle & Meyer, 2004).

More studies assessing how biotic interactions mediate ecological response to fine sediments and the consequences for organisms at higher trophic levels are needed.

2.5 Management issues

Despite being one of the biggest contributors to stream and river impairment worldwide, no biotic metric for assessing or monitoring sediment effects has so far been successfully produced, as opposed to acidification (AWIC) and organic pollution (e.g. BMWP). Because of the complex multi-scale interactions among i) catchment character, ii) sediment sources and associated stressors, iii) particle-size distribution and iv) the variable ecological responses, more empirical data are needed to develop a predictive model with clear understanding of causal relationships and magnitude of response.

Also, although there are no specific sediment management guidelines at the European level, one of the aims of the European Water Framework Directive WFD is the identification of appropriate target for nutrient, water flows and fine sediments in water courses (Greig, Sear & Carling, 2005; Owens *et al.*, 2005).

One of the biggest obstacles in the development of statistical models or metrics is the problematic comparison of quantitative relationships estimated by different studies. Most of the limitation stems from the various ways used to quantify fine sediments, especially when deposited.

The suspended fraction is usually expressed as solid concentration (mg/l) or by associated optical properties, either nephelometric units or Secchi disk visibility (Davies-Colley *et al.*, 1992).

The deposited fraction, on the other hand, is more difficult to measure and several approaches have been proposed including: estimation of size classes distribution based on direct measurement of particles (Wolman, 1954; Minshall, 1984); particle geometric mean diameter and fredle index (Shirazi & Seim, 1979; Beschta, 1982); visual estimation of the percentage of fines (Zweig & Rabeni, 2001; Kreutzweiser *et al.*, 2005); visual estimation of stream bed embeddedness

(Zweig & Rabeni, 2001; Bolliet *et al*, 2005); resuspension technique (Owens, Walling & Leeks, 1999; Collier, 2002; Niyogi *et al*, 2007a; Larsen *et al.*, 2009); weight of different size fractions (Angradi, 1999; Kaller & Hartman, 2004).

The relative volume of fine sediments stored in pools has been shown to be a good indicator of sediment supply in gravel bed streams (Lisle & Hilton, 1992). Whitman et al.(2003) also proposed an interesting photographic technique for characterising bed particles sizes that will eventually reduce costs, field time and stream bed disturbance.

Mebane (2001) stressed the importance of measuring fine sediments over the whole bankfull channel, since it would better indicate upstream disturbances as a result of floods compared to the submerged portion of the channel where sediment are easily diluted. Finally, Cover *et al* (2008) adopted a large grid laid over the stream bed and counted the number of grid intersections occurring over fine sediment patches.

Such diverse array of quantification methods obviously precludes valid cross-study comparisons or meta-analyses.

2.6 Main effects on primary production

The first and most obvious effect of suspended solids in the water column is the modification of the water optical properties. Early work by Ellis (1936) showed how erosion silt can screen out light and change heat radiation. Suspended particles scatter light and increase diffusion. Photons then travel longer pathways increasing their chance to be absorbed (Kirk, 1985). Reduced light penetration due to suspended particles has resulted in decreased benthic primary production and subsequent reduction in periphyton biomass and phototrophic content (Davies-Colley *et al.*, 1992; Yamada & Nakamura, 2002) as well as in reduced or altered algal species diversity (Hancock, 1973; Cline *et al.*, 1982). Increased turbidity is likely to be the main cause affecting primary production in a stream. Lloyd *et al.* (1987) calculated that a turbidity of only 5 NTUs (nephelometric turbidity units) can decrease primary productivity of a shallow, clear water stream by 3-13%, and an increased of 25 NTUs may decrease it up to 50%.

Furthermore, fine sediments can be incorporated in the epilithic biofilms, reducing its organic content and nutritional value (Cline *et al.*, 1982; Graham, 1990; Davies-Colley *et al.*, 1992) with consequences for primary consumers.

Periphyton and macrophytes can actually trap fine particles, increasing local deposition rates. Fine sediments are generally believed to settle only in marginal and pool areas where current velocity is low and no turbulence occurs, but Graham (1990) showed that periphyton provide a sticky matrix that enable siltation to occur even in fast flowing riffles with considerable flow turbulence. Suspended or saltating bedload particles can then mechanically damage macrophytes leaves and stems (Lewis, 1973a, 1973b), or prevent algal attachment reducing stable surfaces (Brookes, 1986). In these cases, only motile taxa (diatoms) may be able to move onto the top of the newly deposited layer (Dickman, Peart & Yim, 2005). Sandy and unstable beds can also affect the rate and location of primary production and respiration in streams (Atkinson, 2008).

Additionally, Yamada and Nakamura (2002) concluded that the shading effect of trapped particles, even though expected to be limited compared to the particles in suspension, is not negligible as they considered sediment accumulated directly on the periphyton to be responsible for the decrease in chlorophyll *a* content.

Recently however, Parkhill & Gulliver (2002) reported that the whole productivity of a stream receiving sediment loads was not significantly lower than control locations, and suggested that the plant community could compensate the irradiance loss via an increase in overall photosynthetic efficiency. The reduced dark respiratory rate of treated streams reported in their experiment indicates, however, that even small sediment loads can reduce the overall biological activity in streams, even though not all communities will be affected to the same extent. Primary producers might be particularly resistant to sediment stress.

Ryder & Miller (2005) recommended caution in measuring chlorophyll *a* concentration, a structural variable, as a surrogate of algal productivity, and instead suggested directly measuring processes such as Gross Primary Production, or Net Primary Production. Also, more information is needed on the recovery time of periphyton and aquatic plants after sediment inputs and how up-welling zones of river bed may eventually favour the process.

2.7 Main effects on benthic invertebrates

Benthic invertebrates are by definition organisms inhabiting the bottom of streams and rivers. The influence of substratum type on the composition and productivity of bottom fauna is well documented (Cordone & Kelley, 1961; Minshall, 1984), hence any modification of its structure is likely to affect the benthic community. Nonetheless, stream organisms must be adapted to natural variations in suspended and deposited sediments occurring as a result of spates and droughts. However, ecological effects arise when anthropogenic inputs differ in frequency, duration and extent.

Besides smothering the river bed, deposited fines can actually reduce suitable habitat by filling interstices of coarser substrates (Chutter, 1968) and reducing available refugia during floods (Olsen & Townsend, 2005). The diversity of the benthic fauna is generally a function of habitable surface area of the bottom particles, with the greatest productivity and richness found in rocky riffles with coarse particles and the lowest on sandy substrata (Cordone & Kelley, 1961; Rabeni & Minshall, 1977). Inputs of sand and finer particles on stream reaches mostly resulted in a significant decrease in invertebrates density (Gray & Ward, 1982; Quinn *et al*, 1992; Angradi, 1999; Fossati *et al.*, 2001; Zweig & Rabeni, 2001) and richness (Lemly, 1982; Doeg & Koehn, 1994; Larsen *et al.*, 2009). Diversity often shows variable response as rare taxa could disappear with increasing sediment, leaving fewer taxa but more evenly distributed among individuals (Angradi, 1999). Most EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) notably prefer coarse grain substrata and a linear decline in their richness with increasing sediment cover has been observed consistently both in experimental studies (Angradi, 1999; Matthaei *et al.*, 2006) and in larger scale surveys (Zweig & Rabeni, 2001; Kaller & Hartman, 2004; Townsend *et al.*, 2008; Larsen *et al.*, 2009; Pollard & Yuan, 2009). Kaller & Hartman (2004) also suggested that a threshold level of fine sediments accumulation exists (0.8-0.9 %) where EPT taxon richness is significantly reduced.

Besides indirect effects through habitat change, the main mechanisms likely to be involved include i) direct mechanical disturbance of saltating and suspended particles, which increase invertebrates drift rates and redistribution (Culp *et al.*, 1985; Doeg & Koehn, 1994; Suren & Jowett, 2001), ii) impairment of respiratory and feeding structures with consequences for behaviour and energy requirements (Lemly, 1982; Strand & Merritt, 1997; Runde & Hellenthal, 2000) and iii) reduction of the organic content of periphyton and thus its food-value for consumers (Graham, 1990; Quinn *et al.*, 1992; Kent & Stelzer, 2008).

The latter mechanism is clearly affecting grazer organisms not only reducing their growth rate but also altering substrate patch-selection and energy expenditure (Broekenhuizen, Parkyn & Miller, 2001; Suren, 2005). Siltation of coarse particulate organic matter may also affect shredders by reducing resource palatability through a reduction in microbial colonization and conditioning of particulate organic matter surfaces (Kreutzweiser *et al.*, 2005).

Hydrology can strongly mediate sediment-organisms interaction with ecological consequences. Culp (1985), for example, added fine sediments to streams with different current velocities in order to distinguish the effect of deposited and transported particles on benthos. Deposited sediments had little impact on the benthic community whereas sediments transport by saltation reduced total benthic density by 50% influencing the whole benthic community composition. Even low rates of bedload transport are sufficient to denude patches of stream bed by triggering mass invertebrate drift (Gibbins *et al.*, 2007). However, Suren & Jowett (2001) demonstrated that also deposited, non-saltating, fine sediments caused significant drift coupled with decreased benthic densities in some taxa. Sand deposits are an unsuitable habitat for many benthic organisms that can also impede upstream migration and thus represent ecological blockages in the colonization cycle (Luedtke & Brusven, 1976)

Community-wise, the most frequently observed effect is a shift in the existing benthic community towards sediment-tolerant and burrowing or tube-building taxa. In the long term, a reduction in overall abundance of prey-items in the form of drifting animals is also likely. In two early works Nuttal and colleagues (1972, 1973) found a significant increase of Chironomidae, Tubificidae, Naididae and *Baetis rhodani* density in streams receiving sand and china-clay wastes. Discharges from a motorway construction in a UK stream resulted in a marked decrease in leech density and the elimination of the river limpet *Ancylus fluviatilis* from the impacted reaches, certainly due to the absence of suitable size particles for attachment (Extence, 1978). Fossati *et al.* (2001) demonstrated that the whole invertebrate community may be affected by sediment release from road construction in a clean Andean stream. Siltation over and within the substrate had a negative impact on epibenthic invertebrates, particularly gatherers. Increased level of suspended solids affected swimmers such as most Ephemeroptera. Suspended sediments interfered with the filtering processes of Hydropsychidae and Simulidae. Finally, the reduced density of primary and secondary consumers affected predators. Sedimentation could effectively impact benthic communities across all trophic levels. In the short term, however reduced interstitial and sheltering habitat may expose prey organisms and thus favour predator taxa (Wantzen, 2006).

Changes in community composition are not necessarily associated with a decrease in overall benthic density. Chironomidae and oligochaetes may become extremely dominant where deposits are also organically enriched (Hellawell, 1986). In fact, Lenat (1981) suggested that stable sand reaches can host a sand-community that, although very different from the one inhabiting rocky substrata, might reach higher densities.

Although the hyporheos is increasingly acknowledged as an integral part of fluvial ecosystems, the effects of fine sediment deposition on hyporheic habitat and organisms is relatively uninvestigated and most of the studies have focused on the top 10 cm of the bottom fauna.

The hyporheos is the ecotone between streams and groundwater and the exchange processes between the two systems have highly ecological significance (Brunke & Gonser, 1997). Further, the communities inhabiting the hyporheos are responsible of a great proportion of total stream respiration (Fellows, Valett & Dahm, 2001) and the meiofauna, which constitute the great majority of hyporheic organisms, can contribute up to 80% of total species diversity in lotic systems (Robertson, Rundle & Schmid-Araya, 2000). The observation that shortly after periods of high flows a higher number of invertebrates were found deep in the hyporheic zone (Williams & Hynes, 1974; Marchant, 1995) suggested that the hyporheos could act as a refugium during floods, an hypothesis that has been further supported (DoleOlivier, Marmonier & Beffy, 1997; Olsen & Townsend, 2005). Furthermore, the hyporheic zone hosts a variety of early life-stage of many insect species (amphibionts), as well as eggs and pupae, whose sensitivity to sediment deposition and infiltration has been so far neglected. Infiltrating sediments can thus reduce suitable refuge habitats during other disturbances and severely affect stream resistance and resilience.

The composition of the invertebrate community inhabiting the hyporheos is directly determined by habitat characteristics such as particles heterogeneity, percentage of fines, porosity, vertical hydrological exchange, all of which can be dramatically altered by siltation and clogging processes (Turnpenny & Williams, 1980; Maridet *et al*, 1996). Studying the macroinvertebrate colonization in a stream impacted by inputs of fines Richards & Bacon (1994) concluded that within the hyporheos, the abundance of fine sediments was the dominant influence on macroinvertebrate assemblages, while at the surface, stream size appeared more important. In their experiment Radwell & Brown (2006) showed how excessive fines deposition reduced total meiofauna colonization with negative effects on copepods, rotifers and nematodes. Boulton *et al.*(1997) attributed the lower number of taxa and individuals in the hyporheic zone of pasture streams, compared to forested streams, to hill slumping and siltation likely responsible of the development of anoxic zones. Although Richards & Bacon (1994) also showed that the hyporheos accumulated the greatest amount of all size categories of sediments, suggesting that it may be more impacted than the surface, specific studies are still rare.

Variable species response

Sediment effects on communities are obviously the consequence of variable species-specific response and tolerance. For instance, Broekenhuizen *et al.* (2001) experimentally fed the snail *Potamopyrgus antipodarum* and the mayfly *Deleatidium* sp. with organic matter contaminated with different quantity of inorganic sediment, and showed that even the smallest contamination would severely affect the growth rate of the mayfly, whilst the snail showed the greatest growth rate at intermediate levels of contaminations. Their findings are consistent with those of Suren (2005) who concluded that *Potamopyrgus* was more tolerant to sedimentation than *Deleatidium*, which constantly avoided sediment contaminated cobbles. The snail tolerance was attributed either to the ingestion of trace nutrients in the sediment, or to the abrasive mechanism of sediment rupturing algal cells thus increasing snail grazing rate.

Suren & Jowett (2001) found an increased number drifting individuals of the mayflies *Deleatidium* sp., the amphipod *Paracalliope fluviatilis* and the caddisfly *Hydrobiosis* sp. from sediment treated artificial channel, but could not determine whether the increased drift was caused by a reduction of suitable habitat, periphyton quality or which mechanism was more relevant to each taxon.

Extreme sedimentation events resulting in burial of benthic organisms are probably rare, but the relatively few studies concerning burial response have shown how different taxa behave in markedly different ways.

In an ex-situ experiment Wood *et al.* (2005) analysed the response of four common taxa to burial by different sediment sizes at two depth. While *Baetis rhodani* nymphs were unable to excavate themselves from any of the sediment, the plecopteran *Nemoura cambrica* excavated itself from all the sediment classes and depth of burial. The isopod *Asellus aquaticus*, which is normally associated with fine sediments (Extence, 1981), escaped rapidly from sediments <1mm, but needed much longer time to escape from sediment >1mm, and was entrapped by sediment >4mm. Finally, the trichopteran *Hydropsyche pellucidula* was trapped in particles <500μm.

Wood *et al.* (2001), describing the response of the Limnephilidae *Malampophylax mucoreus* to rapid sedimentation, demonstrated that variability within different life stages also occur, for the response was size dependent; larvae that became trapped were generally smaller.

The Chironomidae family also showed inconsistent response to sediments accumulation in both surveys and experiments. The sub-family Chironominae, commonly associated with organic-rich silt, often appeared to be negatively affected by increasing fines, contrary to expectations. Both Angradi (1999) and Cover *et al.* (2008) attributed this trend to the filling of interstitial habitat and a dilution of organic matter by inorganic particles.

Also, two grazers with similar habitat requirements (*Rithrogena* and *Glossosoma*) responded differently to reduce periphyton quality in silted locations, with *Rithrogena* displaying increased drift rates and reduced densities and *Glossosoma* showing milder responses. Differences in feeding-appendages morphology and in feeding efficiency under resource competition were invoked as possible explanations in this case (Molinos & Donohue, 2009). These considerations also show that caution is needed when interpreting functional changes in sediment impacted locations.

Individual adaptation may also mask sediment effects. In a paired mesocosm experiment using invertebrates from upland and lowland locations, Connolly & Pearson (2007) observed the stronger responses of Baetidae, Leptophlebiidae and Chironomidae from upland locations compared to the same taxa from lowland sites where sediment loads where already higher.

2.8 Main effects on fish

Fish have great economical importance throughout the world, both as resource and as recreational items. For this reason the literature on the effect of suspended sediment has been mostly focused on these organisms (Waters, 1995). As with other taxa, fish are certainly adapted to short time increases in sediment concentration due to natural events, and obviously certain species are much more tolerant than others. Species inhabiting natural clear water such as salmonids are likely to be more sensitive, therefore much of the research was limited to salmon and trout streams, whilst studies on warmwater fish are relatively few (Waters, 1995).

The effects of sedimentation and turbidity on fish have been thoroughly reviewed by Cordone & Kelley (1961), Bruton (1985) and Waters (1995).

Direct mortality due to suspended sediment is quite rare, especially in adults, which will avoid impacted reaches. Reynolds *et al.*(1989) observed 50% mortality in Arctic grayling sac fry exposed to sediments from a placer gold mine compared to 19% mortality in the control reaches. Scullion and Edwards (1980) observed an extremely high (>80%) mortality of Rainbow trout eggs and alevins in stream receiving ferruginous and suspended solid wastes.

Sublethal effects of suspensoids are much more documented and involve: reduced tolerance to diseases and toxicants (Redding, Schreck & Everest, 1987); impairment of respiratory functions by clogging and damaging gills (Bruton, 1985); reduced feeding capability and growth rate for visual feeders (Bruton, 1985; Rowe & Dean, 1998); avoidance behaviour, which in terms of stream productivity is equal to total fish mortality (Waters, 1995). Bottom-up effects are certainly affecting most predator taxa when sediment inputs are reducing benthic invertebrate abundance and diversity (Suttle *et al.*, 2004).

Sedimentation, however, is most detrimental to the reproductive success of salmon and trout. Almost all salmonids in flowing waters build redds for egg deposition that also represent very efficient sediment traps. Since eggs and embryos rely on intragravel flow as the main source of oxygen, deposition of fines and even larger particles within the redd can dramatically reduce gravel permeability and dissolved oxygen supply; this can result in declined egg and alevins survival and reduced fry weight (Turnpenny & Williams, 1980; Waters, 1995; Argent & Flebbe, 1999; Julien & Bergeron, 2006). More specifically, sediment infiltrating within the redds inhibit incubation success by: (1) reducing gravel permeability, and thus the passage of oxygenated water (Heywood & Walling, 2003); (2) reducing intragravel oxygen concentration when sediments are associated with O_2 consuming material (Dumas *et al*, 2007); (3) reducing the oxygen exchange across the egg membrane via clay-size particles deposition (Turnpenny & Williams, 1980). In addition, when a layer of consolidated sediments is deposited over the redd, emerging fry could be trapped (Waters, 1995).

Not only deposited fines can reduce the reproductive success and food resources but can dramatically alter the physical environment required by fish at different life stages. Rearing habitats, providing necessary protection for both juveniles and adults progressively disappear with increasing deposition. Particles filling the interstitial spaces of riffles reduce vital space for fry as retreats, and deposition in pools reduces water depth necessary for larger fish (Waters, 1995; Zuellig *et al.*, 2002).

In addition, other benthic fishes such as sculpins and bullies (Jowett & Boustead, 2001) may be severely affected by siltation with reduced density and unbalanced age classes frequently observed (Harvey, 1986; Mebane, 2001). The entire fish assemblage might be altered by anthropogenic changes in sediment regimes (Sutherland, Meyer & Gardiner, 2002). Richardson & Jowett (2002) observed a reduced abundance and diversity of the whole fish community with increasing sediment loads with up to nine fish species in streams with low sediment concentration and only two species in sediment impacted streams. In 30 piedmont streams north of Atlanta catchment urbanization was associated with reduced bed-particle sizes and increased baseflow NTU thus favouring cosmopolitan fish species over endemic taxa (Walters, Leigh & Bearden, 1993). Rabeni & Smale (1995) considered feeding and reproductive guilds of fish communities as useful indicators of siltation, with benthic insectivores and lithophilous spawners being the most sensitive. Mol & Ouboter (2004), reported altered age structure, higher proportion of surface feeding fish and lower proportion of visually orienting fish in a tropical stream draining a gold-mine. Mebane (2001) also proposed fish species age class structure as a valid indicator of sediment stress. In fact, different life-stages of fish have different tolerance to sediment, thus studying single life-stages in isolation could lead to incorrect predictions of population-level effects (Curry & MacNeill, 2004). More generally, the effects detected on certain life stages might be the result of earlier life-stage response.

Also, as previously noted with invertebrates, individual tolerance may contribute to variable response to sediment stress. In their innovative study, Bunt *et al*, (2004) measured the physiological response (cardiovascular performance) of rock bass to experimental silt loads. Specimen from river habitats that already experienced high silt loads acclimatised rapidly and showed no stress response, while specimen from silt-free lakes showed cardiac and respiratory impairment.

2.9 Knowledge gaps and research needs

Ecosystem and larger scale processes

Despite the fact that research on ecological effects of fine sediment in aquatic environments has increasingly focused on functional aspects of ecological responses, our understanding of how the effects observed at smaller scale actually scale-up to influence large scale dynamics and ecosystem-wide consequences is relatively poor (Fig. 2.2; Table 2.2). Besides primary production (Graham, 1990; Davies-Colley *et al.*, 1992; Yamada & Nakamura, 2002), albeit with some discordances (Parkhill & Gulliver, 2002), the effects of siltation on other ecosystem processes (e.g. nutrient cycling, organic matter retention) are largely unknown (Table 2.3).

Also, as the biological conditions of stream and rivers are naturally changing along the longitudinal axis, organisms' responses to sediment are likely to show complex relationship with the catchment across a wide range of spatial scales. For instance, I may know patterns of local deposition processes, but the final fate of fine particles entraining the river channel and their pattern of deposition and resuspension along the river as a whole are unclear (Wood & Armitage, 1999). The longitudinal reduction of sediment sizes also suggests that lowland reaches may support fine sediment-adapted taxa relatively tolerant to further supply of fines. However, this may be only partly correct as many rivers are characterised by so called "sedimentary links" separated by recruitment points of coarser substrata (tributaries, landslides) (Rice & Church, 1998; Rice, Greenwood & Joyce, 2001). Manipulative experiments over larger spatial scales along the river continuum and in diverse catchment contexts would certainly aid our understanding of realistic biological responses and ecosystem consequences of sediments effects.

Sources and confounds

Probably the most challenging research needs to develop predictive models of ecological sediments effects are to i) recognise a "signal" of anthropogenic alteration of sediment regimes over a background of natural processes, ii) identify likely sources in a given stream section and catchment, and iii) disentangle sediments effects from that of many associated stressors in impacted environments.

Defining a benchmark of sediment yield in a completely natural and undisturbed context is rarely possible (Reid & Frostick, 1994), therefore understanding what is the natural range of sediment regime for a given catchment, and how it differs from an anthropogenic modified regime is a problematic task. Besides the frequency and rate of supply, anthropogenic sediments are likely to differ from naturally occurring one in many aspects including grain size / sorting and chemical properties (organic matter content, nutrients, contaminants). In this perspective, stream conservation and management would benefit from further development of fingerprinting techniques able to identify catchments sediment sources with significant confidence (Walling, 2005). This would facilitate the control of anthropogenic sediment inputs via prevention, interdiction and restoration (Waters, 1995): if the primary source is recognized as being the catchment surface, it is likely to derive from bare soil erosion, excessive land-use or increased runoff from urban areas and attention must be paid on better land management. If the main source is the channel, sediment delivery can be reduced controlling bank erosion by impeding livestock grazing in the channel and promoting riparian buffer strips.

Finally, most of the current knowledge on fine sediment effects derives from either surveys or small scale experiments, which either have the disadvantages of dealing with multiple uncontrolled confounds or suffer from limited realism. Larger manipulative field experiments, although logistically demanding, would help us to identify the individual and combined effects of multiple stream stressors (Townsed *et al.* 2008). For example' following a factorial BACI approach, different sediment types (e.g. grain sizes, associated nutrients) could be used to impact streams in variable pre-existing conditions or draining diverse land-uses. However, disentangling sediment effects from the multi-scale multi-factor web of influences within lotic systems is virtually impossible (Fig. 2.3).

As mentioned before, further studies should also aim to understand how biotic interactions mediate sediment effects and how such effects scale up in the trophic chain. For example, very few studies have specifically assessed the response of different life stages of amphibians, although high sensitivity is expected (Welsh & Ollivier, 1998; Wood & Richardson, 2009). Further, bottom-up effects are also likely to affect other semi-aquatic organisms such as river birds and otters (Collier, 2004). Resent research also showed that riparian terrestrial invertebrates may be negatively affected by stream bed embeddedness, but formal testing is very scarce (Paetzold, Yoshimura & Tockner, 2008). Even less is known about the effects of sediment deposition on microbial metabolism and the trophic transfer across the microbial web. For example, denitrification rates have been shown to significantly increase in sediment deposits of less then 2mm in grain size (Solomon *et al*, 2009). Also, there is evidence that, especially in small streams, benthic bacteria are far more abundant and active than suspended bacteria (Allan, 1995); increasing sediment deposits and organic matter might then favour microbial production.

2.10 References

Aitken, W.W. (1936) The relatioin of soil erosion to stream improvement and fish life. *Journal of Forestry* **34,** 1059-1061.

Aldridge, D.W. (1987) The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels *Environmental Pollution,* **45,** 17-28.

Allan, J.D. (1995) *Stream Ecology. The Structure and Function of Running Waters,* Chapman & Hall, London.

Allan, J.D. (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics,* **35,** 257-284.

Angradi, T.R. (1999) Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications *Journal of the North American Benthological Society* **18,** 49-66

Argent, D.G. & Flebbe, P.A. (1999) Fine sediment effects on brook trout eggs in laboratory streams. *Fisheries Research,* **39,** 253-262.

Atkinson, B.L., Grace, M.R., Hart, B.T. & Vanderkruk, K. E. N. (2008) Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream. *Journal of the North America Benthological Society* **27,** 581-529.

Barton, B.A. (1977) Short-Term Effects of Highway Construction on Limnology of a Small Stream in Southern Ontario. *Freshwater Biology,* **7,** 99-108.

Bêche, L.A., Mcelravy, E.P. & Resh, V.H. (2006) Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. *Freshwater Biology,* **51,** 56-75.

Benstead, J.P., Deegan, L.A., Peterson, B.J., Huryn, A.D., Bowden, W.B., Suberkropp, K., Buzby, K.M., Green, A.C. & Vacca, J.A. (2005) Responses of a beaded Arctic stream to short-term N and P fertilisation. *Freshwater Biology,* **50,** 277-290.

Beschta, R.L. (1982) Comment on "A stream system evaluation: an emphasis on spawning habitat for salmonids" by Shirazi M.A. and Seim W.K. *Water Resources research,* **18,** 1292-1295.

Bickerton, M., Petts, G., Armitage, P. & Castella, E. (1993) Assessing the Ecological Effects of Groundwater Abstraction on Chalk Streams - 3

Examples from Eastern England. *Regulated Rivers-Research & Management,* **8,** 121-134.

Bolliet, V., Bardonnet, A., Jarry, M., Vignes, J.C. & Gaudin, P. (2005) Does embeddedness affect growth performance in juvenile salmonids? An experimental study in brown trout, *Salmo trutta* L. *Ecology of Freshwater Fish,* **14,** 289–295.

Bond, N.R. (2004) Spatial variation in fine sediment transport in small upland streams: the effects of flow regulation and catchment geology. *River Research and applications,* **20,** 705-717.

Boulton, A.J., Scarsbrook, M.R., Quinn, J.M. & Burrell, G.P. (1997) Land-use effects on the hyporheic ecology of five small streams near Hamilton, New Zealand. *New Zealand Journal of Marine and Freshwater Research,* **31,** 609-622.

Braccia, A. & Voshell, J.R. (2006) Environmental factors accounting for benthic macroinvertebrate assemblage structure at the sample scale in streams subjected to a gradient of cattle grazing. *Hydrobiologia,* **573,** 55-73.

Broekenhuizen, N., Parkyn, S. & Miller, D. (2001) Fine sediment effects on feeding and growth in the invertebrate grazers Potamopyrgus antipodarum (Gastropoda, Hydrobiidae) and Deleatidium sp. (Ephemeroptera, Leptophlebiidae). *Hydrobiologia,* **457,** 125-132.

Brookes, A. (1986) Response of Aquatic Vegetation to Sedimentation Downstream from River Channelization Works in England and Wales. *Biological Conservation,* **38,** 351-367.

Brunke, M. & Gonser, T. (1997) The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* **37,** 1-33.

Bruton, M.N. (1985) The effects of sospensoids on fish. *Hydrobiologia,* **125,** 221-241.

Bunt, C.M., Cook, S.J., Schreer, J.F. & Philipp, D.P. (2004) Effects of incremental increases in silt load on the cardiovascular performance of riverine and lacustrine rock bass, Ambloplites rupestris. *Environmental Pollution,* **128,** 437-444.

Cairns, J.J. (1977) Aquatic ecosystem assimilative capacity. *Fisheries* **2,** 5-7.

Cardinale, B.J., Gelmann, E.R. & Plamer, M.A. (2004) Net spinning caddisflies as stream ecosystem engineers: the influence of Hydropsyche on benthic substrate stability. *Functional Ecology,* **18,** 381–387.

Cardinale, B.J., Palmer, M.A., Swan, C.M., Brooks, S. & Poff, N.L. (2002) The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology,* **83,** 412-422.

Chutter, F.M. (1968) The effects of silt and sand on the invertebrate fauna of stream and rivers. *Hydrobiologia,* **34,** 57-76.

Cline, L.D., Short, R.A. & Ward, J.V. (1982) The Influence of Highway Construction on the Macroinvertebrates and Epilithic Algae of a High Mountain Stream. *Hydrobiologia,* **96,** 149-159.

Collier, K.J. (2002) Effects of flow regulation and sediment flushing on stream habitat and benthic invertebrates in a New Zealand river influenced by a vulcanic eruption. *River Research and Applications,* **18,** 213-226.

Collier, K.J. (2004) Perturbation pathways affecting the avian lotic predator, blue duck, following a volcanic eruption. *Freshwater Biology,* **49,** 818-834.

Connolly, N.M. & Pearson, R.G. (2007) The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: a comparison using flowthrough artificial stream channels and recirculating mesocosms. *Hydrobiologia,* **592,** 423-438.

Cordone, A.J. & Kelley, D.W. (1961) The influences of inorganic sediment on the quatic life of streams. *California Fish and Game,* **47.**

Cover, M.R., May, C.L., Dietrich, W.E. & Resh, V.H. (2008) Quantitative linkages among sediment supply, streambed fine sediment, and benthic macroinvertebrates in northern California streams. *Journal of the North American Benthological Society,* **27,** 135-149.

Culp, J.M., Wrona, F.J. & Davies, R.W. (1985) Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology,* **64,** 1345-1351.

Curry, A.R. & Macneill, W.S. (2004) Population-level responses to sediment during early life in brook trout. *Journal of The North American Benthological Society,* **23,** 140-150.

Davies-Colley, R.J., Hickey, C.W., Quinn, M.J. & Ryan, P.A. (1992) Effects of clay discharges on streams. Optical properties and ephilithon. *Hydrobiologia,* **248,** 215-234.

Davies-Colley, R.J. & Smith, D.G. (2001) Turbidity, suspended sediment, and water clarity: A review. *Journal of the American Water Resources Association,* **37,** 1085-1101.

Davies, P.E. & Nelson, M. (1993) The effect of steep slope logging on fine sediment infiltration into the beds of ephemeral and perennial streams of the Dazzler Range, Tasmania, Australia. *Journal of Hydrology,* **150,** 481-504.

Dickman, M.D., Peart, M.R. & Yim, W.W.S. (2005) Benthic diatoms as indicators of stream sediment concentration in Hong Kong. *International Review of Hydrobiology,* **90,** 412-421.

Dobson, M., Poynter, K. & Cariss, H. (2000) Case Abandonment as a Response to Burial by Potamophylax cingulatus (Trichoptera: Limnephilidae) Larvae. *Aquatic Insects,* **22,** 99–107.

Doeg, T.J. & Koehn, J.D. (1994) Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. . *Regulated Rivers-Research & Management* **9,** 263-277.

Doledec, S., Phillips, N., Scarsbrook, M., Riley, R.H. & Townsend, C.R. (2006) Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. *Journal of the North American Benthological Society,* **25,** 44-60.

Doleolivier, M.J., Marmonier, P. & Beffy, J.L. (1997) Response of invertebrates to lotic disturbance: Is the hyporheic zone a patchy refugium? *Freshwater Biology,* **37,** 257-276.

Dumas, J., Bassenave, J.G., Jarry, M., Barriere, L. & Glise, S. (2007) Effects of fish farm effluents on egg-to-fry development and survival of brown trout in artificial redds. *Journal of Fish Biology,* **70,** 1734-1758.

Ellis, M.M. (1936) Erosion silt as factor in aquatic environments. *Ecology,* **17,** 29-42.

Englund, G., Johansson, F., Olofsson, P., Salonsaari, J. & Ohman, J. (2009) Predation leads to assembly rules in fragmented fish communities. *Ecology Letters,* **12,** 663-671.

Extence, C.A. (1978) The effects of motorway constructions on an urban stream. *Environmental Pollution,* **17,** 245-252.

Extence, C.A. (1981) The Effect of Drought on Benthic Invertebrate Communities in a Lowland River. *Hydrobiologia,* **83,** 217-224.

Fellows, C.S., Valett, H.M. & Dahm, C.N. (2001) Whole-stream metabolism in two montane streams: Contribution of the hyporheic zone. *Limnology and Oceanography,* **46,** 523-531.

Fossati, O., Wasson, J.G., Hery, C., Salinas, G. & Marin, R. (2001) Impact of sediment releases on water chemistry and mocroinvertebrate communities in clear water Andean stream (Bolivia). *Archiv fur Hydrobiologie,* **151,** 33-50.

Gafner, K. & Robinson, C.T. (2007) Nutrient enrichment influences the responses of stream macroinvertebrates to disturbance. *Journal of the North American Benthological Society,* **26,** 92-102.

Gard, M.F. (2002) Effects of sediment loads on the fish and invertebrates of Sierra Nevada river, California. *Journal of aquatic ecosystem stress and recovery,* **9,** 227-238.

Gayraud, S., Herouin, E. & Philippe, M. (2002) The clogging of stream beds: A review of mechanisms and consequences on habitats and macroinvertebrate communities. *Bulletin Francais de le Peche et se la Pisciculture,* **365,** 339-355

Gayraud, S. & Philippe, M. (2003) Influence of Bed-Sediment Features on the Interstitial Habitat Available for Macroinvertebrates in 15 French Streams. *Internatinal Review of Hydrobiology,* **88,** 77–93.

Gibbins, C., Vericat, D., Batalla, R.J. & Gomez, C.M. (2007) Shaking and moving: low rates of sediment transport trigger mass drift of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences,* **64,** 1-5.

Graham, C.K. (1990) Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentration in suspension. *Hydrobiologia,* **199,** 107-115.

Gray, J.L. & Ward, J.V. (1982) Effects of sediment releases from a reservoir on stream macroinvertebrates. *Hydrobiologia,* **96,** 177-184.

Greig, S.M., Sear, D.A. & Carling, P.A. (2005) The impact of fine sediment accumulation on the survival of incubating salmon progreny: Implications for sediment management. *Science of the Total Environment,* **344,** 241-258.

Hancock, F.D. (1973) Algal Ecology of a Stream Polluted through Gold Mining on Witwatersrand. *Hydrobiologia,* **43,** 189-229.

Harvey, B.C. (1986) Effects of Suction Gold Dredging on Fish and Invertebrates in Two California Streams. *North American Journal of Fisheries Management* **6,** 401–409.

Hellawell, J.R. (1986) *Biological indicators of freshwater pollution and environmental management,* Elsevier Applied Science Publishers, London.

Heywood, M.J.T. & Walling, D.E. (2003) Suspended sediment fluxes in chalk streams in the Hampshire Avon catchment, U.K. *Hydrobiologia,* **494,** 111-117.

Holomuzki, J.R. & Biggs, B.J.F. (2003) Sediment texture mediates high-flow effects on lotic macroinvertebrates. *Journal of the North American Benthological Society,* **22,** 542-553.

Jowett, I.G. & Boustead, N.C. (2001) Effects of substrate and sedimentation on the abundance of upland bullies (Gobiomorphus breviceps). *New Zealand Journal of Marine and Freshwater Research,* **35,** 605-613.

Julien, H.P. & Bergeron, N.E. (2006) Effect of fine sediment infiltration during the incubation period on atlantic salmon (Salmo salar) embryo survival. *Hydrobiologia,* **563,** 61-71.

Kaller, M.D. & Hartman, K.J. (2004) Evidence of a threshold level of fine sediment accumulation for altering benthic macroinvertebrate communities. *Hydrobiologia,* **518,** 95 -104.

Kent, T.R. & Stelzer, R.S. (2008) Effects of deposited fine sediment on life history traits of Physa integra snails. *Hydrobiologia,* **596,** 329-340.

Kirk, J.T.O. (1985) Effects of Suspensoids (Turbidity) on Penetration of Solar-Radiation in Aquatic Ecosystems. *Hydrobiologia,* **125,** 195-208.

Knighton, D. (1998) *Fluvial Forms and Processes: A New Perspective,* Hodder Arnold, London.

Kreutzweiser, D.P. & Capell, S.S. (2001) Fine sediment deposition in streams after selective forest harvesting without riparian buffers. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* **31,** 2134-2142.

Kreutzweiser, D.P., Capell, S.S. & Good, K.P. (2005) Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology,* **39,** 55-66.

Larsen, S., Vaughan, I.P. & Ormerod, S.J. (2009) Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology,* **54,** 203-219.

Lemly, D. (1982) Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia,* **87,** 229-245.

Lenat, D.R. (1984) Agriculture and Stream Water-Quality - a Biological Evaluation of Erosion Control Practices. *Environmental Management,* **8,** 333-343.

Lenat, R.D., Penrose, D.L. & Eagleson, W.K. (1981) Variable effects of sediment addiction on stream benthos. *Hydrobiologia,* **79,** 187-194.

Lewis, K. (1973a) The effect of suspended coal particles on the life forms of the aquatic moss Eurhynchium riparoides (Hedw). I. The gamethophyte plant. *Freshwater Biology,* **3,** 251-257.

Lewis, K. (1973b) The effect of suspended coal particles on the life forms of the aquatic moss Eurhynchium riparoides (Hedw).II. The effect on spore germination and regeration of apical tips. *Freshwater Biology,* **3,** 391-395.

Lisle, T.E. & Hilton, S. (1992) The Volume of Fine Sediment in Pools - an Index of Sediment Supply in Gravel-Bed Streams. *Water Resources Bulletin,* **28,** 371-383.

Lloyd, D.S., Koenings, J.P. & Laperriere, J.D. (1987) Effects of turbidity in fresh waters in alaska. *North American Journal of Fisheries Management,* **7,** 18-33.

Luedtke, R.J. & Brusven, M.A. (1976) Effects of Sand Sedimentation on Colonization of Stream Insects. *Journal of the Fisheries Research Board of Canada,* **33,** 1881-1886.

Manel, S., Buckton, S.T. & Ormerod, S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology,* **37,** 756-770.

Marchant, R. (1995) Seasonal-Variation in the Vertical-Distribution of Hyporheic Invertebrates in an Australian Upland River. *Archiv Fur Hydrobiologie,* **134,** 441-457.

Maridet, L., Philippe, M., Wasson, J.G. & Mathieu, J. (1996) Spatial and temporal distribution of macroinvertebrates and trophic variables within the bed sediment of three streams differing by their morphology and riparian vegetation. *Archiv Fur Hydrobiologie,* **136,** 41-64.

Matthaei, C.D., Weller, F., Kelly, D.W. & Townsend, C.R. (2006) Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology,* **51,** 2154-2172.

Mebane, C.A. (2001) Testing bioassessment metrics: macroinvertebrate, sculpin, and salmonid responses to stream habitat, sediment and metals. *Environmental Monitoring and Assessment,* **67,** 293-322.

Metzler, G.M. & Smock, L.A. (1990) Storage and Dynamics of Subsurface Detritus in a Sand-Bottomed Stream. *Canadian Journal of Fisheries and Aquatic Sciences,* **47,** 588-594.

Minshall, G.W. (1984) Aquatic insect-substratum relationships. In: *The ecology of aquatic insects.* (Eds V.H. Resh & D.M. Rosenberg), pp. 358-400. Preager publishers, New York.

Mol, J.H. & Ouboter, P.E. (2004) Downstream effects of erosion from small-scale gold mining on the instream habitat and fish community of a small neotropical rainforest stream. *Conservation Biology,* **18,** 201-214.

Molinos, J.G. & Donohue, I. (2009) Differential contribution of concentration and exposure time to sediment dose effects on stream biota. *Journal of the North American Benthological Society,* **28,** 110-121.

Nakano, D., Yamamoto, M. & Okino, T. (2005) Ecosystem engineering by larvae of net-spinning stream caddisflies creates a habitat on the upper surface of stones for mayfly nymphs with a low resistance to flows. *Freshwater Biology,* **50,** 1492-1498.

Newcombe, C.P. & Jensen, J.O.T. (1996) Channel suspended sediment and fisheries: a synthesis of quantitative assessment of risk and impact. *North American Journal of Fisheries Management,* **16,** 693-727.

Newcombe, C.P. & Macdonald, D.D. (1991) Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management,* **11,** 72-82.

Niyogi, D.K., Koren, M., Arbuckle, C.J. & Townsend, C.R. (2007a) Longitudinal changes in biota along four New Zealand streams: declines and improvements in stream health related to land use. *New Zealand Journal of Marine and Freshwater Research,* **41,** 63-75.

Niyogi, D.K., Koren, M., Arbuckle, C.J. & Townsend, C.R. (2007b) Stream communities along a catchment land-use gradient: Subsidy-stress responses to pastoral development. *Environmental Management,* **39,** 213-225.

Nuttall, P.M. (1972) The effect of sand deposition upon the macro-invertebrate fauna of the river Camel, Cornwall. *Freshwater Biology,* **2,** 181-186.

Nuttall, P.M. & Bielby, G.H. (1973) The effect of china-clay wastes on stream invertebrates. *Environmental Pollution,* **5,** 77-86.

Olley, J.M. & Wasson, R.J. (2003) Changes in the flux of sediment in the Upper Murrumbidgee catchment, Southeastern Australia, since European settlement. *Hydrological Processes,* **17,** 3307-3320.

Olsen, D.A. & Townsend, C.L. (2003) Hyporheic community composition in a gravel-bed stream: influence of vertical hydrological exchange,sediment structure and physicochemistry. *Freshwater Biology,* **48,** 1363–1378.

Olsen, D.A. & Townsend, C.R. (2005) Flood effects on invertebrates, sediments and particulate organic matter in the hyporheic zone of a gravel-bed stream. *Freshwater Biology,* **50,** 839-853.

Osmundson, D.B., Ryel, R.J., Lamarra, V.L. & Pitlick, J. (2002) Flow-sediment-biota relations: Implications for river regulation effects on native fish abundance. *Ecological Applications,* **12,** 1719-1739.

Owens, P.N., Batalla, R.J., A. J. Collins, B. Gomez, D. M. Hichs, A. J. Horowitz, Kondolf;, G.M., M. Marden, M. J. Page, D. H. Peacock, E. L. Petticrew, W. Salomons & N. A. Trustrumi (2005) Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications,* **21,** 693–717.

Owens, P.N., Walling, D.E. & Leeks, G.J.L. (1999) Deposition and storage of fine-grained sediment within the main channel system of the river tweed, scotland. *Earth Surface Processes and Landforms,* **24,** 1061-1076.

Paetzold, A., Yoshimura, C. & Tockner, K. (2008) Riparian arthropod responses to flow regulation and river channelization. *Journal of Applied Ecology,* **45,** 894-903.

Parkhill, K.L. & Gulliver, J.S. (2002) Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia,* **472,** 5-17.

Platts, W.S., Torquemada, R.J., Mchendry, M.L. & Graham, C.K. (1989) Changes in salmon spawing and rearing habitat from increased delivery of fine sediment to the South Fork Salmon River. *Transactions of the American Fisheries Society,* **118,** 274-283.

Pollard, A.I. & Yuan, L.L. (2009) Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity-based measures. *Freshwater Biology,* **in press**.

Pringle, C.M., Blake, G.A., Covich, A.P., Buzby, K.M. & Finley, A. (1993) Effects of Omnivorous Shrimp in a Montane Tropical Stream - Sediment Removal, Disturbance of Sessile Invertebrates and Enhancement of Understory Algal Biomass. *Oecologia,* **93,** 1-11.

Pye, K. (1994) Properties of sediment particles. In: *Sediment transport and depositional processes.* (Eds K. Pye). Blackwell Scientific Publication, Oxford.

Quinn, M.J., Davies-Colley, R.J., Hickey, C.W., Vickers, M.L. & Ryan, P.A. (1992) Effects of clay discharge on streams. Benthic invertebrates. *Hydrobiologia,* **248,** 235-247.

Rabeni, C.F., Doisy, K.E. & Zweig, L.D. (2005) Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences,* **67,** 395-402.

Rabeni, C.F. & Minshall, G.W. (1977) Factors affecting microdistribution of stream benthic insects. *Oikos,* **29,** 33-43.

Rabeni, C.F. & Smale, M.A. (1995) Effects of Siltation on Stream Fishes and the Potential Mitigating Role of the Buffering Riparian Zone. *Hydrobiologia,* **303,** 211-219.

Radwell, A.J. & Brown, A.V. (2006) Influence of fine sediments on meiofauna colonization densities in artificial stream channels. *Archiv Fur Hydrobiologie,* **165,** 63-75.

Rathburn, S.L. & Whol, E.E. (2001) One-dimensional sediment transport modeling of pool recovery along a mountain channel after a reservoir sediment release. *Regulated Rivers: Research & Management,* **17,** 251-273.

Redding, J.M., Schreck, C.B. & Everest, F.H. (1987) Physiological-Effects on Coho Salmon and Steelhead of Exposure to Suspended-Solids. *Transactions of the American Fisheries Society,* **116,** 737-744.

Rehg, J.K., Packman, A.I. & Ren, J. (2005) Effects of suspended sediment characteristics and bed sediment transport on streambed clogging. *Hydrological Processes,* **19,** 413–427.

Reid, I. & Frostick, L.E. (1994) Fluvial sediment trasnport and deposition In: *Sediment transport and depositional processes.* (Eds K. Pye). Blackwell Scientific Publication.

Reynolds, J.B., Simmons, R.C. & Burkholder, A.R. (1989) Effects of Placer Mining Discharge on Health and Food of Arctic Grayling. *Water Resources Bulletin,* **25,** 625-635.

Rice, S. & Church, M. (1998) Grain size along two gravel-bed rivers: Statistical variation, spatial pattern and sedimentary links. *Earth Surface Processes and Landforms,* **23,** 345-363.

Rice, S.P., Greenwood, M.T. & Joyce, C.B. (2001) Macroinvertebrate community changes at coarse sediment recruitment points along two gravel bed rivers. *Water Resources Research,* **37,** 2793-2803.

Richards, C. & Bacon, K.L. (1994) Influence of Fine Sediment on Macroinvertebrate Colonization of Surface and Hyporheic Stream Substrates. *Great Basin Naturalist,* **54,** 106-113.

Richardson, J. & Jowett, I.J. (2002) Effects of sediment on fish communities in East Cape streams, North Island, New Zealand *New Zealand Journal of Marine and Freshwater Research* **36,** 431-442.

Robertson, A.L., Rundle, S.D. & Schmid-Araya, J.M. (2000) Putting the meio- into stream ecology: current findings and future directions for lotic meiofaunal research. *Freshwater Biology,* **44,** 177-183.

Rowe, D.K. & Dean, T.L. (1998) Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine and Freshwater Research,* **32,** 21-29.

Runde, J.M. & Hellenthal, R.A. (2000) Behavioral Responses of *Hydropsyche sparna* (Trichoptera:Hydropsychidae) and Related Species to Deposited Bedload Sediment. *Environmental Entomology,* **29,** 704-709.

Ryan, P.A. (1991) Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research,* **25,** 207-221.

Ryder, D.S. & Miller, W. (2005) Setting goals and measuring success: linking patterns and processes in stream restoration. *Hydrobiologia,* **552,** 147-158.

Sable, K.A. & Wohl, E. (2006) The relationship of lithology and watershed characteristics to fine sediment deposition in streams of the Oregon Coast Range. *Environmental Management,* **37,** 659-670.

Schalchli, U. (1992) The Clogging of Coarse Gravel River Beds by Fine Sediment. *Hydrobiologia,* **235,** 189-197.

Schoener, T.W. (1983) Field Experiments on Interspecific Competition. *American Naturalist,* **122,** 240-285.

Schofield, K.A., Pringle, C.M. & Meyer, J.L. (2004) Effects of increased bedload on algal- and detrital-based stream food webs: Experimental manipulation of sediment and macroconsumers. *Limnology and Oceanography,* **49,** 900-909.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekotter, T., Hendrickx, F., Herzog, F., Liira, J., Maelfait, J.P., Speelmans, M. & Dziock, F. (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos,* **116,** 461-472.

Scullion, J. & Edward, R.W. (1980) The effects of coal industry pollutants on macroinvertebrate fauna of a small river in the South Wales coalfield. *Freshwater Biology,* **10,** 141-162.

Shaw, A.E. & Richardson, J.S. (2001) Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*oncorhynchus mykiss*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences,* **58,** 2213-2221.

Shirazi, M.A. & Seim, W.K. (1979) A stream system evaluation: an emphasis on spawning habitat for salmonids. In: *EPA Report.* (Ed^Eds. U.S. Environmental Protection Agency
Washington DC.

Solomon, C.T., Hotchkiss, E.R., Moslemi, J.M., Ulseth, A.J., Stanley, E.H., Hall, R.O. & Flecker, A.S. (2009) Sediment size and nutrients regulate denitrification in a tropical stream. *Journal of the North American Benthological Society,* **28,** 480-490.

Spanhoff, B., Augspurger, C. & Kusel, K. (2007) Comparing field and laboratory breakdown rates of coarse particulate organic matter: Sediment dynamics mask the impacts of dissolved nutrients on CPOM mass loss in streams. *Aquatic Sciences,* **69,** 495-502.

Stone, M. & Droppo, I.G. (1994) In-Channel Surficial Fine-Grained Sediment Laminae .2. Chemical Characteristics and Implications for Contaminant Transport in Fluvial Systems. *Hydrological Processes,* **8,** 113-124.

Strand, M.R. & Merritt, R.W. (1997) Effects of episodic sedimentation on the netspinning caddisflies *Hydropsyche betteni* and *Ceratopsyche sparna* (trichoptera: hydropsychidae). *Environmental Pollution,* **98,** 129-134.

Suren, A.M. (2005) Effects of deposited sediment on patch selection by two grazing stream invertebrates. *Hydrobiologia,* **549,** 205-218.

Suren, A.M. & Jowett, I.J. (2001) Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research,,* **35,** 725-737.

Sutherland, A.B., Meyer, J.L. & Gardiner, E.P. (2002) Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology,* **47,** 1791–1805.

Suttle, K.B., Power, M.E., M.;, L.J. & Mcneely, C. (2004) How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications,* **14,** 969–974.

Townsend, C.R., Uhlmann, S.S. & Matthaei, C.D. (2008) Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology,* **45,** 1810-1819.

Turnpenny, A.W.H. & Williams, R. (1980) Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology,* **17,** 681-693.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37,** 130-137.

Walling, D.E. (1990) Linking the field to river: sediment delivery from agricultural land. In: *Soil erosion and agricultural land.* (Eds J. Boardman & D.L. Foster & J.A. Dearing), pp. 129-152. John Wiley, Chichester.

Walling, D.E. (2005) Tracing suspended sediment sources in catchments and river systems. *Science of the Total Environment,* **344,** 159– 184.

Walling, D.E. & Amos, M. (1999) Source, storage and mobilisation of fine sediment in a chalk stream system. *Hydrological Processes,* **13,** 323-340.

Walters, D.M., Leigh, D.S. & Bearden, A.B. (1993) Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River Basin, USA *Hydrobiologia,* **494,** 5-10.

Wantzen, K.M. (2006) Physical pollution: effects of gully erosion on benthic invertebrates in a tropical clear-water stream. *Aquatic Conservation-Marine and Freshwater Ecosystems,* **16,** 733-749.

Warren, N., Allan, I.J., Carter, J.E., House, W.A. & Parker, A. (2003) Pesticides and other micro-organic contaminants in freshwater sedimentary environments - a review. *Applied Geochemistry,* **18,** 159-194.

Waters, T.F. (1995) *Sediments in streams: sources, biological effects, and control,* AFS Monographs, Bethesda, Maryland.

Welsh, H.H. & Ollivier, L.M. (1998) Stream amphibians as indicators of ecosystem stress: A case study from California's redwoods. *Ecological Applications,* **8,** 1118-1132.

Whitman, M.S., Moran, E.H. & Ourso, R.T. (2003) Photographic techniques for characterizing streambed particle sizes. *Transactions of the American Fisheries Society,* **132,** 605-610.

Wilby, R.L., Dalgleish, H.Y. & Foster, I.D.L. (1997) The impact of weather patterns on historic and contemporary catchment sediment yields. *Earth Surface Processes and Landforms,* **22,** 353-363.

Williams, D.D. & Hynes, H.B.N. (1974) Occurrence of Benthos Deep in Substratum of a Stream. *Freshwater Biology,* **4,** 233-255.

Wolman, M. (1954) A method of sampling coarse river bed material. *Transactions of the American Geophysical Union,* **35,** 951-956.

Wood, P.J. & Armitage, P.D. (1997) Biological Effects of Fine Sediment in the Lotic Environment. *Environmental Management,* **21,** 203-217.

Wood, P.J. & Armitage, P.D. (1999) Sediment deposition in a small lowland stream-management implications. *Regulated Rivers: Research & Management,* **15,** 199–210.

Wood, P.J., Toone, J., Greenwood, M.T. & Armitage, P.D. (2005) The response of four lotic macroinvertebrate taxa to burial by sediments. *Archiv fur Hydrobiologie,* **163,** 145-162.

Wood, P.J., Vannn, A.R. & Wanless, P.J. (2001) The response of *Melampophylax mucoreus* (Hagen) (Trichoptera:Limnephilidae) to rapid sedimentation. *Hydrobiologia,* **455,** 183-188.

Wood, S.L.R. & Richardson, J.S. (2009) Impact of sediment and nutrient inputs on growth and survival of tadpoles of the Western Toad. *Freshwater Biology,* **54,** 1120-1134.

Yamada, H. & Nakamura, F. (2002) Effect of fine sediment deposition and channel works on periphyton biomass in the makomanai river, northern japan. *River Research and Applications,* **18,** 481–493.

Yoshimura, C., Tockner, K., Omura, T. & Moog, O. (2006) Species diversity and functional assessment of macroinvertebrate communities in Austrian rivers. *Limnology,* **7,** 63-74.

Zanetell, B.A. & Peckarsky, B.L. (1996) Stoneflies as ecological engineers - Hungry predators reduce fine sediments in stream beds. *Freshwater Biology,* **36,** 569-577.

Zuellig, R.E., Kondratieff, B.C. & Rhodes, H.A. (2002) Benthos recovery after an episodic sediment release into a Colorado Rocky Mountain River. *Western North American Naturalist,* **62,** 59-72.

Zweig, L.D. & Rabeni, C.F. (2001) Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society,* **20,** 643-657.

2.11 Tables and Figures

Table 2.1- Main anthropogenic activities altering sediment regimes and common associated covariates in flowing waters.

Anthropogenic activity	Sediment change	Main associated covariates
Agriculture (diffuse)	Quantity, chemical properties, particle size	Water quality, loss of riparian buffers
Forestry (point)	Organic content, regime	Loss of riparian buffer, T range
Mining (point)	Quantity, chemical properties, particle size	Water quality, loss of buffer strips
Water abstraction (diffuse)	Regime	Altered hydrology, loss of habitat
Livestock grazing (point)	Quantity, chemical properties	Water quality, bank erosion
Urbanization (point/diffuse)	Regime, chemical properties	Water quality, altered hydrology
Dams / straightening (point)	Quantity, regime	Altered river continuum, lateral exchange

Table 2.2 –Sediment effects on ecosystem processes / properties. Potential consequences of sediment deposition are likely to be context dependent.

Ecological process / property	Potential effect	Rationale
1) Primary production	Reduced	Decrease Chlorophyll *a* content and periphyton biomass, increase non-living periphyton. Reduce algal diversity. However, increased photosynthetic efficiency can compensate irradiance loss (Parkhill & Gulliver, 2002). Also, where sediments are associated with nutrients antagonistic effects are possible.
2) Secondary production	Reduced	Decrease in fish and invertebrate diversity and biomass. However, sediment associated nutrients can favour some taxa through increased primary production (Townsend *et al.*, 2008).
3) Organic matter decomposition.	Variable (?)	Shredders are generally less sensitive to sedimentation (Rabeni *et al.*, 2005), which could, however, decrease resource palatability (Kreutzweiser *et al.*, 2005).
Leaf breakdown		Sediments may bury coarse organic matter, making it inaccessible (Spanhoff, Augspurger & Kusel, 2007), but associated nutrients can enhance decomposition rates (Benstead *et al*, 2005). See also points 5 - 6.
4) Import / Export of organic matter.	(?)	Fine grained deposits could decrease substratum heterogeneity and retentiveness. However, fine sediments could store large amounts of fine detritus (Metzler & Smock, 1990).
Longitudinal transport		Decline in sensitive filter feeding organism could increase POM transport downstream.
5) Assimilative capacity	Reduced (?)	Sedimentation can reduce aquatic plants able to trap nutrients (but see point 1). It also depends on microbial response to sediments (see next point).
6) Bacterial metabolism	Increased (?)	Deposits of fine grains have been shown to increase denitrification rates (Solomon *et al.*, 2009).
7) Resistance / Resilience	Reduced (?)	Loss of hyporheic refugium reduces resilience (Richards & Bacon, 1994; Olsen & Townsend, 2003). However, sediment-rich location could host pre-adapted tolerant taxa. Also, local adaptation may buffer negative effects and increase resistance (e.g. Connolly & Pearson, 2007).

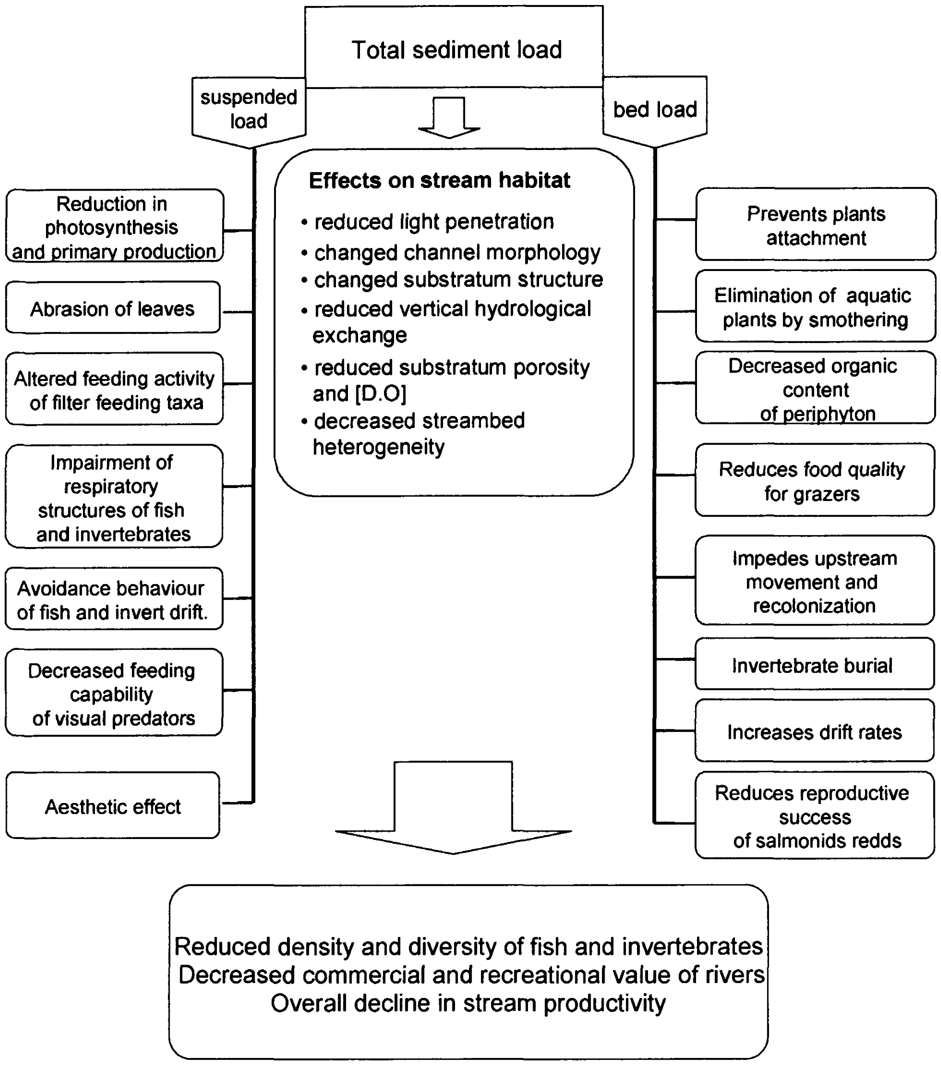


Fig. 2.1 - Flowchart summarising the main effects of suspended and bedload sediments on stream biota and habitat.

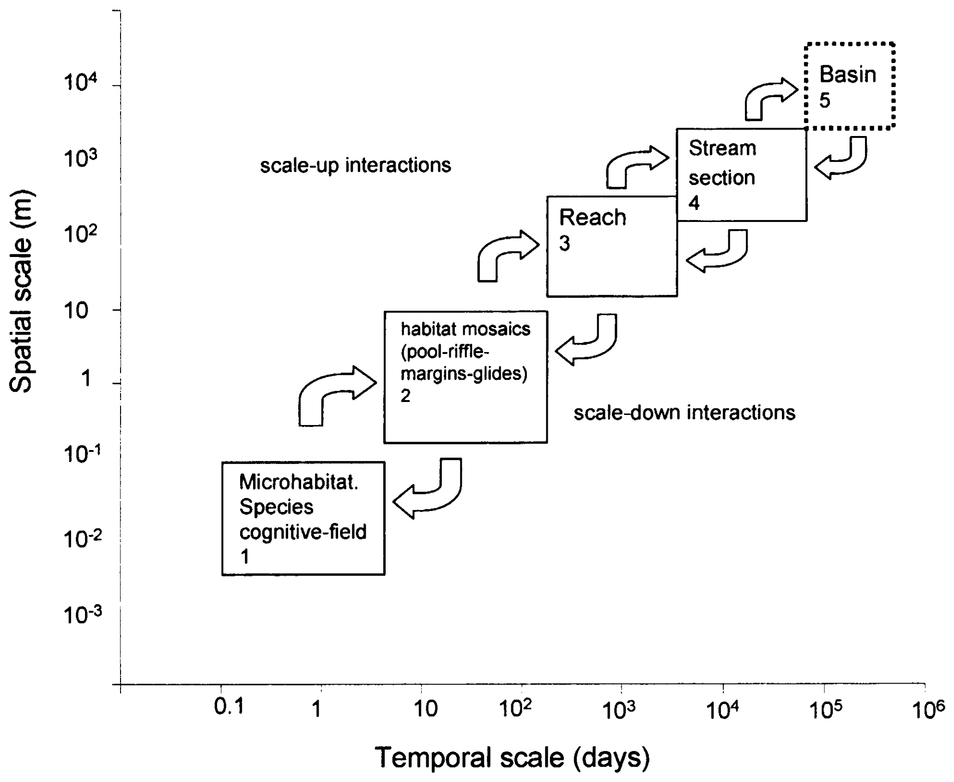


Fig. 2.2. Effects of sediment deposition on stream habitats at different scales.

The temporal scale is not necessarily representing sediment residence time that changes according to flow regime and sediment re-supply.

Effects on 1: direct mechanical stress on organisms; filling interstices; reducing suitable habitat; reducing dissolved oxygen concentration.

Effects on 2: altering habitat mosaics; clogging riffles and filling pools; homogenizing stream bed structure.

Effects on 3: reducing primary production and whole stream metabolism.

Effects on 4 and 5: effects on ecosystem scale processes are not clear.

Interactions among scales are playing a major role in determining the global effects.

-Small scale dynamics scale-up to affect larger scale processes (i.e. loss of hyporheic refugia can reduce ecosystem resistance / resilience; reduced grazers, filterers and detritivores abundance affects whole stream metabolism and organic matter input/export).

-Large scale features influence smaller scale effects (i.e. catchment characteristics such as land-use, soil type and topography affect sediment quality/quantity, regime and in-stream behaviour).

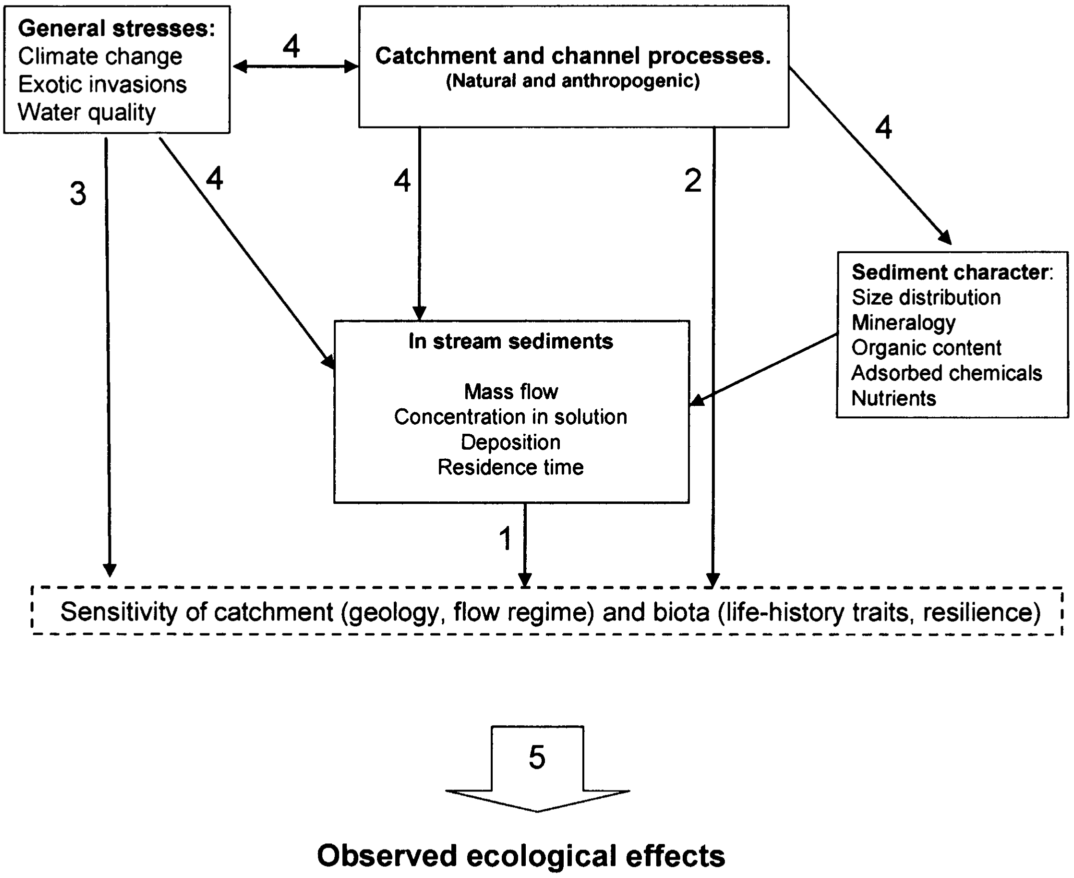


Fig. 2.3. Complex inter-relations of fluvial sediments with other processes and disturbances. The observed ecological effect of sedimentation on stream organisms is the result of: (1) direct impact of in-stream sediments and related characteristics; (2) direct influence of channel and catchment processes and disturbances; (3) direct influence of other general stresses; (4) the reciprocal influence of these factors and processes on each other; (5) the sensitivity of the catchment, stream and organisms. The overall sensitivity depends on catchment and stream physical and chemical features, organism's traits, historical disturbances, individual adaptation and susceptibility to other stresses.

Chapter 3 - Scale-dependent effects of fine sediments on temperate headwater invertebrates

Summary

1. Anthropogenic activities can increase fine sediment supply to streams over multiple spatial and temporal extents. Identifying the processes responsible, and the scale at which any effects on stream organisms become evident, are key management needs, but appropriately scaled surveys are surprisingly few.

2. I surveyed macroinvertebrates and superficial fine sediments at two spatial resolutions (reach- and patch-scale) in tributaries of the River Usk, a temperate, montane catchment in rural Wales (UK). Land use, habitat and geomorphological character were measured on-site or derived from an existing database (= Fluvial Audit). I aimed to identify: i) how in-stream sediments varied with land use and associated geomorphology; ii) likely consequences for macroinvertebrates and iii) any scale-dependence in relationships between macroinvertebrates and sediment character.

3. At both the reach- and patch-scales, bed cover by fine sediment was related directly to the extent of eroding banks 500m upstream. In turn, sedimentation and bank erosion were negatively correlated with catchment or riparian woodland extent.

4. At the reach scale, macroinvertebrate composition varied with catchment land use and stream chemistry, with richness declining as rough grazing or woodland was replaced by improved grassland. There was no response to deposited sediment except for weak increase in the relative abundance of oligochaetes.

5. By contrast, at the patch scale, fine sediments were accompanied by pronounced changes in invertebrate composition, and I ranked the 27 most common taxa according to their apparent sediment tolerance. General estimating equations (GEE) showed that total and EPT richness decreased significantly by 20% and 25% at the most sediment impacted sites (30% cover) by comparison with sediment-free sites.

6. I conclude that sediment deposition in the Usk system reflects local bank erosion, with riparian woodland likely to mediate this process through bank stability. Fine sediment release had marked ecological effects, but these were detectable only at patch-to-patch scales. I suggest that investigation of localised sediment release in streams will benefit from scale-dependent or scale-specific sampling, and some effects could go undetected unless sample resolution is selected carefully.

3.1 Introduction

Many physico-chemical variables that influence benthic invertebrate in rivers are mediated by catchment characteristics (Bunn & Davies, 2000; Imhof *et al.*, 1996; Ankers, Walling & Smith, 2003). These effects are scale-dependent because regional or catchment features influence processes at smaller spatial extents (Ciesielka & Bailey, 2007; Mykra, Heino & Muotka, 2007; Townsend, Doledec, Norris *et al.*, 2003). A good example is where catchment or riparian land-use and geology determine sediment and nutrient runoff into streams (Bond, 2004; Niyogi *et al.*, 2007b; Opperman, Lohse, Brooks *et al.*, 2005; Rabeni & Smale, 1995; McPherson & Riley, 2006; Jones, Neale, Nash *et al.*, 2001). In turn, the deposition of fine sediment, often from anthropogenic activities, can have major consequences for stream organisms (Davies-Colley *et al.*, 1992; Gayraud *et al.*, 2002; Gray & Ward, 1982; Greig, Sear & Carling, 2005a; Luedtke & Brusven, 1976; Newcombe & MacDonald, 1991; Waters, 1995).

In reality, quantitative understanding of the ecological effects of sediments and the mechanisms involved is poor (Angradi, 1999; Davies-Colley *et al.*, 1992; Gard, 2002; Parkhill & Gulliver, 2002; Strand & Merritt, 1997; Broekenhuizen *et al.*, 2001). Knowledge of interactions among catchment land-use, diffuse sediment release and ecological effects is particularly uncertain for several reasons (Matthaei *et al.*, 2006). First, anthropogenic effects on sediment regimes range from catchment modification (e.g. agriculture) to local habitat alteration (e.g. livestock trampling), so that the exact source of sediments in any one location can seldom be identified readily (Imhof *et al.*, 1996). Secondly, much recent research in physical geography has aimed at parameterising sediment regimes without exploring the response of organisms (Collins & Walling, 2007; Walling & Amos, 1999; Walling, Collins, Sichingabula *et al.*, 2001). Thirdly, the ecological effects of sediment from anthropogenic sources, especially over large spatial or temporal extents, can be masked by natural variability. For instance, some types of agricultural intensification or the removal of riparian woodland might increase erosion and fine sediment release to streams, but also they alter temperature, organic matter supply and nutrient fluxes (Osborne & Kovacic, 1993; Roth, Allan & Erickson, 1996). As a result, identifying the scale, severity and impact of altered sediment fluxes in catchments affected by more general chemical or eco-hydromorphological degradation, has become a management need (Feld, 2004). While the extent and resolution (grain) of these investigations can influence findings, scale dependence is seldom explicitly included in monitoring programmes or experimental design. Ideally, in impact-assessment studies, the scales of measurement and organism responses should coincide. By increasing resolution (i.e. using more smaller-size sampling units) variation in response variables and sensitivity of statistical tests should also increase (e.g. Smiley & Dibble, 2008).

By combining two consecutive surveys at different resolution, in this paper I aimed to understand the apparent causes and extent of sediment deposition in a temperate, montane river system (the Usk, Wales), and to identify the scale at which any effects were relevant to stream invertebrates. The Usk catchment is particularly suitable for this purpose because, in comparison with adjacent catchments such as the Wye (e.g. Ormerod & Edwards 1987), dominant geology and major aspects of ionic composition are relatively homogeneous, thereby reducing confounding ecological effects. While effects on stream function from urbanization are negligible and localised, the sandstone-dominated catchments of the Usk are liable to be sensitive to sediment mobilisation (Sable & Wohl, 2006). Finally, land-use varies from semi-natural upland vegetation to modified improved grassland, implying possible effects on sediment release.

Our principal objectives were, first, to identify how in-stream sediment character varied between locations in relation to land use at different scales (riparian *vs* catchment). Secondly, I aimed to assess the extent to which variation in invertebrate composition among sites reflected sediment character or other habitat features in the channel, riparian zone and catchment. Thirdly, I aimed to identify any scale-dependence in apparent relationships between macroinvertebrates and sediment character. Two main predictions were tested:

i) Variation in observed deposited sediments should be explained by riparian and catchment land-use and associated processes, namely bank erosion.

ii) Invertebrates should respond to deposited sediments, but I expected different macroinvertebrate patterns to be detectable by changing spatial resolution. At larger spatial extents, I expected that links between organisms, altitude and dominant land-use should be most evident, while at the patch scale local effects, such as deposited sediments, should be detectable.

3.2 Methods

Study area

The River Usk is one of the largest rivers in Wales, with a main channel 120 km long and catchment area 1358 square km. One the most important game fisheries in England and Wales, the Usk rises in rough grazing land at an altitude of 500 metres on Mynydd Du (National Grid Reference SN819239; 51.52N, 03.50W) before flowing eastwards along the northern face of the Brecon Beacons and then southwards to its confluence with the Severn Estuary.

From its source on the Black Mountain, the river flows over sandstones and mudstones of the Old Red Sandstone Series, with soil types a blend of brown earths or peat and gley soils on wetter plateaus. The dominantly rural area is sparsely populated (< 20 people/km^2) and therefore urbanization has negligible impact. In this temperate and relatively maritime location, annual average precipitation over the catchment averages 1336 mm, but exceeds 2500 mm in some upland locations. Groundwater contributions, even to typical dry weather flow, are modest (c 15%), and river discharges fluctuate rapidly with rainfall (Environment Agency, 1998). This combination of factors brings some risks of both sediment release and sediment in-wash making the Usk an ideal catchment to investigate sedimentation effects. Moreover, stream waters in the rural parts of the Usk catchment are clean and well-oxygenated, and concentrations of plant nutrients are generally low. Otherwise, waters are relatively rich and fairly uniform in carbonate concentration, so that few organisms are limited by base-cation availability (Table 1).

Survey design

The first extensive survey (2006; 'reach-scale survey') comprised 32 reaches along 18 second-order tributaries mainly draining semi-natural upland vegetation (bracken, heath, moorland, acid grassland) and improved grassland used as rough grazing land, while woodland vegetation cover never exceeds 34% of any catchment. Sampling reaches were selected to cover the main land-use typology present in the study area, but selection was restricted to reaches where depth, flow velocity, stream width and particle size distribution were similar. Fourteen streams were sampled on two reaches and four streams on one reach, depending on accessibility and stream length. The altitudinal range was 190-400 m a.s.l. and distance between two reaches in a stream never exceeded 8 km. Although there was a risk that replicate reaches within streams might not be independent, all results and conclusions were unchanged when only one reach per stream was analyzed, thus the entire dataset was used.

The subsequent patch-scale survey, carried out in 2007 at locations nested within 12 previously sampled reaches on eight of the streams (see Table 1), was designed specifically to assess within reach effects of sediment deposition, i.e. at finer resolution. Informed by the results of the reach-scale survey, locations for patch sampling were selected to represent both upland and grassland while covering a range of sediment conditions. Sampling was again restricted to riffle-glide habitats, where depths and velocities were measured. Depending on their availability, three to six patches per reach were sampled in a ~15m long section, for a combined total of 56 patch samples.

Environmental variables

Reach scale survey. I used a combination of field measurements and available data to characterise conditions in each of the 32 survey reaches. In the field, basic measurements of channel width, depth and flow velocity were taken along a 10 m stretch, averaged from three values. The percentage of surface water overhung by riparian vegetation was also estimated. Next, substratum composition was assessed over each 10m section using a modified version of the UK Environment Agency's River Habitat Survey (Environment Agency, 2003), where the proportionate bed-cover of bedrock, boulder, cobble, gravel, sand, fine sand, clay and earth were estimated. Deposited fine sediment (< 2mm) cover within a (300 cm^2) circular quadrat was estimated as the percentage of stream bed, in 5 % increments, covered by fine particles (Platts, Megaham & Minshall, 1983; Rabeni *et al.*, 2005). Twelve estimations in two transects over the 10 m section were combined and the mean determined. Although these twelve observations covered only a small portion of the stream bed, they were sufficient to allow reaches to be ranked along the sedimentation gradient.

To characterise typical size distribution of fine sediments across all reaches, composite samples of fine sediment were collected from ten reaches of seven relatively sediment-rich streams, and then sediment composition determined using dry sieving.

In order to support the field measurements, additional data were retrieved as far as possible for each reach from the 'Fluvial Audit' database for the upper Usk tributaries. Designed and progressively applied across British rivers by the GeoData Institute (Southampton), Fluvial Audit uses contemporary field survey, historical and contemporary maps, documentary information and scientific literature resources to gain a comprehensive understanding of the geomorphological controls on a given river systems (Emery & Hill 2005). The Audit is both qualitative and quantitative, and from the latter data I took the length of eroding banks for 27 of our reaches where direct field observation had been previously been digitalised (Emery & Hill, 2005). The extent of erosion was calculated for 1 km and 500 m upstream of the sample sites using Arc-GIS (ESRI, 2004).

Land-use for each reach was calculated at two spatial extents, respectively a 150 m wide buffer on each side of the stream for 1 km upstream and the whole catchment area draining to each site. Land-use data were extracted from existing GIS land cover layer created by the Countryside Council for Wales (CCW, 2002), the statutory Welsh agency for nature conservation and landscape protection. Catchment areas were derived using a 10 x 10 m resolution Digital Elevation Map of the Usk catchment (CCW, 2002). Slope classes were derived for every catchment, and low and high relief was calculated as the proportion of catchment with slopes <10% and > 30% respectively.

Chemical data, obtained from the UK Environment Agency's Water Management Information System (WMIS) and based on standard methods (Standing Committee of Analysts, 1979; Standing Committee of Analysts, 1981; Standing Committee of Analysts, 1987; Standing Committee of Analysts, 1992), were available for 12 of the reaches (38%) as monthly concentrations of nitrate (mg/l), phosphate (mg/l), Biological Oxygen Demand (BOD mg/l), water hardness as $CaCO_3$ (mg/l) and pH data (Table 1). Means were calculated for the year antecedent to invertebrate sampling. Although incomplete, these chemical data drained both grassland and semi-natural upland vegetation, and allowed an assessment of the extent to which water quality might have confounded or subsumed the ecological effects of fine sediments. Most reaches without chemical data were the highest altitude locations where improved grasslands were less frequent, and nutrient concentrations would have been low.

Patch scale survey. All environmental data for the patch-scale survey were collected in the field. At each sampling site (~ $3m^2$), I made ten visual estimates of deposited sediment immediately around the invertebrate Surber sampler (see below) and averaged these values. To complement these estimates, the amount of suspendable sediment from the stream bed was also measured at 45 of the patch-scale sites, with four measurements made around each Surber location. A large metal box (24 x 18 x 80 cm) was pushed into the substratum and sediments from c 2 cm depth were entrained in the measurable volume of water within the box by mixing with a ruler. Suspended sediments within the range of 0.063-1 mm were filtered from 1 liter of water, dried at 100-105 C° for 24h, weighted and calculated as g /m^2. Organic material was reduced by washing and decanting. Water depth and flow velocity were also recorded at each site.

Macroinvertebrate sampling

Reach-scale survey. Benthic macroinvertebrates were collected, and reach-habitat characteristics recorded, in June and July 2006, when annual discharge was expected to be lowest and deposited sediments were stable and visible. Invertebrate sampling was restricted to fast flowing habitats (glides, riffles, with velocities typically < 55 cm/s) since pools and margins naturally collect fine material. To collect macroinvertebrates, a kick sample of three minutes duration was taken both from riffles and glides over a 10 m reach, using a standard hand-net (Environment Agency, 1999; mesh 0.9mm, area 25 cm^2). For this extensive survey I specifically used a hand net as it is widely used in biological monitoring programmes, such as RIVPACS (Wright, Furse & Moss, 1998), and I have investigated this method extensively (Bradley & Ormerod, 2002).

Note that, in both reach- and patch-scale surveys, I have assumed that a single sampling occasion is sufficient to reflect both assemblage composition and relationship with sediment cover, thus ignoring sediment dynamics or possible sediment release during events (Environment Agency, 1998). This assumption is justifiable because many of the organisms recorded have univoltine life cycles (or longer) so that assemblage composition should reflect antecedent conditions. In addition, our approach was designed to characterise variations between invertebrates and sediments at multiple sites rather than dynamics within sites.

Patch-scale survey. To capture smaller-scale variations, and cover specifically a well-defined area of streambed where sediment conditions were assessed, I collected macroinvertebrates for the patch-scale survey using a Surber sampler in June and July 2007 (0.16 m^2; 0.44mm). Because of this difference timing and methods from the reach-scale survey, I compared reach-scale pattern among invertebrates generated from kick-samples and aggregated within-reach

Surber data. The outcomes of this evaluation are reported at the end of the results section.

Both patch- and reach-scale samples were preserved immediately in ethanol. In the laboratory, macroinvertebrates were sorted and identified as far as possible to species (Edington & Hildrew, 1981; Elliott, Humpesch & Macan, 1988; Friday, 1988; Wallace, Wallace & Philipson, 2003). Diptera were identified to family and oligochaetes were not identified further.

Data analysis

To help interpret reach-scale pattern among invertebrates, I first used principal components analysis (PCA) to derive variates that described substratum (Substratum PCA) conditions as well as catchment and riparian land-use (Catchment PCA and Riparian PCA respectively). I quantified land-use variations in this way because percentages of individual land-use coverage are not independent, and principal components avoided any multicolinearity (Bruns, 2005; Rier & King, 1996). Land-use percentages were arc sin $(x/100)^{0.5}$ transformed prior to PCAs to homogenise variances. Land-use categories quantified were improved grassland, arable farmland, urban, upland vegetation and woodland, but urban land cover was omitted from the Catchment PCA since its extent was small.

Also prior to any other analysis, Detrended Correspondence Analysis (DCA) was used on both sets of invertebrate data (reach and patch) to identify the main variations in macroinvertebrate assemblage composition, which could then be related to measured environmental variables in subsequent analyses. This form of unconstrained ordination was preferred to constrained ordination because it produces easily interpretable plots, it can reveal whether important environmental variables have been overlooked and it is generally regarded as a superior analytical tool because clear hypothesis testing can occur in subsequent steps (Jongman, Ter Braak & Van Tongeren, 1995). Analyses were run with both arithmetic and transformed abundances, but results were similar and only arithmetic abundances were used in subsequent analyses.

To assess how in-stream sediments varied with land use and associated geomorphology (objective i), I assessed relationships between percentage cover by deposited sediments, land use and other environmental variables using Spearman rank correlation. Relationships among ordination axes, PCA axes and physical-chemical variables were examined with Pearson product-moment correlation.

To assess any consequences of sediments for macroinvertebrates (objective ii), based on expectations from previous studies (Angradi, 1999; Braccia & Voshell, 2007; Fossati, Wasson, Hery *et al.*, 2001a; Kreutzweiser *et al.*, 2005; Quinn *et al.*, 1992; Waters, 1995; Zweig & Rabeni, 2001), I examined invertebrate abundance, composition and richness, EPT abundance and richness, Shannon diversity, and the relative abundances of individual taxa (as proportions for example of Coleoptera, Chironomidae and Oligochaeta) in relation to sediment features using generalized estimating equations (GEEs). Since multiple patches per reach were sampled in the 2007 survey, samples could not be treated as independent in conventional regression analyses. GEEs allow the analysis of data collected in clusters where within-cluster correlation is expected (i.e. patches from the same reach might be more similar than patches from different reaches). Accounting for the lack of statistical independence between samples, regression coefficients and variance are adjusted to avoid spurious correlations to be observed (Vaughan, Noble & Ormerod, 2007; Blaustein, Kotler & Ward, 1995; Zorn, 2001). Spatially or temporally correlated data occur often in ecological research and this approach is a valuable tool (Vaughan *et al.*, 2007). GEEs models were run using *R* (Ihaka & Gentleman, 1996) using the program *geeglm* from the library *geepack* (Halekoh, Hojsgaard & Yan, 2006). Sequential Bonferroni correction was not applied because *a priori* hypotheses were formulated about invertebrates metrics and sediment features (Moran, 2003).

I identified any scale-dependence in apparent relationships between macroinvertebrates and sediment character (objective iii) by comparing the patterns generated between the reach- and patch-scale data. From the patch-scale survey, results were sufficiently clear to allow an assessment of the apparent tolerance to deposited sediment for the 27 most widespread taxa, occurring in more than 12 sites (20%). Curves relating the cumulative abundance of each taxon to the amount of deposited sediments were constructed and the percentage sediment cover at which each reached 50% abundance was determined. Following Zweig & Rabeni (2001), I assumed that intolerant taxa should reach 50% of their cumulative abundance at lower levels of deposited sediments.

3.3 Results

Reach scale: deposited sediments, land-use and channel geomorphology

Major patterns in land use and substratum were captured well by principal components analyses. Two principal components explained 66% of the variation in riparian land-use, and up to 90% of the land-use variation at the catchment scale. Both Catchment and Riparian PC1 values represented a gradient from improved grassland to semi-natural upland vegetation, but with inverted signs; PC2 values were mostly related to woodland cover. In other words, land use varied in similar ways in both the riparian zone and catchment ($r = -0.75$; $P<0.01$ for PCs1; $r = -0.5$; $P = 0.03$ for PCs2) with the major gradients a trend from improved grassland to upland vegetation and increasing woodland cover (Table 2.2).

In the stream channel, over 55% of the variance in substratum composition was explained by Substratum PC1. Values correlated positively with the proportion of boulder and bedrock (loadings: 0.82 and 0.74) and negatively with gravel and fine sand (loadings: -0.91 and -0.78) thus describing a gradient from fine to coarse substrata. The amount of the channel surface covered by fine sediments, as estimated from the reach scale survey, ranged from 1 to 75% cover among reaches. Sieving revealed that most fine sediments were mainly (>82%) composed of sand (2–0.25mm) and fine sand (0.25-0.125 mm), whereas silt and clay content was very low.

Up to 500m-1km upstream from each sampling point, the proportion of eroding banks ranged over 0 – 53%, and 0 – 49%, respectively. Fine sediment cover increased strongly with the proportion of eroding banks 500 m upstream (r_S = 0.77; P<0.001; n =27) and more weakly to bank erosion 1 km upstream (r_S = 0.59; P= 0.001; n = 27). Sediment cover was also related to land use PC2 in both the riparian zone and catchment. This mostly reflected trends with woodlands (Fig.3), fine sediments on the bed declining with both riparian (r_S = 0.39; P = 0.02; n =32) and catchment woodland cover (r_S = 0.62; P<0.001; n =31). Proportions of eroding banks (1 km upstream) and riparian woodland were also negatively correlated (r_S =0.6; P<0.001; n =27; Fig. 3.3). Interestingly, and contrary to expectation, steep slopes did not increase sediment delivery, and instead sediment cover declined as the proportion of catchment with slope > 30% increased (r_S = -0.39; P = 0.02; n =31). This effect arose because woodland cover increased on the steeper slopes (r_S = 0.54; P = 0.001; n = 31).

Deposited sediments were unrelated to either upland or improved grassland vegetation, but nitrate concentrations (r_S=0.6; P=0.04; n = 11) and BOD (r_S = 0.72; P = 0.01; n =11) increased where catchments had more improved grass. There was some correlation between cover by fine deposited sediment and nitrate (r_S=0.6, P=0.02; n =12), but this largely reflected the effect of just two streams (Honddu and Rhiangoll. See Table 3.1). On these grounds, any sediment effects would be unlikely to be confounded by nutrients, but nutrients effects could reflect variations in land use (c.f. Niyogi *et al.*, 2007b).

Reach-scale: assemblage composition

Over 70,000 individual invertebrates from 74 taxa were collected during the 2006 reach-scale surveys, but 16 taxa present in fewer than 5 samples were not considered in multivariate analyses (Table 3.5). *Ephemerella ignita* was the most abundant species, followed by chironomids, *Baetis rhodani*, simuliids and *Gammarus pulex*. (All naming authorities are given in Table 3.5.).

In DCA, two axes explained >37 % of species variation, with *Caenis rivulorum, Baetis muticus, Rhithrogena semicolorata, Chloroperla* *tripuncatata, Dinocras cephalotes, Perla bipunctata* and Helodidae all increasing along axis 1 while *Gammarus pulex, B. scambus, B. fuscatus*, Ceratopogonidae and the coleopteran *Oreodytes sanmarkii* declined. However, no trends in species composition were related to in-stream sediments or other channel features. DCA axis 1 (24%) instead varied with nitrate concentration ($r = -0.66$; $P=0.01$; $n = 12$), Catchment land use PC1 ($r = -0.49$; $P<0.01$; $n = 31$) and Riparian land use PC1 ($r = 0.36$; $P=0.04$; $n = 32$). There was also a tendency for DCA axis 1 scores to vary with water hardness ($r = -0.58$; $P=0.04$; $n = 12$). No correlations were evident for DCA axis 2.

In other words, despite wide variations in fine sediment cover and bank erosion, reach-scale variations among invertebrates were most closely related to catchment land use and water quality, following a gradient from upland to improved grassland vegetation.

Reach-scale: invertebrate metrics

Besides a weak increase in the relative abundance (%) of Oligochaeta with increasing sediment cover ($r_s=0.36$; $P = 0.04$; $n = 32$), assemblage metrics at the reach scale were unrelated to fine sediment. However, in keeping with the apparent effects on species composition, macroinvertebrate diversity, % coleoptera and % chironomids were reduced in improved grasslands as represented by Catchment PC1 ($r_s = -0.48$ to -0.43; $P=0.008$ to 0.01; $n = 31$).

Patch-scale: deposited sediments

Among the 56 locations in the patch-scale survey, depth ranged over 8 – 27 cm and current velocity 11 – 57 cm/s. Observed variation in sediment cover at this scale ranged over 1 – 35 % and, while these values are lower than those for the reach-scale survey, these detailed estimations were once again related to the extent of eroding banks 500m upstream ($r_s = 0.66$; $P = 0.02$; $n = 11$). Suspendable sediments ranged from 2 – 147 g/m^2 and were directly related to deposited sediment cover ($r_s = 0.74$; $P < 0.001$; $n = 45$). Flow velocity did not influence deposited or suspendable sediments over the range observed ($p > 0.05$), but both sediment cover ($r_s = 0.33$; $P = 0.01$; $n = 56$) and suspendable sediments ($r_s = 0.37$; $P = 0.01$; $n = 45$) increased with depth.

Patch-scale: assemblage composition

Around 23,000 individual invertebrates from 69 taxa were collected in the 2007 patch-scale survey, this richness being comparable to the reach scale survey (74) despite the smaller number of animals collected. *Ephemerella ignita*, *Baetis rhodani* and chironomids were again the most abundant organisms. However, after removing taxa occurring in <5 samples, only 40 were included in the DCA (Fig.3.4).

In contrast to the reach-scale survey, ordination patterns from the patch data were related strongly to sediments. The first two DCA axes explained 35 % of the variation in species composition, with axis 1 (23%) representing a gradient from shallower sites with less suspendable sediments ($r_s = -0.47$; $P<0.01$) to deeper sites ($r_s = 0.36$; $P = 0.006$). Axis 2 (12%) was also positively correlated with suspendable sediments ($r_s = 0.61$; $P<0.001$), more weakly to sediment cover ($r_s = 0.35$; $P = 0.007$) and negatively with flow velocity ($r_s = - 0.32$; $P = 0.01$).

Patch-scale: invertebrate metrics

Also in contrast to the reach-scale survey, GEE modeling showed that several invertebrate metrics were related to sediment cover and suspendable sediments. For example, total taxon richness and EPT richness were reduced in sediment-rich sites (Table 3.3). On average, total richness declined by c 5 taxa, and EPT richness by 4 taxa at the most sediment-impacted locations (c 30% cover), or respectively 20% and 25% of richness at sites free of any sediment (Fig. 3.5). Except for an increase in the relative abundance of Oligochaeta with depth ($r = 0.36$; $P <0.01$), there were no relationships between invertebrate metrics and either depth or current velocity, which might have been expected if these factors were confounding effects ascribed to sediments.

Because of the apparent effects on invertebrates of land use detected in the reach-scale survey, I investigated how fine-scaled effects might be reflected within land use types. Reduction in richness was consistent between the upland

and improved grassland areas, but there were more significant relationships between sediments and invertebrates in the former (Table 3.3). At upland locations (n = 24), sediment cover and suspendable sediments increased from 1 to 23 % and 2 to 49 g/m^2, leading apparently to increased invertebrate abundances (particularly oligochaetes) but reductions in EPT richness, Shannon diversity and the relative abundance of both Coleoptera and Chironomidae. At grassland locations (n = 32), sediment cover and suspendable sediments increased from 3 to 35 % and 1.7 to 147 g/m^2 respectively, accompanied by reductions in taxon richness and total abundance. Other metrics were only marginally affected (e.g. *P* values c 0.09).

Patch-scale: individual species tolerance to sediments

Far clearer relationships with sediments at the patch scale allowed some assessment of varying tolerance among species. Based on their cumulative abundance curves (Fig.3.6), the most common taxa were ordered from the most sensitive to the most tolerant (Table 3.4). The trichopteran *Hydropsyche instabilis* and the plecopteran *Perla bipunctata* were apparently the most sediment-intolerant species, along with Helodidae and Simulidae. By contrast, Tipulidae, Oligochaeta and the coleopteran *Oreodytes sanmarkii,* appeared the most tolerant.

Methodological evaluations

In the 12 reaches where invertebrates were collected in subsequent years by both kick-samples and aggregated Surber samples, axis 1 DCA scores were highly inter-correlated between the two methods ($r = 0.86$, $n = 12$; $P<0.001$) implying that both collected near-identical assemblages. Moreover, besides a decrease in the proportion of Coleoptera ($r_S = -0.7$; $P<0.01$), there were no other significant correlations between reach-wide metrics based on aggregated Surber samples and sediment features averaged at the reach-scale. In other words, when using fine-scale methods at the same sampling resolution as the reach-scale survey, sediment effects were far less detectable. This result confirms that differences in survey outcome between the patch and reach-scale survey were not due to differences in the timing or method of invertebrate collection.

In a second methodological evaluation, I assessed whether patch-scale effects of sediments were still apparent within those streams with sufficient variation in sediment cover. In the Afon Cynrig (sediment cover 2.5-35%) and Ysgir Fechan (10 – 27%) EPT richness declined consistently with increasing suspendable sediments or sediment cover ($r_S = -0.81$ to -0.88, n = 6-7; $P = 0.02$-0.01). In the Afon Honndu (9.5 - 28.7%) %EPT declined with increasing suspendable sediments ($r_s = -0.76$; n=8; P=0.02). However, in the Bran (6.5 – 31%) no effects were evident on community metrics.

Also, in the Cynrig, total taxon richness declined with increasing sediments ($r_s = -0.84$; $P = 0.01$, n = 7) and in the Ysgir Fechan the relative abundance of Oligochaeta increased ($r_s = 0.81$; $P = 0.04$; n =6). Therefore, the responses of invertebrates to sediments were generally consistent within streams and even with reduced sample size.

3.4 Discussion

Linkages among riparian or catchment land-use, erosion and sediment behaviour in streams are increasingly well established (Opperman *et al.*, 2005; Rabeni & Smale, 1995; McPherson & Riley, 2006). Awareness of the ecological significance of suspended and bedload sediments is growing, particularly in anthropogenically modified catchments and where there are important resources such as salmonids or other organisms of high conservation value (Owens *et al.*, 2005; Walling, Collins & McMellin, 2003). Understanding the factors controlling the spatial variability of sediments and their effects is therefore an important management requirement. Although derived from an extensive, correlative survey across locations, our data offer some support for these needs in upland, temperate streams.

In support of the first of our hypotheses, more than 59% of the variation in deposited sediments in the Usk was explained by local (500 m) bank erosion. Catchment woodland cover was also an important correlate, supporting its role in preventing the release of fine sediments into the channel (Opperman *et al.*, 2005; Zimmerman, Vondracek & Westra, 2003). In turn, bank erosion appeared to be mediated by riparian land use, with wooded vegetation likely to limit sediment release by stabilising stream banks. This finding accords with the general pattern of sediment sources for other rivers in this region, as assessed by fingerprinting methodologies, where channel and sub-surface sources are the major contributors to in-stream sediments (Walling *et al.*, 2003). Also, fine sediments collected in our streams were mostly composed of coarser sand fractions likely to originate from the channel (Knighton, 1998). However, other factors beside woodland cover must affect sediment supply in the study area, since relatively low sedimentation was also observed in some grassland reaches with eroded banks. Although Townsend *et al.* (2004) suggested that marginal pastures could increase stock trampling and bank instability, there is evidence that grassland buffers can be effective sediment filters, especially of the coarse fraction (Dosskey, Hoagland & Brandle, 2007; Le Bissonnais, Lecomte & Cerdan, 2004; Mankin, Ngandu, Barden *et al.*, 2007). Temporal variability and seasonality in bed sediment cover and direct livestock access to streams might also be involved (McIver & McInnis, 2007; Walling *et al.*, 2003). In these instances, destabilization of stream banks due to over-grazing coupled with footpaths and roads running across steep slopes can be responsible for disproportionately large increases in sediment delivery – even very locally – but no such occurrences were apparent in our data.

Scale-dependent effects

Our second hypothesis, that relationships between invertebrates and sediments should be scale dependent, was also supported strongly, and this result raises some methodological and management issues. Few other studies have addressed this hypothesis (e.g. Smiley & Dibble, 2008; Townsend, Scarsbrook & Doledec, 1997), and in all cases significant effects were observed mostly at the finest spatial resolution.

At broader, reach-scales, neither assemblage nor invertebrate metrics revealed any large effects of sediments, with most invertebrate variations instead tracking land-use change from upland to improved grassland. Such significant land-use effects on stream biota occur often where native vegetation changes to pasture or agriculture (Braccia & Voshell, 2007; Niyogi *et al.*, 2007b), and mechanisms include altered hydrology (Allan et al. 1997, Davies-Colley 1997), nutrient release, and allochthonous or solar energy flux (Burdon & Harding, 2008; Osborne & Kovacic, 1993). Reduced invertebrate diversity observed in pasture reaches in the Usk is likely to have reflected changes in water quality as both nitrates and BOD were higher in grassland. Even small changes in these variables, similar to those detected here, were sufficient to affect invertebrates in the adjacent Wye (Clews & Ormerod, 2009). Most of the remaining reach-scale variation in invertebrate composition remained unexplained, as is common in surveys, and largely depends on the number of sites and taxa (Leps & Smilauer, 2003). Nevertheless, the increased abundance of oligochaetes in sediment-enriched reaches showed that some localised effects were detectable even at this scale.

Apparent sediment effects on organisms became far clearer at increased sampling resolution, i.e. in units of decreased sample size that captured within-reach variation. Overall composition and associated invertebrate metrics responded predictably to increasing fine sediments measured as both bed cover and suspendable material, with overall taxon richness and EPT taxon richness respectively 20% and 25% lower at the most sediment-impacted sites than in locations free of sediments. Besides the proportion of Oligochaeta, none of the invertebrate metrics related to sediments correlated with other micro-habitat features, such as current velocity or water depth, implying that the correlations were not spurious. However, one interesting methodological point to emerge was that estimates of sediment cover differed between surveys at reach- and patch-scales. Although the values were correlated with each other ($r_s=0.62$; $P=0.03$) and with measures of bank erosion, the latter produced lower estimates (1-35% cover) than the former (1-75%). A further corollary is the patch-scale measurements evidently detected sedimentation effects on organisms at substantially lower values of cover than could occur at the reach scale without such effects. Almost certainly, these differences reflect the gain in measurement accuracy at the finer scale, when 10 observations were made immediately around each Surber sampler as opposed to 12 estimates spread sparsely in two transects over entire reaches. Not only were there more measurements per unit area at the finer scale, but also they were taken directly adjacent to the point of biological sampling. At the same time, there is a potential sampling bias in that Surber sampling is constrained to operate in substrata of finer particle sizes (i.e. avoiding boulders and bedrock) where sediment deposition effects could be greatest.

The net outcome from the patch-scale survey was that variations in composition, invertebrate diversity and EPT richness could be related to sediment cover, with results supporting previous work. Generally consistent effects of sedimentation on overall diversity and EPT taxa in North America (Fossati *et al.*, 2001a; Kreutzweiser *et al.*, 2005; Zweig & Rabeni, 2001), Australia and New Zealand (Downes, Lake, Glaister *et al.*, 2005; Matthaei *et al.*, 2006; Quinn *et al.*, 1992) imply that the same general processes must be involved, linked also with shared biological traits among sensitive organisms. Similarly, Braccia & Voshell (2006) found relative abundance of Coleoptera to be consistently related to fine sediment in cattle impacted streams. In some cases, where sediment cover reaches 100%, effects can be even stronger than those I detected (Zweig & Rabeni, 2001). In our example, those taxa most sensitive to sediments, as identified from the cumulative abundance curves, were *Hydropsyche instabilis* and *Perla bipunctata,* both species normally associated with fast-flowing and sediment-free habitats. For hydropsychids, previous data suggest that sensitivity can arise due to the effects of suspended sediments on feeding nets (e.g. Strand & Merritt, 1997), and similar mechanisms might be responsible for the decreased abundance among filter-feeding simuliids. With some authors calling for the development of more pressure-specific metrics through which stream organisms can be used to diagnose reasons for stream impairment, rather than just detecting it (Clews & Ormerod, 2009), further data ranking the specific sensitivities of invertebrates to fine sediments would be valuable.

Interestingly, the patch-scale data revealed that some effects of varying sediment occurred only within land-use types. Invertebrate assemblages in upland locations showed the stronger response to sediments, with almost all invertebrate metrics highly significantly affected by sedimentation. The response of Chironomidae to sedimentation must, however, be interpreted with caution considering their wide ranging habitat and feeding strategies. Even at the sub-family level, Orthocladiinae and Chironominae respond respectively negatively and positively to sediment accumulation, so that family level identification is inadequate to appraise response (Angradi, 1999). Increased invertebrate abundance in upland locations with increasing sediment cover is somewhat contrary to expectation but linked to the increased abundance of sediment tolerant oligochaetes as well as the stonefly, *Leutra moselyi.*

By contrast, sediment effects on invertebrates in grassland locations were weaker, even though this is where the largest sediment accumulations occurred. One possibility is that effects were masked here because invertebrate diversity was already lower than in upland locations, linked possibly to nutrient concentrations. These results support those from experiments by Matthaei *et al.*(2006), who showed that sediments affect streams with the greatest invertebrate diversity where previous sediment effects have been small. As in our upland sites, these workers also observed a moderate increase in invertebrate density with increasing sediment cover. In combination, this previous study and ours suggest that sediment effects on macroinvertebrate communities might depend on the diversity and sensitivity of organisms present, with streams in semi-natural catchments at greatest risk of impairment.

Overview

Overall, I conclude that sediment deposition in this upland, temperate river system mostly reflects local bank erosion, particularly interacting with riparian and catchment woodland cover. Ecological effects on organisms occur mostly in upland locations, where reductions in richness at the most sediment-affected sites were substantial, and there are three general implications.

First, the interaction between woodland, sediment release and ecological effects is important in this British river catchment where many riparian trees have been removed for agriculture, and only now are being restored through a range of agri-environment and riparian management schemes. Sediment controls are only one such benefit from carefully riparian-zone maintenance (Petersen, Masters, Hildrew *et al.*, 2004).

Secondly, ecological effects in the Usk occurred even though most of the fine sediments involved were coarser, non-flocculating sand rather than silt and clay. Elsewhere, these finer fractions substantially alter substratum quality, reduce interstitial flow, alter oxygen exchange and increase ion-exchange capacity (Schalchli, 1992; Brunke & Gonser, 1997), and are considered to be responsible for many of the negative effects on stream organisms (Waters, 1995). This fraction was a minor substratum component in our study streams, yet some effects were still detectable.

Thirdly, the detection of such effects was scale-dependent. This implies that sediment effects may be influenced by larger catchment controls, while requiring also a finer-scale approach that might have been more accurate for sediment effects in the Usk. I suggest that the assessment of the effects of diffuse anthropogenic sediment can benefit from a scale-specific approach, in which local (i.e. reach-based) effects can be separated from broader (i.e. whole-stream, catchment) influences. Of more direct management importance, sediment effects could go undetected without appropriately scaled investigation.

3.5 References

Angradi, T.R. (1999) Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications *Journal of the North American Benthological Society* **18,** 49-66

Ankers, C., Walling, D.E. & Smith, R.P. (2003) The influence of catchment characteristics on suspended sediment properties. *Hydrobiologia,* **494,** 159-167.

Bond, N.R. (2004) Spatial variation in fine sediment transport in small upland streams: the effects of flow regulation and catchment geology. *River Research and applications,* **20,** 705-717.

Braccia, A. & Voshell, J.R. (2006) Environmental factors accounting for benthic macroinvertebrate assemblage structure at the sample scale in streams subjected to a gradient of cattle grazing. *Hydrobiologia,* **573,** 55-73.

Braccia, A. & Voshell, J.R. (2007) Benthic macroinvertebrate responses to increasing levels of cattle grazing in Blue Ridge Mountain streams, Virginia, USA. *Environmental Monitoring and Assessment,* **131,** 185-200.

Bradley, D.C. & Ormerod, S.J. (2002) Evaluating the precision of kick-sampling in upland streams for assessments of long-term change: the effects of sampling effort, habitat and rarity. *Archiv Fur Hydrobiologie,* **155,** 199-221.

Broekenhuizen, N., Parkyn, S. & Miller, D. (2001) Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). *Hydrobiologia,* **457,** 125-132.

Brunke, M. & Gonser, T. (1997) The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* **37,** 1-33.

Bruns, D.A. (2005) Macroinvertebrate response to land cover, habitat, and water chemistry in a mining-impacted river ecosystem: A GIS watershed analysis. *Aquatic Sciences,* **67,** 403-423.

Bunn, S.E. & Davies, P.M. (2000) Biological processes in running waters and their implications for the assessment of ecological integrity. *Hydrobiologia,* **422-423,** 61-70.

Ciesielka, I.K. & Bailey, R.C. (2007) Hierarchical structure of stream ecosystems: consequences for bioassessment. *Hydrobiologia,* **586,** 57-67.

Clews, E. & Ormerod, S.J. (2009) Improving bio-diagnostic monitoring using simple combinations of standard biotic indices. *River Research and Applications,* **25,** 348 - 361.

Collins, A.L. & Walling, D.E. (2007) Fine-grained bed sediment storage within the main channel systems of the Frome and Piddle catchments, Dorset, UK. *Hydrological processes,* **21,** 1448-1459.

Countryside Council for Wales (2002) *Phase 1 Survey from the Countryside Council for Wales,* CCW Geographic Information Unit.

Davies-Colley, R.J., Hickey, C.W., Quinn, M.J. & Ryan, P.A. (1992) Effects of clay discharges on streams. Optical properties and ephilithon. *Hydrobiologia,* **248,** 215-234.

Dosskey, M.G., Hoagland, K.D. & Brandle, J.R. (2007) Change in filter strip performance over ten years. *Journal of Soil and Water Conservation,* **62,** 21-32.

Downes, B.J., Lake, P.S., Glaister, A. & Bond, N.R. (2005) Effects of sand sedimentation on the macroinvertebrate fauna of lowland streams: are the effects consistent? *Freshwater Biolology,* **50.**

Edington, J.M. & Hildrew, A.G. (1981) *A key to the caseless Caddis larvae of the British Isles with notes on their ecology* Freshwater Biological Association, Ambleside, Cumbria

Elliott, J., Humpesch, U. & Macan, T. (1988) *Larvae of the British Ephemeroptera: Akey with Ecological notes. Scientific Publication 49,* Freshwater Biological Association, Ambleside.

Emery, J.C. & Hill, C.T. (2005) Fluvial Audit of the Upper Usk tributaries. CCW Review of Consents Report No 15, Bangor, Countryside Council for Wales.

Environment Agency (1998) *Rural Usk LEAP Consultation Report,* Environment Agency Wales.

Environment Agency (2003) *River Habitat Survey in Britain and Ireland, Field Survey Guidance Manual,* Environment Agency, Bristol.

Environment Agency (1999) *Procedures for collecting and analysing macroinvertebrate samples. Quality Management Systems for Environmental Monitoring: Biological Techniques,* Environment Agency, Bristol.

Esri (2004) ArcGIS 9.1. E.S.R.I. Inc.). Environmental System Research Institute Inc., Redlands.

Feld, C.K. (2004) Identification and measure of hydromorphological degradation in Central European lowland streams. *Hydrobiologia,* **516,** 69-90.

Fossati, O., Wasson, J.G., Hery, C., Salinas, G. & Marin, R. (2001) Impact of sediment releases on water chemistry and macroinvertebrate communities in clear water Andean stream (Bolivia). *Archiv fur Hydrobiologie,* **151,** 33-50.

Friday, L. (1988) *A Key to the Adults of British Water Beetles,* Field Studies Council, Preston Montford.

Gard, M.F. (2002) Effects of sediment loads on the fish and invertebrates of Sierra Nevada river, California. *Journal of aquatic ecosystem stress and recovery,* **9,** 227-238.

Gayraud, S., Herouin, E. & Philippe, M. (2002) The clogging of stream beds: A review of mechanisms and consequences on habitats and macroinvertebrate communities. *Bulletin Francais de le Peche et se la Pisciculture,* **365,** 339-355

Gray, J.L. & Ward, J.V. (1982) Effects of sediment releases from a reservoir on stream macroinvertebrates. *Hydrobiologia,* **96,** 177-184.

Greig, S.M., Sear, D.A. & Carling, P.A. (2005) The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management. *Science of the Total Environment,* **344,** 241-258.

Halekoh, U., Hojsgaard, S. & Yan, J. (2006) The R Package geepack for Generalized Estimating Equations. *Journal of Statistical Software,* **15.**

Harding, J.S., Young, R.G., Hayes, J.W., Shearer, K.A. & Stark, J.D. (1999) Changes in agricultural intensity and river health along a river continuum. *Freshwater Biology,* **42,** 345-357.

Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics,* **5,** 299-314.

Imhof, J.G., Fitzgibbon, J. & Annable, W.K. (1996) A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences,* **53,** 312-326.

Jones, K.B., Neale, A.C., Nash, M.S., Van Remortel, R.D., Wickham, J.D., Riitters, K.H. & O'neill, R.V. (2001) Predicting nutrient and sediment loadings to streams from landscape metrics: A multiple watershed study from the United States Mid-Atlantic Region. *Landscape Ecology,* **16,** 301-312.

Jongman, R.H.G., Ter Braak, C.J.F. & Van Tongeren, O.F.R. (1995) *Data analysis in community and landscape ecology,* Cambridge University Press, Cambridge.

Knighton, D. (1998) *Fluvial forms and processes: A new perspective,* Hodder Arnold, London.

Kreutzweiser, D.P., Capell, S.S. & Good, K.P. (2005) Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology,* **39,** 55-66.

Le Bissonnais, Y., Lecomte, V. & Cerdan, O. (2004) Grass strip effects on runoff and soil loss. *Agronomie,* **24,** 129-136.

Leps, J. & Smilauer, P. (2003) *Multivariate analysis of ecological data using CANOCO,* Cambridge University Press.

Luedtke, R.J. & Brusven, M.A. (1976) Effects of sand sedimentation on colonization of stream insects. *Journal of the Fisheries Research Board of Canada,* **33,** 1881-1886.

Mankin, K.R., Ngandu, D.M., Barden, C.J., Hutchinson, S.L. & Geyer, W.A. (2007) Grass-shrub riparian buffer removal of sediment, phosphorus, and nitrogen from simulated runoff. *Journal of the American Water Resources Association,* **43,** 1108-1116.

Matthaei, C.D., Weller, F., Kelly, D.W. & Townsend, C.R. (2006) Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology,* **51,** 2154-2172.

Mciver, J.D. & Mcinnis, M.L. (2007) Cattle grazing effects on macroinvertebrates in an Oregon mountain stream. *Rangeland Ecology & Management,* **60,** 293-303.

Moran, M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos,* **100,** 403-405.

Mykra, H., Heino, J. & Muotka, T. (2007) Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography,* **16,** 149-159.

Newcombe, C.P. & Macdonald, D.D. (1991) Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management,* **11,** 72-82.

Niyogi, D.K., Koren, M., Arbuckle, C.J. & Townsend, C.R. (2007) Stream communities along a catchment land-use gradient: Subsidy-stress responses to pastoral development. *Environmental Management,* **39,** 213-225.

Opperman, J.J., Lohse, K.A., Brooks, C., Kelly, N.M. & Merenlender, A.M. (2005) Influence of land use on fine sediment in salmonid spawning gravels within the Russian River Basin, California. *Canadian Journal of Fisheries and Aquatic Sciences,* **62,** 2740-2751.

Osborne, L.L. & Kovacic, D.A. (1993) Riparian Vegetated Buffer Strips in Water-Quality Restoration and Stream Management. *Freshwater Biology,* **29,** 243-258.

Owens, P.N., Batalla, R.J., A. J. Collins, B. Gomez, D. M. Hichs, A. J. Horowitz, Kondolf;, G.M., M. Marden, M. J. Page, D. H. Peacock, E. L. Petticrew, W. Salomons & N. A. Trustrumi (2005) Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications,* **21,** 693–717.

Parkhill, K.L. & Gulliver, J.S. (2002) Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia,* **472,** 5-17.

Petersen, I., Master, Z., Hildrew, A.G. & Ormerod, S.J. (2004) Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Apllied Ecology* **41,** 934-950.

Platts, W.S., Megaham, W.F. & Minshall, G.W. (1983) Mehods for evaluating stream, riparian, and biotic conditions. General Technical Report INT-138. Intermountain Forest Range Experiment Station. United States department of Agriculture, Ogden, Utah.

Quinn, M.J., Davies-Colley, R.J., Hickey, C.W., Vickers, M.L. & Ryan, P.A. (1992) Effects of clay discharge on streams. Benthic invertebrates. *Hydrobiologia,* **248,** 235-247.

Rabeni, C.F., Doisy, K.E. & Zweig, L.D. (2005) Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences,* **67,** 395-402.

Rabeni, C.F. & Smale, M.A. (1995) Effects of siltation on stream fishes and the potential mitigating role of the buffering riparian zone. *Hydrobiologia,* **303,** 211-219.

Rier, S.T. & King, D.K. (1996) Effects of inorganic sedimentation and riparian clearing on benthic community metabolism in an agriculturally-disturbed stream. *Hydrobiologia,* **339,** 111-121.

Riley, R.H., Townsend, C.R., Niyogi, D.K., Arbuckle, C.A. & Peacock, K.A. (2003) Headwater stream response to grassland agricultural development in New Zealand. *New Zealand Journal of Marine and Freshwater Research,* **37,** 389-403.

Roth, N.E., Allan, J.D. & Erickson, D.L. (1996) Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology,* **11,** 141-156.

Sable, K.A. & Wohl, E. (2006) The relationship of lithology and watershed characteristics to fine sediment deposition in streams of the Oregon Coast Range. *Environmental Management,* **37,** 659-670.

Schalchli, U. (1992) The clogging of coarse gravel river beds by fine sediment. *Hydrobiologia,* **235,** 189-197.

Smiley, P.C. & Dibble, E.D. (2008) Influence of spatial resolution on assessing channelization impacts on fish and marcoinvertebrate communities in a warmwater stream in the southeastern United States. *Environmental Monitoring and Assessment,* **138,** 17-29.

Standing Committee of Analysts (1979) *Dissolved oxygen in natural and waste waters,* HMSO, London.

Standing Committee of Analysts (1981) *Biological oxygen demand,* HMSO, London.

Standing Committee of Analysts (1987) *Kjeldahl nitrogen in waters,* HSMO, London.

Standing Committee of Analysts (1992) *Phosphorus and Silicon in waters, effluents and sludges,* HMSO, London.

Strand, M.R. & Merritt, R.W. (1997) Effects of episodic sedimentation on the netspinning caddisflies *Hydropsyche betteni* and *Ceratopsyche sparna* (Trichoptera: Hydropsychidae). *Environmental Pollution,* **98,** 129-134.

Townsend, C.R., Doledec, S., Norris, R., Peacock, K. & Arbuckle, C. (2003) The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology,* **48,** 768-785.

Townsend, C.R., Downes, B.J., Peacock, K. & Arbuckle, C.J. (2004) Scale and the detection of land-use effects on morphology, vegetation and macroinvertebrate communities of grassland streams. *Freshwater Biology,* **49,** 448-462.

Townsend, C.R., Scarsbrook, M.R. & Doledec, S. (1997) The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography,* **42,** 938-949.

Vaughan, I.P., Noble, D.G. & Ormerod, S.J. (2007) Combining surveys of river habitats and river birds to appraise riverine hydromorphology. *Freshwater Biology,* **52,** 2270-2284.

Wallace, I., Wallace, B. & Philipson, G. (2003) *Keys to the Case-bearing Caddis larvae of Britain and Ireland. Scientific Publication 61* Freshwater Biological Association, Ambleside.

Walling, D.E. & Amos, M. (1999) Source, storage and mobilisation of fine sediment in a chalk stream system. *Hydrological Processes,* **13,** 323-340.

Walling, D.E., Collins, A.L. & Mcmellin, K.G. (2003) A reconnaissance survey of the source of interstitial fine sediment recovered from salmonid spawning gravels in England and Wales. *Hydrobiologia,* **497,** 91-108.

Walling, D.E., Collins, A.L., Sichingabula, H.M. & Leeks, G.J.L. (2001) Integrated assessment of catchment suspended sediment budgets: a Zambian example. *Land degradation & development,* **12,** 387-415.

Ward, P. & Myers, R.A. (2007) Bait loss and its potential effects on fishing power in pelagic longline fisheries. *Fisheries Research,* **86,** 69-76.

Waters, T.F. (1995) *Sediments in streams: sources, biological effects, and control,* AFS Monographs, Bethesda, Maryland.

Wright, J.F., Furse, M.T. & Moss, D. (1998) River classification using invertebrates: RIVPACS applications. *Aquatic Conservation-Marine and Freshwater Ecosystems,* **8,** 617-631.

Zimmerman, J.K.H., Vondracek, B. & Westra, J. (2003) Agricultural land use effects on sediment loading and fish assemblages in two Minnesota (USA) watersheds. *Environmental Management,* **32,** 93-105.

Zorn, C.J.W. (2001) Generalized estimating equation models for correlated data: A review with applications. *American Journal of Political Science,* **45,** 470-490.

Zweig, L.D. & Rabeni, C.F. (2001) Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society,* **20,** 643-657.

Table 3.1 Means (± sd) of the main physico-chemical and channel characteristics of the study streams in the Usk catchment, south-east Wales. The number (2) indicates that two reaches were sampled in the 2006 survey while * indicates those streams selected for the 2007 patch-scale survey. NA indicates that data were not available for the given stream.

River	Nitrate (mg/l)	Phosphate (mg/l)	Hardness (mg/l)	BOD (mg/l)	Flow velocity (m/s)	Width (m)	Depth (cm)
Afon Ysgir *	0.99 (0.39)	0.01 (0.01)	68.2 (26.7)	1.18 (0.77)	0.34 (0.10)	6.50 (0.5)	19.5 (7.4)
Bran (2) *	0.86 (0.51)	0.01 (0.01)	58.4 (20.5)	1.13 (0.72)	0.32 (0.08)	4.7 (0.35)	19 (7.7)
Caerfanell	0.65 (0.33)	0.01 (0.01)	60.6 (57.9)	1.0 (0.38)	0.22 (0.02)	3.0 (0.5)	12 (2.1)
Camlais (2)	NA	NA	NA	NA	0.34 (0.03)	3.0 (0.9)	15.7 (3.1)
Cilieni (2)	NA	NA	NA	NA	0.32 (0.09)	4.2 (2.47)	12 (0.7)
Crai (2)	0.67 (0.89)	0.03 (0.18)	49.5 (16.2)	1.20 (0.34)	0.37 (0.03)	5.5 (0.70)	13.7 (1.7)
Cynrig (2) *	0.92 (0.38)	0.01 (0.01)	95.6 (191)	1.1 (0.50)	0.38 (0.12)	3.00 (1.0)	13.9 (3.6)
Eithrim	NA	NA	NA	NA	0.22 (0.06)	1.50 (0.3)	12.5 (1.2)
Grwyne Fawr (2)	1.20 (0.2)	0.02 (0.06)	90.1 (27.1)	1.1 (0.50)	0.37 (0.18)	5 (1.41)	18.9 (10)
Grwyne Fechan (2)	NA	NA	NA	NA	0.41 (0.15)	3.2 (0.35)	16 (6.3)
Honddu (2) *	1.58 (0.6)	0.02 (0.02)	92.6 (28.2)	1.24 (0.80)	0.45 (0.19)	5 (2.83)	20.4 (7.5)
Hydfer *	0.68 (1.1)	0.01 (0.02)	50.5 (20.2)	0.97 (0.50)	0.40 (0.20)	5.00 (0.7)	9.4 (3.2)
Menascin (2)	0.90 (0.8)	0.01 (0.02)	74.3 (33.1)	0.97 (0.35)	0.25 (0.02)	3.2 (0.35)	12.8 (3.1)
Rhiangoll (2)	1.50 (0.4)	0.02 (0.01)	146.9 (38.5)	1.29 (0.92)	0.34 (0.06)	2 (0.71)	13.4 (1.2)
Senni (2) *	0.92 (0.64)	0.04 (0.01)	76.8 (29.0)	1.19 (0.51)	0.23 (0.03)	4.5 (3.52)	13.3 (2.4)
Tarell (2) *	0.96 (0.33)	0.02 (0.02)	96.9 (154.1)	1.08 (0.65)	0.55 (0.01)	5 (2.12)	20.5 (4.6)
Ysgir Fawr (2)	NA	NA	NA	NA	0.34 (0.01)	3.7 (1.77)	15.2 (3.3)
Ysgir Fechan (2) *	NA	NA	NA	NA	0.30 (0.13)	4 (1.41)	15 (1.8)

Table 3.2 Loadings onto the first two Principal Components revealing trends in catchment and riparian land-use in the Usk catchment, south-east Wales. Values in parentheses are the percentages of variance explained by each principal component.

	Catchment PCs		Riparian PCs	
Land use type	PC1 (68%)	PC2 (22%)	PC1 (39%)	PC2 (27%)
Improved grassland	0.91	-0.22	-0.91	0.05
Upland vegetation	-0.98	-0.05	0.74	0.59
Woodland	0.52	0.84	0.42	-0.76
Urban	N.A.	N.A.	-0.13	-0.59
Arable	0.82	-0.35	-0.61	0.25

Table 3.3 Invertebrate response shown by General Estimating Equations in the catchment of the River Usk to sediment cover and measured suspendable sediments at the patch-scale at all sites and in upland and improved grassland locations. Values of r are shown at * = $P < 0.05$ and ** = $P < 0.01$. (See Fig. 5 for an example).

	All locations		Upland locations		Grassland locations	
Metrics	Sediment cover (%) (N=56)	Suspendable sediments (N=45)	Sediment cover (%) (N=24)	Suspendable sediments (N=18)	Sediment cover (%) (N=32)	Suspendable sediments (N=27)
Taxon richness	- 0.41 **	- 0.40 **	- 0.29 *	N.S.	-0.42 *	N.S.
EPT richness	- 0.45 **	- 0.44 **	- 0.52 **	N.S.	N.S.	N.S.
% EPT	N.S.	N.S.	0.51 **	0.57 **	N.S.	N.S.
Shannon Index	N.S.	N.S.	- 0.47 **	- 0.63 **	N.S.	N.S.
Total abundance	N.S.	N.S.	0.50 *	0.80 **	- 0.41 *	- 0.40 *
% Chironomidae	N.S.	N.S.	- 0.49 **	- 0.65 **	N.S.	N.S.
% Coleoptera	N.S.	N.S.	- 0.64 **	- 0.69 **	N.S.	N.S.
% Oligochaeta	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

Table 3.4 Ranking of 27 common taxa based on their 50% abundance in relation to cumulative sediment cover (see Fig. 6).

Taxon	Order	Sediment cover (%) for 50% abundance
Hydropsyche instabilis	Trichoptera	1.5
Perla bipunctata	Plecoptera	2.5
Helodidae	Coleoptera	3.1
Simulidae	Diptera	3.5
Caenis rivulorum	Ephemeroptera	4.5
Sericostoma personatum	Trichoptera	4.7
Hydraena gracilis	Coleoptera	4.7
Hydropsyche siltalai	Trichoptera	5.3
Baetis scambus	Ephemeroptera	6
Elmis aenea	Coleoptera	6.3
Rhyacophila spp.	Trichoptera	6.3
Chironomidae	Diptera	6.3
Esolus parallelepipedus	Coleoptera	6.6
Heptagenia lateralis	Ephemeroptera	8.3
Rhithrogena semicolorata	Ephemeroptera	8.9
Ephemerella ignita	Ephemeroptera	9.1
Limnius volkmari	Coleoptera	9.1
Baetis rhodani	Ephemeroptera	9.5
Leuctra geniculata	Plecoptera	9.8
Baetis muticus	Ephemeroptera	10
Leuctra moselyi	Plecoptera	10
Ecdyonurus sp.	Ephemeroptera	10.6
Chloroperla torrentium	Plecoptera	11.2
Odontocerum albicorne	Trichoptera	12
Tipulidae	Diptera	12
Oligochaeta	Anellida	12.7
Oreodytes sanmarkii	Coleoptera	13.1

Table 3.5 Complete list of taxa collected in the 2006 and 2007 surveys in the Usk catchment, South-east Wales.

Agapetus sp.
Amphinemura sulcicollis (Stephens)
Ancylidae
Asellus sp.
Athericidae
Baetis fuscatus (Linnaeus)
Baetis muticus (Linnaeus)
Baetis rhodani (Pictet)
Baetis scambus Eaton
Brachycentrus subnubilus Curtis
Caenis rivulorum Eaton
Centroptilium pennatulum Eaton
Ceratopogonidae
Chironomidae
Chloroperla torrentium (Pictet)
Chloroperla tripunctata (Scopoli)
Dinocras cephalotes (Curtis)
Dytiscidae
Dixidae
Drusus annulatus Stephens
Ecdyonurus torrentis Kimmins
Ecdyonurus venosus (Fabricus)
Elmis aenea (Muller)
Empididae
Ephemera danica Muller
Ephemerella ignita (Poda)
Esolus parallelepipedus (Muler)
*Gammarus pulex*Linnaeus
Gyrinidae
Glossosoma sp.
Goeridae
Habrophlebia fusca (Curtis)
Halesus spp.
Helodidae
Helophorus brevipalpis Bedel
Heptagenia lateralis (Curtis)
Heptagenia sulphurea (Muller)
Hydaena gracilis Germar
Hydropsyche instabilis (Curtis)
Hydropsyche siltalai Dohler
Hydroptilia sp.
Irudinea
Isoperla grammatica (Poda)
Lepidostoma hirtum (Fabricus)
Leptophlebiidae
Leuctra geniculata (Stephens)
Leuctra inermis Kempny
Leuctra moselyi Morton
Leuctraa nigra (Oliver)
Limnius volckmari (Panzer)
Lumbricidae
Lymneidae
Notonectidae
Odontocerum albicorne (Scopoli)
Oligochaeta
Oreodytes sanmarkii (Sahlberg)
Oulimnius tuberculatus (Muller)
Perla bipunctata Pictet
Philopotamus montanus (Donovan)
Pisidium sp.
Planorbidae
Plectrocnemia conspersa (Curtis)
Polycelis spp.
Potamophylax sp.
Poycentropus flavomaculatus(Pictet)
Rhyacophila dorsalis (Curtis)
Rhyacophila munda McLachlan
Rhyacophila obliterata McLachlan
Rhyacophila septentrionis McLachlan
Rhithrogena semicolorata (Curtis)
Sericostoma personatum (Spence)
Silo pallipes (Fabricus)
Simulidae
Sphaerium sp.
Tabanids
Tipulidae
Womaldia subnigra McLachlan
Wormaldia occipitalis (Pictet)

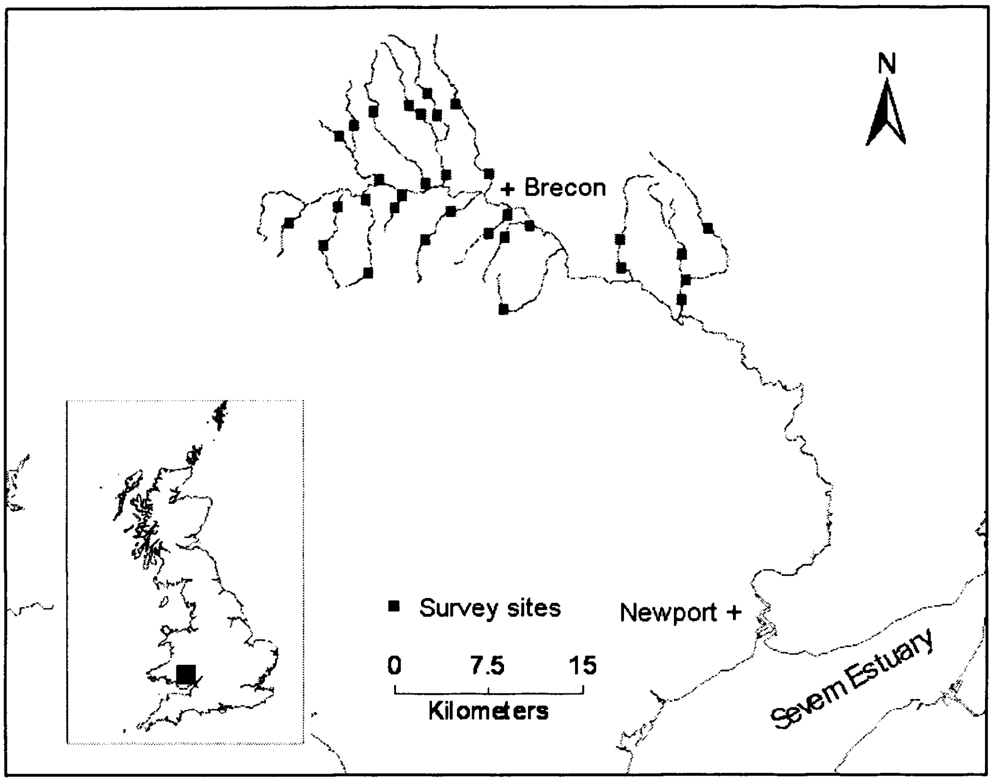


Fig. 3.1 Scaled schematic map of the Usk River system, Wales, showing sites selected for the 2006 reach-scale survey.

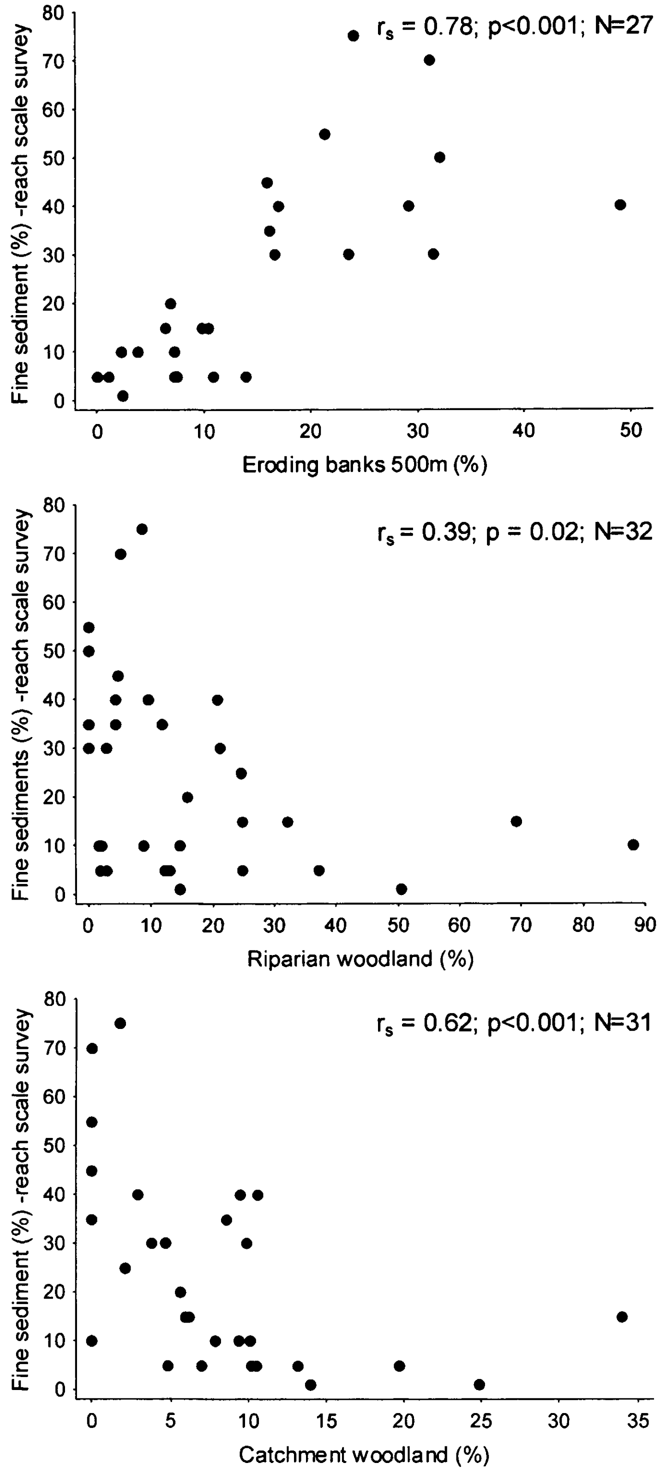


Fig. 3.2 Significant relationships between fine sediment cover, estimated from the reach scale survey, and the extent of eroding banks for 500 upstream, riparian and catchment woodland cover in the Usk catchment, south-east Wales.

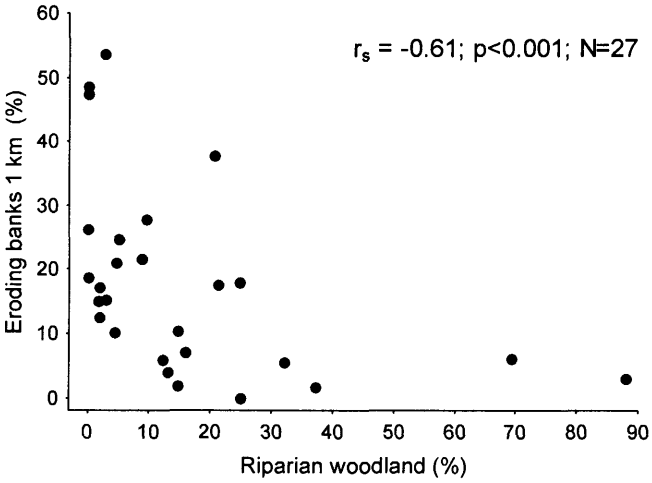


Fig 3.3 Relationship between the extent of eroding banks for 1 km upstream and riparian woodland cover in the Usk catchment south-east Wales.

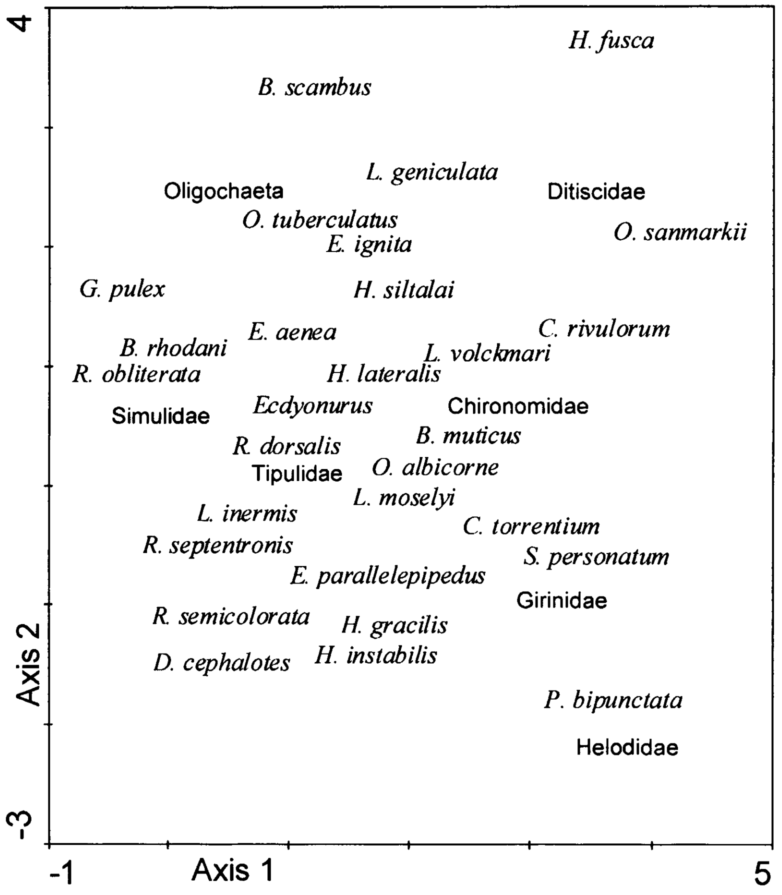
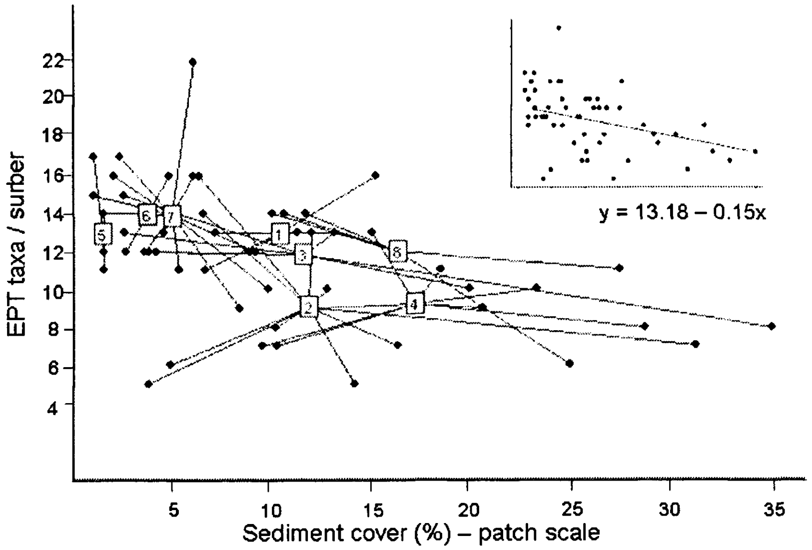


Fig. 3.4 Detrended Correspondence Analysis (DCA) plot of taxa from the 2007 patch -scale survey. Axis 1 mainly represented increased water depth, while fine sediment cover and suspendable sediments increased along axis 2. For clarity not all taxa are included.



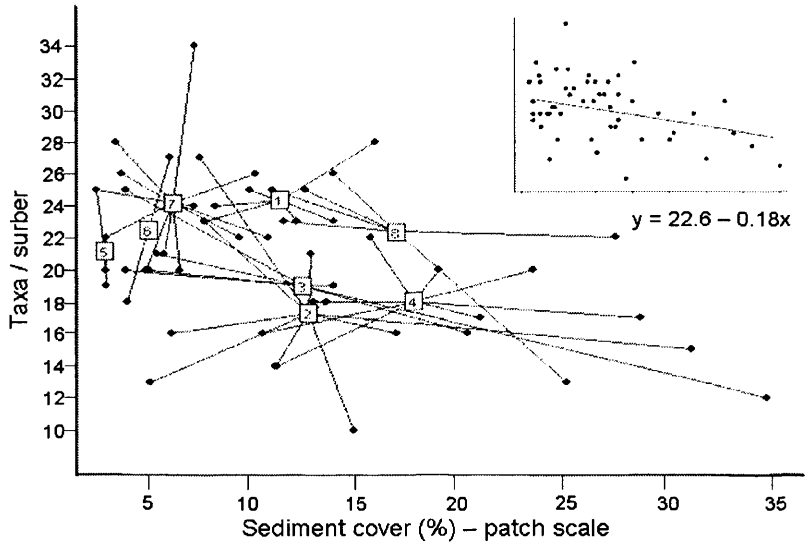


Fig. 3.5 Response of EPT taxon richness and total taxon richness to increasing sediment cover. Samples are grouped by stream (labelled as numbers). Regression coefficients are based on GEE models.

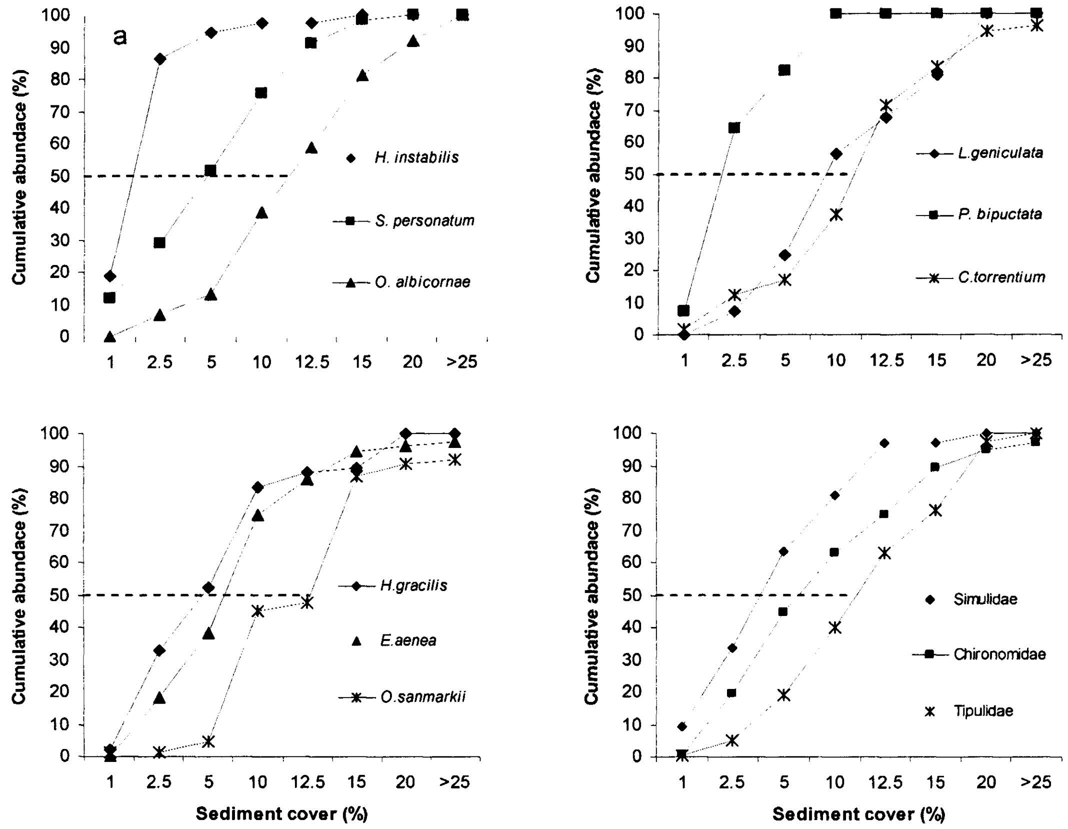


Fig. 3.6 Examples of cumulative abundance curves for three species of Trichoptera (a), Plecoptera (b), Coleoptera (c) and three dipteran families (d) in relation to sediment cover. Tolerance values (Table 4) were estimated where 50% cumulative abundance ourred (dotted line).

Chapter 4 - Habitat modification and the conservation of species' traits in temperate river invertebrates

Summary

1. Freshwaters have rapid rates of species' extinction and compositional change resulting from anthropogenic modification at multiple spatial scales. Biological traits offer a means to appraise the conservation impacts, but there have been few investigations. In the Usk river system (Wales, UK), I sampled macroinvertebrates at two spatial extents to investigate how catchment-scale intensification and patch-scale deposition of sediments affected overall trait diversity as well as species of contrasting trait character.

2. Species-trait composition varied as semi-natural catchments gave way to intensified pasture. Larger, longer-lived organisms declined while modified sites were occupied by resilient taxa with small body size, polivoltinism, ovoviviparity and strong dispersal. At the patch-scale, sedimentation was accompanied by changes in behavioural or feeding-trait representation; detritivores, herbivores, deposit feeders and burrowers increased while filterers, predators and attached taxa declined. Trait diversity was reduced by modification at both scales. Sites affected by land-use intensification and local sedimentation were occupied by nested subsets of species, implying that modified locations lost specialist taxa while retaining generalists.

3. I conclude that habitat modification in this catchment has had systematic effects on species of contrasting character. Sedimentation has altered feeding-trait representation substantially, but only locally. By contrast, large-scale intensification has apparently reduced the frequency of specialised, longer-lived invertebrates. These K-strategists might be at risk from the loss of semi-natural habitats in river catchments more generally, implying the need to conserve river-catchment integrity. Biological traits provide unique insight to the conservation impacts of anthropogenic modification in rivers, and parallels between the traits of affected organisms in aquatic and terrestrial ecosystems suggest that similar ecological processes might operate.

4.1 Introduction

Biodiversity loss and impairment are occurring at unprecedented rates, with climate change, habitat modification and habitat loss among the major drivers (Travis, 2003). Although such effects are widely recognised in terrestrial habitats, particularly in the tropics, less attention has been paid to freshwaters, where extinction rates now appear to be rapid (Ricciardi & Rasmussen, 1999; Clausnitzer *et al*, in press). These effects arise from the array and extent of stressors on freshwaters not only directly, for example from pollution, water abstraction, impoundment and introduced species, but also indirectly from the extensive conversion of river and lake catchments for agriculture or other human uses (Allan, 1995; Richter *et al*, 1997).

Despite long-standing efforts to quantify the biological impairment of streams and rivers, there is still only limited understanding of the types of organisms at risk, and of the conservation consequences. This is partly because different stressors combine to affect river systems at multiple scales (Vannote *et al*, 1980; Allan, 2004; Townsend, Uhlmann & Matthaei, 2008), but also because most ecological assessment in freshwaters focuses on the taxonomic identity of affected organisms rather their ecological character (e.g. Hellawell, 1986; Rosenber & Resh, 1993; e.g. Davy-Bowker *et al*, 2005). This taxonomically-led approach not only prevents regional comparison of stressor effects, organism sensitivities and conservation impacts, but also it limits mechanistic understanding, predictability and transportability of management responses (Gayraud & Philippe, 2003).

Evidence that species' sensitivities to environmental change are non-random has stimulated attempts to identify the ecological or biological traits of vulnerable organisms. For example, across many biological systems, extinction proneness is related to life-history specialization, body mass and reproductive rate (Duffy, 2003; Kotiaho *et al*, 2005; Olden, Hogan & Vander Zanden, 2007). These effects arise because environmental constraints shape local species assemblages by 'filtering' specific species' traits in such a way that only organisms whose resource requirements are met in any given location can establish or maintain viable populations (Southwood, 1977; Usseglio-Polatera & Tachet, 1994; Richards *et al*, 1997). Conversely, other species are excluded, where resources are lost, so rapidly through environmental change that they can neither persist nor establish in new locations (Duffy, 2003).

Trait-based approaches to understanding environmental change and selection, initially developed in entomology, have been applied increasingly to freshwater invertebrates, mostly in Europe, where information on species life-history is readily available (Statzner, Hildrew & Resh, 2001). So far, however, most applications have focused on biological monitoring, pollution assessment and restoration (Gayraud & Philippe, 2003; Statzner, Bonada & Doledec, 2007; Horrigan & Baird, 2008; Paillex *et al*, 2009; Tullos *et al*, 2009). Applications aimed at understanding how wider environmental change in river systems affects species loss, ecological impairment and conservation have been scarcer (Bonada, Doledec & Statzner, 2007; Dolédec & Statzner, 2008; Townsend *et al.*, 2008). This is despite clear relevance to river conservation biology, and to the comparison of impairment processes between terrestrial and aquatic environments (Purvis *et al*, 2000).

Among the anthropogenic impairments that affect streams and rivers, modifications to catchment land-use and alterations in sediment release are among the most widespread (Waters, 1995). At the catchment scale or in the riparian zone, the conversion of semi-natural habitats to agriculture typically alters energy flux, hydrology, hydrochemistry, thermal regimes and habitat availability (e.g. Manel, Buckton & Ormerod, 2000). Associated alterations in sediment release can have effects on aquatic organisms (Lemly, 1982; Newcombe & MacDonald, 1991; Waters, 1995; Gayraud, Herouin & Philippe, 2002; Parkhill & Gulliver, 2002; Greig, Sear & Carling, 2005), but their detection is problematic where sediments occur against a background of wider land-use change. In the Usk Catchment in Wales, for instance, localised sediment release had effects on invertebrates that were only detectable by either experiments or scale-specific approaches that separated local sedimentation from larger catchment influences (Larsen, Vaughan & Ormerod, 2009; Larsen & Ormerod, in press). These circumstances, where effects at different scales might mask each others' conservation implications, make this problem a particularly interesting one in which to examine the value of trait-based assessments.

In this paper, I investigate how anthropogenic modification of a temperate river catchment at two spatial extents, reach/catchment change in land use and patch-scale sediment deposition, has been associated with effects on macroinvertebrates of contrasting trait character, overall trait diversity and the relative drop-out of specialist versus generalist species.

First, based on observations relating trait representation to land use change and sedimentation, I formulated *a priori* hypotheses regarding specific trait response to modification. As natural catchment vegetation is converted into improved pasture, traits conferring rapid population growth and increased resilience should be favoured (Doledec *et al*, 2006). Species with resilience traits should also be more common in patches impaired by sedimentation where effects on feeding and behavioural character should also arise (Richards *et al.*, 1997; Rabeni, Doisy & Zweig, 2005; Townsend *et al.*, 2008). Specifically, burrowing organisms should be more common in sediment-affected patches while filter feeding and grazing organisms should be impaired (Table 1). Secondly, I examined whether overall trait diversity was affected by either land-use intensity or local sediment deposition.

All of these foregoing effects would have intrinsic conservation ramifications if they resulted in the systematic loss or impairment of organisms of specific trait character. Additional conservation effects might arise if the resulting losses altered species representation, for example by eliminating specialists rather than generalists. I examined this possibility by assessing patterns of nestedness across communities at impaired versus less-impaired locations. Nested patterns occur where species present at species-poor sites form a sub-set of the species occurring in richer locations (Atmar & Patterson, 1993; Rodriguez-Girones & Santamaria, 2006). In a perfectly nested matrix, rarer species are exclusive to species-rich locations, whereas in a non-nested system rare species could also occur in species-poor locations and common species may be absent from richer sites. Although sometimes criticised for apparent limitations in predicting extinction-prone species (e.g. Donlan *et al*, 2005), this method is being applied increasingly to appraise conservation effects in different ecosystem types (Fernandez-Juricic, 2002; Schouten *et al*, 2007; Horsak & Cernohorsky, 2008). I wanted to know whether trait-dependent sensitivity to land use and sediments affected species composition through such nested effects (Fleishman *et al*, 2007). I hypothesised that, because species differ in their sensitivities to modification, then, local selection, extinction (i.e. local drop-out) and colonisation should generate nested patterns as increasingly intensive land-use or increased sedimentation favour generalists over specialist taxa (Cutler, 1991; Atmar & Patterson, 1993; Heino, Mykra & Muotka, 2009).

4.2 Methods

Study area

The Usk, in south-central Wales (UK), is notified as a Special Area of Conservation under the Habitats Directive (92/43/EEC) and holds one of the most important game fisheries in England and Wales. The catchment is suitable for appraising combined land-use and sedimentation effects because ionic composition and geology are relatively homogeneous across the catchment (e.g. total oxidised nitrogen 0.65-1.58 mg/L hardness 49.5-146 mg/L), while urbanization is negligible. Moreover, land-use varies from semi-natural upland vegetation to increasingly intensive pastoral grassland over a sandstone dominated catchment that is sensitive to sediment mobilisation (Larsen et al., 2009).

Survey design

The overall survey design, study locations and analytical approaches have been described by Larsen et al. (2009), who also demonstrated statistical independence among the survey sites. Briefly, a reach-scale survey was carried on in summer 2006 to assessed catchment and reach-scale influences on invertebrates and their trait structure. It involved 32 catchment reaches over an altitudinal range of 190-400 m a.s.l. along 18 second-order tributaries draining semi-natural upland vegetation (bracken, heath, moorland, acid grassland) and improved pasture grassland. Deciduous woodland never exceeded 34% of any catchment. While covering the main land-uses, reaches were selected to minimize variations in depth, flow velocity, stream width and particle size distribution. Fourteen streams were sampled along two reaches and four streams on one reach, depending on accessibility and stream length.

In 2007, a patch-scale survey assessed within-reach effects of sediment deposition at locations nested within 12 previously sampled reaches on eight streams, again focussing on invertebrates and their traits. Stream patches (*c.* 3m^2) represented both upland and pasture grassland while covering a wide range of sediment conditions. Only riffle-glide habitats were included. According to availability, three to six patches per reach were sampled in a ~15m long section, for a combined total of 56 patches.

Environmental variables – reach-scale

Land-use data were extracted from an existing GIS land-cover layer created by the Countryside Council for Wales (CCW, 2002). For every reach, land-use was calculated for the whole catchment area as well as for a 150 m wide buffer on each side of the stream up to 1 km upstream. Variation among macroinvertebrate species assemblages at this scale is mostly related to catchment and riparian land-use, namely the percentage of pasture grassland (Larsen et al., 2009). Because riparian and catchment land-use are correlated closely, I use only improved grassland as a primary descriptor of land-use intensity.

Monthly concentrations of nitrate (mg/L), phosphate (mg/L), Biochemical Oxygen Demand (BOD mg/L), water hardness as $CaCO_3$ (mg/L) and pH were available for 12 reaches from the UK Environment Agency's Water Management Information System (WMIS) based on standard methods (Standing Committee of Analysts, 1981, 1979, 1987, 1992) . Means for each determinand were calculated for the year antecedent to invertebrate sampling. Although incomplete, the chemical data from streams draining both pasture grassland and semi-natural upland vegetation allowed to assess the extent to which water quality might influence invertebrates. Most reaches without chemical data were higher altitude locations likely to have the lowest nutrient concentrations (Clews & Ormerod, 2009).

Environmental variables – patch-scale

Patch-sale environmental data were collected in the field. Water depth and flow velocity were measured in each patch, and deposited fine sediment (< 2mm) in each sampling site (c.3m^2) measured using a circular quadrat (300 cm^2) where the percentage of stream bed covered by fine particles was estimated in 5 % increments (Zweig & Rabeni, 2001). Ten observations immediately around Surber samplers used for invertebrates were averaged. In addition, the amount of suspendable sediment from the stream bed was measured at 49 of the patches sampled, with four measurements made around each Surber location. A metal box (24 x 18 cm) was pushed into the substratum and sediments from *c.* 2 cm depth were entrained in the measurable volume of water. Suspended sediments within the range of 0.063-1 mm were filtered from 1 liter of water, dried, weighted and calculated as g /m^2. Organic material from the collected sediments was reduced by washing and decanting.

Invertebrate sampling

Reach-scale survey (June-July 2006). Benthic macroinvertebrates were collected using kick-samples of three minutes duration across riffles and glides (typical < 55 cm/s) over a 10 m reach. I used a standard hand-net (mesh 0.9mm, 25 x 25 cm) to mimic typically biological monitoring (Wright, Furse & Moss, 1998), and the method has been validated on similar streams (Bradley & Ormerod, 2002).

Patch-scale survey (June-July 2007). A Surber sampler (0.16 m^2; 0.44mm) was used to assess smaller-scale variations in composition and to cover the defined area of stream bed where sediment character was also assessed. The two collection methods, although differing in spatial extent, provide similar qualitative information about assemblage composition (Larsen et al., 2009).

Invertebrate biological traits

The functional composition of all invertebrate samples was defined using 51 categories of 11 biological traits (Table 1) based on available information (Richoux, 1994; Tachet, Usseglio-Polatera & Roux, 1994; Usseglio-Polatera, 1994; Usseglio-Polatera & Tachet, 1994; Tachet *et al*, 2000). Trait information was collected for a total of 50 taxa, mostly genera, but Oligochaeta and Hirudinea were omitted because of incomplete information. Fuzzy coding was used to determine the affinity of each taxon for categories (Chevenet, Doledec & Chessel, 1994) that ranged between 0 and 3, or 0 and 5. Affinity scores were rescaled as proportions (sum = 1) for each taxon, while group-wide averages were used for taxa identified at coarser level (e.g. Diptera families). Taxon × trait-categories at each site were multiplied by the log(x+1) abundance to produce a site × trait abundance matrix, and abundance-weighted trait profiles converted to frequency distributions for each trait (Dolédec, Olivier & Statzner, 2000; Archaimbault, Usseglio-Polatera & Bossche, 2005).

Data analysis

Trait diversity (TD) in each sample for both surveys was calculated as the average Simpson diversity (S) across all traits:

$$TD = S = 1 - D_i, \text{ where } D_i = \Sigma(n_j/N)^2$$

With D_i = Dominance index of trait i; n_j = relative abundance of trait category j; N = total abundance of all trait categories. The average of S across all traits was calculated to account for the lack of independence (e.g. Bêche & Resh, 2007). In addition, because traits can have multiple categories (e.g. feeding traits are divided into filterer, grazers, predators, etc.) I also assessed how diversity within traits varied across locations using Simpson's diversity index.

Correlation (Pearson product-moment) between overall trait diversity and taxonomic richness was examined to appraise occurrence of functional redundancy at the two scales (Micheli & Halpern, 2005; Bêche & Resh, 2007).

To obtain synthetic scores of sites based on overall trait composition I used Fuzzy Principal Component Analysis (FPCA) on the traits matrix for both surveys (Chevenet et al., 1994). At the reach-scale, relationship between catchment improved grassland, water chemistry and trait composition and diversity was analysed using Pearson product-moment correlation.

At the patch-scale, relationship between sediment measures (cover and suspendable sediments) and trait composition and diversity was assessed using General Estimating Equations (GEEs). This approaches accounts for the non-independence among patches within reaches by adjusting regression coefficients (see Zorn, 2001; Vaughan, Noble & Ormerod, 2007). In addition, I used Spearman rank correlations to assess how the proportions of each trait category varied with either catchment land-use and associated water physiochemical variables or patch-scale sediment features (Bêche, McElravy & Resh, 2006). I corrected alpha values (= 0.05) by dividing by the number of categories within each trait (e.g. if a given trait has six categories, for significance $\alpha = 0.008$). Results from this analysis were also checked by GEEs to control for independence among sites, but there were no departures from standard Spearman rank correlations.

To quantify the level of nestedness across communities in both surveys, I used the binary-matrix nestedness temperature calculator (BINMATNEST; Rodriguez-Girones & Santamaria, 2006), which is an improvement of the nested-temperature method of Atmar and Patterson (1993). The temperature method is relative insensitive to matrix size, and also correlates well with other metrics (Wright et al., 1998). BINMATNEST works on the species presence / absence matrix, re-ordering rows and columns to maximise matrix nestedness to calculate a temperature (ranging over 0 – 100 °C) which reflects the matrix deviation from an ideal nested structure; perfectly nested matrices with rare taxa in rich locations have $T = 0°C$ while totally random matrices have $T = 100°C$. The statistical significance of the observed temperature was assessed using a Monte-Carlo approach involving comparison with simulated temperatures of 400 random generated matrices. In the more conservative null-model III used here, the probability of a cell being occupied equals the average probabilities of occupancy of its row and column. This null model is considered the most reliable as it is less sensitive to species richness and occurrences (Rodriguez-Girones & Santamaria, 2006). The order with which sites are sorted in the maximally packed matrix can then be compared with independent correlates to assess the likely determinants of nestedness. I used Spearman-rank correlation to evaluate the influence of land-use and sediment measures on the nested patterns of communities from the reach and patch-survey respectively (Schouten *et al.*, 2007; Heino *et al.*, 2009).

4.3 Results

Reach-scale trends

The percentage of improved grassland in the catchments ranged from 0 to 64 %, representing a clear intensification gradient. Phosphate concentration never exceeded 0.04 mg/l, while mean nitrate concentrations were in the range 0.65 – 1.58 mg/l. These variations, in turn, were accompanied by changes in species trait composition across locations.

The first two axes of the fuzzy PCA explained 40% and 23% of variation in trait composition across reaches, respectively. Both axes were significantly correlated with the extent of improved grassland (Axis 1: r = -0.38; P=0.03; Axis 2: r = 0.48; P=0.004; Fig. 4.1), implying that invertebrate trait composition followed this dominant land-use gradient. Aggregate trait representation shifted from ovoviviparity, multiple generations per year, medium-small body size, short life-cycle and high dispersal potential in improved grassland reaches to taxa characterised by larger body size and longer life-cycles (Fig. 4.1). There were also relationships between individual trait categories and improved grasslands (Table 4.3), with smaller size, shorter life cycles, ovoviviparity and high dispersal potential all increasing with grassland, whereas larger size, lower dispersal potential and laying free-egg clutches declined. By contrast, chemical trends across sites were reflected by only two significant trends in trait representation respectively involving a decline in the tendency of species to lay free eggs with increasing nitrate (r_s = -

0.8; $P<0.001$; N=12) and an increase in ovoviviparity with water hardness ($r_s = 0.71$; $P=0.009$; N=12).

Further evidence of a land-use effect arose from a significant decline in overall trait diversity with increasing cover of intensive grassland (r = -0.46; $P=0.008$). There were also trends in individual trait diversity, for example in maximal size (r = -0.7; $P<0.001$), life-cycle duration (r = -0.36; $P=0.04$) and resistance forms (r = -0.35; $P=0.04$). Interestingly trait diversity per reach was not related to taxonomic richness (Fig.4.2; $P = 0.6$).

Communities showed a significantly nested sub-structure (T = 36.4°; $P<0.001$). Site ranking in the maximally packed matrix (i.e. the species-by-site matrix when ordered to most emphasise patterns of nesting) was significantly correlated with grassland intensity ($r_s = 0.43$; $P=0.01$), suggesting that land-use was implicated in the observed nested-subset pattern.

Patch-scale trends

Deposited sediments covered 1 – 35% of the benthos across the 56 patches sampled, with suspendable sediments reaching 2 – 147 g/m^2. Depth ranged over 8 – 27 cm and current velocity 11 – 57 cm/s. Species' trait profiles varied markedly in response, with the two principal components explaining c 44% of trait variation among patches (Fig. 4.3).

GEE models showed that trait axis 1 was strongly related to both deposited and suspendable sediments (r = -0.55; $P<0.001$ and r = -0.57; $P<0.001$ respectively). Fuzzy PCA axis 1 was correlated with water depth, but only weakly (r = -0.3; $P=0.03$). From the ordination plot (Fig. 4.3), it appeared that trait categories most common in sediment-rich patches were related to locomotion and feeding habits, with burrowers, interstitial taxa, and fine sediment or detrital feeders most favoured. In contrast, predators, scrapers and filterers were more common in sediment-free patches, along with larger taxa characterised by semi-voltine life cycles. However, very small body size was also more common on this side of the gradient. These multivariate trends were confirmed in bivariate correlations: deposit and detrital feeders, macrophyte herbivores, burrowers, shredders and organisms laying endophytic eggs were all associated with increased sediment loads, while filterers, predators, scrapers and taxa attached to the substratum were negatively impacted. Semivoltine taxa also declined at sites with suspendable sediments (Table 4.3).

Variations in trait composition were accompanied by variation in global trait diversity, which declined as deposited sediments increased ($r = -0.33$; $P<0.001$; $N=56$). Specific traits were responsible for this trend as the diversity of maximal size, dispersion potential and feeding habits all declined with increasing sedimentation ($r = -0.39$; $P=0.003$; $r = -0.35$; $P=0.008$; $r = -0.46$; $P<0.001$, respectively). At this scale, trait diversity was correlated significantly with taxon richness ($r = 0.5$; $P<0.001$; Fig. 4.2).

Communities again showed significant nestedness across patches with different sediment character (matrix T= 31.5 °C; $P<0.001$). Ranking of sites according to both sediment cover and suspendable sediments showed significant correlations with nestedness ($r_s = 0.29$; $p=0.02$; $r_s = 0.44$; $P=0.001$, respectively) implying that sedimentation was accompanied by the drop-out of taxa that occurred elsewhere.

No correlations were observed between trait axis 2 and the measured patch-scale or sediment variables. When grouped by reach and plotted on the factorial plane, the position of sample patches overlapped across reaches, implying that local habitat character (i.e. sediment features) influenced invertebrate communities locally within reaches (Fig. 4.3).

4.4 Discussion

In revealing that river invertebrate traits vary systematically with catchment-scale intensification and patch-scale sediments in the Usk, these extensive data supported our initial hypotheses. While there is a caveat in that the tests used surveys rather than experimental manipulations (Doledec *et al.*, 2006; Townsend *et al.*, 2008), the resulting data offer an insight into how basin-scale changes affect river organisms over large spatial and temporal extents (Manel *et al.* 2000). Indeed, three important results emerged, each of which has the potential to expand the use of traits in assessing how river ecosystem respond to modification, and to predicting the organisms at greatest risk of adverse change. First, the use of trait-based approaches in rivers extends beyond evolutionary ecology (Townsend & Hildrew, 1994) or biomonitoring (Statzner *et al*, 2001) into conservation biology, in this case revealing how river-catchment intensification affects larger, longer-lived organisms. Secondly, processes at different spatial extents can have contrasting effects on the trait composition of river organisms, in this case local sediment deposition as distinct from modified land-use. Thirdly, some important ecological responses to modification transcended scale, and in our example trait diversity as well as the representation of larger organisms with longer life-cycles was reduced by both local sediment deposition and by extensive land-use modification. Effects on patterns of nestedness also transcended spatial scale.

Effects of catchment modification

Across entire reaches in the Usk system, individual traits apparently responded to land-use intensification, with characteristics related to population resilience, short generation time and high dispersal potential prevailing in pasture by comparison with semi-natural grassland and/or riparian woodlands. The overall trait composition of invertebrates followed this land-use gradient, so that larger-bodied and typically K-selected taxa became least abundant in more modified locations. Typical taxa lost were large predators such as *Perla*, *Dinocras* and *Isoperla* while typical *r*-strategists such as *Baetis* and ceratopogonids increased in grassland (Table 3.5 – Chapter 3). These observations followed our *a priori* hypotheses regarding higher population resilience with increasing land-use intensity and confirmed trends observed elsewhere (Doledec *et al.*, 2006). Conversely, Townsend and Thompson (2007) found that average body-size increased with land-use intensity perhaps as a result of higher stream productivity; however, they were unable to demonstrate any associated nutrient effect. They argued that unmeasured contaminants in farmed pasture reaches could have affected smaller invertebrates disproportionately, thus increasing average body size.

It is, in fact, problematic to appraise the effects of single factors on trait structure using survey data in such multivariate circumstances where many factors change simultaneously. Rather than any single, major environmental driver, effects observed here most likely reflect a combined, multivariate trend through which semi-natural, climax vegetation (mixed deciduous woodland) has been replaced by more intensively managed grassland. Habitat structure, sediment regimes, nutrient concentrations, thermal conditions, hydrology, relative sources of energy from autochthonous relative to allochthonous sources, and a range of other in-stream features are all modified as a consequence (Allan, Erickson & Fay, 1997; Harding *et al*, 1999). Our own data from the Usk and adjacent Wye illustrate some of these effects, including nutrient concentrations (Clews & Ormerod, 2009), sediment release (Larsen et al., 2009) and increased summer temperatures in tributaries draining grasslands (E. Clews, I. Durance and S. J. Ormerod unpubl. data). In turn, catchment and riparian land-use may well act through these factors as larger-scale filters that select or support organisms with life-history traits appropriate to the prevailing conditions - specifically those that accommodate disturbance in less natural, agricultural circumstances in contrast to the organisms with longer life-cycles that appear to persist more readily in stable, semi-natural catchments (Richards *et al.*, 1997; Hector *et al*, 1999; Diaz, Alonso & Gutierrez, 2008).

Similar multiple mechanisms were the likely drivers of the nested subset pattern observed in the invertebrate assemblage at this scale. The degree of nestedness is in line with what observed in other studies on stream invertebrates (Heino et al., 2009), and confirms that nestedness was relatively low compared to other biological systems in archipelagos, isolated ponds and habitat fragments (Fernandez-Juricic, 2002; Hecnar *et al*, 2002; McAbendroth *et al*, 2005). While such nestedness could be generated by either selective colonization or extinction and direct human disturbance, in river systems it is likely that a continuous disturbance-mediated colonization-extinction dynamic is responsible (Heino et al., 2009). In the Usk system, species sensitivity to land-use intensity appeared trait-specific, and a progressive loss of taxa resulted in the formation of a nested pattern along the land-use gradient.

With land-use modification and intensification in river catchments now widespread, any wider repetition of the ecological response I observed could have considerable significance for the conservation of river organisms. Parallel trends in species traits are already apparent elsewhere in modified river environments (Doledec *et al.*, 2006; Diaz *et al.*, 2008; Townsend *et al.*, 2008; Tullos *et al.*, 2009), and there are at least two important corollaries. First, large merovoltine or bivoltine organisms might be effective indicators of river and catchment stability or integrity, and further data to assess this possibility are required. Secondly, and more critically, their survival and persistence may require the greater protection or restoration of semi-natural river catchments than hitherto; the patterns I observed in the Usk occur in spite of the fact that the whole river system is a Special Area of Conservation under the EU Habitats Directive (92/43/EEC), and hence part of the Natura 2000 network of sites. More information is required on how such response traits – those sensitive to disturbance or land-use modification – are related to effects trait that represent ecosystem function. There is evidence, especially from animals, that extinction proneness is often associated with dominant ecosystem functions such that the first species to disappear are also more functionally efficient (Duffy, 2003). Here, larger taxa and predators appeared most sensitive to both land-use change and sedimentation. Such size-biased loss of species can affect function in whole ecological networks, but evidence from rivers is scarce (Duffy, 2003).

At a more fundamental level, one of the challenges in using traits as conservation indicators will be to separate traits that reflect a direct adaptation to certain habitat features from others that simply co-evolved and may be selectively neutral. As an example, ovoviviparity increased in pasture grasslands, but this reproductive mode is specific to crustaceans and some molluscs and might well be unconnected with habitat conditions. Abundance of such organisms may simply reflect higher calcium concentration and indeed, our results showed that ovoviviparity was more common in harder waters. A possible method to account for these phylogenetic constraints is to focus indicator effort on evolutionary labile traits that result from adaptive convergence independently of phylogeny. Poff *et al.* (2002) investigated this problem in North American river insects and showed that size at maturity, trophic habit, locomotion and voltinism were the most labile traits (i.e. those most independent of phylogeny), and it is interesting that these were among the traits responding apparently most clearly to environmental features in the Usk.

Scale-dependent effects

In addition to assessing the apparent influence of land use on trait composition, our survey was designed to detect patch-to-patch variations. At this scale, variation in life-cycle traits were again apparent, with depositional conditions apparently favouring *r*-strategists in these lower stability, transient environments characterised by suspendable or saltating material (Culp, Wrona & Davies, 1985). Besides a disturbance-driven pattern, it is also possible that deposited fine materials reduced streambed porosity thus disfavouring larger organisms requiring larger interstitial space. Perhaps a combination of both mechanisms is responsible for the decline of larger K-selected organisms at this scale. However, local sedimentation also affected traits related to feeding and behaviour. This apparent scale-dependence in trait response to habitat modification in the Usk mirrors the magnitude of sedimentation effects, which are more readily detectable at finer scales (Larsen et al., 2009).

Few studies have assessed explicitly the influence of fine sediment deposition on invertebrate trait composition (Richards *et al.*, 1997; Rabeni *et al.*, 2005; Doledec *et al.*, 2006; Townsend *et al.*, 2008), but our data contained several examples consistent with previous specific observations. Trait categories negatively affected by sediments included filter-feeding, with this effect known to reflect the impairment of filtering devices, such as nets (e.g. Strand & Merritt, 1997). Conversely, Townsend et al. (2008) observed that filter feeding was favoured by fine sediments, likely reflecting the associated increase in available nutrients with fine particles. In the Usk system however, deposited sediments are relatively coarser and not necessarily associated with increasing nutrient levels (Larsen et al., 2009).

Sediment deposition also affected taxa requiring temporary attachment to the substratum, and scrapers that graze clean surfaces. Some proportional decrease in flying insects and plastron respiration reflected reduction among coleopterans such as *Oulimnius* and *Hydraena*, which are mostly grazers and hence sediment-intolerant (Braccia & Voshell, 2006; Larsen *et al.*, 2009). In contrast, detrital feeders, macrophyte herbivores, burrowers and shredders were apparently favoured in sediment-rich patches, consistent with previous data that show both the retention of detrital material in depositing habitats as well as the response of associated taxa (Rabeni et al., 2005). Groups involved in the Usk included *Leuctra*, *Odontocerum* and Tipulidae, all apparently relatively sediment-tolerant (Larsen et al., 2009). Other trait categories apparently benefiting in depositing conditions are more difficult to interpret, for example, egg-laying in vegetation (endophytic), rather than on terrestrial substrata. Dolédec et al. (2006) observed a similar trend and suggested that, in habitats likely to be smothered with fine particles, ovoposition sites in vegetation were more likely to be available with possible benefits to egg survival. While it can be argued that such a reproductive strategy is characteristic of many Odonata that are also borrowers, no Odonata occurred in our samples.

Interestingly, assemblages at the patch-scale showed similar degree of nestedness as at the larger reach-scale, although the process generating it appeared to differ. At this local scale, trait-related tolerance to sedimentary conditions determined assemblage composition and the formation of a nested pattern. This result also confirms previous findings on the scalar property of nestedness, which can be generated by different processes at different scales (Summerville, Veech & Crist, 2002). While extinction and colonization can promote nestedness at broad spatial scales, behavioural and feeding related differences in patch use can be invoked at much finer scales.

Trait diversity

At least as interesting as scale-dependence in trait response to habitat modification in the Usk was the fact that some effects transcended the scales involved in our assessment. Specifically, both patch-scale sedimentation and land-use conversion to agriculture were accompanied by reductions in overall trait diversity. This may well be a widespread consequence of habitat modification, but its explicit relevance to conservation biology in river ecosystems is still poorly understood. Two key areas of investigation are whether the effect reflects the systematic reduction in the frequency of traits that also predispose species to extirpation (Olden, Poff & Bestgen, 2008) and whether there are any consequences of trait simplification for ecosystem function. In contrast to research on links between biodiversity loss and ecosystem functioning, links between trait representation and ecosystem function are scarce (Loreau, 2000). On the first theme, our data are interesting in revealing that reductions in trait diversity can arise from different effects, at different scales and through variations in different trait responses. While body size diversity appeared affected by both land-use modification and localised sedimentation, pasture intensity mostly affected the diversity of traits associated with voltinism and resistance. Reduction in the diversity of feeding modes and dissemination potentials reflected instead increasing sediment smothering.

On the second theme, I used functional diversity as a surrogate for assessing ecosystem function directly, examined by calculating trait diversity (TD). Functional diversity in a community is normally expected to be a function of species richness, although the shape of this function varies between systems (Stevens *et al*, 2003; Micheli & Halpern, 2005). In our data, this relationship was scale-dependent, with trait diversity increasing linearly with taxon richness at the patch-scale, but not at the reach scale. The shape of such relation suggests a saturating effect of taxonomic richness on functional groups (e.g. Bêche & Resh, 2007), where patterns observed at the larger scale may represent an asymptote and imply some functional redundancy in the communities. However, this apparent redundancy could not compensate for the progressive loss of taxa (and functional groups) along the land-use gradient, which clearly reflected the nested non-random nature of species removal dictated by their biological traits.

4.5 Conclusion

I began this case study wishing to examine whether trait-based approaches could reveal any effects of two widespread ecosystem stressors, sedimentation and land-use intensification, that were relevant to river conservation biology. The results are clear, and illustrate the value of trait-based assessment, as opposed to conventional taxonomy, in detecting distinct effects of habitat modification that varied with the life-cycles, dispersal capabilities, behaviour and feeding methods of the organisms at risk. Moreover, the use of nested subset analysis showed how different processes can generate nestedness at different scales and further illustrate the potential benefits of using such approach in conservation studies at finer scales (Summerville et al., 2002).

Parallels with other trait-based studies illustrate that results of this type may well be comparable not only across rivers in different geographical locations (e.g. Diaz et al., 2008), but also between rivers and terrestrial environments. The latter comparison is particularly striking in revealing similarities in the specific (e.g. feeding trait) and generic (e.g. life cycle, body mass) characteristics of organisms that appear to be affected by habitat modification and loss (Ribera *et al*, 2001: Hauser, Yoccoz & Ims, 2003: Cardillo *et al*, 2005: Magura, Tothmeresz & Lovei, 2006). River ecosystems are linked to terrestrial systems not only because they are both affected by catchment intensification, but also because there are apparently similarities in the ecological processes through which habitat impairment leads to changes in species' composition. As envisaged by Dolédec et al. (1999) the standardisation of trait-based approaches across ecosystems could allow further testing of such aquatic-terrestrial parallels thereby allowing both a common theoretical ground for cross systems conservation, and also parallel assessment of how ecosystem modification results in systematic effects on biodiversity.

4.6 References

Allan, J.D. (1995) *Stream Ecology. The Structure and Function of Running Waters,* Chapman & Hall, London.

Allan, J.D. (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics,* **35,** 257-284.

Allan, J.D., Erickson, D.L. & Fay, J. (1997) The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biology,* **37,** 149-161.

Archaimbault, V., Usseglio-Polatera, P. & Bossche, J.P.V. (2005) Functional differences among benthic macroinvertebrate communities in reference streams of same order in a given biogeographic area. *Hydrobiologia,* **551,** 171-182.

Atmar, W. & Patterson, B.D. (1993) The Measure of Order and Disorder in the Distribution of Species in Fragmented Habitat. *Oecologia,* **96,** 373-382.

Bêche, L.A., Mcelravy, E.P. & Resh, V.H. (2006) Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. *Freshwater Biology,* **51,** 56-75.

Bêche, L.A. & Resh, V.H. (2007) Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Fundamental and Appled Limnology,* **169,** 1-23.

Bonada, N., Doledec, S. & Statzner, B. (2007) Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology,* **13,** 1658-1671.

Braccia, A. & Voshell, J.R. (2006) Environmental factors accounting for benthic macroinvertebrate assemblage structure at the sample scale in streams subjected to a gradient of cattle grazing. *Hydrobiologia,* **573,** 55-73.

Bradley, D.C. & Ormerod, S.J. (2002) Evaluating the precision of kick-sampling in upland streams for assessments of long-term change: the effects of sampling effort, habitat and rarity. *Archiv Fur Hydrobiologie,* **155,** 199-221.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005) Multiple causes of high extinction risk in large mammal species. *Science,* **309,** 1239-1241.

Cardinale, B.J., Palmer, M.A., Swan, C.M., Brooks, S. & Poff, N.L. (2002) The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology,* **83,** 412-422.

Chevenet, F., Doledec, S. & Chessel, D. (1994) A Fuzzy Coding Approach for the Analysis of Long-Term Ecological Data. *Freshwater Biology,* **31,** 295-309.

Clausnitzer, V., Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E.M., Bedjanič, M., Dartwall, W.R.T., Dijkstra, K.B., Dow, R., Hawking, J., Karube, H., Malikova, E., Paulson, P., Schütte, K., Suhling, F., Villanueva, R.J., Von Ellenrieder, N. & Wilson, K. (in press) Odonata enter the biodiversity crisis debate: The first global assessment of an insect group. *Biological Conservation.*

Clews, E. & Ormerod, S.J. (2009) Improving bio-diagnostic monitoring using simple combinations of standard biotic indices. *River Research and Applications,* **25,** 348 - 361.

Culp, J.M., Wrona, F.J. & Davies, R.W. (1985) Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology,* **64,** 1345-1351.

Cutler, A. (1991) Nested Faunas and Extinction in Fragmented Habitats. *Conservation Biology,* **5,** 496-505.

Davy-Bowker, J., Murphy, J.F., Rutt, G.R., Steel, J.E.C. & Furse, M.T. (2005) The development and testing of a macroinvertebrate biotic index for detecting the impact of acidity on streams. *Archiv Fur Hydrobiologie,* **163,** 383-403.

Diaz, A.M., Alonso, M.L.S. & Gutierrez, M. (2008) Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. *Freshwater Biology,* **53,** 1-21.

Dolédec, S., Olivier, J.M. & Statzner, B. (2000) Accurate description of the abundance of taxa and their biological traits in stream invertebrate communities: effects of taxonomic and spatial resolution. *Archiv Fur Hydrobiologie,* **148,** 25-43.

Doledec, S., Phillips, N., Scarsbrook, M., Riley, R.H. & Townsend, C.R. (2006) Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. *Journal of the North American Benthological Society,* **25,** 44-60.

Dolédec, S. & Statzner, B. (2008) Invertebrate traits for the biomonitoring of large European rivers: an assessment of specific types of human impact. *Freshwater Biology,* **53,** 617-634.

Dolédec, S., Statzner, B. & Bournard, M. (1999) Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology,* **42,** 737-758.

Donlan, C.J., Knowlton, J., Doak, D.F. & Biavaschi, N. (2005) Nested communities, invasive species and Holocene extinctions: evaluating the power of a potential conservation tool. *Oecologia,* **145,** 475-485.

Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters,* **6,** 680-687.

Fernandez-Juricic, E. (2002) Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia,* **131,** 269-278.

Fleishman, E., Donnelly, R., Fay, J.P. & Reeves, R. (2007) Applications of nestedness analyses to biodiversity conservation in developing landscapes. *Landscape and Urban Planning,* **81,** 271-281.

Gayraud, S., Herouin, E. & Philippe, M. (2002) The clogging of stream beds: A review of mechanisms and consequences on habitats and macroinvertebrate communities. *Bulletin Francais de le Peche et se la Pisciculture,* **365,** 339-355

Gayraud, S. & Philippe, M. (2003) Influence of Bed-Sediment Features on the Interstitial Habitat Available for Macroinvertebrates in 15 French Streams. *Internatinal Review of Hydrobiology,* **88,** 77–93.

Greig, S.M., Sear, D.A. & Carling, P.A. (2005) The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management. *Science of the Total Environment,* **344,** 241-258.

Harding, J.S., Young, R.G., Hayes, J.W., Shearer, K.A. & Stark, J.D. (1999) Changes in agricultural intensity and river health along a river continuum. *Freshwater Biology,* **42,** 345-357.

Hausner, V.H., Yoccoz, N.G. & Ims, R.A. (2003) Selecting indicator traits for monitoring land use impacts: Birds in northern coastal birch forests. *Ecological Applications,* **13,** 999-1012.

Hecnar, S.J., Casper, G.S., Russell, R.W., Hecnar, D.R. & Robinson, J.N. (2002) Nested species assemblages of amphibians and reptiles on islands in the Laurentian Great Lakes. *Journal of Biogeography,* **29,** 475-489.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-

Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. & Lawton, J.H. (1999) Plant diversity and productivity experiments in European grasslands. *Science,* **286,** 1123-1127.

Heino, J., Mykra, H. & Muotka, T. (2009) Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. *Diversity and Distributions,* **15,** 198-206.

Hellawell, J.R. (1986) *Biological indicators of freshwater pollution and environmental management,* Elsevier Applied Science Publishers, London.

Horrigan, N. & Baird, D.J. (2008) Trait patterns of aquatic insects across gradients of flow-related factors: a multivariate analysis of Canadian national data. *Canadian Journal of Fisheries and Aquatic Sciences,* **65,** 670-680.

Horsak, M. & Cernohorsky, N. (2008) Mollusc diversity patterns in Central European fens: hotspots and conservation priorities. *Journal of Biogeography,* **35,** 1215-1225.

Kotiaho, J.S., Kaitala, V., Komonen, A. & Paivinen, J. (2005) Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences of the United States of America,* **102,** 1963-1967.

Larsen, S. & Ormerod, S.J. (in press) Low-level effects of inert sediments on temperate stream invertebrates.

Larsen, S., Vaughan, I.P. & Ormerod, S.J. (2009) Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology,* **54,** 203-219.

Lemly, D. (1982) Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia,* **87,** 229-245.

Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos,* **91,** 3-17.

Magura, T., Tothmeresz, B. & Lovei, G.L. (2006) Body size inequality of carabids along an urbanisation gradient. *Basic and Applied Ecology,* **7,** 472-482.

Manel, S., Buckton, S.T. & Ormerod, S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology,* **37,** 756-770.

Mcabendroth, L., Foggo, A., Rundle, S.D. & Bilton, D.T. (2005) Unravelling nestedness and spatial pattern in pond assemblages. *Journal of Animal Ecology,* **74,** 41-49.

Micheli, F. & Halpern, B.S. (2005) Low functional redundancy in coastal marine assemblages. *Ecology Letters,* **8,** 391-400.

Newcombe, C.P. & Macdonald, D.D. (1991) Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management,* **11,** 72-82.

Olden, J.D., Hogan, Z.S. & Vander Zanden, M.J. (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography,* **16,** 694-701.

Olden, J.D., Poff, N.L. & Bestgen, K.R. (2008) Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology,* **89,** 847-856.

Paillex, A., Doledec, S., Castella, E. & Merigoux, S. (2009) Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology,* **46,** 250-258.

Parkhill, K.L. & Gulliver, J.S. (2002) Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia,* **472,** 5-17.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **267,** 1947-1952.

Rabeni, C.F., Doisy, K.E. & Zweig, L.D. (2005) Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences,* **67,** 395-402.

Ribera, I., Doledec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology,* **82,** 1112-1129.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology,* **13,** 1220-1222.

Richards, C., Haro, R.J., Johnson, L.B. & Host, G.E. (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology,* **37,** 219-&.

Richoux, P. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Aquatic Coleoptera in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 377-395.

Richter, B.D., Braun, D.P., Mendelson, M.A. & Master, L.L. (1997) Threats to imperiled freshwater fauna. *Conservation Biology,* **11,** 1081-1093.

Rodriguez-Girones, M.A. & Santamaria, L. (2006) A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography,* **33,** 924-935.

Rosenber, D.M. & Resh, V.H. (1993) *Freshwater biomonitoring and benthic macroinvertebrates,* Chapman and Hall, New York.

Schouten, M.A., Verweij, P.A., Barendregt, A., Kleukers, R.J.M. & De Ruiter, P.C. (2007) Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life-history traits. *Journal of Biogeography,* **34,** 1938-1946.

Southwood, T.R.E. (1977) Habitat, Templet for Ecological Strategies - Presidential-Address to British-Ecological-Society, 5 January 1977. *Journal of Animal Ecology,* **46,** 337-365.

Standing Committee of Analysts (1979) *Dissolved oxygen in natural and waste waters,* HMSO, London.

Standing Committee of Analysts (1981) *Biological oxygen demand,* HMSO, London.

Standing Committee of Analysts (1987) *Kjeldahl nitrogen in waters,* HSMO, London.

Standing Committee of Analysts (1992) *Phosphorus and Silicon in waters, effluents and sludges,* HMSO, London.

Statzner, B., Bis, B., Doledec, S. & Usseglio-Polatera, P. (2001) Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition on invertebrate communities in European running waters. *Basic and Applied Ecology,* **2,** 73-85.

Statzner, B., Bonada, N. & Doledec, S. (2007) Conservation of taxonomic and biological trait diversity of European stream macroinvertebrate communities: a case for a collective public database. *Biodiversity and Conservation,* **16,** 3609-3632.

Statzner, B., Hildrew, A.G. & Resh, V.H. (2001) Species traits and environmental, constraints: Entomological research and the history of ecological theory. *Annual Review of Entomology,* **46,** 291-316.

Stevens, R.D., Cox, S.B., Strauss, R.E. & Willig, M.R. (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters,* **6,** 1099-1108.

Strand, M.R. & Merritt, R.W. (1997) Effects of episodic sedimentation on the netspinning caddisflies *Hydropsyche betteni* and *Ceratopsyche sparna* (trichoptera: hydropsychidae). *Environmental Pollution,* **98,** 129-134.

Summerville, K.S., Veech, J.A. & Crist, T.O. (2002) Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? *Oikos,* **97,** 195-204.

Tachet, H., Richoux, P., Bournaud, M. & Usseglio-Polatera, P. (2000) *Invertebres d'eau Douce. Systematique, Biologie, Ecologie,* CNRS Editions, Paris.

Tachet, H., Usseglio-Polatera, P. & Roux, C. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Trichoptera in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 397-415.

Townsend, C.R. & Hildrew, A.G. (1994) Species Traits in Relation to a Habitat Templet for River Systems. *Freshwater Biology,* **31,** 265-275.

Townsend, C.R. & Thompson, R.M. (2007) Body size in streams: macroinvertebrate community size composition along natural and human-induced environmental gradients. In: *Body size: The structure and function of aquatic ecosystems.* (Eds A.G. Hildrew & D. Raffaelli & R. Edmonds-Brown). Cambridge University Press, Cambridge.

Townsend, C.R., Uhlmann, S.S. & Matthaei, C.D. (2008) Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology,* **45,** 1810-1819.

Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **270,** 467-473.

Tullos, D.D., Penrose, D.L., Jennings, G.D. & Cope, W.G. (2009) Analysis of functional traits in reconfigured channels: implications for the bioassessment and disturbance of river resoration. *Journal of the North American Benthological Society,* **28,** 80-92.

Usseglio-Polatera, P. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Aquatic Insects in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 417-437.

Usseglio-Polatera, P. & Tachet, H. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Plecoptera and Ephemeroptera in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 357-375.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences,* **37,** 130-137.

Vaughan, I.P., Noble, D.G. & Ormerod, S.J. (2007) Combining surveys of river habitats and river birds to appraise riverine hydromorphology. *Freshwater Biology,* **52,** 2270-2284.

Waters, T.F. (1995) *Sediments in streams: sources, biological effects, and control,* AFS Monographs, Bethesda, Maryland.

Wright, J.F., Furse, M.T. & Moss, D. (1998) River classification using invertebrates: RIVPACS applications. *Aquatic Conservation-Marine and Freshwater Ecosystems,* **8,** 617-631.

Zorn, C.J.W. (2001) Generalized estimating equation models for correlated data: A review with applications. *American Journal of Political Science,* **45,** 470-490.

Zweig, L.D. & Rabeni, C.F. (2001) Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society,* **20,** 643-657.

4.7 Tables and Figures

Table 4.1 - *A priori* hypotheses about increasing (+) or decreasing (-) invertebrates trait representation in relation to catchment grassland development and patch-scale sediment deposition in the Usk catchment, Wales.

Impact	Trait	Category	Mechanism / Rationale
Catchment grassland	Maximal size	Small-medium (+)	Rapid growth and increased resilience in more frequently disturbed habitats
	Life-cycle duration	< 1 year (+)	
	No. generation / year	> 1 (+)	
Fine sediments	Maximal size	Small-medium (+)	
	Life-cycle duration	< 1 year (+)	
	No. generation / year	> 1 (+)	
	Feeding habits	Scraper (-)	Affected by algae smothering and clogging of filtering devices
		Filterers (-)	
	Locomotion	Burrowers (+)	Adapted to fine substrata
		Temporarily attached (-)	Lack of stable surfaces

Table 4.2 - Biological trait and categories considered in assessing variations in trait composition across the Usk catchment, Wales. (* labels used in Figures 3.1 and 3.3 for categories)

Trait	Categories	Code*
Maximal size	2.5-5 mm	2.5-5
	5-10 mm	5-10
	10-20 mm	10-20
	20-40 mm	20-40
Life-cycle duration	< 1 year	lc<1
	> 1 year	lc>1
No. of potential generations per year	< 1	gy<1
	1	gy=1
	>1	gy>1
Dissemination potential	< 10m	<10m
	10-100m	10-100m
	100m-1km	100m-1km
	> 1km	>1km
Aquatic stage	Egg	egg
	Larva	larva
	Nymph	nymph
	Adult	adult
Reproduction	ovoviviparity	ovovip
	Isolated eggs, free	eggsfr
	Isolated eggs, cemented	eggsc
	Clutches, fixed	clutfx
	Clutches, free	clutfr
	Clutches, in vegetation	clutv
	Clutches, terrestrial	clutt
Resistance forms	Eggs, statoblasts	egg-stbl
	Cocoons	cocoon
	Diapause	diaps
	No resistance forms	no rest
Food	Fine sediments	fine-sed
	Detritus <1mm	fdet
	Detritus >1mm	cdet
	Living microphytes	lmph
	Living macrophytes	lMph
	Dead animal <1mm	sdan
	Living microinvertebrates	lminv
	Living macroinvertebrates	lMinv
Feeding habits	Deposit feeder	dep feed
	Shredder	shred
	Scraper	scraper
	Filterer	filter
	Predators	predat
Respiration	Tegument	tegum
	Gill	gill
	Plastron	plastr
	Aerial	aerial
Locomotion	Flier	fly
	Full water swimmer	full sw
	Crawler	crawl
	Burrower	burrow
	Interstitial	interst
	Temporarily attached	tem att

Table 4.3 - Spearman correlation coefficients (r_S) between trait categories and the % of improved grassland (n = 32; reach-scale survey), sediment cover (n = 56; patch-scale survey) and suspendable sediments (n = 49; patch-scale survey) in the Usk catchment. Only categories showing at least one significant correlation are shown. Bold r_S-values are significant after correction based on number of categories.

Trait	Categories	Improved grassland (Reach scale)	Sediment cover (%) (Patch-scale)	Suspendable sediments (Patch-scale)
Maximal size	2.5-5 cm	**0.52**	-0.34	-0.39
	5-10 cm	0.25	**0.38**	**0.46**
	20-40 cm	**-0.72**	**-0.57**	**-0.41**
Life-cycle duration	< 1 year	**0.40**	0.19	**0.34**
	> 1 year	**-0.40**	-0.19	**-0.34**
No. of potential generations per year	< 1	**-0.47**	-0.20	**-0.51**
	>1	**0.49**	0.20	**0.38**
Dissemination potential	< 10m	-0.21	**-0.64**	**-0.65**
	10-100m	**-0.52**	-0.19	-0.14
	> 1km	**0.46**	**0.52**	**0.67**
Aquatic stage	Nymph	0.03	**-0.44**	-0.24
Reproduction	ovoviviparity	**0.53**	0.24	0.37
	Clutches, fixed	-0.14	**-0.47**	**-0.52**
	Clutches, free	**-0.51**	-0.24	-0.08
	Clutches, in vegetation	0.21	**0.45**	**0.43**
Resistance forms	Cocoons	-0.38	**0.44**	0.32
Food	Detritus >1mm	0.27	**0.52**	**0.54**
	Living macrophytes	0.25	**0.63**	**0.46**
	Dead animal <1mm	0.38	**0.40**	**0.48**
	Living macroinvertebrates	-0.31	**-0.41**	**-0.43**
Feeding habits	Deposit feeder	0.16	**0.44**	0.23
	Shredder	-0.09	**0.50**	0.34
	Scraper	0.20	**-0.29**	-0.30
	Filterer	0.11	**-0.62**	-0.30
Respiration	Tegument	0.07	**0.49**	0.28
	Plastron	-0.03	**-0.46**	**-0.51**
Locomotion	Flier	0.02	**-0.38**	**-0.47**
	Burrower	-0.36	**0.50**	**0.40**
	Temporarily attached	0.16	**-0.64**	-0.35

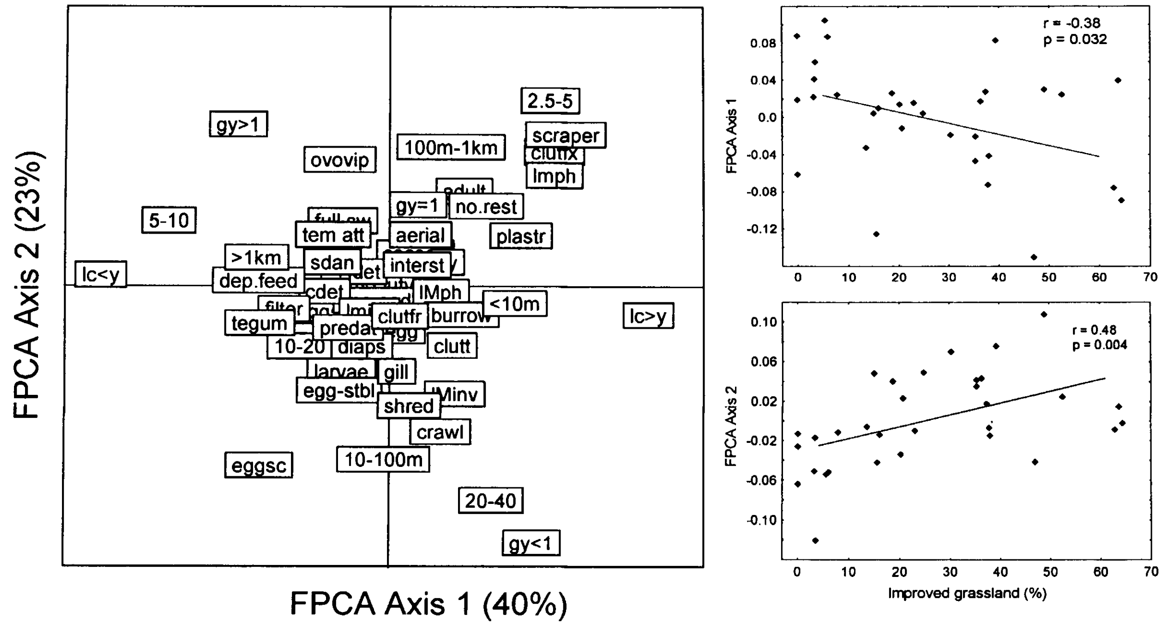


Fig. 4.1 - Position of trait categories on the first Fuzzy PCA plane from a reach-scale survey of the Usk catchment, Wales. The relationship between the first and second axes with increasing catchment cover by improved grassland is also shown. Trait codes are in Table 4.2.

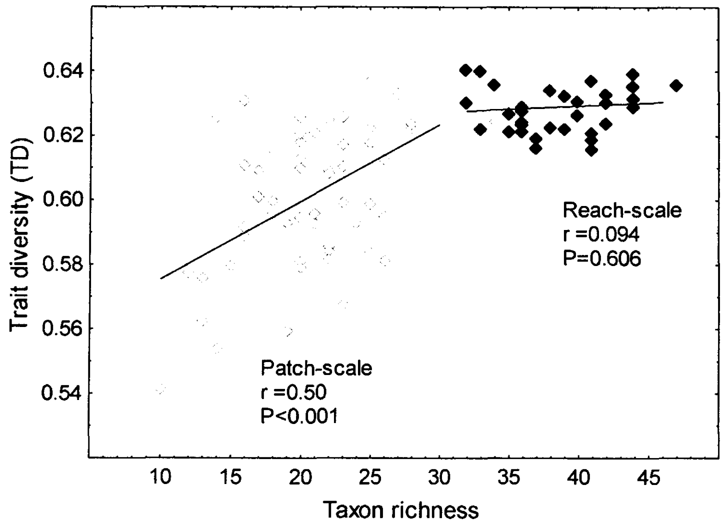


Fig. 4.2 - Relationship between macroinvertebrate trait diversity (TD) and taxon richness at reach and patch-scales in the Usk catchment, Wales.

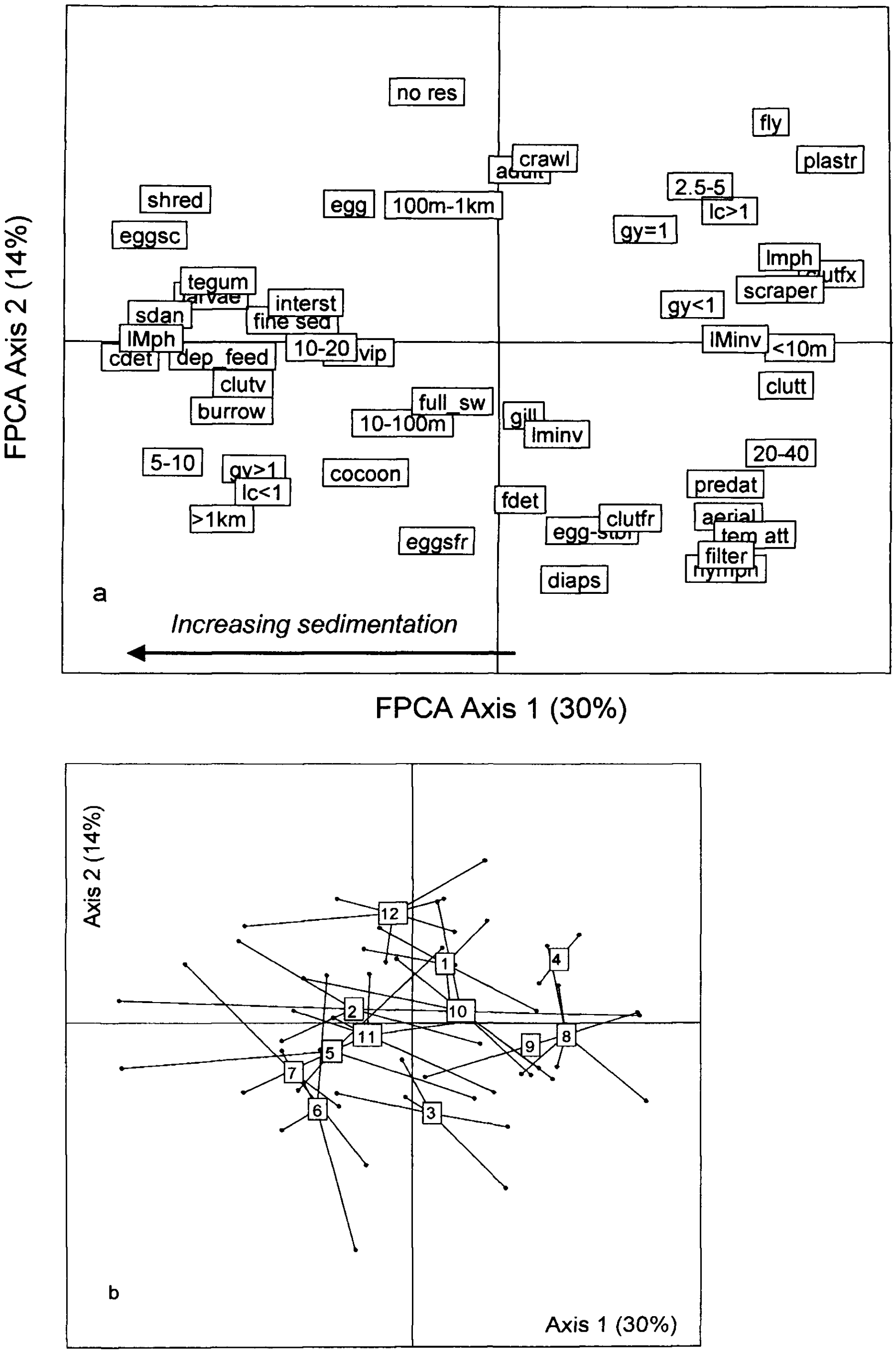


Fig. 4.3 - a) Position of trait categories from a patch-scale survey in the Usk river catchment, Wales, on the first Fuzzy PCA plane. Sediment cover and suspendable sediments decrease along Axis 1. b) Position of study patches on the first factorial plane; patches are grouped by reaches, labelled here as reach numbers).

Chapter 5 - Low-level effects of inert sediments on temperate stream invertebrates

Summary

1. The delivery, entrainment and deposition of inert fine sediments are among the most significant contributors to stream and river impairment worldwide. Associated ecological effects have been observed frequently, but specific experiments to identify sensitivity and avoidance behaviour in stream organisms are few, particularly in headwaters.

2. In a field experiment, I added fine sand at low levels (c 4-5 kg/m^2) to 10m reaches of two replicate headwater streams in the Usk catchment (Wales, UK) over two periods (autumn and summer). Upstream reaches were used as control in a classic BACIP design. Invertebrate drift and benthic composition were measured for two days before and one day after sediment impact.

3. Sediment addition significantly increased overall drift density (by 45%) and propensity (by 200%), with effects largest on the night following addition rather than immediately (i.e. within 9 hrs). The mayflies *Baetis rhodani, B. muticus* and *Ecdyonurus* spp, simuliid and chironomid dipterans, and helodid beetles were the strongest contributors.

4. There were no marked effects on benthic composition, but density declined in treated reaches by 30-60%, particularly in *Baetis rhodani*, *Ecdyonurus* spp. and *Leuctra* (*hippopus* + *moselyi*).

5. All effects were consistent between both seasons and streams.

6. These data show how even low-level, short-term, increases in fine sediment loading to upland, stony streams can reduce overall benthic density through increased drift. I suggest that the likely cause of the delayed drift response was a change in habitat quality which prompted avoidance behaviour. Longer-term experiments are required to assess whether these effects reduce fitness or explain the losses of some types of organisms observed recently in sediment-impaired reaches of this and other catchments.

5.1 Introduction

Catchment agriculture, urbanisation, forestry and mining not only alter energy fluxes, hydrology, thermal regimes and habitat availability in rivers (Osborne & Kovacic, 1993; Roth, Allan & Erickson, 1996; Manel, Buckton & Ormerod, 2000), but can also increase fine sediment delivery and alter sediment quality with profound consequences for aquatic organisms (reviewed by Ryan, 1991; Waters, 1995; Wood & Armitage, 1997). These ecological effects depend on sediment character, size distribution, particle shape and associated pollutants (Lemly, 1982; Wood, Vannn & Wanless, 2001), as well as catchment and stream characteristics (Culp, Wrona & Davies, 1985; Collins, Walling & Leeks, 1997; Kreutzweiser, Capell & Good, 2005; Larsen, Vaughan & Ormerod, 2009). Organisms at all trophic levels are affected, for example through a reduction of available light for primary producers and visual predators (Rowe & Dean, 1998; Parkhill & Gulliver, 2002), alteration of substratum structure and habitat quality for benthic organisms (Chutter, 1968; Turnpenny & Williams, 1980), decline in feeding efficiency of filter feeders and grazers (Graham, 1990; Broekenhuizen, Parkyn & Miller, 2001) and reduced oxygen supply to salmonids eggs via interstitial occlusion (Argent & Flebbe, 1999; Greig, Sear & Carling, 2005). Shorter-term effects are also possible through the displacement or avoidance behaviour of organisms affected by suspended, saltating or deposited particles (Gibbins *et al.* 2007).

However, identifying sediment effects on stream organisms, and the processes involved, is hindered by two major problems. First, sediments occur often alongside other stressors which might exacerbate or mask effects (Townsend, Uhlmann & Matthaei, 2008). In agricultural catchments, such confounds include nutrients, pesticides, alteration in runoff pattern and habitat modification. Secondly, sediments in any one location can arise from a diverse array of catchment sources. For example, point-sources associated with the effects of livestock on bank erosion might be locally important, but small by comparison with larger-scale releases from tillage, from the wider conversion of catchment forests to grassland, or even from large-scale natural release. In these circumstances, experimental investigations can have major advantages over observational approaches, with sediment additions, artificial substrates of varying grain-size, flumes or experimental streams all used in the past (Doeg & Milledge 1991; Angradi,1999; Bond & Downes 2003; Connolly & Pearson, 2007).

In the Upper Usk catchment, in south-central Wales (UK), recent surveys have suggested that local sediment deposition is associated with decreased woodland cover and increased bank erosion (Larsen *et al.*, 2009). Apparent effects on stream invertebrates include altered assemblage composition, reduced richness, reductions in the density of sensitive species, and an overall reduction in trait diversity (Larsen & Ormerod in review). However, the exact mechanisms are unclear. There are a range of possibilities (see above), but here I turn our attention to the possibility that sediment deposition and sediment movement might cause short-term invertebrate losses and redistribution through drift.

While the drift of invertebrates is a natural process in streams, representing emigration and immigration between patches of different quality, changes in substratum character can alter drift behaviour (e.g.Holomuzki & Biggs, 2003). Evidence from several studies has shown that sediment transport and increased turbidity can promote invertebrate drift causing a reduction in benthic density and richness (Rosenberg & Wiens, 1978; Culp *et al.*, 1985; Suren & Jowett, 2001). Laboratory data suggest that such effects can also arise due to small changes in bedload or saltating particles (Gibbins *et al*, 2007). However, not all results have been consistent (Connolly & Pearson, 2007). Moreover, early experiments on the effects of sediments on drift were characterised by limited replication (Rosenberg & Wiens, 1978; Culp *et al.*, 1985), while those carried out in artificial channels might not scale-up to represent real stream ecosystems (Suren & Jowett, 2001; Bond & Downes, 2003). Most of all, considering the sensitivity of streams and stream organisms to sediments (Matthaei *et al*, 2006; Connolly & Pearson, 2007), realistic experiments to investigate the effects of sediments on invertebrate drift have been surprisingly few.

Following experimental approaches used previously (Rosenberg & Wiens, 1978; Culp *et al.*, 1985), I describe a replicated field-experiment in which I manipulated fine sediment supply to two 2nd- 3rd order streams to test the hypothesis that relatively small increases in sediment deposition and transport can increase the short-term drift of sensitive benthic invertebrates. Specifically, I expected that any invertebrates showing an immediate avoidance or displacement reaction to sediment addition might occur rapidly in the drift. Alternatively, alterations in habitat quality for invertebrates would be reflected in increased behavioural drift as part of the normal nocturnal drift pattern. Both responses could reduce benthic density and I evaluated this possibility. A secondary aim of the experiment was to compare the apparent sensitivity of individual species to sediments as shown by their short-term drift with apparent tolerance to longer-term sediment effects indicated by our previous surveys (Larsen, Vaughan & Ormerod 2009).

5.2 Methods

Study area

The Senni and Grwyne Fawr are two small, third-order tributaries (3-5 m wide) of the Usk River in Wales at 290-300 m above sea level (National Grid Reference: SN925207 and SO266251, respectively), and these upland locations have been shown previously to be sensitive to sediment deposition (Larsen *et al.* 2009). One of the largest rivers in Wales, the Usk is dominantly rural, sparsely populated and one of the most important game fisheries in Britain (see Larsen *et al.*, 2009 for more details). The reaches selected for the experiment drained semi-natural rough pasture and woodland, and had substrata of bedrock, boulders and cobbles, moderately shaded by deciduous or conifer trees. The streams have similar ionic composition, rich in carbonates with high pH (c. pH 7.8-8) but low in nutrients (average nitrate 0.9 mg/l; phosphate 0.02 mg/l), and invertebrate communities are diverse and dominated by Ephemeroptera, Plecoptera and Trichoptera. The local geology of Devonian Old-red Sandstone has given rise to relatively sandy soils and alluvial deposits that, in the upper catchment, enter streams through bank-face erosion in locations where broadleaf trees have been removed. There are also point sediment sources where livestock trampling or local bank manipulations have caused sediment release. I wished to mimic the effects of such low-level sediment additions experimentally under controlled conditions.

Experimental design

In each of the two replicate streams I selected one downstream reach for sediment addition ('impact') and one upstream control reach to be as similar physiographically as possible within the same 40 m section. Invertebrate drift patterns were measured simultaneously in both reaches for two x 24 hour periods before sediment addition ('Before 1', 'Before 2') and for 24 hours after sediment addition ('After'), thus following a classic before-after-control-impact (BACIP) design (Stewart-Oaten & Bence, 2001). Experiments were carried out in autumn 2007 (September 21st - October 10th) and repeated in entirety at each site in summer 2008 (June 26th -July 19th), giving a total 12 days (288 hours) of drift sampling.

In each case (i.e. each season and each stream), at the beginning of the 'After' period (t. 12:00 pm), clean childrens' play-sand (0.25 – 0.125 mm = ~60% in dry weight and 2 – 0.5 mm = ~30%) was added as evenly as possible to the 10m impact reaches at a concentration of c 4-5 kg /m^2 (corresponding to approximately to 25-35 % bed cover). I chose this material because it was unaffected by contaminants or nutrients that would confound sedimentation effects and it had a size-distribution near-identical to naturally occurring sediments in the Usk (0.25 mm – 2 mm; Larsen *et al.* 2009). Additions were made mostly from the banks to limit substratum disturbance, and I aimed to cover up to 35% of the benthos to mimic values at which longer-term effects occur (Larsen *et al.*, 2009). Water temperature, pH and conductivity were measured on each day of the experiment.

Invertebrate sampling

Throughout all experiments, steel poles fixed to the streambed held two adjacent rectangular drift nets (40 x 24 cm) in both impact and control reaches, respectively of two mesh sizes (0.9 and 0.44 mm) thereby attempting to capture differently sized organisms. The twin control nets were positioned at least 6 m from the upstream end of the sand-impacted reaches. Net contents were collected at 3 hours intervals for 24 hours starting at 12:00 on each sample day, with all drift samples combined from the contents from the two nets in each reach. The volumes of water filtered were estimated from three measurements of current velocity and water depth at the beginning, middle and end of each day.

In addition to drift samples, four pooled Surber samples (30 x 30 cm; 0.44 mm mesh) were collected in both impact and control reaches at the end of each drift sampling day. Invertebrates were immediately preserved in 70% ethanol and then sorted and identified as far as possible in the laboratory (Edington & Hildrew, 1981; Elliott, Humpesch & Macan, 1988; Friday, 1988; Wallace, Wallace & Philipson, 2003).

Data analysis

Analyses were carried out to assess variations in both drift density (N/100 m^3) and drift propensity (drift density / benthic density), thereby accounting for differences in discharge and benthic composition among times and locations. Invertebrate abundances were log (x+1) transformed when necessary. Although invertebrate composition differed slightly between the streams (see Results), dominant taxa were the same and could be included in the same analyses.

Drift variations were assessed using mixed-effects models because I had longitudinal data (repeated measures). Season and stream were included as random factors, while experimental period (before and after) was treated as a fixed factor to assess differences in drift response. Analyses were run on R (Ihaka & Gentleman, 1996), using the “nlme” extension (Pinheiro & Bates, 2000).

The BACIP design used allowed us to derive the main variables for analysis from the differences between impact and control locations; H_0 was that the impact-control difference before treatment was equal to the impact-control difference after treatment. This is equivalent to measuring the interaction term between reach type (control, impact) and time (before, after) in a classic Analysis of Variance (Weiss & Reice, 2005; James, Dewson & Death, 2008). Response variables thus described the total drift densities and propensity, drift densities and propensities of each dominant taxon, and benthic densities. No correction for multiple tests was performed, and I give exact *P* values in each case.

I used Detrended Correspondence Analysis (DCA; Hill & Gauch, 1980) to assess whether sand addition had any gross effects on either benthic or drift composition. This exploratory method is a well-known, simple approach to indirect gradient ordination that uses reciprocal averaging to order samples objectively according to the frequency of co-occurrence of their constituent taxa. Sample scores reflect turnover in taxonomic composition along orthogonal axes, and these can be related to sample attributes or environmental conditions, in this case before and after sediment addition, and benthic versus drift samples. Although DCA has received some criticism associated with the detrending algorithm used to remove any curvilinear relationships between axes (i.e. "the arch effect") (Wartenberg, Ferson & Rohlf, 1987), in our case identical ordination patterns were produced by DCA and non-metric multidimensional scaling based on Bray-Curtis Similarity.

5.3 Results

Autumn and summer water temperatures during the experiment ranged were 9-12 C° and 12-17 C°, respectively, while conductivities during both seasons was c 150 µs/cm and pH 7.2-8. Current velocities in the study streams over the two seasons typically ranged over 20-60 $cm.s^{-1}$

Seventy-two macroinvertebrate taxa occurred in the drift, but most were at low abundance. *Baetis rhodani*, *Ecdyonurus* spp., chironomids and simuliids accounted for more than 60% of total drift abundance, with aquatic drift densities peaking at c 60-80 individuals per 100 m^3 prior to any treatment. The contribution of terrestrial invertebrates to total drift in any single 24 hours reached 50 % in the summer, but fell to < 10% throughout the autumn experiments. Overall, terrestrial invertebrates, mostly dipterans, accounted for up to 16% of total drift.

Drift response to sediments

Sediment addition increased both drift density and drift propensity (Table 5.1, Fig. 5.1). Sand additions, on average, resulted in 15 more individuals drifting per 100 m^3, and drift density in the impact reach increased by 35% in autumn, 60% in summer and 45% overall. Although there was a slight increase in drift in the autumn experiment immediately after sediment input, significantly increased drift was not immediate (i.e. within the first 9 hours after addition). Instead, drift patterns maintained the expected diel variation, with densities increasing after sunset (around 19:00 in autumn and 21:00 in summer; Fig.5.2). Invertebrate response to treatment therefore appeared to be delayed, and contributed to night-time drift in the impacted reaches compare to control (Fig. 5.2).

Much of the additional drift was explained by commonly drifting taxa; drift density in the mayflies *Baetis rhodani,* and *Ecdyonurus* spp., as well as simuliid dipterans, all increased after sediment input (Table 5.1). Overall changes in drift propensity in the impact reach were large (200%), particularly in the aforementioned taxa, and in *Baetis muticus*, chironomids and larval Helodidae. There was no effect on some other taxa that were relatively common in the drift, such as the mayflies *Baetis scambus*, *Heptagenia lateralis* and the coleopterans *Elmis aenea*, *Limnius volkmarii* or *Oulimnius tuberculatus*.

Visual inspection of DCA plots for both seasons illustrated that sediment addition had no marked effects on the taxonomic composition of the drift (Fig. 5.3), and drifting invertebrates formed assemblages that were equally distinct from the benthos both before and after sediment addition. Even though general assemblage composition apparently differed between the two streams according to ordination, drift responses to sediments were highly consistent across both streams and seasons (Fig. 5.4).

Benthic response to sediments

Benthic samples produced 56 taxa, with *Baetis rhodani, Ephemerella ignita, Ecdyunurus* spp. and chironomids the most abundant. Average densities in the treated reaches were slightly higher than control reaches before sediment input (Fig. 5.1), but sediment addition reversed this position, resulting in a significant reduction in overall benthic density of > 300 individual / m^2 (Fig. 5.1). In particular, densities of *Baetis rhodani*, *Ecdyonurus* sp. and *Leuctra* (*hippopus* + *mosleyi*) were significantly reduced in impacted reaches after sand addition by 26-63% (Table 5.1). Ordination showed that there were no changes in overall taxonomic composition (Fig. 5.3). As with the drift, benthic invertebrate in the two study streams formed distinct groups in DCA plots for both seasons, but sediment effects on density were consistent across sites and seasons (Fig. 5.4).

5.4 Discussion

These results support the hypothesis that small increases in sediment loads to stony streams increase invertebrate drift and reduce benthic density, at least over short time-periods. Sediment additions of just 4-5 kg /m^2, covering the benthos to levels typically seen at the lower range of deposition of this same catchment, increased drift density or propensity in simuliids, chironomids and several mayflies, with the latter also declining consistently in benthic numbers. Drift responses were not immediate (Rosenberg & Wiens, 1978; Culp *et al.*, 1985; Doeg & Koehn, 1994), but delayed into the first period of darkness following sediment addition, suggesting avoidance of apparently impaired habitat rather than immediate behavioural displacement (Fairchild *et al*, 1987; Matthaei *et al.*, 2006). This form of behavioural drift and redistribution is well-known as a response to local carrying capacity and habitat conditions, particularly where reduced food quality or availability prompts individuals to seek new patches (Hildebrand, 1974). However, because drift carries a predation risk, it is mostly nocturnal in locations occupied by drift-feeding fishes, and it is interesting that drift from sediment-impacted patches here was deferred into darkness. Diel activity patterns in epilithic grazers such as mayflies also mean that surface-deposited sediments might not be encountered until darkness (Glozier & Culp, 1989). Interestingly, leuctrid stoneflies also declined in the benthos following sediment addition despite showing no change in drift suggesting that other avoidance behaviours might also have occurred, such as movement into the hyporheos.

Despite apparently straightforward support for the hypothesis under test, several aspects of our results require cautious interpretation. As well as water quality or temperature, biotic factors such as food scarcity, competition and the presence of predators can influence drift densities (e.g. James *et al.*, 2008). Drift can therefore vary significantly not only through the diel cycle, but even between days in the same week (Brittain & Eikeland, 1988). Variations also occur among streams, as well as vertically and horizontally within streams, potentially affecting estimates based on small numbers of observations (Jones *et al*, 2001). Variations around the drift profiles during our experiment reflect some of these differences between sampling sessions and streams after accounting for varying discharge. However, our experimental BACIP design, with matched control with impact reaches and analysis focussed on the differences between them, meant that any confounding effects were unlikely (Stewart-Oaten & Bence, 2001). Moreover, despite some variability, the direction of all results was consistent between seasons and study streams, allowing a more confident interpretation of observed effects.

Three particular methodological aspects of our study were not controlled by our design and require particular attention. First, the possibility exists that extreme invertebrate drift distances might have exceeded the length of our experimental reaches, so that not all invertebrates captured in the drift had necessarily originated from the treated areas (Brittain & Eikeland, 1988). However, changes in such effects during the experiment would be an unlikely explanation for apparently enhanced drift in both treated reaches and on both experimental occasions. Moreover, typical drift distances are much less than our experimental reaches, and typically < 2-20m (Allan, 1995). Secondly, and linked to the previous point, upstream drift nets in the reference reaches might have intercepted drifting invertebrates and therefore contributed to the reduction in treatment-reach density over the course of the experiment. I rule out this possibility because any such effects should already have been apparent before sediment addition (i.e. on the second 'Before' day) rather than following sediment addition. Thirdly, the type of sediments I added, although formed from siliceous sand comparable in size and composition to the naturally occurring fine fraction in the Usk system, may have differed in other features, such as sphericity and angularity. These features can be relevant ecologically (Holomuzki & Biggs, 2003). However, any such effects would limit the application of the results to the Usk rather than their general relevance to other locations where sandy sediments enter streams.

Although not common, other studies have reported the effects of experimental sediment additions and turbidity on drift, but comparisons with our experiment are complicated by the differences in the methods, designs and sediment characteristics used. For example, Rosenmberg & Wiens (1978) and Doeg & Milledge (1994) detected an immediate drift response to increased suspended clay and silt sediments in natural channels, but neither measured behavioural drift at night nor used a replicated or controlled design. Culp *et al.* (1985) added sand to two contrasting streams and recorded immediate and delayed drift only where sand particles were transported downstream by saltation, suggesting that sediment-flow interactions are important to invertebrate redistribution. Similarly, working in a flume, Gibbins *et al.* (2007) showed that fine sediment movement could trigger substantial drift, concluding that even low bed loads could denude stream patches of invertebrates. In our study, I did not measure the rate of sand displacement, but most of the material added was transported away from the treated reaches after 24 hours illustrating that saltation and/or suspension must have been occurring. However, Suren & Jowett (2001) demonstrated that even deposited, non-saltating, fine sediments (~12 kg/m^2) caused significant drift coupled with decreased benthic densities in some taxa. In complete contrast, Bond & Downes (2003) concluded from experimental manipulations that suspended sediment additions to experimental streams had no additional effects in displacing invertebrates over those caused by flow increase alone. The sediment size range was very similar to that in our study, although drift was recorded over a much shorter, diurnal period that, if used in our experiment, would have failed to detect the subsequent increase in nocturnal drift. With the exception of this last study, and notwithstanding some variations with respect to the timing and possible mechanisms involved, overall our work is consistent with previous data in confirming that invertebrates drift in response to sediments even at the low loadings used.

Despite their limitations, freshwater ecology has a long history of using experiments at small spatio-temporal extents to examine the potential effects of larger-scale phenomena. Examples include investigating the role of drift or refuge effects in large-scale disturbance and recolonization (Townsend & Hildrew, 1976; Palmer, Bely & Berg, 1992), or assessing the short-term (< 24h) sensitivity of invertebrates to globally widespread pollutants (Ormerod & Edwards, 1987). In all these cases, there are difficulties in scaling-up, but equally there are major benefits in understanding whether effects observed at one support patterns observed at other scales. In keeping with these concepts, a secondary aim of this experiment was to examine how drift responses to sediments might corroborate previous survey work in the same river system that related invertebrate assemblages, trait composition and apparent species sensitivity to large-scale sediment cover (Larsen, Vaughan & Ormerod 2009; Larsen & Ormerod, in review). There are limitations here because the 24h treatment period was apparently insufficient to reduce benthic richness or alter community composition. Moreover, the limited reach length in our experiment means also that drift responses will have represented local redistribution of organisms between patches rather than larger-scale impairment. Additionally, because experiments on drift are likely to capture a different set of taxa from benthic sampling (see Fig. 5.4), there are also difficulties in comparisons with taxa whose sensitivity to sediments was shown from benthic data. Nevertheless, substantially reduced density in treated reaches is an illustration of how longer-term sediment effects on benthic organisms might arise and develop where sediment delivery is sustained.

In our larger-scale surveys, the overall richness of Ephemeroptera, Plecoptera and Trichoptera was reduced at sediment-treated sites, to which a longer-term displacement of *Baetis rhodani*, *B muticus* and *Ecdyonurus* spp. could contribute. *Baetis* spp, generally avoid fine substrata (Wagner, 1989; Wood *et al*, 2005), and also drift rapidly as bedload transport increases (Gibbins *et al.*, 2007). Simuliids, also, are intolerant to smothering in agreement with the increased drift densities in our impacted reaches (Minshall, 1984; Larsen *et al.*, 2009). Our previous work showed that taxa sensitive to sediments were characterised by particular feeding or behavioural traits (Larsen & Ormerod, in review), and this is again consistent with the drift and density data here. For example, simuliids are filter-feeders whose mouthparts can be impaired by fine particles (Strand & Merritt, 1997). *Baetis* and *Ecdyonurus* species are mostly scrapers in which feeding would be quickly impaired on smothered periphyton even if the short duration of the experiment will not have altered underlying periphyton quality.

Overall, even if the temporal and spatial scale of this experiment was limited, the data show how even small increases in fine sediment supply to upland streams can reduce benthic density by promoting drift. Many temperate river catchments are now characterised by land use practices that increase sediment delivery to streams, for example through the conversion of natural vegetation to pasture and the removal of riparian trees. Both appear to increase the risks of sediment release in the Usk (Larsen *et al.*, 2009). Small-scale effects like those observed here could, therefore, form part of a larger scale attrition of stream integrity. I suggest that larger, longer-term experiments would be a valuable means of assessing this possibility.

5.5 References

Allan, J.D. (1995) *Stream Ecology. The Structure and Function of Running Waters,* Chapman & Hall, London.

Argent, D.G. & Flebbe, P.A. (1999) Fine sediment effects on brook trout eggs in laboratory streams. *Fisheries Research,* **39,** 253-262.

Bond, N.R. & Downes, B.J. (2003) The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams *Freshwater Biology* **48,** 455-465

Brittain, J.E. & Eikeland, T.J. (1988) Invertebrate Drift - a Review. *Hydrobiologia,* **166,** 77-93.

Broekenhuizen, N., Parkyn, S. & Miller, D. (2001) Fine sediment effects on feeding and growth in the invertebrate grazers Potamopyrgus antipodarum (Gastropoda, Hydrobiidae) and Deleatidium sp. (Ephemeroptera, Leptophlebiidae). *Hydrobiologia,* **457,** 125-132.

Chutter, F.M. (1968) The effects of silt and sand on the invertebrate fauna of stream and rivers. *Hydrobiologia,* **34,** 57-76.

Collins, A.L., Walling, D.E. & Leeks, G.J.L. (1997) Source type ascription for fluvial suspended sediment based on a quantitative composite fingerprinting technique. *Catena,* **29,** 1-27.

Connolly, N.M. & Pearson, R.G. (2007) The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: a comparison using flowthrough artificial stream channels and recirculating mesocosms. *Hydrobiologia,* **592,** 423-438.

Culp, J.M., Wrona, F.J. & Davies, R.W. (1985) Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology,* **64,** 1345-1351.

Doeg, T.J. & Koehn, J.D. (1994) Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. . *Regulated Rivers-Research & Management* **9,** 263-277.

Edington, J.M. & Hildrew, A.G. (1981) *A key to the caseless Caddis larvae of the British Isles with notes on their ecology* Freshwater Biological Association, Ambleside, Cumbria

Elliott, J., Humpesch, U. & Macan, T. (1988) *Larvae of the British Ephemeroptera: Akey with Ecological notes. Scientific Publication 49,* Freshwater Biological Association, Ambleside.

Fairchild, J.F., Boyle, T., English, W.R. & Rabeni, C. (1987) Effects of Sediment and Contaminated Sediment on Structural and Functional Components of Experimental Stream Ecosystems. *Water Air and Soil Pollution,* **36,** 271-293.

Friday, L. (1988) *A Key to the Adults of British Water Beetles,* Field Studies Council, Preston Montford.

Gibbins, C., Vericat, D., Batalla, R.J. & Gomez, C.M. (2007) Shaking and moving: low rates of sediment transport trigger mass drift of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences,* **64,** 1-5.

Glozier, N.E. & Culp, J.M. (1989) Experimental Investigations of Diel Vertical Movements by Lotic Mayflies over Substrate Surfaces. *Freshwater Biology,* **21,** 253-260.

Graham, C.K. (1990) Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentration in suspension. *Hydrobiologia,* **199,** 107-115.

Greig, S.M., Sear, D.A. & Carling, P.A. (2005) The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management. *Science of the Total Environment,* **344,** 241-258.

Hildebrand, S.G. (1974) Relation of Drift to Benthos Density and Food Level in an Artificial Stream. *Limnology and Oceanography,* **19,** 951-957.

Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence-analysis - an improved ordination technique. *Vegetatio,* **42,** 47-58.

Holomuzki, J.R. & Biggs, B.J.F. (2003) Sediment texture mediates high-flow effects on lotic macroinvertebrates. *Journal of the North American Benthological Society,* **22,** 542-553.

Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics,* **5,** 299-314.

James, A.B.W., Dewson, Z.S. & Death, R.G. (2008) The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications,* **24,** 22-35.

Jones, K.B., Neale, A.C., Nash, M.S., Van Remortel, R.D., Wickham, J.D., Riitters, K.H. & O'neill, R.V. (2001) Predicting nutrient and sediment loadings to streams from landscape metrics: A multiple watershed study from the United States Mid-Atlantic Region. *Landscape Ecology,* **16,** 301-312.

Kreutzweiser, D.P., Capell, S.S. & Good, K.P. (2005) Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology,* **39,** 55-66.

Larsen, S., Vaughan, I.P. & Ormerod, S.J. (2009) Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology,* **54,** 203-219.

Lemly, D. (1982) Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia,* **87,** 229-245.

Manel, S., Buckton, S.T. & Ormerod, S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology,* **37,** 756-770.

Matthaei, C.D., Weller, F., Kelly, D.W. & Townsend, C.R. (2006) Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology,* **51,** 2154-2172.

Minshall, G.W. (1984) Aquatic insect-substratum relationships. In: *The ecology of aquatic insects.* (Eds V.H. Resh & D.M. Rosenberg), pp. 358-400. Preager publishers, New York.

Ormerod, S.J. & Edwards, R.W. (1987) The Ordination and Classification of Macroinvertebrate Assemblages in the Catchment of the River Wye in Relation to Environmental-Factors. *Freshwater Biology,* **17,** 533-546.

Osborne, L.L. & Kovacic, D.A. (1993) Riparian Vegetated Buffer Strips in Water-Quality Restoration and Stream Management. *Freshwater Biology,* **29,** 243-258.

Palmer, M.A., Bely, A.E. & Berg, K.E. (1992) Response of Invertebrates to Lotic Disturbance - a Test of the Hyporheic Refuge Hypothesis. *Oecologia,* **89,** 182-194.

Parkhill, K.L. & Gulliver, J.S. (2002) Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia,* **472,** 5-17.

Pinheiro, J. & Bates, D. (2000) *Mixed Effects Models in S and S-Plus,* Springer, New York.

Rosenberg, D.M. & Wiens, A.P. (1978) Effects of Sediment Addition on Macrobenthic Invertebrates in a Northern Canadian River. *Water Research,* **12,** 753-763.

Roth, N.E., Allan, J.D. & Erickson, D.L. (1996) Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology,* **11,** 141-156.

Rowe, D.K. & Dean, T.L. (1998) Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine and Freshwater Research,* **32,** 21-29.

Ryan, P.A. (1991) Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research,* **25,** 207-221.

Stewart-Oaten, A. & Bence, J.R. (2001) Temporal and spatial variation in environmental impact assessment. *Ecological Monographs,* **71,** 305-339.

Strand, M.R. & Merritt, R.W. (1997) Effects of episodic sedimentation on the netspinning caddisflies *Hydropsyche betteni* and *Ceratopsyche sparna* (trichoptera: hydropsychidae). *Environmental Pollution,* **98,** 129-134.

Suren, A.M. & Jowett, I.J. (2001) Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research,,* **35,** 725-737.

Townsend, C.R. & Hildrew, A.G. (1976) Field Experiments on Drifting, Colonization and Continuous Redistribution of Stream Benthos. *Journal of Animal Ecology,* **45,** 759-772.

Townsend, C.R., Uhlmann, S.S. & Matthaei, C.D. (2008) Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology,* **45,** 1810-1819.

Turnpenny, A.W.H. & Williams, R. (1980) Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology,* **17,** 681-693.

Wagner, R. (1989) The Influence of Artificial Stream Bottom Siltation on Ephemeroptera in Emergence Traps. *Archiv Fur Hydrobiologie,* **115,** 71-80.

Wallace, I., Wallace, B. & Philipson, G. (2003) *Keys to the Case-bearing Caddis larvae of Britain and Ireland. Scientific Publication 61* Freshwater Biological Association, Ambleside.

Wartenberg, D., Ferson, S. & Rohlf, F.J. (1987) Putting Things in Order - a Critique of Detrended Correspondence-Analysis. *American Naturalist,* **129,** 434-448.

Waters, T.F. (1995) *Sediments in streams: sources, biological effects, and control,* AFS Monographs, Bethesda, Maryland.

Weiss, J.M. & Reice, S.R. (2005) The aggregation of impacts: Using species-specific effects to infer community-level disturbances. *Ecological Applications,* **15,** 599-617.

Wood, P.J. & Armitage, P.D. (1997) Biological Effects of Fine Sediment in the Lotic Environment
Environmental Management, **21,** 203-217.

Wood, P.J., Toone, J., Greenwood, M.T. & Armitage, P.D. (2005) The response of four lotic macroinvertebrate taxa to burial by sediments. *Archiv fur Hydrobiologie,* **163,** 145-162.

Wood, P.J., Vannn, A.R. & Wanless, P.J. (2001) The response of *Melampophylax mucoreus* (Hagen) (Trichoptera:Limnephilidae) to rapid sedimentation. *Hydrobiologia,* **455,** 183-188.

5.6 Tables and Figures

Table 5.1 Mixed effect model (N=12) BACIP F and P values of the effect of sand addition to drift and benthic variables for the two streams and seasons combined. See text for details.

Drift variables	F (2, 6)	P	% change in Impact reach
Total density	15.9	0.004	+ 45%
Total propensity	66.7	0.0001	+ 200%
Baetis rhodani density	15.8	0.004	+ 63%
Ecdyonurus spp. density	47.7	0.0002	+ 26%
Simulidae density	10.4	0.01	+ 81%
Baetis rhodani propensity	12.2	0.007	+ 155%
Ecdyonurus sp. propensity	15.8	0.004	+ 422%
Baetis muticus propensity	6.0	0.03	+ 437%
Helodidae propensity	4.5	0.05	+ 121%
Chironomidae propensity	7.2	0.02	+ 433%
Benthic variables			
Total density	14.0	0.005	- 30%
Baetis rhodani	4.75	0.05	- 63%
Ecdyonurus sp.	11.0	0.009	- 26%
Leuctra (hippopus+moselyi)	29.5	0.0008	- 50%

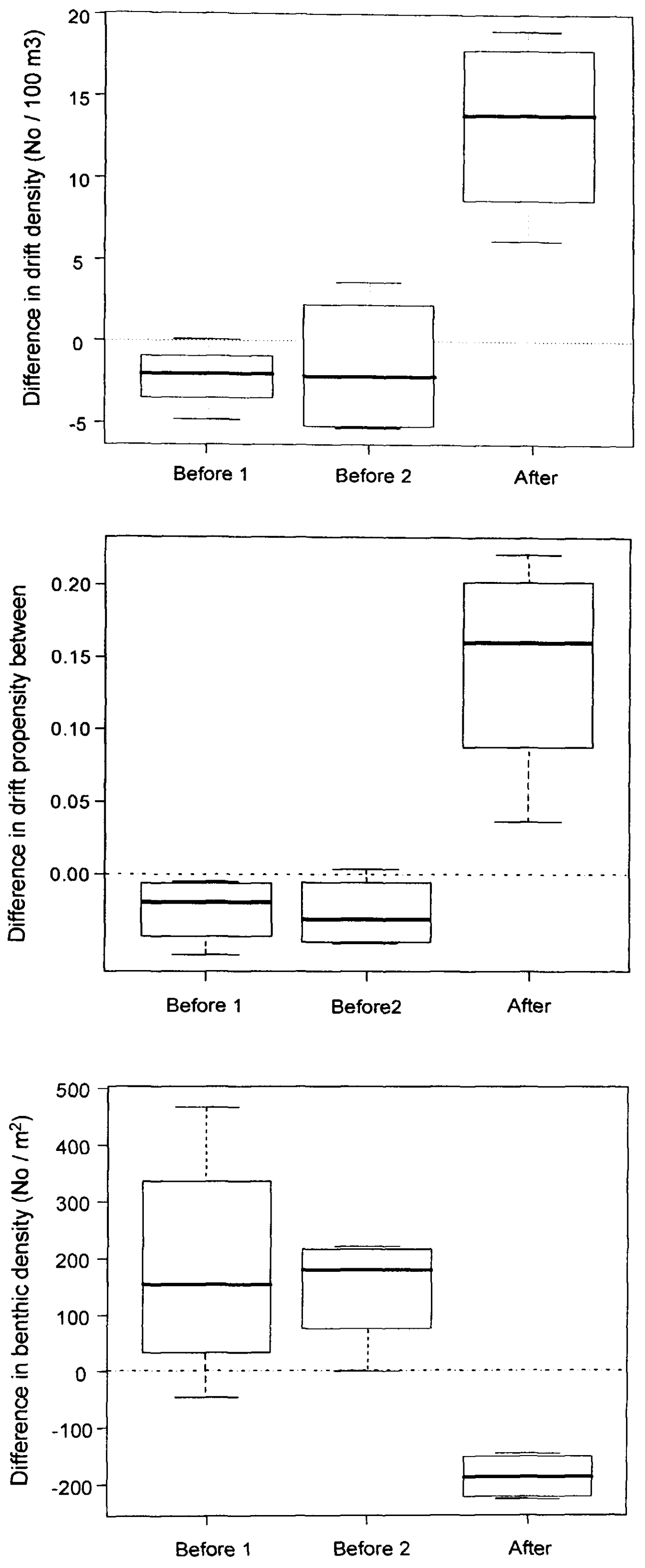


Fig. 5.1 Box-Whisker plots, showing mean and inter-quartile range to illustrate the differences in drift and benthic measures between impact and control reaches before and after sediment addition. Drift propensity = drift density / benthic density. Note that transformed abundances were used in analyses.

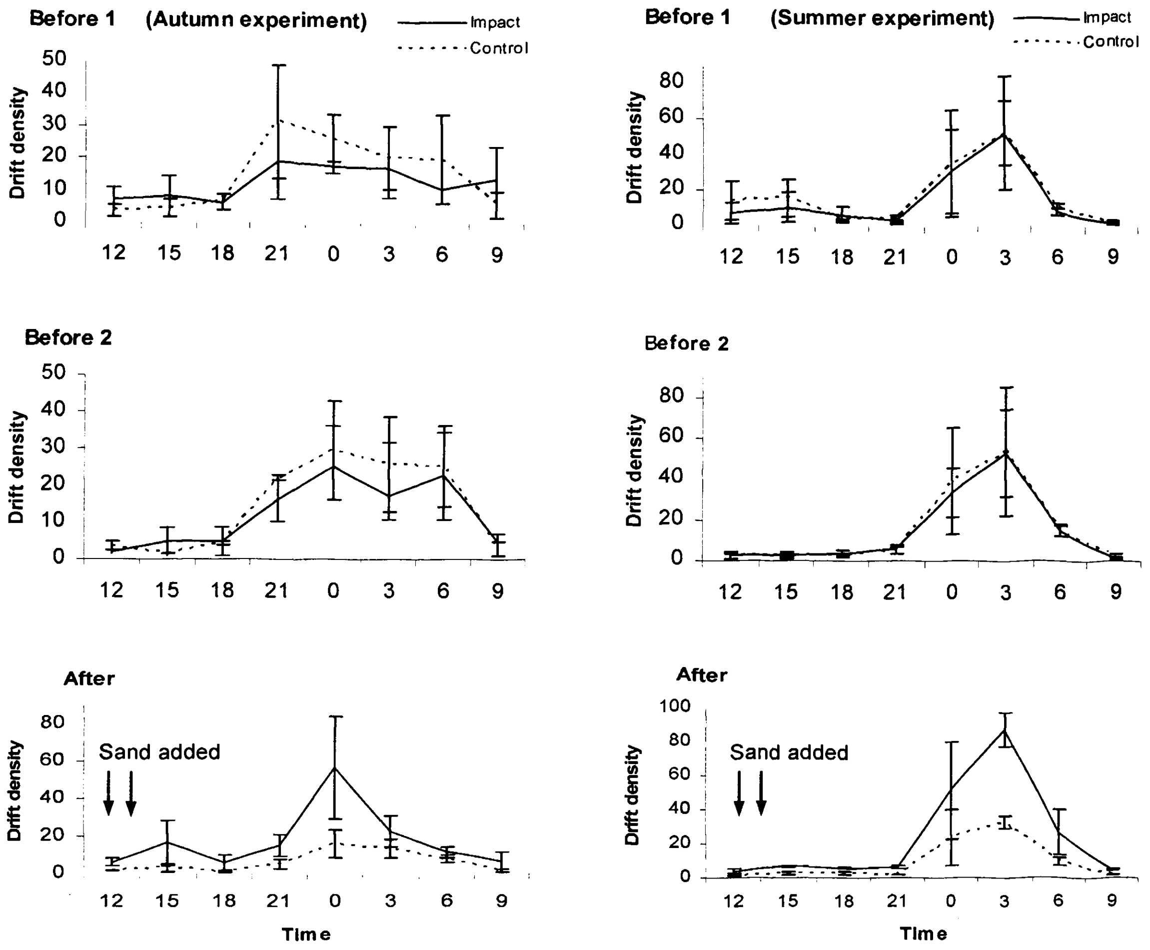


Fig. 5.2 Diel drift density (No/100m^3 ± SE) profiles of aquatic invertebrates autumn and summer experiments for the two days before and immediately after sediment addition. The X axis represents time of day. Note changes in Y axis.

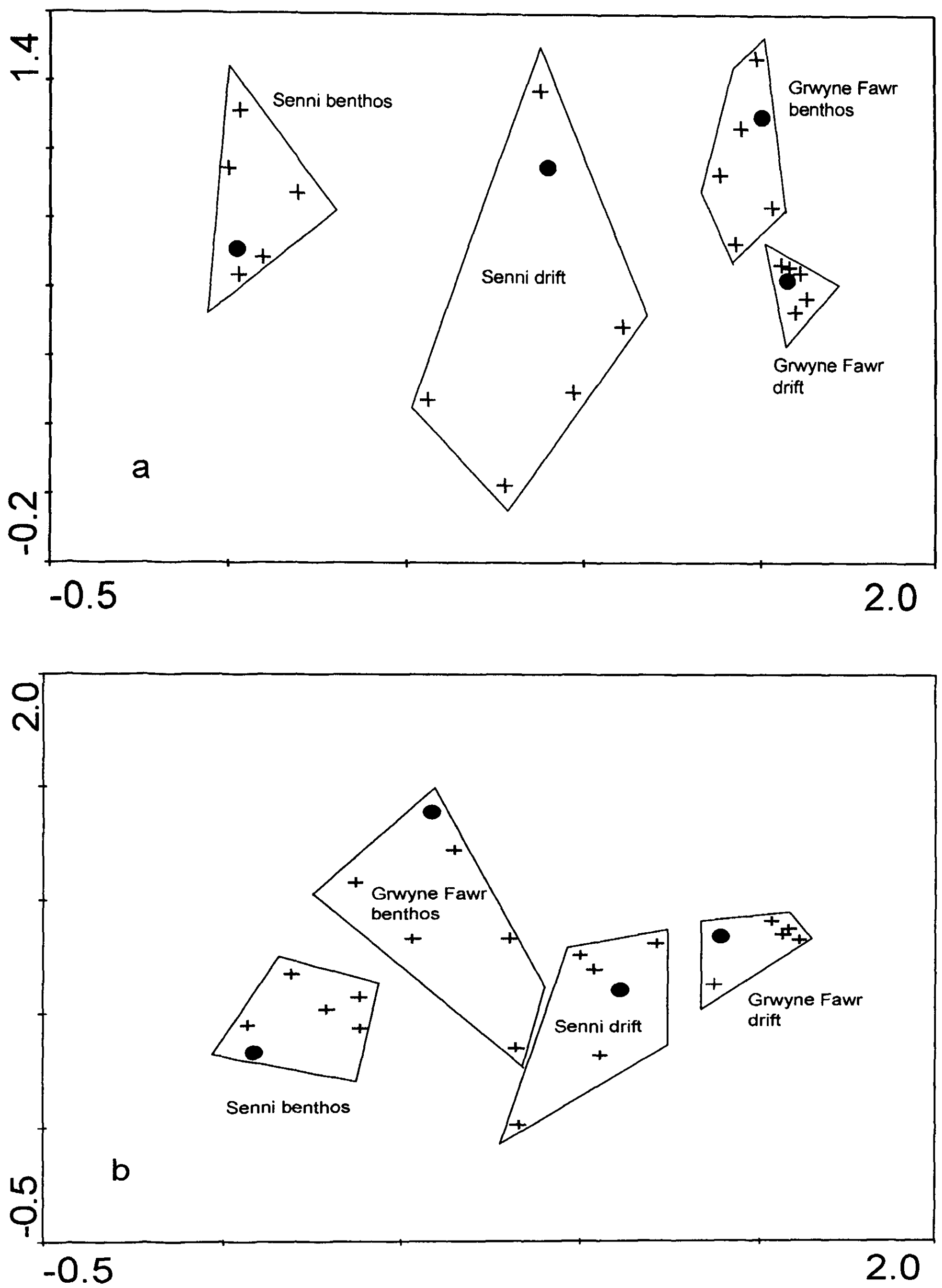


Fig 5.3 DCA plots of summer (a) and autumn (b) experiments. Each group has six samples corresponding to either drift or benthic samples taken twice before and once after sediment addition in both control and impact reaches. Black circles represent impact locations after sediment addition. Drift and benthic assemblages formed distinct groups for both streams. Note that the axes are in units of standard deviation such that 4 SD represents c 100% turnover in species composition.

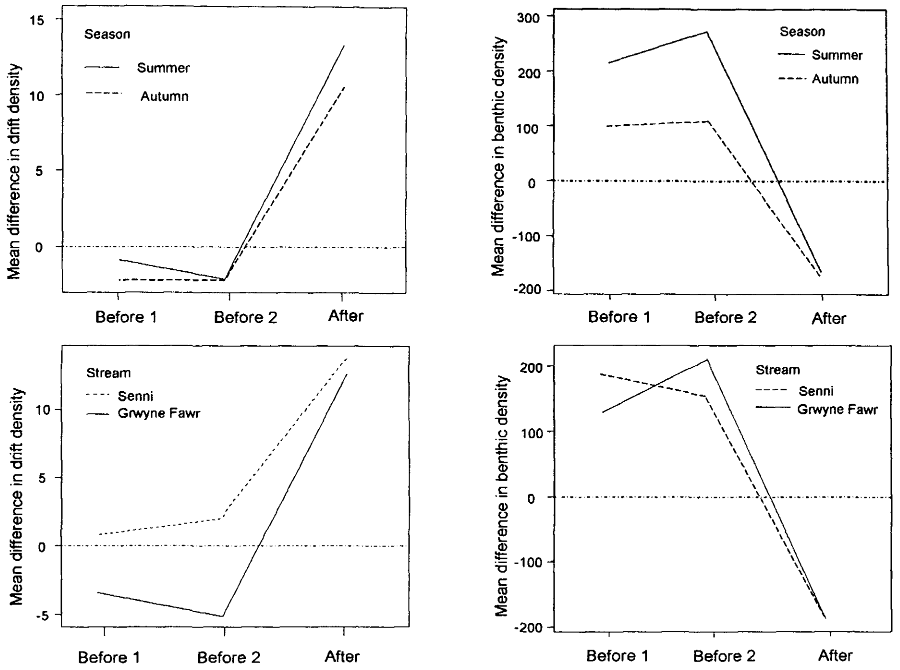


Fig 5.4 Interaction plots showing the contribution of streams or seasons on the mean differences of drift and benthic density between impact and control reaches before and after sediment addition.

Chapter 6 - Experimental effects of sediment deposition on macroinvertebrate structure and function in temperate streams

Summary

1. Fine sediment in streams and rivers is one of the most globally widespread of all freshwater pollutants. However, the ecological implications are still poorly quantified, and field experiments to assess likely functional and structural effects are scarce.

2. I assessed the response of stream invertebrates to fine sediment (i.e. inert sand) added to trays (n = 65) containing otherwise natural substrata over a three-week period in three replicate streams in the Usk catchment, Wales.

3. Sediment addition to 0.6 – 18 kg/m^2 affected both the structure and functional composition of invertebrate communities. Abundance also declined significantly in total and in common species (*Baetis rhodani*, *Ecdyonurus* sp., and *Leuctra geniculata*)

4. Sediment reduced richness and overall trait diversity, while different life-history traits were either favoured (polivoltinism, tegumental respiration and burrowing behaviour) or disfavoured (swimmers, attached taxa, gill respiration). Moreover, sediments appeared to promote a nested sub-set pattern in species composition, with generalists favoured at the expense of specialists either through exclusion or impaired colonisation. Effects were due largely to the loss of five species that contributed to the significant nestedness across the sand gradient.

5. This short-term experiment supports recent surveys and drift experiments in indicating how sedimentation can changes the structural and functional composition of stream invertebrates even in low to moderate quantities. In revealing direct effects on trait diversity, trait representation and nestedness, the data are also consistent with survey data in indicating that sediments have conservation ramifications.

6.1 Introduction

The entrainment and deposition of inert fine particles, arising from catchment and riparian modification, is one of the most widespread of all pollution problems affecting freshwaters globally (Waters, 1995). In United States, siltation is the principal source of impairment on the basis of stream distance impacted (USEPA 2000), while sediment fluxes throughout the world are increasing as catchments are progressively modified (Owens *et al*, 2005). Consequent changes in water quality and habitat character affect aquatic organisms across all trophic levels through mechanisms that include (i) increasing turbidity, reducing primary production and available light for visual predators (Davies-Colley *et al*, 1992; Davies-Colley & Smith, 2001); (ii) changing substratum structure and benthic habitat (Schalchli, 1992; Rehg, Packman & Ren, 2005); (iii) filling interstices, thus altering hydrological exchange between surface and groundwater while decreasing nutrient and oxygen supply to the hyporheos (Turnpenny & Williams, 1980; Richards & Bacon, 1994) and iv) reducing salmonids eggs survival and affecting other hyporheic organisms via oxygen depletion (Argent & Flebbe, 1999; Greig, Sear & Carling, 2005).

In agricultural catchments, sediments can arise from point-sources, such as livestock poaching and bank erosion, or from large-scale diffuse release, for example from tillage and deforestation (Kreutzweiser, Capell & Good, 2005; Larsen, Vaughan & Ormerod, 2009). In these cases, increasing sedimentation is often associated with wider habitat modifications and other in-stream stressors resulting in complex synergistic or antagonistic ecological responses (Townsend, Uhlmann & Matthaei, 2008). For example, nutrients, pesticides and altered hydraulic and thermal regimes can potentially mask or exacerbate biological effects of sediments. Global climate change is also likely to modify precipitation and hydrologic regimes therefore altering soil erosion rates and sediment transport (Wilby, Dalgleish & Foster, 1997). Under all these circumstances, improved quantification of the ecological effects of sediments and improved understanding of the underlying mechanisms is a major requirement.

In the River Usk, a temperate, upland river draining a sandstone-rich catchment in Wales (UK), recent surveys have shown how localised sediment delivery and patch-to-patch variation in sediment deposition have been associated with reduced richness and densities of sensitive taxa, altered representation of certain life-history or behavioural traits, and reduced trait diversity (Larsen *et al.*, 2009; Larsen & Ormerod, in review). As is typical with large-scale surveys, however, these data were correlative rather than clear indications of cause and effect (Manel, Buckton & Ormerod, 2000). Here, and elsewhere, laboratory or field manipulations of sediment character or deposition rate offer a method of corroborating larger-scale effects (Angradi, 1999; Townsend *et al.*, 2008), investigating the possible mechanisms involved (Larsen and Ormerod in review), or appraising directly the functional responses of impacted organisms (Rabeni, Doisy & Zweig, 2005; Townsend *et al.*, 2008).

In this paper, I describe the results of a field experiment in the Usk river system, replicated at the stream scale, designed to mimic the patch-scale effects of sediments. I increased the deposition of fine sand in trays filled with natural substrata held *in situ* to investigate effects on macroinvertebrate composition, abundance and functional characteristics. Based on previous findings from this catchment and elsewhere (Angradi, 1999; Doledec *et al*, 2006; Matthaei *et al*, 2006; Townsend *et al.*, 2008; Larsen *et al.*, 2009; Larsen & Ormerod, in review), I tested the following predictions:

i) invertebrate density, diversity and richness should decline with increasing sediments;

ii) the representation of shorter life -cycles, smaller sizes, tegumental respiration, detrital feeding and burrowing traits should be favoured in sediment-rich trays, while longer life cycles, larger size, gill respiration, filtering, grazing and temporary attachment should be disfavoured;

iii) overall trait diversity should decline with increasing sediments.

The experiment also allowed us to test the hypothesis that local sedimentation can alter colonization patterns and promote nestedness in invertebrate community structure (Larsen and Ormerod, in review). Nested sub-set patterns occur where species present in depauperate locations constitute a subset of the species in richer locations. In perfectly nested systems, rare taxa only occur in the richest site and generalists at most sites. While nestedness analysis was initially developed as a mean of testing biogeographical theories (Atmar & Patterson, 1993; Hecnar *et al*, 2002), applications to conservation and management are increasing (Fleishman *et al*, 2007). This is because nested subsets in species composition can arise not only from extinction and colonization processes over broad spatio-temporal extents, but also from human disturbance, habitat alteration and even behavioural effects on patch use (Fernandez-Juricic, 2002; Summerville, Veech & Crist, 2002; Hylander *et al*, 2005). I examined the possibility that sediment deposition could promote a nested sub-set pattern in species occurrence across trays, for example by impairing colonization by specialist and rare taxa during the experiment.

6.2 Methods

Study area

The river Crai, Cynrig and Tarell are three, third-order tributaries (3-5 m wide) of the River Usk, in Wales, at 250-300 m. above sea level (National Grid Reference: SN881235, SO048247, SO009269, respectively). The reaches selected for the experiment (c 30 m) drained a blend of scattered deciduous woodland, improved grassland and rough pasture. Each was partially shaded by deciduous trees with substrata mainly of boulders, cobbles and pebbles and some gravel. Stream reaches were chosen for their relative similarity in geomorphology, faunal composition and riparian / catchment land-use as informed by previous surveys (Larsen *et al.*, 2009).

Stream waters were relatively clean, well oxygenated and rich in carbonates, with pH 7.2-8 and plant nutrients generally low (< 2 mg nitrate/L). In some locations, where natural riparian vegetation has been removed and livestock have access to the stream banks, erosion has resulted in localised release and deposition of relatively coarse sediments (Larsen *et al.*, 2009). I attempted to recreate such patch-scale variation in deposited sediments under controlled conditions *in situ* in the three selected streams.

Experimental design

Following an approach similar to that of Angradi (1999), 22 plastic trays (18 x 12 x 5 cm), filled with natural substrata collected on site and composed of gravel, pebble and cobble, were deployed in each of the three streams on the 19th of July 2008 across a 30 m stretch within glide / run habitats with relatively homogeneous flow (c 20 -30 cm/s). Each filled tray weighed c. 2 kg and was positioned in the stream bed so that the substratum surface in the tray was flush with the stream bed. In each stream, immediately after installation, trays were either covered with 1 kg of sand (33% in weight, or c 40 kg/m^2; n = 6), with 2 kg of sand (50% in weight, or c 80 kg/m^2; n = 6) or left as controls (no sand added; n = 6). Additionally, to maintain the intended sediment concentration over the experimental period and to simulate sediment re-supply, four additional trays in each stream were covered with 1 kg of sand on two occasions; at the beginning of the experiment and then again after a week, thus receiving 2 kg in total. Size distribution of sand used here (0.2 – 1 mm) was similar to natural occurring sediments in the catchment (Larsen *et al.*, 2009).

Trays were left in the streams for 19 days, with this interval determined by the risk and impact of high-flow events during this abnormally wet summer. Water velocity and depth immediately in front of each tray was monitored every three days for the duration of the experiment, while water temperature, conductivity and pH were also measured on three occasions. Although the experiment covered a relatively short period, associated work showed that sediment effects on stream invertebrates in the Usk can develop even within 24h (Larsen & Ormerod, in press). Moreover, a longer colonization period would have decreased the sediment gradient towards ambient conditions.

Trays were eventually retrieved paying attention not to lose any invertebrates or organic detritus by covering them with a net at the time of collection (mesh 0.2 mm). In addition, two pooled Surber samples (0.09 m^2; 0.44mm) were taken at the time of tray collection to assess how closely assemblages in trays represented the faunal composition in each stream. The contents of each tray and Surber sample were sorted in the laboratory where invertebrates were separated from coarse particulate organic matter (CPOM), which was then dried and weighed. A sieve of 2 mm was used to retain the fine sediment fraction which was also dried and weighed to assess how closely sediment additions had produced the intended sediment cover. Invertebrates were identified, where practicable, to species.

Data analysis

Because background sediment accumulation in each tray would cause variations relative to the nominal additions, I used the exact mass of sand per-unit-area of tray substrate as a continuous variable to express sediment effects on the invertebrates. Data from all the three streams were combined in analysis in order to maximise sample size and decrease the risk that species occurred in individual trays by chance.

Prior to any further analysis, I used Detrended Correspondence Analysis to parameterise variations in invertebrate assemblages among samples (DCA; Hill & Gauch, 1980). This ordination technique arranges samples with similar composition onto orthogonal axes that can be used in subsequent analyses. Preliminary investigation showed that species responded unimodally to sediment cover rather than rectilinearly, suggesting that this technique was appropriate (Jongman, Ter Braak & Van Tongeren, 1995). After removing taxa that did not occur in all four streams, 18 were included in the ordination. Arithmetic and transformed abundances gave near-identical ordination results, and only analyses based on arithmetic abundances are presented.

To assess treatment effects on the taxonomic richness, diversity, individual abundances and community composition (i.e. sample ordination scores) of invertebrates, I used mixed-effects models, where stream identity was included as a random factor in analysis, while fine sediments and CPOM were considered fixed factors. Mixed models are appropriate for the data, providing flexibility in representing the covariance structure induced by data grouping (Pinheiro & Bates, 2000). In other words, the analysis takes into account the difference in species composition and biological response to treatment among the streams. I also assessed the influence of water flow on sediment levels, and measured the correlation between sediment and CPOM in trays.

Similarity in taxonomic composition among trays and adjacent Surber samples was assessed using the Bray-Curtis Similarity index. Specifically, I plotted the similarity between control trays and treated trays, and between all trays and Surber samples, against sediment content. To allow direct comparison of richness between control trays and Surbers, I used EcoSim simulation software (Gotelli & Entsminger, 1997) to rarefy Surber richness based on the average abundance in control trays.

To describe communities according to their functional trait representation, I defined 48 categories of 11 life-history and behavioural traits using available information (Richoux, 1994; Tachet, Usseglio-Polatera & Roux, 1994; Usseglio-Polatera, 1994; Usseglio-Polatera & Tachet, 1994; Tachet *et al*, 2000). The affinity of each taxon for each trait category was described using fuzzy coding (Chevenet, Doledec & Chessel, 1994). Information on trait coding was available only at the genus level, so I used this level of identification for all trait analysis. Each taxon was given an affinity score that ranged between 0 (no affinity) and 3, or 0 and 5. When no exact information was available for a given taxon for a given trait, an affinity of 0 was applied so that the taxon was treated as though it had the average profile of the corresponding trait (Dolédec, Statzner & Bournard, 1999). Affinity scores were rescaled as proportions (sum = 1) for each taxon, thus representing the probability that any taxon belonged to a particular category. For each site, the resulting species × trait-category matrix was multiplied by the site × species-abundance matrix to give a site × trait abundance matrix. The abundance-weighted trait matrix were then defined as a frequency distribution of categories for each trait (Dolédec, Olivier & Statzner, 2000; Archaimbault, Usseglio-Polatera & Bossche, 2005). Fuzzy Correspondence Analysis (FCA) was used on the trait matrix to obtain scores of each tray based on overall trait composition (Chevenet *et al.*, 1994). The scores were then used to assess if sediment affected overall trait representation again using mixed modelling. Trait diversity (TD) in each tray was calculated as the average Simpson diversity (S) across all categories within each trait:

$TD = S = 1 - D_i$, where $D_i = \sum(n_j/N)^2$

With D_i = Dominance index of trait *i*; n_j = relative abundance of trait category *j*; N = total abundance of all trait categories. The average of S across all traits was calculated to reduce lack of independence among traits (e.g. Bêche & Resh, 2007).

To assess if specific traits varied with sediment content, the proportion of trait categories describing maximal size, life cycles, numbers of generations per year, respiration, feeding and locomotion were analysed using mixed effect models as before. Proportions were arcsin $\sqrt{x}$ transformed before analysis to homogenize variances. For this particular test on trait categories, I corrected alpha values (= 0.05) by dividing by the number of categories within each trait (e.g. if a given trait has five categories, for significance alpha = 0.01; Bêche, McElravy & Resh, 2006).

Nestedness across sites was calculated using the binary-matrix nestedness temperature calculator (BINMATNEST; Rodriguez-Girones & Santamaria, 2006), which is a recent improvement of the nested-temperature method of Atmar and Patterson (1993) in that it uses a more robust algorithm for matrix packing. The temperature method was chosen as it is relatively insensitive to matrix size and correlates well with other existing metrics (Wright, Furse & Moss, 1998). Working on the species presence / absence matrix, BINMATNEST re-orders rows and columns maximising matrix nestedness and then calculates a temperature (ranging over 0 – 100 °C), which reflects the matrix deviation from an ideal nested structure; perfectly nested matrices with rare taxa in rich locations have T = 0°C while totally random matrices have T = 100°C. The temperatures of 400 simulated matrices using Monte-Carlo randomization were used to calculate the statistical significance of the observed temperature against chance expectation. In the matrix simulations, I used the more conservative null-model III where the probability of a cell being occupied equals the average probabilities of occupancy of its row and column. This model is particularly reliable as it is less sensitive to species richness and occurrences (Rodriguez-Girones & Santamaria, 2006). The order with which the maximally packed matrix is sorted can then be compared with independent correlated to assess the likely drivers of nestedness. I used Spearman-rank correlation to evaluate the influence of sediment levels on the nested patterns of communities in trays (see Schouten *et al*, 2007; Heino, Mykra & Muotka, 2009 for a similar approach).

To examine which taxa contributed significantly to the overall nestedness I used the Mann-Whitney test on individual taxa. This is a two group test where presences (1) and absences (0) constitute the groups in the presence-absence matrix. For each taxon, the test gives the probability that the observed sequence of presences and absences differs from a random one (i.e. conforms to a nested pattern). To test specifically whether sediment treatment promoted "nestedness" of individual taxa I first sorted the presence-absence matrix by increasing sediments. In this case, a perfectly "nested" species would have no presences ("1") after the first absence ("0") along the sediment gradient. This approach has been used by Fernandez-Juricic (2002), Hecnar *et al.* (2002) and Summerville *et al.* (2002). Although this method assesses the "nestedness" of individual taxa and it is useful to appraise specific contribution to the formation of nested subset patterns, real nestedness remains a property of assemblages since, by definition, it has a multi-species basis.

6.3 Results

Physical conditions

Throughout the experiment, average current velocity in the steams ranged between 7 and 26 cm/s across trays, with water depths 6 – 18 cm. Average conductivity was c. 140 µs/cm, pH c. 7.5, and stream temperature 14.5 – 17 C°.Nitrate concentrations were similar across streams, averaging 1.3 mg/L, while phosphates were very low (c. 0.01 mg/L).

Upon retrieval, fine sediments accumulation in the trays ranged over 13 – 414 g (c 0.6 – 18 kg/m^2), or c. 1 – 23 % in proportional weight. In the untreated control trays (ambient substratum mixture), sediment weight ranged over 13 – 66 g (mean

= 50 g ± 13 S.D.). One tray was lost so that the final sample size was 65 trays. There was a tendency for lower sediment retention with increasing current velocity, but this trend was only marginally significant ($p = 0.07$). Compared to controls, CPOM content decreased by about 70% in the most sediment-affected trays (slope = -0.006; P=0.007; Fig. 6.1).

Invertebrate structure

Among the 34 taxa collected, *Baetis rhodani*, *Ecdyonurus* sp., *Leuctra moselyi, Ephemerella ignita* and Chironomidae were the most common. Taxon richness ranged between 4 and 14 (mean = 7 ± 2.16 S.D.) across trays, while abundances were 7 – 111 individuals / tray.

Mixed models showed that abundances and taxon richness were affected negatively by fine sediments, but not taxonomic diversity (Simpson index; Table 6.1; Fig. 6.2). Among individual taxa, the abundances of *B. rhodani*, *Ecdyonurus* sp., *Leuctra geniculata*, and *Gammarus pulex* were all affected by sediments (Table 6.1).

In community assessment, two DCA axes explained c 50 % of species variation across trays, with both axes showing significant relationships with sediment amount (Table 6.1 and Fig. 6.3). Most species in the ordination appeared to prefer sediment-free conditions, being located mostly in the upper right quadrant of the factorial plane (Fig. 6.1). Taxa apparently more common in sediment rich trays included chironomids, dytiscids and the mayfly *Habrophlebia fusca*. In contrast, the amount of CPOM in trays appeared to have no significant effects on species composition (DCA axes), richness or the abundance of individual taxa, implying that sediment affects were direct rather than being mediated through effects on organic detritus.

Comparison between Surber samples and control trays revealed some differences, and in particular average rarefied richness in Surber samples was 12-15 taxa, while the average richness in control trays was eight. *Hydropsyche siltalai, H. instabilis, Rithrogena semicolorata, Rhyacophila obliterata, Halesus* sp., *Perla bipunctata,* Tipulidae, Dytiscidae and *Oreodytes sanmarchii* were exclusive to

Surber samples. Despite having reduced richness, 70% (i.e. 21) of the 30 taxa collected by Surber samplers were also present in control trays. Interestingly five taxa collected in control trays were not observed in Surbers: *Habrophlebia fusca, Odontocerum albicorne, Melampophylax mucoreus, Silo pallipes* and Psychodidae. Mostly these were rare taxa, with only few occurrences in control trays.

Average Bray-Curtis Similarity between Surber samples and trays (control + treatment) declined significantly with increasing sediment content, with control trays distinctively more similar to Surbers (Fig. 6.4). Sediment addition also reduced the average similarity between treatment trays and controls (Fig. 6.4).

Functional response

The first factorial plane of the FCA explained > 74 % of the variation in biological traits across sites. Both axes were significantly related to fine sediment amount in trays implying that overall trait representation was affected by sediment addition (Table 6.1).

Further effect of sediments on the trait structure was evident from the significant decline in overall trait diversity with increasing sediments (Table 6.1). Mixed models showed that several trait categories responded to sediments (Table 6.2). In particular, taxa characterised by shorter life cycles, detrital feeding and burrowing were all represented more in sediment-rich trays, while ovoviviparity, gill respiration, and temporarily attached taxa were disfavoured. There was no effect on the representation of different body sizes and number of generations per year.

Except for a proportional increase in shredder representation with increasing coarse organic matter ($P = 0.016$; not significant after correction based on number of categories), no effect of CPOM on trait representation was observed.

Nested subset pattern

Across the experimental trays, macroinvertebrate communities were significantly nested ($T = 16.4$; $P < 0.001$). Site ranking in the maximally-packed species-matrix (i.e. the matrix ordered to maximise nestedness) was significantly correlated with sediment ranking across trays. In other words, there was a progressive loss of taxa with increasing sediment accumulation. The Mann -Whitney test showed that the loss of five taxa contributed to the significant nestedness along the sedimentation gradient (Table 6.3): *B. rhodani, Ecdyonurus* sp., *Leuctra geniculata,* simuliids and, to a lesser extent, *Ephemerella ignita.*

6.4 Discussion

These experimental data confirm that even low to moderate amounts of sediment can alter the patch-scale richness, abundance, community composition, trait diversity and trait composition of invertebrates: feeding, attachment, respiration and life-cycle traits all appeared to increase species' sensitivity to sediment addition. As with all experimental manipulations in ecology, there are some limitations in our approach, related mostly to the small-scale and short-term nature of the experiment. In large part, however, the data are consistent with other large-scale surveys and experiments in indicating how sediments can change benthic invertebrate assemblages. In particular, the results mirrored the effects of patch-scale (c. 1m^2) variation in deposited sediments on invertebrates in the same catchments (Larsen *et al.*, 2009). I expand on these points in the discussion that follows.

Ecological experiments at small spatio-temporal scales are used often to investigate the mechanisms involved in larger-scale phenomena. However, care is needed in scaling-up biological responses to larger-scale patterns. Both the duration of the experiment and size of our sample units were particularly small, so that limited colonisation time, patch-scale variability in invertebrate distribution, species-area effects, edge effects, representativeness and chance could all limit realism (Angradi, 1999). The clearest evidence for the restricted realism of our experiment came from differences in invertebrate composition between the Surber samples and trays, with species such as *Hydropsiche siltalai, H. instabilis, Perla bipunctata* and Simuliidae absent or underrepresented in the experimental tray units. As observed by Angradi (1999), their absence may be linked to the absence of larger, stable substrata (e.g. boulders) in trays that are used by some of these taxa for anchorage or refuge (e.g. Hydropsychidae, Simuliidae). Species are also inherently variable in their ability to colonise newly created conditions – in this case those represented by introduced substrates (Boothroyd & Dickie, 1991; Olomukoro & Okologume, 2008). In addition to limits imposed by drift propensity among species, the enclosed nature of the trays could have altered interstitial flow and interstitial colonisation routes. Notwithstanding such effects, the fact that trays held 70% of the 30 taxa collected by Surber samplers illustrates that they represented benthic assemblages reasonably well. Moreover, progressive dissimilarity between manipulated trays and controls or Surber samples with increasing sediment deposition shows that any limits on tray colonisation did not mask sediment effects. Previous work on drift and changes in density in the Usk show that these effects can be generated very rapidly, and even within 24h (Larsen and Ormerod, in press).

One further positive feature of our experimental approach is that it allowed relatively high power through replication within streams, and also replication at the stream scale. With this design, sediment addition clearly altered invertebrate assemblage composition, abundance, and functional structure. Most of the observed responses were in-line with findings from previous surveys and experiments in the same catchment and elsewhere, thus reinforcing the validity and generalisation of our results. The observed decline in overall macroinvertebrates richness with increasing fine sediments likely reflects the negative effect on Ephemeroptera, Plecoptera and Trichoptera (EPT), which are among the dominant taxa in the Usk system, and are reported to be sensitive to fine sediments: a linear decline of EPT taxon richness with increasing sediment cover has been observed frequently both in experimental studies (Angradi, 1999; Matthaei *et al.*, 2006) and in larger scale surveys (Zweig & Rabeni, 2001; Kaller & Hartman, 2004; Townsend *et al.*, 2008; Larsen *et al.*, 2009; Pollard & Yuan, 2009). Contrary to some studies (e.g. Lenat, Penrose & Eagleson, 1981), deposited sediments did not affect diversity indices of benthic communities in our trays possibly because the loss of rarer taxa at greater sediment cover led to fewer taxa that were more evenly distributed among individuals. This is a well recognised difficulty in interpreting diversity indices as opposed to richness.

Sediment treatments also reduced dramatically overall invertebrate abundance by up to 90% with six common taxa significantly affected at effect sizes of c 40-90%. While this effects probably reflected reduced interstitial space (Bo *et al*, 2007), it is possible that a longer-term experiment would have allowed invertebrates composition to adjust to the sediment conditions and even result in increased density of tolerant taxa (Lenat *et al.*, 1981). In grassland sites similar to those used here, the lower abundance I observed is consistent with previous data (Larsen *et al.*, 2009). Among the taxa affected, the mayflies *Baetis rhodani* and *Ecdyonurus* sp. are both grazers reportedly intolerant of sediment deposition (Rabeni *et al.*, 2005) and *Ecdyonurus* is also a clinger requiring clean interstitial spaces to maintain position in the substratum (Rabeni *et al.*, 2005; Pollard & Yuan, 2009). *Leuctra geniculata* appeared to be relatively sediment-intolerant in previous surveys and the abundance of both *L. geniculata* and *L. moselyi* was affected by a short-term experimental sediment addition in nearby streams (Larsen and Ormerod, in press). The amphipod *Gammarus pulex* was also negatively affected by sediment addition, although this trend was mostly due to one stream (Cynrig) where *Gammarus* dominated tray assemblages. Waters and Hokenstrom (1980) also reported reduced biomass of *Gammarus* in a small tributary of the upper Mississippi River after severe siltation.

In addition to changes in density and richness, I expected from previous findings that organisms with certain life-history traits would be affected by sediments (e.g. Rabeni & Smale, 1995; Doledec *et al.*, 2006; Townsend *et al.*, 2008). Typically, the representation of filter feeders and K-selected (i.e. larger, long-lived) taxa is affected negatively by fine-sediment deposition. Filterers are intolerant to sediments because fine particles impair filtering devices (Lemly, 1982), while K-selected taxa could be excluded by the unstable and transient environments that occur in fine sediments (Richards *et al*, 1997; Townsend & Thompson, 2007; Larsen and Ormerod, in review). The reduced representation in the experimental trays of Hydropsychidae, Simuliidae and large stoneflies (e.g. *Perla*), prevented us from formally testing these hypotheses. Nevertheless, overall trait diversity declined with increasing sediment cover, and other life-history or behavioural traits responded as predicted to treatment. The observed reduction of invertebrate trait diversity with increasing fine sediments is in line with findings from previous surveys and reflects the specific selection (or filtering) of taxa according to their functional traits.

Evidence is increasingly clear that anthropogenic effects (e.g. land-use) can reduce functional diversity in ecological communities (Charvet *et al*, 2000; Houghton, 2007; Schweiger *et al*, 2007; Flynn *et al*, 2009) Across the experimental trays in this study, the representation of shorter life cycles, burrowers, fine detritus feeders and tegumental respiration all increased with fine sediments. These traits reflect some adaptation to habitats dominated by fine substrata, and the taxa which possess them can be favoured in sediment-rich environments (Rabeni *et al.*, 2005; Doledec *et al.*, 2006; Townsend *et al.*, 2008). Groups with these traits in our experiment included chironomids, oligochaetes and, to a lesser extent, the trichopterans *Odontocerum albicorne* and *Sericostoma personatum*. Reproduction via free egg-clutches also appeared to be favoured by sedimentation, mostly due to the proportional increase of chironomids with increasing sediments. Similarly, reduced representation of ovoviviparity with sediment accumulation reflected negative effects on *Gammarus*, as no other taxon possessed this particular trait. Conversely, the decline in gill respiration, swimmers and taxa requiring attachment to the substratum appeared to be more community wide, consistent with previous observations (e.g. Townsend *et al.*, 2008). Organisms relying on gill respiration are particularly sensitive to fine particles that can impair their delicate respiratory structures (Lemly, 1982). In this instance, negative effects reflect the three common mayflies, *B. rhodani*, *Ecdyonurus* sp. and *E. ignita*. Also, particle-free surfaces are needed for those taxa requiring temporary attachment to the substratum and this could explain why simuliids colonized only untreated trays.

The consequences of alterations caused by sediments to the composition and diversity of trait representation in stream communities, for example for ecosystem function, are still poorly understood. This is also true of changes in the pattern of nestedness among stream species, where rarer taxa are lost in some locations where only commoner taxa persist. In this small-scale experiment, simuliids, *B. rhodani*, *Ecdyonurus* sp. and *L. geniculata* all contributed to the significant nestedness in species occurrences with increasing sedimentation. In other words, these taxa were absent more than expected by chance. Further evidence that experimental treatment promoted nestedness came from the significant rank-correlation between nestedness order of the presence / absence matrix (as calculated by BINMATNEST algorithm) and the amount of sediment in each tray. As with many other of the results from our experiment, similar patterns of nestedness have been shown at sediment-rich sites over larger areas (Larsen and Ormerod, in review), and it seems that trait-mediated sensitivity to sediments causes a non-random colonization – extinction pattern that transcends scale to cause a nested sub-set pattern in species composition. This is also consistent with the nested habitats hypothesis (Hylander *et al.*, 2005), where the sediment gradient could reflect changing heterogeneity or complexity where sediment-free trays or sites harboured a wider range of micro-habitats (and thus a wider range of species from the available pool) than did sediment-impacted trays or locations. These results also suggest that nestedness can derive not only from large scale biogeographical processes, but also from variations in habitat quality and impairment (Fernandez-Juricic, 2002; Hylander *et al.*, 2005). Elsewhere, I have considered that alterations in both trait composition and nestedness caused by sediments may well have ramifications for conservation, by selectively removing not only key invertebrate traits and organism types, but also by changing the organisation of assemblages (Larsen and Ormerod, in review): if sediment impacted location can support only a sub-set of pre-adapted generalist species, increasing sedimentation worldwide could lead to the selective loss of certain species types. This possibility requires wider examination

6.5 References

Angradi, T.R. (1999) Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications *Journal of the North American Benthological Society* **18,** 49-66

Archaimbault, V., Usseglio-Polatera, P. & Bossche, J.P.V. (2005) Functional differences among benthic macroinvertebrate communities in reference streams of same order in a given biogeographic area. *Hydrobiologia,* **551,** 171-182.

Argent, D.G. & Flebbe, P.A. (1999) Fine sediment effects on brook trout eggs in laboratory streams. *Fisheries Research,* **39,** 253-262.

Atmar, W. & Patterson, B.D. (1993) The Measure of Order and Disorder in the Distribution of Species in Fragmented Habitat. *Oecologia,* **96,** 373-382.

Bêche, L.A., Mcelravy, E.P. & Resh, V.H. (2006) Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. *Freshwater Biology,* **51,** 56-75.

Bêche, L.A. & Resh, V.H. (2007) Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Fundamental and Appled Limnology,* **169,** 1-23.

Bo, T., Fenoglio, S., Malacarne, G., Pessino, M. & Sgariboldi, F. (2007) Effects of clogging on stream macroinvertebrates: An experimental approach. *Limnologica,* **37,** 186-192.

Boothroyd, I.K.G. & Dickie, B.N. (1991) Macroinvertebrate Drift and Community Colonization on Perspex Artificial Substrates in the Ohinemuri River, New-Zealand. *New Zealand Journal of Marine and Freshwater Research,* **25,** 167-176.

Charvet, S., Statzner, B., Usseglio-Polatera, P. & Dumont, B. (2000) Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology,* **43,** 277-296.

Chevenet, F., Doledec, S. & Chessel, D. (1994) A Fuzzy Coding Approach for the Analysis of Long-Term Ecological Data. *Freshwater Biology,* **31,** 295-309.

Davies-Colley, R.J., Hickey, C.W., Quinn, M.J. & Ryan, P.A. (1992) Effects of clay discharges on streams. Optical properties and ephilithon. *Hydrobiologia,* **248,** 215-234.

Davies-Colley, R.J. & Smith, D.G. (2001) Turbidity, suspended sediment, and water clarity: A review. *Journal of the American Water Resources Association,* **37,** 1085-1101.

Dolédec, S., Olivier, J.M. & Statzner, B. (2000) Accurate description of the abundance of taxa and their biological traits in stream invertebrate communities: effects of taxonomic and spatial resolution. *Archiv Fur Hydrobiologie,* **148,** 25-43.

Doledec, S., Phillips, N., Scarsbrook, M., Riley, R.H. & Townsend, C.R. (2006) Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. *Journal of the North American Benthological Society,* **25,** 44-60.

Dolédec, S., Statzner, B. & Bournard, M. (1999) Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology,* **42,** 737-758.

Fernandez-Juricic, E. (2002) Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia,* **131,** 269-278.

Fleishman, E., Donnelly, R., Fay, J.P. & Reeves, R. (2007) Applications of nestedness analyses to biodiversity conservation in developing landscapes. *Landscape and Urban Planning,* **81,** 271-281.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. & Declerck, F. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters,* **12,** 22-33.

Gotelli, N.J. & Entsminger, G.L. (1997) EcoSim: Null models software for ecologists. *Bulletin of the Ecological Society of America,* **78.**

Greig, S.M., Sear, D.A. & Carling, P.A. (2005) The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management. *Science of the Total Environment,* **344,** 241-258.

Hecnar, S.J., Casper, G.S., Russell, R.W., Hecnar, D.R. & Robinson, J.N. (2002) Nested species assemblages of amphibians and reptiles on islands in the Laurentian Great Lakes. *Journal of Biogeography,* **29,** 475-489.

Heino, J., Mykra, H. & Muotka, T. (2009) Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. *Diversity and Distributions,* **15,** 198-206.

Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence-analysis - an improved ordination technique. *Vegetatio,* **42,** 47-58.

Houghton, D.C. (2007) The effects of landscape-level disturbance on the composition of Minnesota caddisfly (Insecta : Trichoptera) trophic functional groups: evidence for ecosystem homogenization. *Environmental Monitoring and Assessment,* **135,** 253-264.

Hylander, K., Nilsson, C., Jonsson, B.G. & Gothner, T. (2005) Differences in habitat quality explain nestedness in a land snail meta-community. *Oikos,* **108,** 351-361.

Jongman, R.H.G., Ter Braak, C.J.F. & Van Tongeren, O.F.R. (1995) *Data analysis in community and landscape ecology,* Cambridge University Press, Cambridge.

Kaller, M.D. & Hartman, K.J. (2004) Evidence of a threshold level of fine sediment accumulation for altering benthic macroinvertebrate communities. *Hydrobiologia,* **518,** 95 -104.

Kreutzweiser, D.P., Capell, S.S. & Good, K.P. (2005) Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology,* **39,** 55-66.

Larsen, S. & Ormerod, S.J. (in press) Low-level effects of inert sediments on temperate stream invertebrates.

Larsen, S. & Ormerod, S.J. (in review) Habitat modification and the conservation of species' traits in temperate river invertebrates.

Larsen, S., Vaughan, I.P. & Ormerod, S.J. (2009) Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology,* **54,** 203-219.

Lemly, D. (1982) Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia,* **87,** 229-245.

Lenat, R.D., Penrose, D.L. & Eagleson, W.K. (1981) Variable effects of sediment addiction on stream benthos. *Hydrobiologia,* **79,** 187-194.

Manel, S., Buckton, S.T. & Ormerod, S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology,* **37,** 756-770.

Matthaei, C.D., Weller, F., Kelly, D.W. & Townsend, C.R. (2006) Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology,* **51,** 2154-2172.

Olomukoro, J.O. & Okologume, U. (2008) Macroinvertebrate colonisation of artificial substrates in a Nigerian river I: gravel and leaf litter. *African Journal of Aquatic Science,* **33,** 143-148.

Owens, P.N., Batalla, R.J., A. J. Collins, B. Gomez, D. M. Hichs, A. J. Horowitz, Kondolf;, G.M., M. Marden, M. J. Page, D. H. Peacock, E. L. Petticrew, W. Salomons & N. A. Trustrumi (2005) Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications,* **21,** 693–717.

Pinheiro, J. & Bates, D. (2000) *Mixed Effects Models in S and S-Plus,* Springer, New York.

Pollard, A.I. & Yuan, L.L. (2009) Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity-based measures. *Freshwater Biology,* in press.

Rabeni, C.F., Doisy, K.E. & Zweig, L.D. (2005) Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences,* **67,** 395-402.

Rabeni, C.F. & Smale, M.A. (1995) Effects of Siltation on Stream Fishes and the Potential Mitigating Role of the Buffering Riparian Zone. *Hydrobiologia,* **303,** 211-219.

Rehg, J.K., Packman, A.I. & Ren, J. (2005) Effects of suspended sediment characteristics and bed sediment transport on streambed clogging. *Hydrological Processes,* **19,** 413–427.

Richards, C. & Bacon, K.L. (1994) Influence of Fine Sediment on Macroinvertebrate Colonization of Surface and Hyporheic Stream Substrates. *Great Basin Naturalist,* **54,** 106-113.

Richards, C., Haro, R.J., Johnson, L.B. & Host, G.E. (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology,* **37,** 219-&.

Richoux, P. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Aquatic Coleoptera in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 377-395.

Rodriguez-Girones, M.A. & Santamaria, L. (2006) A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography,* **33,** 924-935.

Schalchli, U. (1992) The Clogging of Coarse Gravel River Beds by Fine Sediment. *Hydrobiologia,* **235,** 189-197.

Schouten, M.A., Verweij, P.A., Barendregt, A., Kleukers, R.J.M. & De Ruiter, P.C. (2007) Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life-history traits. *Journal of Biogeography,* **34,** 1938-1946.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekotter, T., Hendrickx, F., Herzog, F., Liira, J., Maelfait, J.P., Speelmans, M. & Dziock, F. (2007)

Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos,* **116,** 461-472.

Summerville, K.S., Veech, J.A. & Crist, T.O. (2002) Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? *Oikos,* **97,** 195-204.

Tachet, H., Richoux, P., Bournaud, M. & Usseglio-Polatera, P. (2000) *Invertebres d'eau Douce. Systematique, Biologie, Ecologie,* CNRS Editions, Paris.

Tachet, H., Usseglio-Polatera, P. & Roux, C. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Trichoptera in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 397-415.

Townsend, C.R. & Thompson, R.M. (2007) Body size in streams: macroinvertebrate community size composition along natural and human-induced environmental gradients. In: *Body size: The structure and function of aquatic ecosystems.* (Eds A.G. Hildrew & D. Raffaelli & R. Edmonds-Brown). Cambridge University Press, Cambridge.

Townsend, C.R., Uhlmann, S.S. & Matthaei, C.D. (2008) Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology,* **45,** 1810-1819.

Turnpenny, A.W.H. & Williams, R. (1980) Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology,* **17,** 681-693.

Usepa (U.S. Environmental Protection Agency) (2000) Atlas of America's Polluted Waters. Office of Water, Unites States Environmental Protection Agency, Washington, DC.

Usseglio-Polatera, P. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Aquatic Insects in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 417-437.

Usseglio-Polatera, P. & Tachet, H. (1994) Theoretical Habitat Templets, Species Traits, and Species Richness - Plecoptera and Ephemeroptera in the Upper Rhone River and Its Floodplain. *Freshwater Biology,* **31,** 357-375.

Waters, T.F. (1995) *Sediments in streams: sources, biological effects, and control,* AFS Monographs, Bethesda, Maryland.

Waters, T.F. & Hokenstrom, J.C. (1980) Annual Production and Drift of the Stream Amphipod Gammarus-Pseudolimnaeus in Valley Creek, Minnesota. *Limnology and Oceanography,* **25,** 700-710.

Wilby, R.L., Dalgleish, H.Y. & Foster, I.D.L. (1997) The impact of weather patterns on historic and contemporary catchment sediment yields. *Earth Surface Processes and Landforms,* **22,** 353-363.

Wright, J.F., Furse, M.T. & Moss, D. (1998) River classification using invertebrates: RIVPACS applications. *Aquatic Conservation-Marine and Freshwater Ecosystems,* **8,** 617-631.

Zweig, L.D. & Rabeni, C.F. (2001) Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society,* **20,** 643-657.

6.6 Tables and Figures

Table 6.1. The results of mixed-effects models showing the response of macroinvertebrate community variables and individual abundance to experimental sediment addition in the Usk catchment, Wales. Percentage change in each variable over the range of sediments accumulated is also shown.

Response variable	Slope	% change	*p*
Richness	-0.11	- 30%	0.001
EPT richness	-0.12	- 46%	<0.0001
Abundance	-2.6	- 90%	<0.0001
DCA axis 1	0.03		<0.0001
DCA axis 2	-0.03		0.0004
Baetis rhodani	-0.018	- 42%	0.003
Ephemerella ignita	-0.014	- 59%	0.018
Ecdyonurus sp.	-0.021	- 71%	<0.0001
Leuctra moselyi	-0.016	- 48%	0.011
Leuctra geniculata	-0.017	- 90%	0.002
Gammarus pulex	-0.04	- 70%	<0.0001
Trait diversity	-0.0003	- 24%	0.001
FCA axis 1	0.016		<0.0001
FCA axis 2	-0.012		0.0004

Notes:

1. N= 65; d.f = 61.
2. Study streams (3) were included as random factors. Only significant models are shown.

Table 6.2. The results of mixed effects models showing how the representation of individual trait category responded to experimental sediment addition in the Usk catchment, Wales. Percentage change over the range of accumulated sediment is also shown. Conventions as in Table 6.1

Trait	Category	Slope	% change	*p*
Life-cycle duration	< 1 year	0.47	+ 20%	0.001
Reproduction	ovoviviparity	-1.01	- 70%	<0.001
	Clutches, free	0.7	+ 80%	<0.001
Food	Detritus >1mm	0.4	+ 40%	<0.001
Respiration	Tegument	0.32	+ 24%	0.012
	Gill	-0.4	- 16%	-0.005
Locomotion	Full swimmers	-0.52	- 26%	<0.001
	Interstitial	0.13	+ 14%	0.008
	Burrower	0.41	+ 50%	<0.001
	Temporarily attached	-0.14	- 24%	0.008

Table 6.3. Mann-Whitney U test (z-scores) showing "nestedness" of individual taxa along the sediment gradient induced experimentally in three streams in the Usk catchment, Wales. * $p<0.05$; only taxa included in the ordination are shown.

Taxon	z-score	*p*
Baetis rhodani	-3.19	0.001*
Baetis scambus	-0.85	0.20
Ephemerella ignita	-1.68	0.04*
Ecdyonurus sp.	-2.86	0.002*
Habrophlebia fusca	-0.05	0.48
Leuctra moselyi	-0.6	0.27
Leuctra geniculata	-2.27	0.01*
Drusus annulatus	-1.13	0.13
Sericostoma personatum	-1.2	0.11
Odontocerum albicorne	-0.84	0.20
Simuliidae	-2.42	0.007*
Chironomidae	-1.6	0.06
Elims aenea	-0.92	0.18
Esolus parallelepipedus	-0.81	0.20
Limnius volckmari	-0.92	0.18
Dytiscidae	-1.14	0.13
Oligochaetes	-0.84	0.20
Gammarus pulex	-0.11	0.45

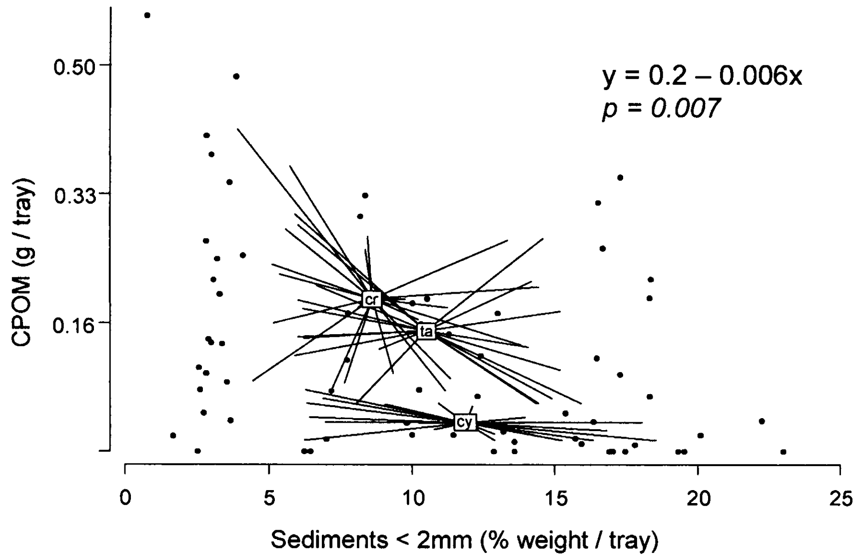


Fig. 6.1. Relationship between CPOM (g / tray) and fine sediments in trays across the three replicate streams in the Usk catchment, Wales. Samples are grouped by stream (lines connecting samples to labels); Cr = Crai; Cy = Cynrig; Ta = Tarell. Parameters are based on mixed-effects model with streams as random factors.

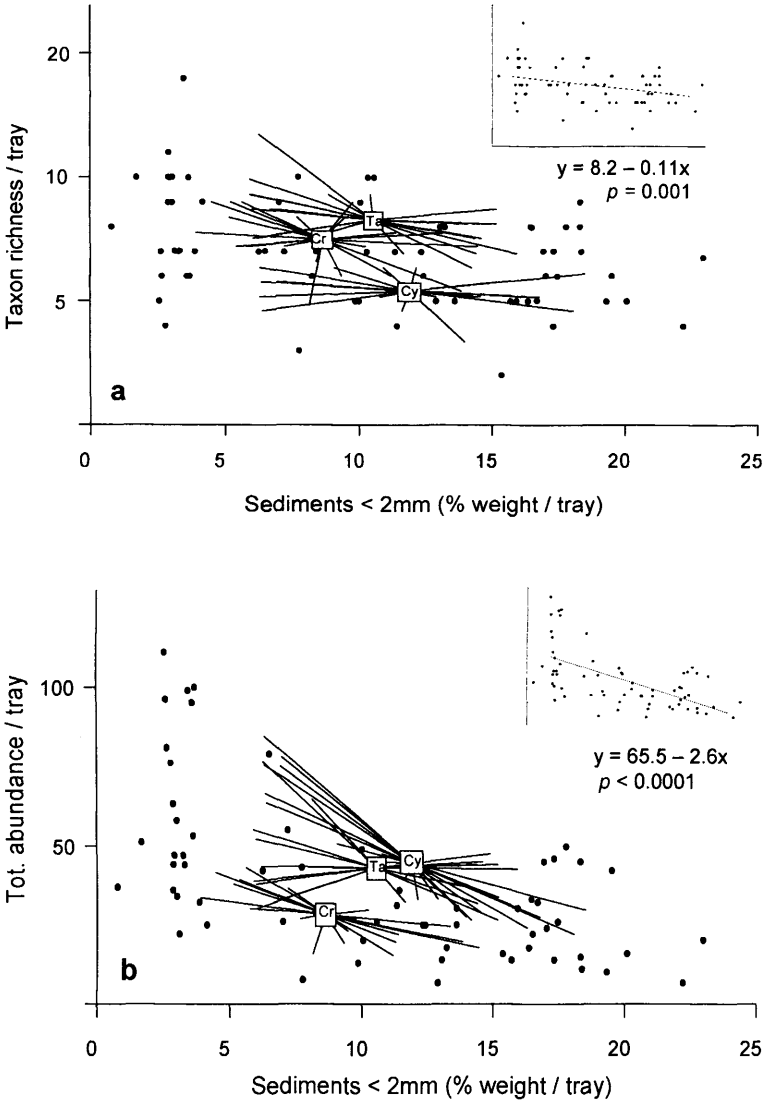


Fig. 6.2. Relationship between taxon richness (a) and abundance (b) and fine sediment content in trays across the three replicate streams in the Usk catchment, Wales. Details as in Fig. 1.

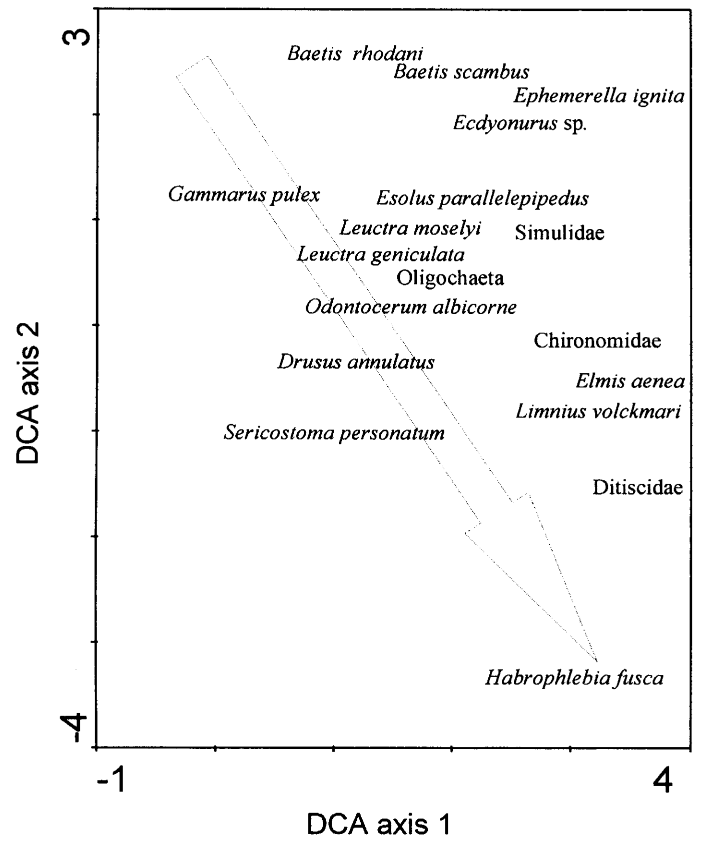


Fig. 6.3. Plot of taxa collected during the experiment on the first DCA plane. Only taxa occurring more than four times were included. Arrow represents increasing fine sediments as reflected by correlation with both axes.

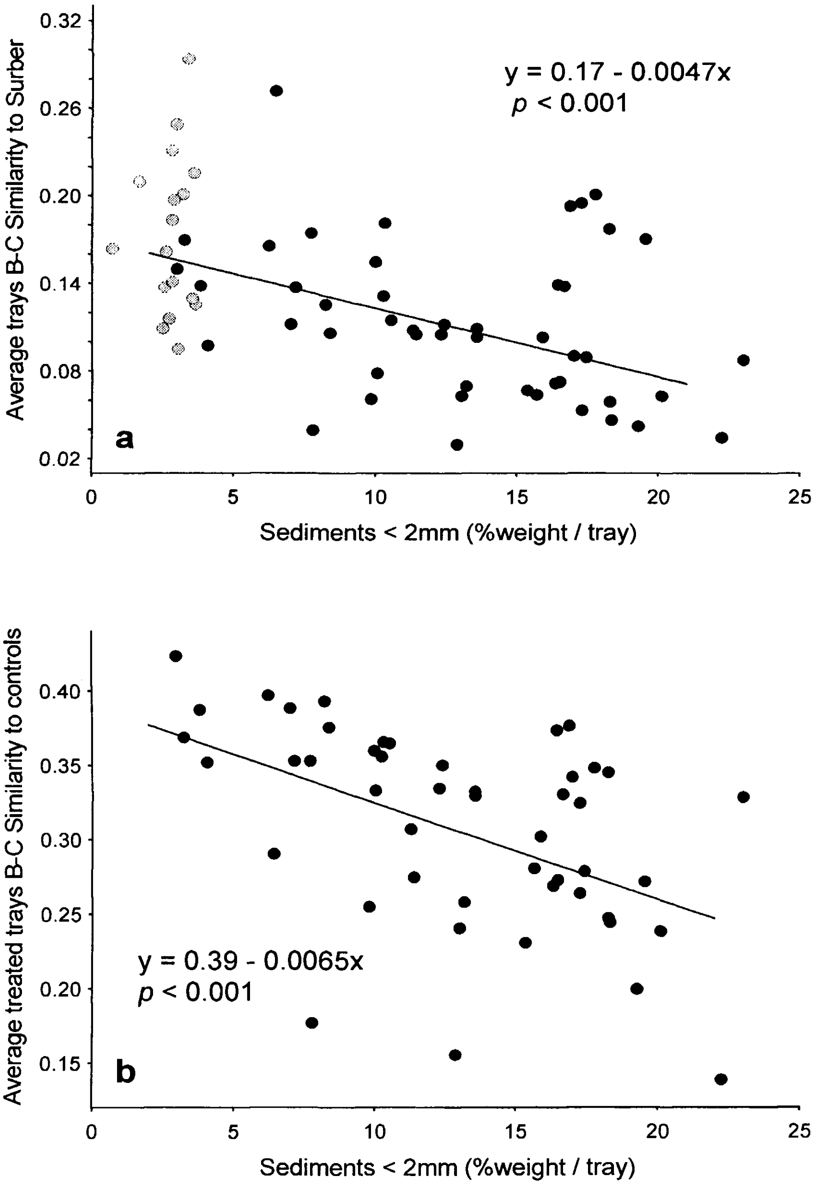


Fig. 6.4. a) Plot showing average similarity between trays (control + treatment) to Surber samples in relation to fine sediment content during an experiment involving sediment addition to three streams in the Usk catchment, Wales. Control trays are in grey. b) Average similarity of treated trays to control trays in relation to fine sediment content. Parameters are based on mixed-effects model.

Chapter 7 - General discussion

Most of the UK landscape was covered by woodland until c 5000 years ago, when Mesolithic settlements resulted in increasing clearings of woodland areas (Owens & Walling, 2002). Since then, land clearance and cultivation associated with population growth have significantly accelerated land erosion and altered geomorphic processes on land and in river systems (Evans, 1990). There is now widespread recognition that catchment and floodplain modification by humans have been responsible for altered sediment regimes across all continents (Owens *et al*, 2005) with such trends superimposed over climate-change effects. Despite increasing research effort, current knowledge on the ecological effects of increased sediments supply to lotic systems is dominated by a structural approach describing community changes and species-specific tolerance. Functional response and conservation implications have been assessed only recently, but our understanding is still limited by the variable nature of sediment character and the associated multi-scale covariables.

As noted in the introduction, work on this thesis began with the challenge of quantifying the ecological effects of sediments in the Usk system, and separating them from other possible confounding effects on the distribution, composition and trait character of organisms. By adopting field surveys and experiments, as well as ready-available data on land-use and geomorphology, the work was able to assess the extent and the potential causes of sediment delivery in the Upper Usk catchment, Wales. Also, in demonstrating how stream-invertebrate richness, composition and specific trait representation were affected by increasing deposited sediments, most of the initial hypotheses were supported. More importantly, several response patterns of benthic invertebrates appeared consistent between surveys and experiments, thus reinforcing their generalisation. This also shed light on some of the potential mechanisms involved. Finally, the thesis also highlighted important aspects related to conservation of benthic taxa and their functional diversity in face of increasing sediment delivery to lotic waters worldwide.

Land-use and fine sediments in the upper Usk catchment

In the Upper Usk catchment, land-use and, in particular, the extent of woodland cover and bank erosion appeared to influence sediment delivery in streams. As seen in Chapter 2, these relatively coarse sediments are likely generate from within the channel (Knighton, 1998), as previously estimated for other catchments in the region (Walling, Collins & McMellin, 2003). Both surveys at catchment and patch scale were obviously no more than a snapshot and it is likely that in-stream sediment conditions may vary rapidly in these flashy streams (Environment Agency, 1998). Relatively low sediment cover was in fact observed also in grassland locations with eroded banks, so that other factors besides woodland cover may influence sediment loads. Nonetheless, this localised variation in sediment character was accompanied by significant structural and functional effects on macroinvertebrates communities that were revealed only at the higher spatial resolution (patch scale). Sediment effects were negligible at the reach scale as the larger stream bed area covered with the hand-net likely comprised many sediment free patches or refugia. Larger scale differences in dominant land-use and associated stream water quality (BOD, nitrates) appeared to influence the benthic fauna at this scale. In addition, dominant land-use appeared to mediate sediment effects at the patch scale where invertebrates' response differed between upland and grassland sites. This is consistent with other findings where sediment effects were stronger for streams in semi-natural conditions (Matthaei *et al*, 2006). Therefore, despite the Usk river system being a Special Area of Conservation under the EU Habitats Directive (92/43/EEC), results show that even extensive land-use practises and limited sediment release could have important ecological consequences in semi-natural catchments. Although localised, bank erosion and livestock grazing adjacent stream channels could have far-reaching effects on in-stream habitat (Braccia & Voshell, 2007).

Certainly, specific research is needed to identify patterns of sediment mobilisation, transport and storage as well as the main sediment sources across the catchment with confidence (e.g. fingerprinting), but future management should consider investing in impeding livestock access to stream channels (by fencing or moving field access away from water courses) and riparian reforestation. Livestock trampling not only could directly increase the supply of fine grains to streams, but could result in channel widening with associated reduction in flow velocity and consequences for sediment mobilisation and residence time (Waters, 1995). By prioritising areas with high susceptibility to erosion, even limited reforestation could be cost-effective in reducing sediment supply. In a New Zealand pasture catchment, for example, reforestation of selected areas (8 % of basin) was estimated to reduce landslide derived sediment by 30%, whereas 25% of land would need to be reforested to achieve similar reductions without prioritisation (Reid & Page, 2003). Also, where water abstraction and impoundment affect stream discharges, care should be taken in maintaining sufficient water flow and frequent spates to limit sediment residence time or gravel compacting.

As the timing and duration of sedimentation episodes are crucial to both fauna and flora in coming seasons, future research should assess temporal dynamics of sediment entrainment and deposition by using sediment traps collected seasonally from different locations; observed patterns could be related then to flow regimes and precipitation.

Macroinvertebrates response

Over the range of deposited sediment observed in the study area (1 – 35%) taxon richness and EPT richness declined by c 20-25%. In the artificial tray experiment reduction of overall and EPT richness approached 30-45% in the most sedimented sites. Direct quantitative comparison is not straightforward, however, since in the experiment sediments were expressed as a fraction of weight, but sediment cover in the most impacted trays was more than 60% (visual estimation upon retrieval).

Such responses were expected and frequently observed in other surveys and experiments across continents (Extence, 1978; Fossati *et al*, 2001; Kreutzweiser, Capell & Good, 2005; Doledec *et al*, 2006; Matthaei *et al.*, 2006) and imply that similar mechanisms may be involved that are certainly linked to common biological traits of sensitive taxa. Impairment of feeding and respiratory activity, for example, has been frequently invoked as the main source of stress for grazers, filter feeders and organisms with external gills (Lenat, Penrose & Eagleson, 1981; Lemly, 1982; Strand & Merritt, 1997;

Rabeni, Doisy & Zweig, 2005; Doledec *et al.*, 2006). Not only were such effects confirmed here for the Usk catchment, but by examining trends in the representation of diverse biological traits along both land-use and sediment gradients this thesis also showed how process at different spatial extents may have contrasting effects on trait composition. Representation of feeding and behavioural traits was mostly related to local sediment character while traits associated with population growth and resilience were influenced by wider catchment modification. Interestingly, the response of some life-history traits appeared to transcend scale. Larger organisms with longer life-cycles were disfavoured by both basin scale land-use and patch scale sedimentation, likely reflecting sensitivity towards frequently disturbed or unstable conditions. Richards *et al.* (1997) also hypothesised that fine substrata may represent transient habitats unsuitable for K-strategists. These observations show that fine sediment delivery to streams can affect benthic organisms through a wide range of mechanisms including direct effects on feeding and respiratory structures and efficiency and indirect effects on habitat character.

These results were not simply based on observational approaches, but their validity was further reinforced by follow-up experiments where benthic density and richness were significantly reduces by sand addition and traits related to feeding and locomotion appeared similarly affected. Although with some limitations associated with experimental artefacts (discussed in Chapter 6 and below), the field experiment provided further evidence for the causal relation between in-stream sediments and trait composition. On the same theme, and linked to the selective elimination or limitation of functional groups (and taxa), trait diversity appeared markedly reduced where sediment content was high in both survey and experiment.

The transient unstable nature of fine sediment deposits is not only likely to affect K-selected organisms in the long term, but as particles are constantly redistributed in-stream, even episodic events and small bed-loads can reduce benthic densities over very short periods (e.g. Gibbins *et al*, 2007). This possibility was formally tested and confirmed in the Usk catchment by the replicated BACI experiment involving two similar upland reaches (Chapter 5).

Low-level increases in deposited and saltating sediments resulted in significant decline of benthic densities and increased drift over just 24 hours. Interestingly, such responses appeared to be delayed until darkness, reflecting the diel activity patterns of many sensitive taxa (e.g. epilithic grazers). As noted before, however, scaling-up these small-scale, short-term effects so as to explain larger scale patterns requires caution. Nonetheless, substantial reduction in benthic densities over 24 hours may indicate how negative effects are likely where sediment delivery is sustained.

As previously discussed, organisms' sensitivity to sediments appeared dictated by their biological traits, whose overall diversity also declined in impacted locations.

This process, the selective filtering of taxa and traits, appeared the likely driver of nestedness in species composition along sediment gradients observed in surveys and in the experiment. Local extinction and impaired colonization of sensitive taxa resulted in a progressive loss of rare species as sedimentation increased. Such patterns clearly conform to a non-random species loss that is commonly observed in natural systems and may have consequences for ecosystem functioning (e.g. Larsen, Williams & Kremen, 2005). To my knowledge studies on the role of sediment smothering in the formation of nested subset patterns in benthic organisms have yet to be published, but these trends suggest that similar mechanisms may be operating where catchments are modified with important conservation implications. Also, in revealing how processes at different spatial scale, catchment land-use and local sediment deposition, apparently determined nestedness in communities, the thesis also confirmed the scalar nature of nested patterns (Summerville, Veech & Crist, 2002); not only biogeographic processes and speciation over long time scale, but also small scale variation in habitat quality and patch selection can influence the degree of nestedness in natural communities.

Certainly, nestedness analysis cannot establish a sure causal relationship between an environmental variable and species occurrences, but the trends observed here should help refine future process-based hypotheses testing of sediment effects.

Ecological implications

The consequences of catchment land-use intensification on lotic systems are well documented (Manel, Buckton & Ormerod, 2000; Allan, 2004) with habitat structure, hydrology, temperature, water quality and ratio of allochthonous to autochthonous energy sources all likely to be modified. Although agricultural practices were generally extensive in the Usk system they resulted in altered water quality with apparent effects on benthic fauna. Similar trends in water quality were sufficient to affects invertebrates in the adjacent Wye catchment (Clews & Ormerod, 2009). Interestingly, these land-use influences apparently masked most sediment effects, probably linked to higher nutrient concentrations (Niyogi *et al*, 2007; Townsend, Uhlmann & Matthaei, 2008). Overall however, invertebrate response to sediments as revealed by surveys and experiments illustrates that any repetition of these trends could have important ramification for the conservation of certain taxa and ecosystem functioning. Here, for example, larger, long-lived taxa and predators appeared most sensitive to land-use and sedimentation; this selective loss of taxa and functional groups along with the evidence that size-biased loss of species could affect functions of whole ecological networks, suggest that wider ecosystem consequences are likely (Duffy, 2003; Larsen *et al.*, 2005). However, even if overall functional diversity declined in face of habitat changes, it has to be demonstrated whether effects on specific trait representation would ultimately result in local extinction of sensitive taxa (Olden, Hogan & Vander Zanden, 2007; Olden, Poff & Bestgen, 2008). On the same theme, more information is needed in order to link response-traits, those sensitive to disturbance, to effect-traits, those determining species influence on ecosystem functions. For example, a decline in filter feeding taxa in the face of increasing sediment regimes could have consequences for long term longitudinal transport of particulate matter in impacted streams. Moreover, loss of sensitive filter feeding hydropsychids may results in destabilised gravel beds with consequences for other organisms (Cardinale, Gelmann & Plamer, 2004).

The observed decline in benthic richness and density and the higher proportion of burrowers with deposited sediments may as well have bottom-up effects on insectivorous and drift-feeding fish in this important game fishery (Suttle *et al*, 2004). If accompanied by effects on spawning habitats, sustained sediment delivery could also have important economic consequences.

Limitations of the study

Despite several similarities in apparent organism response between surveys and experiments, this study has some limitations that need brief discussion.

As explained above, both surveys represented a snapshot of habitat and biological conditions that certainly could vary between seasons and years. Nonetheless, most of the organisms sampled had univoltine or longer life-cycles so that assemblages should reflect antecedent conditions.

The extent of sediment deposition in the sampled locations was only limited to c 35% (accurate patch-scale survey). Observed biological responses were certainly similarly limited and did not illustrate all range of possible ecological implications. However, extending sample locations to the most impaired sites would have strongly increased the risk of ascribing sediment effects to other factors (e.g. eutrophication).

Both field experiments were spatially and temporally limited, so that scaling-up need caution. The duration of the drift experiment (24 hours) was insufficient to reduce benthic richness or change community composition. Also, drifting and benthic organisms constitute separate sets so that direct comparison with the survey is not straightforward.

Some experimental artefacts were instead associated with the experiment involving small plastic trays held *in situ*, as discussed in Chapter 6. Briefly, the limited colonization period and the enclose nature of the trays resulted in the absence or under representation of some taxa relatively common in the benthos. This partly limited the representation of biological traits observed under natural conditions. However, any limited colonization did not appear to mask sediment effects that clearly reduced density, richness and trait composition.

7.1 Conclusion

Throughout the study sites sediment entrainment and deposition appeared to be localised phenomena associated with banks erosion and riparian clearing. This clearly illustrates the potential benefits of appropriate agri-environment and management schemes in maintaining riparian habitats (Petersen *et al*, 2004). Considering the rapid fluctuation of discharge with rainfall, if fencing and conservation of riparian buffers are implemented across the Usk system, the study streams are likely to be only moderately affected by sedimentation in the near future.

Although variation in land-use and altitude appeared the most important factors affecting the benthic community at the catchment scale, fine sediment deposition had clear ecological effects and macroinvertebrates showed consistent responses across scales. Besides validating some of the frequently observed effects on benthic structure (reduced taxon richness, EPT richness, abundance), the study showed how sedimentation could alter overall trait diversity and composition with potential effects on ecosystem functioning and ramification for invertebrates conservation. The thesis also provided further support for the use of trait-based measures for freshwater biological monitoring; by identifying mechanistic link between sensitive traits and sediment character, similar measures could be tested and eventually adopted across biogeographic boundaries.

Future work should certainly aim to assess invertebrates' community variation over a wider range of natural sediment cover, possibly comprising hyporheic habitat and organisms. Also longer term field experiments and laboratory work would be necessary to understand better the link between sensitive traits, sediment features and species proneness to local extinction.

7.2 References

Allan, J.D. (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics,* **35,** 257-284.

Braccia, A. & Voshell, J.R. (2007) Benthic macroinvertebrate responses to increasing levels of cattle grazing in Blue Ridge Mountain streams, Virginia, USA. *Environmental Monitoring and Assessment,* **131,** 185-200.

Cardinale, B.J., Gelmann, E.R. & Plamer, M.A. (2004) Net spinning caddisflies as stream ecosystem engineers: the influence of Hydropsyche on benthic substrate stability. *Functional Ecology,* **18,** 381–387.

Clews, E. & Ormerod, S.J. (2009) Improving bio-diagnostic monitoring using simple combinations of standard biotic indices. *River Research and Applications,* **25,** 348 - 361.

Doledec, S., Phillips, N., Scarsbrook, M., Riley, R.H. & Townsend, C.R. (2006) Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. *Journal of the North American Benthological Society,* **25,** 44-60.

Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters,* **6,** 680-687.

Environment Agency (1998) *Rural Usk LEAP Consultation Report,* Environment Agency Wales.

Evans, R. (1990) Soil erosion: its impact on the English and Welsh landscape since woodland clearance. In: *Soil Erosion in Agricultural Land.* (Eds J. Boardman & D.L. Foster & J.A. Dearing), pp. 232-254. Wiley, Chichester.

Extence, C.A. (1978) The effects of motorway constructions on an urban stream. *Environmental Pollution,* **17,** 245-252.

Fossati, O., Wasson, J.G., Hery, C., Salinas, G. & Marin, R. (2001) Impact of sediment releases on water chemistry and mocroinvertebrate communities in clear water Andean stream (Bolivia). *Archiv fur Hydrobiologie,* **151,** 33-50.

Gibbins, C., Vericat, D., Batalla, R.J. & Gomez, C.M. (2007) Shaking and moving: low rates of sediment transport trigger mass drift of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences,* **64,** 1-5.

Knighton, D. (1998) *Fluvial Forms and Processes: A New Perspective,* Hodder Arnold, London.

Kreutzweiser, D.P., Capell, S.S. & Good, K.P. (2005) Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology,* **39,** 55-66.

Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters,* **8,** 538-547.

Lemly, D. (1982) Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia,* **87,** 229-245.

Lenat, R.D., Penrose, D.L. & Eagleson, W.K. (1981) Variable effects of sediment addiction on stream benthos. *Hydrobiologia,* **79,** 187-194.

Manel, S., Buckton, S.T. & Ormerod, S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology,* **37,** 756-770.

Matthaei, C.D., Weller, F., Kelly, D.W. & Townsend, C.R. (2006) Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology,* **51,** 2154-2172.

Niyogi, D.K., Koren, M., Arbuckle, C.J. & Townsend, C.R. (2007) Stream communities along a catchment land-use gradient: Subsidy-stress responses to pastoral development. *Environmental Management,* **39,** 213-225.

Olden, J.D., Hogan, Z.S. & Vander Zanden, M.J. (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography,* **16,** 694-701.

Olden, J.D., Poff, N.L. & Bestgen, K.R. (2008) Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology,* **89,** 847-856.

Owens, P.N., Batalla, R.J., A. J. Collins, B. Gomez, D. M. Hichs, A. J. Horowitz, Kondolf;, G.M., M. Marden, M. J. Page, D. H. Peacock, E. L. Petticrew, W. Salomons & N. A. Trustrumi (2005) Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications,* **21,** 693–717.

Owens, P.N. & Walling, D.E. (2002) Changes in sediment sources and floodplain deposition rates in the catchment of the river Tweed, Scotland, over the last 100 years: the impact of climate and land use change. *Earth Surface Processes and Landforms,* **27,** 403–423.

Petersen, I., Master, Z., Hildrew, A.G. & Ormerod, S.J. (2004) Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology* **41,** 934-950.

Rabeni, C.F., Doisy, K.E. & Zweig, L.D. (2005) Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences,* **67,** 395-402.

Reid, L.M. & Page, M.J. (2003) Magnitude and frequency of landsliding in a large New Zealand catchment. *Geomorphology,* **49,** 71-88.

Richards, C., Haro, R.J., Johnson, L.B. & Host, G.E. (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology,* **37,** 219-&.

Strand, M.R. & Merritt, R.W. (1997) Effects of episodic sedimentation on the netspinning caddisflies *Hydropsyche betteni* and *Ceratopsyche sparna* (trichoptera: hydropsychidae). *Environmental Pollution,* **98,** 129-134.

Summerville, K.S., Veech, J.A. & Crist, T.O. (2002) Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? *Oikos,* **97,** 195-204.

Suttle, K.B., Power, M.E., M.;, L.J. & Mcneely, C. (2004) How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications,* **14,** 969–974.

Townsend, C.R., Uhlmann, S.S. & Matthaei, C.D. (2008) Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology,* **45,** 1810-1819.

Walling, D.E., Collins, A.L. & Mcmellin, K.G. (2003) A reconnaissance survey of the source of interstitial fine sediment recovered from salmonid spawning gravels in England and Wales. *Hydrobiologia,* **497,** 91-108.

Waters, T.F. (1995) *Sediments in streams: sources, biological effects, and control,* AFS Monographs, Bethesda, Maryland.

Appendix 1

Published version of Chapters 3, 5 and 6

Larsen S., Vaughan I. & Ormerod S.J. 2009. Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology* 54: 203-219

Larsen S. and Ormerod S.J. 2010. Low-level effects of inert sediments on temperate stream invertebrates. *Freshwater Biology* 55: 476-486.

Larsen S., Pace G. & Ormerod S.J. 2010. Experimental effects of sediment deposition on the structure and function of macroinvertebrate assemblages in temperate streams. *River Research and Application*, in press.

Freshwater Biology (2009) **54**, 203–219 doi:10.1111/j.1365-2427.2008.02093.x

APPLIED ISSUES

Scale-dependent effects of fine sediments on temperate headwater invertebrates

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SUMMARY

1. Anthropogenic activities can increase fine sediment supply to streams over multiple spatial and temporal extents. Identifying the processes responsible, and the scale at which any effects on stream organisms become evident, are key management needs, but appropriately scaled surveys are surprisingly few.

2. We surveyed macroinvertebrates and superficial fine sediments at two spatial resolutions (reach- and patch-scale) in tributaries of the River Usk, a temperate, montane catchment in rural Wales (U.K.). Land use, habitat and geomorphological character were measured on-site or derived from an existing database (=Fluvial Audit). We aimed to identify: (i) how in-stream sediments varied with land use and associated geomorphology; (ii) likely consequences for macroinvertebrates and (iii) any scale-dependence in relationships between macroinvertebrates and sediment character.

3. At both the reach- and patch-scales, bed cover by fine sediment was related directly to the extent of eroding banks 500 m upstream. In turn, sedimentation and bank erosion were negatively correlated with catchment or riparian woodland extent.

4. At the reach scale, macroinvertebrate composition varied with catchment land use and stream chemistry, with richness declining as rough grazing or woodland was replaced by improved grassland. There was no response to deposited sediment except for weak increase in the relative abundance of oligochaetes.

5. By contrast, at the patch scale, fine sediments were accompanied by pronounced changes in invertebrate composition, and we ranked the 27 most common taxa according to their apparent sediment tolerance. General estimating equations showed that total and Ephemeroptera, Plecoptera and Trichoptera richness decreased significantly by 20% and 25% at the most sediment impacted sites (30% cover) by comparison with sediment-free sites.

6. We conclude that sediment deposition in the upper Usk system mostly reflects local bank erosion, with riparian woodland likely to mediate this process through bank stability. Fine sediment release had marked ecological effects, but these were detectable only at patch-to-patch scales. We suggest that investigation of localized sediment release in streams will benefit from scale-dependent or scale-specific sampling, and some effects could go undetected unless sample resolution is selected carefully.

Keywords: catchment, land-use, macroinvertebrates, scale, sediment

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Introduction

Many physicochemical variables that influence benthic invertebrate in rivers are mediated by catchment characteristics (Imhof, Fitzgibbon & Annable, 1996; Bunn & Davies, 2000; Ankers, Walling & Smith, 2003). These effects are scale-dependent because regional or catchment features influence processes at smaller spatial extents (Townsend *et al.*, 2003; Ciesielka & Bailey, 2007; Mykra, Heino & Muotka, 2007). A good example is where catchment or riparian land-use and geology determine sediment and nutrient runoff into streams (Rabeni & Smale, 1995; Jones *et al.*, 2001; Riley *et al.*, 2003; Bond, 2004; Opperman *et al.*, 2005; Niyogi *et al.*, 2007). In turn, the deposition of fine sediment, often from anthropogenic activities, can have major consequences for stream organisms (Luedtke & Brusven, 1976; Gray & Ward, 1982; Newcombe & Macdonald, 1991; Davies-Colley *et al.*, 1992; Waters, 1995; Gayraud, Herouin & Philippe, 2002; Greig, Sear & Carling, 2005).

In reality, quantitative understanding of the ecological effects of sediments and the mechanisms involved is poor (Davies-Colley *et al.*, 1992; Strand & Merritt, 1997; Angradi, 1999; Broekenhuizen, Parkyn & Miller, 2001; Gard, 2002; Parkhill & Gulliver, 2002). Knowledge of interactions among catchment land-use, diffuse sediment release and ecological effects is particularly uncertain for several reasons (Matthaei *et al.*, 2006). First, anthropogenic effects on sediment regimes range from catchment modification (e.g. agriculture) to local habitat alteration (e.g. livestock trampling), so that the exact source of sediments in any one location can seldom be identified readily (Imhof *et al.*, 1996). Secondly, much recent research in physical geography has aimed at parameterizing sediment regimes without exploring the response of organisms (Walling & Amos, 1999; Walling *et al.*, 2001; Collins & Walling, 2007). Thirdly, the ecological effects of sediment from anthropogenic sources, especially over large spatial or temporal extents, can be masked by natural variability. For instance, some types of agricultural intensification or the removal of riparian woodland might increase erosion and fine sediment release to streams, but also they alter temperature, organic matter supply and nutrient fluxes (Osborne & Kovacic, 1993; Roth, Allan & Erickson, 1996). As a result, identifying the scale, severity and impact of altered sediment fluxes in catchments affected by more general chemical or eco-hydromorphological degradation, has become a management need (Feld, 2004). While the extent and resolution (grain) of these investigations can influence findings, scale dependence is seldom explicitly included in monitoring programmes or experimental design. Ideally, in impact-assessment studies, the scales of measurement and organism responses should coincide. By increasing resolution (i.e. using more smaller-size sampling units) variation in response variables and sensitivity of statistical tests should also increase (e.g. Smiley & Dibble, 2008).

By combining two consecutive surveys at different resolution, in this paper we aimed to understand the apparent causes and extent of sediment deposition in a temperate, montane river system (the Usk, Wales), and to identify the scale at which any effects were relevant to stream invertebrates. The Usk catchment is particularly suitable for this purpose because, in comparison with adjacent catchments such as the Wye (e.g. Ormerod & Edwards 1987), dominant geology and major aspects of ionic composition are relatively homogeneous, thereby reducing confounding ecological effects. While effects on stream function from urbanization are negligible and localized, the sandstone-dominated catchments of the Usk are liable to be sensitive to sediment mobilization (Sable & Wohl, 2006). Finally, land-use varies from semi-natural upland vegetation to modified improved grassland, implying possible effects on sediment release.

Our principal objectives were, first, to identify how in-stream sediment character varied between locations in relation to land use at different scales (riparian versus catchment). Secondly, we aimed to assess the extent to which variation in invertebrate composition among sites reflected sediment character or other habitat features in the channel, riparian zone and catchment. Thirdly, we aimed to identify any scale-dependence in apparent relationships between macroinvertebrates and sediment character. Two main predictions were tested: (i) variation in observed deposited sediments should be explained by riparian and catchment land-use and associated processes, namely bank erosion and (ii) invertebrate should respond to deposited sediments, but we expected different macroinvertebrate patterns to be detectable by changing spatial resolution. At larger spatial extents, we expected that links between organisms, altitude and dominant land-use should be most evident, while at the patch scale local effects, such as deposited sediments, should be detectable.

Methods

Study area

The River Usk is one of the largest rivers in Wales, with a main channel 120 km long and catchment area 1358 km^2. One of the most important game fisheries in England and Wales, the Usk rises in rough grazing land at an altitude of 500 m on Mynydd Du (National Grid Reference SN819239; 51.52 N, 03.50 W) before flowing eastwards along the northern face of the Brecon Beacons and then southwards to its confluence with the Severn Estuary.

From its source on the Black Mountain, the river flows over sandstones and mudstones of the Old Red Sandstone Series, with soil types a blend of brown earths or peat and gley soils on wetter plateaus. The dominantly rural area is sparsely populated (<20 people per km^2) and therefore urbanization has negligible impact. In this temperate and relatively maritime location, annual average precipitation over the catchment averages 1336 mm, but exceeds 2500 mm in some upland locations. Groundwater contributions, even to typical dry weather flow, are modest (*c.* 15%), and river discharges fluctuate rapidly with rainfall (Environment Agency, 1998). This combination of factors brings some risks of both sediment release and sediment in-wash making the Usk an ideal catchment to investigate sedimentation effects. Moreover, stream waters in the rural parts of the Usk catchment are clean and well-oxygenated, and concentrations of plant nutrients are generally low. Otherwise, waters are relatively rich and fairly uniform in carbonate concentration, so that few organisms are limited by base-cation availability (Table 1).

Survey design

The first extensive survey (2006; 'reach-scale survey') comprised 32 reaches along 18 second-order tributaries mainly draining semi-natural upland vegetation (bracken, heath, moorland, acid grassland) and improved grassland used as rough grazing land, while woodland vegetation cover never exceeds 34% of any catchment. Sampling reaches were selected to cover the main land-use typology present in the study area, but selection was restricted to reaches where depth, flow velocity, stream width and particle size distribution were similar. Fourteen streams were sampled on two reaches and four streams on one

Table 1 Mean (±SD) of the main physicochemical and channel characteristics of the study streams in the Usk catchment, south-east Wales

River	Nitrate (mg L^{-1})	Phosphate (mg L^{-1})	Hardness (mg L^{-1})	BOD (mg L^{-1})	Flow velocity (m s^{-1})	Width (m)	Depth (cm)
Afon Ysgir*	0.99 (0.39)	0.01 (0.01)	68.2 (26.7)	1.18 (0.77)	0.34 (0.10)	6.50 (0.5)	19.5 (7.4)
Bran (2)*	0.86 (0.51)	0.01 (0.01)	58.4 (20.5)	1.13 (0.72)	0.32 (0.08)	4.7 (0.35)	19 (7.7)
Caerfanell	0.65 (0.33)	0.01 (0.01)	60.6 (57.9)	1.0 (0.38)	0.22 (0.02)	3.0 (0.5)	12 (2.1)
Camlais (2)	NA	NA	NA	NA	0.34 (0.03)	3.0 (0.9)	15.7 (3.1)
Cilieni (2)	NA	NA	NA	NA	0.32 (0.09)	4.2 (2.47)	12 (0.7)
Crai (2)	0.67 (0.89)	0.03 (0.18)	49.5 (16.2)	1.20 (0.34)	0.37 (0.03)	5.5 (0.70)	13.7 (1.7)
Cynrig (2)*	0.92 (0.38)	0.01 (0.01)	95.6 (191)	1.1 (0.50)	0.38 (0.12)	3.00 (1.0)	13.9 (3.6)
Eithrim	NA	NA	NA	NA	0.22 (0.06)	1.50 (0.3)	12.5 (1.2)
Grwyne Fawr (2)	1.20 (0.2)	0.02 (0.06)	90.1 (27.1)	1.1 (0.50)	0.37 (0.18)	5 (1.41)	18.9 (10)
Grwyne Fechan (2)	NA	NA	NA	NA	0.41 (0.15)	3.2 (0.35)	16 (6.3)
Honddu (2)*	1.58 (0.6)	0.02 (0.02)	92.6 (28.2)	1.24 (0.80)	0.45 (0.19)	5 (2.83)	20.4 (7.5)
Hydfer*	0.68 (1.1)	0.01 (0.02)	50.5 (20.2)	0.97 (0.50)	0.40 (0.20)	5.00 (0.7)	9.4 (3.2)
Menascin (2)	0.90 (0.8)	0.01 (0.02)	74.3 (33.1)	0.97 (0.35)	0.25 (0.02)	3.2 (0.35)	12.8 (3.1)
Rhiangoll (2)	1.50 (0.4)	0.02 (0.01)	146.9 (38.5)	1.29 (0.92)	0.34 (0.06)	2 (0.71)	13.4 (1.2)
Senni (2)*	0.92 (0.64)	0.04 (0.01)	76.8 (29.0)	1.19 (0.51)	0.23 (0.03)	4.5 (3.52)	13.3 (2.4)
Tarell (2)*	0.96 (0.33)	0.02 (0.02)	96.9 (154.1)	1.08 (0.65)	0.55 (0.01)	5 (2.12)	20.5 (4.6)
Ysgir Fawr (2)	NA	NA	NA	NA	0.34 (0.01)	3.7 (1.77)	15.2 (3.3)
Ysgir Fechan (2)*	NA	NA	NA	NA	0.30 (0.13)	4 (1.41)	15 (1.8)

The number (2) indicates that two reaches were sampled in the 2006 survey; NA, data were not available for the given stream.
*Those streams selected for the 2007 patch-scale survey.

reach, depending on accessibility and stream length (Fig. 1). The altitudinal range was 190–400 m.a.s.l. and distance between two reaches in a stream never exceeded 8 km. Although there was a risk that replicate reaches within streams might not be independent, all results and conclusions were unchanged when only one reach per stream was analysed.

The subsequent patch-scale survey, carried out in 2007 at locations nested within 12 previously sampled reaches on eight of the streams (see Table 1), was designed specifically to assess within reach effects of sediment deposition, i.e. at finer resolution. Informed by the results of the reach-scale survey, locations for patch sampling were selected to represent both upland and grassland while covering a range of sediment conditions. Sampling was again restricted to riffle-glide habitats, where depths and velocities were measured. Depending on availability, three to six patches per reach were sampled in a *c.* 15 m long section, for a combined total of 56 patch samples.

Environmental variables

Reach scale survey. We used a combination of field measurements and available data to characterize conditions in each of the 32 survey reaches. In the field, basic measurements of channel width, depth and flow velocity were taken along a 10 m stretch, averaged from three values. The percentage of surface water overhung by riparian vegetation was also estimated. Next, substratum composition was assessed over each 10 m section using a modified version of the U.K. Environment Agency's River Habitat Survey (Environment Agency, 2003), where the proportionate bed-cover of bedrock, boulder, cobble, gravel, sand, fine sand, clay and earth were estimated. Deposited fine sediment (<2 mm) cover within a (300 cm^2) circular quadrat was estimated as the percentage of stream bed, in 5% increments, covered by fine particles (Platts, Megaham & Minshall, 1983; Rabeni, Doisy & Zweig, 2005). Twelve estimations in two transects over the 10 m section were combined and the mean determined. Although these 12 observations covered only a small portion of the stream bed, they were sufficient to allow reaches to be ranked along the sedimentation gradient.

To characterize typical size distribution of fine sediments across all reaches, composite samples of fine sediment were collected from 10 reaches of seven relatively sediment-rich streams, and then sediment composition determined using dry sieving.

In order to support the field measurements, additional data were retrieved as far as possible for each reach from the 'Fluvial Audit' database for the upper Usk tributaries. Designed and progressively applied across British rivers by the GeoData Institute (Southampton), Fluvial Audit uses contemporary field survey, historical and contemporary maps, documentary information and scientific literature resources to gain a comprehensive understanding of the geomorphological controls on a given river systems (Emery & Hill, 2005). The Audit is both qualitative and quantitative, and from the latter data we took the length of eroding banks for 27 of our reaches where direct field observation had been previously been digitalized (Emery & Hill, 2005). The extent of erosion was calculated for 1 km and 500 m upstream of the sample sites using ARC-GIS (ESRI, 2004).

Land-use for each reach was calculated at two spatial extents, respectively, a 150 m wide buffer on each side of the stream for 1 km upstream and the whole catchment area draining to each site. Land-use data were extracted from existing GIS land cover layer created by the Countryside Council for Wales (CCW, 2002), the statutory Welsh agency for nature conservation and landscape protection. Catchment areas were derived using a 10 × 10 m resolution Digital Elevation Map of the Usk catchment (CCW, 2002). Slope classes were derived for every catchment, and low and high relief was calculated as the proportion of catchment with slopes <10% and >30% respectively.

Chemical data, obtained from the U.K. Environment Agency's Water Management Information System and based on standard methods (Standing Committee of Analysts, 1979, 1981, 1987, 1992), were available for 12 of the reaches (38%) as monthly concentrations of nitrate (mg L^{-1}), phosphate (mg L^{-1}), biochemical oxygen demand (BOD mg L^{-1}), water hardness as $CaCO_3$ (mg L^{-1}) and pH data (Table 1). Means were calculated for the year antecedent to invertebrate sampling. Although incomplete, these chemical data drained both grassland and semi-natural upland vegetation, and allowed an assessment of the extent to which water quality might have confounded or subsumed the ecological effects of fine sediments. Most reaches without chemical data

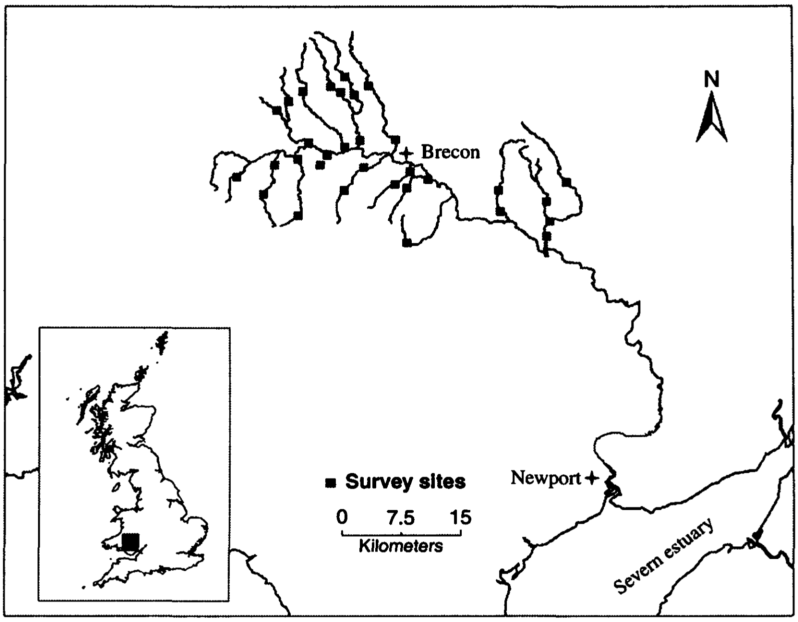

Fig. 1 Scaled schematic map of the Usk River system, Wales, showing sites selected for the 2006 reach-scale survey.

were the highest altitude locations where improved grasslands were less frequent, and nutrient concentrations would have been low.

Patch scale survey. All environmental data for the patch-scale survey were collected in the field. At each sampling site (*c.* 3 m^2), we made 10 visual estimates of deposited sediment immediately around the invertebrate Surber sampler (see below) and averaged these values. To complement these estimates, the amount of suspendable sediment from the stream bed was also measured at 45 of the patch-scale sites, with four measurements made each Surber location. A large metal box (24 x 18 cm) was pushed into the substratum and sediments from *c.* 2 cm depth were entrained in the measurable volume of water within the cylinder by mixing with a ruler. Suspended sediments within the range of 0.063–1 mm were filtered from 1 L of water, dried at 100–105 °C for 24 h, weighted and calculated as g m^{-2}. Organic material was reduced by washing and decanting. Water depth and flow velocity were also recorded at each site.

Macroinvertebrate sampling

Reach-scale survey. Benthic macroinvertebrates were collected, and reach-habitat characteristics recorded, in June and July 2006, when annual discharge was expected to be lowest and deposited sediments were stable and visible. Invertebrate sampling was restricted to fast flowing habitats (glides, riffles, with velocities typically <55 cm s^{-1}) since pools and margins naturally collect fine material. To collect macroinvertebrates, a kick sample of 3 min duration was taken both from riffles and glides over a 10 m reach, using a standard hand-net (Environment Agency, 1999; mesh 0.9 mm, area 25 cm^2). For this extensive survey we specifically used a hand net as it is widely used in biological monitoring programmes, such as RIVPACS (Wright, Furse & Moss, 1998), and we have investigated this method extensively (Bradley & Ormerod, 2002).

Note that, in both reach- and patch-scale surveys, we have assumed that a single sampling occasion is sufficient to reflect both assemblage composition and relationship with sediment cover, thus ignoring sediment dynamics or possible sediment release during events (Environment Agency, 1998). This assumption is justifiable because many of the organisms recorded have univoltine life cycles (or longer) so that assemblage composition should reflect antecedent conditions. In addition, our approach was designed to characterize variations between invertebrates and sediments at multiple sites rather than dynamics within sites.

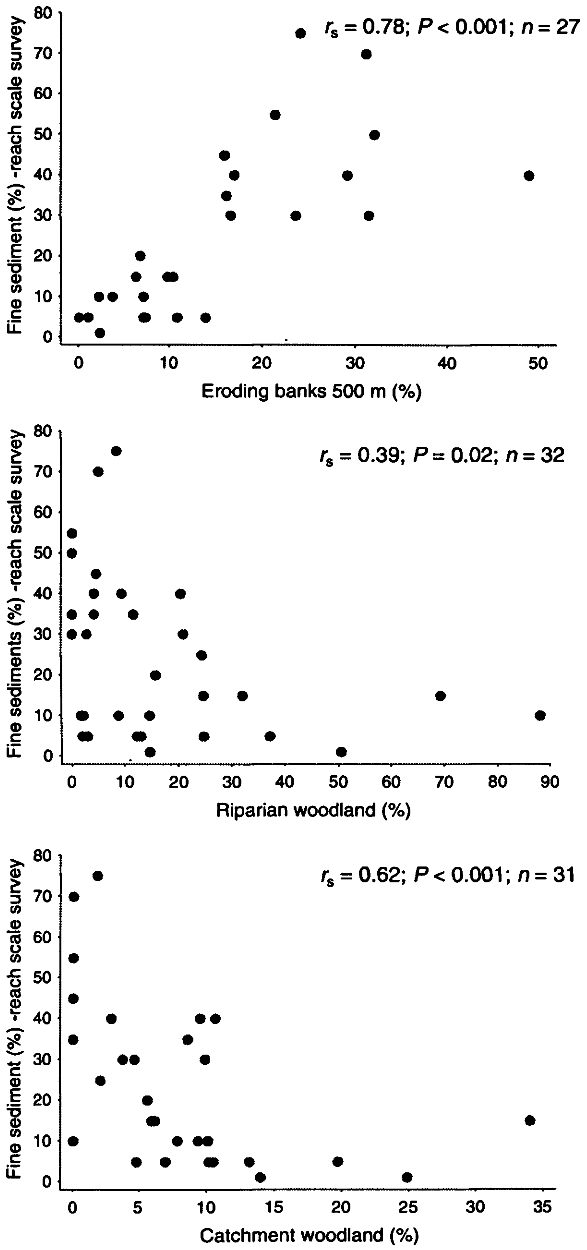

Fig. 2 Significant relationships between fine sediment cover, estimated from the reach scale survey and the extent of eroding banks for 500 upstream, riparian and catchment woodland cover in the Usk catchment, south-east Wales.

Patch-scale survey. To capture smaller-scale variations, and cover specifically a well-defined area of streambed where sediment conditions were assessed, we collected macroinvertebrates for the patch-scale survey using a Surber sampler in June and July 2007 (0.16 m^2; 0.44 mm). Because of this difference in timing and methods from the reach-scale survey, we compared reach-scale pattern among invertebrates generated from kick-samples and aggregated within-reach Surber data. The outcomes of this evaluation are reported at the end of the results section.

Both patch- and reach-scale samples were preserved immediately in ethanol. In the laboratory, macroinvertebrates were sorted and identified as far as possible to species (Edington & Hildrew, 1981; Elliott, Humpesch & Macan, 1988; Friday, 1988; Wallace, Wallace & Philipson, 2003). Diptera were identified to family and oligochaetes were not identified further.

Data analysis

To help interpret reach-scale pattern among invertebrates, we first used principal components analysis (PCA) to derive variates that described substratum (substratum PCA) conditions as well as catchment (Catchment PCA) and riparian land-use (riparian PCA). We quantified land-use variations in this way because percentages of individual land-use coverage are not independent, and principal components avoided any multicolinearity (Rier & King, 1996; Bruns, 2005). Land-use percentages were arcsin(x/100)$^{0.5}$ transformed prior to PCAs to homogenize variances. Land-use categories quantified were improved grassland, arable farmland, urban, upland vegetation and woodland, but urban land cover was omitted from the catchment PCA since its extent was small.

Also prior to any other analysis, we used detrended correspondence analysis (DCA) on both sets of invertebrate data (reach and patch) to identify the main variations in macroinvertebrate assemblage composition which could then be related to measured environmental variables in subsequent analyses. This form of unconstrained ordination was preferred to constrained ordination because it produces easily interpretable plots, it can reveal whether important environmental variables have been overlooked and it is generally regarded as a superior analytical tool because clear hypothesis testing can occur in subsequent steps (Jongman, Ter Braak & Van Tongeren, 1995). Analyses were run with both arithmetic and transformed abundances, but results were similar and only arithmetic abundances were used in subsequent analyses.

To assess how in-stream sediments varied with land use and associated geomorphology (objective i), we assessed relationships between percentage cover by deposited sediments, land use and other environmental variables using Spearman's rank correlation. Relationships among ordination axes, PCA axes and physicochemical variables were examined with Pearson's product–moment correlation.

To assess any consequences of sediments for macroinvertebrates (objective ii), based on expectations from previous studies (Quinn *et al.*, 1992; Waters, 1995; Angradi, 1999; Fossati *et al.*, 2001; Zweig & Rabeni, 2001; Kreutzweiser, Capell & Good, 2005; Braccia & Voshell, 2007), we examined invertebrate abundance, composition and richness, Ephemeroptera, Plecoptera and Trichoptera (EPT) abundance and richness, Shannon diversity and the relative abundances of individual taxa (as proportions for example of Coleoptera, Chironomidae and Oligochaeta) in relation to sediment features using generalized estimating equations (GEEs). Since multiple patches per reach were sampled in the 2007 survey, samples could not be treated as independent in conventional regression analyses. GEEs allow the analysis of data collected in clusters where within-cluster correlation is expected (i.e. patches from the same reach might be more similar than patches from different reaches). Accounting for the lack of statistical independence between samples, regression coefficients and variance were adjusted to avoid spurious correlations to be observed (Zorn, 2001; Vaughan, Noble & Ormerod, 2007; Ward & Myers, 2007). Spatially or temporally correlated data occur often in ecological research and this approach is a valuable tool (Vaughan *et al.*, 2007). GEEs models were run using R (Ihaka & Gentleman, 1996) using the program *geeglm* from the library *geepack* (Halekoh, Hojsgaard & Yan, 2006). Sequential Bonferroni correction was not applied because *a priori* hypotheses were formulated about invertebrates metrics and sediment features (Moran, 2003).

We identified any scale-dependence in apparent relationships between macroinvertebrates and sediment character (objective iii) by comparing the patterns generated between the reach- and patch-scale data. From the patch-scale survey, results were sufficiently clear to allow an assessment of the apparent tolerance to deposited sediment for the 27 most widespread taxa, occurring in more than 12 sites (20%). Curves relating the cumulative abundance of each taxon to the amount of deposited sediments were constructed and the percentage sediment cover at which each reached 50% abundance was determined. Following Zweig & Rabeni (2001), we assumed that intolerant taxa should reach 50% of their cumulative abundance at lower levels of deposited sediments.

Results

Reach scale: deposited sediments, land-use and channel geomorphology

Major patterns in land use and substratum were captured well by PCA. Two principal components explained 66% of the variation in riparian land-use, and up to 90% of the land-use variation at the catchment scale. Both Catchment and Riparian PC1 values represented a gradient from improved grassland to semi-natural upland vegetation, but with inverted signs; PC2 values were mostly related to woodland cover. In other words, land use varied in similar ways in both the riparian zone and catchment ($r = -0.75$; $P < 0.01$ for PCs1; $r = -0.5$; $P = 0.03$ for PCs2) with the major gradients a trend from improved grassland to upland vegetation and increasing woodland cover (Table 2).

In the stream channel, over 55% of the variance in substratum composition was explained by substratum PC1. Values correlated positively with the proportion of boulder and bedrock (loadings: 0.82 and 0.74) and negatively with gravel and fine sand (loadings: −0.91 and −0.78) thus describing a gradient from fine to coarse substrata. The amount of the channel surface

Table 2 Loadings onto the first two principal components (PC) revealing trends in catchment and riparian land-use in the Usk catchment, south-east Wales

	Catchment PCs		Riparian PCs	
Land-use type	PC1 (68%)	PC2 (22%)	PC1 (39%)	PC2 (27%)
Improved grassland	0.91	−0.22	−0.91	0.05
Upland vegetation	−0.98	−0.05	0.74	0.59
Woodland	0.52	0.84	0.42	−0.76
Urban	N.A.	N.A.	−0.13	−0.59
Arable	0.82	−0.35	−0.61	0.25

Values in parentheses are the percentages of variance explained by each PC.

covered by fine sediments, as estimated from the reach scale survey, ranged from 1% to 75% cover among reaches. Sieving revealed that most fine sediments were mainly (>82%) composed of sand (2–0.25 mm) and fine sand (0.25–0.125 mm), whereas silt and clay content was very low.

Up to 500 m–1 km upstream from each sampling point, the proportion of eroding banks ranged over 0–53%, and 0–49% respectively. Fine sediment cover increased strongly with the proportion of eroding banks 500 m upstream ($r_s = 0.77$; $P < 0.001$; $n = 27$) and more weakly to bank erosion 1 km upstream ($r_s = 0.59$; $P = 0.001$; $n = 27$) (Fig. 2). Sediment cover was also related to land use PC2 in both the riparian zone and catchment. This mostly reflected trends with woodlands (Fig. 3), fine sediments on the bed declining with both riparian ($r_s = 0.39$; $P = 0.02$; $n = 32$) and catchment woodland cover ($r_s = 0.62$; $P < 0.001$; $n = 31$). Proportions of eroding banks (1 km upstream) and riparian woodland were also negatively correlated ($r_s = 0.6$; $P < 0.001$; $n = 27$; Fig. 3). Interestingly, and contrary to expectation, steep slopes did not increase sediment delivery, and instead sediment cover declined as the proportion of catchment with slope >30% increased ($r_s = -0.39$; $P = 0.02$; $n = 31$). This effect arose because woodland cover increased on the steeper slopes ($r_s = 0.54$; $P = 0.001$; $n = 31$).

Deposited sediments were unrelated to either upland or improved grassland vegetation, but nitrate concentrations ($r_s = 0.6$; $P = 0.04$; $n = 11$) and BOD ($r_s = 0.72$; $P = 0.01$; $n = 11$) increased where catchments had more improved grass. There was some correlation between cover by fine deposited sediment and nitrate ($r_s = 0.6$, $P = 0.02$; $n = 12$), but this largely reflected the effect of just two streams (Honddu and Rhiangoll; see Table 1). On these grounds, any sediment effects would be unlikely to be confounded by nutrients, but nutrients effects could reflect variations in land use (cf. Niyogi *et al.*, 2007).

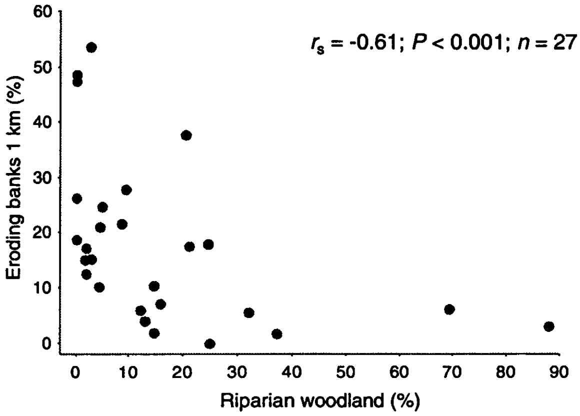

Fig. 3 Relationship between the extent of eroding banks for 1 km upstream and riparian woodland cover in the Usk catchment south-east Wales.

Reach-scale: assemblage composition

Over 70 000 individual invertebrates from 74 taxa were collected during the 2006 reach-scale surveys, but 16 taxa present in fewer than five samples were not considered in multivariate analyses (Appendix S1). *Ephemerella ignita* was the most abundant species, followed by chironomids, *Baetis rhodani*, simuliids and *Gammarus pulex*. (All naming authorities are given in Appendix S1.).

In DCA, two axes explained >37% of species variation, with *Caenis rivulorum, Baetis muticus, Rhithrogena semicolorata, Chloroperla tripuncatata, Dinocras cephalotes, Perla bipunctata* and Helodidae all increasing along axis 1 while *G. pulex, B. scambus, B. fuscatus*, Ceratopogonidae and the coleopteran *Oreodytes sanmarkii* declined. However, no trends in species composition were related to in-stream sediments or other channel features. DCA axis 1 (24%) instead varied with nitrate concentration ($r = 0.66$; $P = 0.01$; $n = 12$), Catchment land use PC1 ($r = -0.49$; $P < 0.01$; $n = 31$) and Riparian land use PC1 ($r = 0.36$; $P = 0.04$; $n = 32$). There was also a tendency for DCA axis 1 scores to vary with water hardness ($r = -0.58$; $P = 0.04$; $n = 12$). No correlations were evident along DCA axis 2. In other words, despite wide variations in fine sediment cover and bank erosion, reach-scale variations among invertebrates were most closely related to catchment land use and water quality, following a gradient from upland to improved grassland vegetation.

Reach-scale: invertebrate metrics

Besides a weak increase in the relative abundance (%) of Oligochaeta with increasing sediment cover ($r_s = 0.36$; $P = 0.04$; $n = 32$), assemblage metrics at the reach scale were unrelated to fine sediment. However, in keeping with the apparent effects on species composition, macroinvertebrate diversity, % coleoptera and % chironomids were reduced in improved grasslands as represented by Catchment PC1 ($r_s = -0.48$ to -0.43; $P = 0.008$–0.01; $n = 31$).

Patch-scale: deposited sediments

Among the 56 locations in the patch-scale survey, depth ranged over 8–27 cm and current velocity 11–57 cm s^{-1}. Observed variation in sediment cover at this scale ranged over 1–35% and, while these values are lower than those for the reach-scale survey, these detailed estimations were once again related to the extent of eroding banks 500 m upstream ($r_s = 0.66$; $P = 0.02$; $n = 11$). Suspendable sediments ranged from 2–147 g m^{-2} and were directly related to deposited sediment cover ($r_s = 0.74$; $P < 0.001$; $n = 45$). Flow velocity did not influence deposited or suspendable sediments over the range observed ($P > 0.05$), but both sediment cover ($r_s = 0.33$; $P = 0.01$; $n = 56$) and suspendable sediments ($r_s = 0.37$; $P = 0.01$; $n = 45$) increased with depth.

Patch-scale: assemblage composition

Around 23 000 individual invertebrates from 69 taxa were collected in the 2007 patch-scale survey, this richness being comparable to the reach scale survey (74) despite the smaller number of animals collected. *Ephemerella ignita*, *B. rhodani* and chironomids were again the most abundant organisms. However, after removing taxa occurring in less than five samples, only 40 were included in the DCA (Fig. 4).

In contrast to the reach-scale survey, ordination patterns from the patch data were related strongly to sediments. The first two DCA axes explained 35% of the variation in species composition, with axis 1 (23%) representing a gradient from shallower sites with less suspendable sediments ($r_s = -0.47$; $P < 0.01$) to deeper sites ($r_s = 0.36$; $P = 0.006$). Axis 2 (12%) was also positively correlated with suspendable sediments ($r_s = 0.61$; $P < 0.001$), more weakly to sediment cover ($r_s = 0.35$; $P = 0.007$) and negatively with flow velocity ($r_s = -0.32$; $P = 0.01$).

Patch-scale: invertebrate metrics

Also in contrast to the reach-scale survey, GEE modelling showed that several invertebrate metrics were related to sediment cover and suspendable sediments. For example, total taxon richness and EPT richness were reduced in sediment-rich sites (Table 3). On average, total richness declined by approximately five taxa, and EPT richness by four taxa at the most sediment-impacted locations (*c.* 30% cover), or respectively 20% and 25% of richness at sites free of any sediment (Fig. 5). Except for an increase in the relative abundance of Oligochaeta with depth ($r = 0.36$; $P < 0.01$), there were no relationships between invertebrate metrics and either depth or current velocity, which might have been expected if these factors were confounding effects ascribed to sediments.

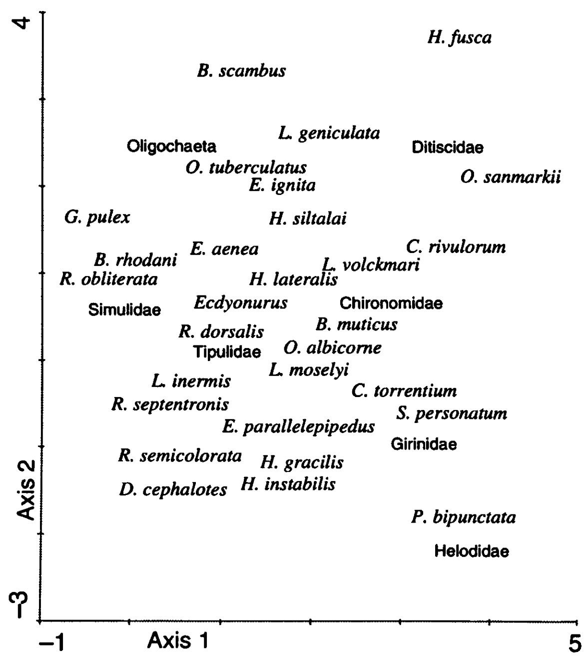

Fig. 4 Detrended correspondence analysis (DCA) plot of taxa from the 2007 patch -scale survey. Axis 1 mainly represented increased water depth, while fine sediment cover and suspendable sediments increased along axis 2. For clarity not all taxa are included.

Because of the apparent effects of land use on invertebrates detected in the reach-scale survey, we investigated how fine-scaled effects might be reflected within land use types. Reduction in richness was consistent between the upland and improved grassland areas, but there were more significant relationships between sediments and invertebrates in the former (Table 3). At upland locations ($n = 24$), sediment cover and suspendable sediments increased from 1% to 23% and 2–49 g m^{-2}, leading apparently

Table 3 Invertebrate response shown by general estimating equations in the catchment of the River Usk to sediment cover and measured suspendable sediments at the patch-scale at all sites and in upland and improved grassland locations

	All locations		Upland locations		Improved grasslands	
Metrics	Sediment cover (%) (n = 56)	Suspendable sediments (n = 45)	Sediment cover (%) (n = 24)	Suspendable sediments (n = 18)	Sediment cover (%) (n = 32)	Suspendable sediments (n = 27)
Taxon richness	−0.41**	−0.40**	−0.29*	NS	−0.42*	NS
EPT richness	−0.45**	−0.44**	−0.52**	NS	NS	NS
% EPT	NS	NS	0.51**	0.57**	NS	NS
Shannon index	NS	NS	0.47**	−0.63**	NS	NS
Total abundance	NS	NS	0.50*	0.80**	−0.41*	−0.40*
% Chironomidae	NS	NS	−0.49**	−0.65**	NS	NS
% Coleoptera	NS	NS	−0.64**	−0.69**	NS	NS
% Oligochaeta	NS	NS	NS	NS	NS	NS

Values of r are shown: $^*P < 0.05$; $^{**}P < 0.01$ (see Fig. 5 for an example).

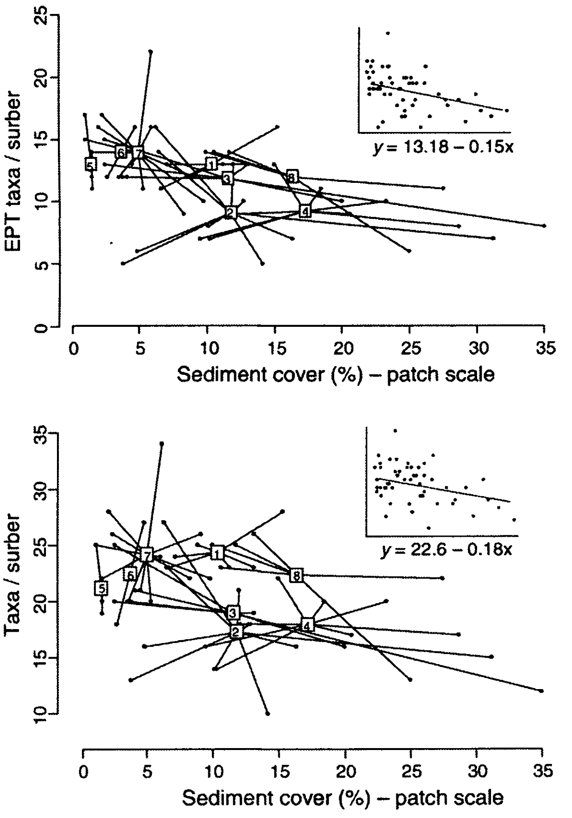

Fig. 5 Response of EPT taxon richness and total taxon richness to increasing sediment cover. Samples are grouped by stream (labelled as numbers). Regression coefficients are based on GEE models.

to increased invertebrate abundances (particularly oligochaetes) but reductions in EPT richness and proportion, Shannon diversity and the relative abundance of both Coleoptera and Chironomidae. At grassland locations (n = 32), sediment cover and suspendable sediments increased from 3% to 35% and 1.7–147 g m^{-2}, respectively, accompanied by reductions in taxon richness and total abundance. Other metrics were only marginally affected (e.g. P-values c. 0.09).

Patch-scale: individual species tolerance to sediments

Far clearer relationships with sediments at the patch scale allowed some assessment of varying tolerance among species. Based on their cumulative abundance curves (Fig. 6), the most common taxa were ordered from the most sensitive to the most tolerant (Table 4). The trichopteran *Hydropsyche instabilis* and the plecopteran *P. bipunctata* were apparently the most sediment-intolerant species, along with Helodidae and Simulidae. By contrast, Tipulidae, Oligochaeta and the coleopteran *O. sanmarkii*, appeared the most tolerant.

Methodological evaluations

In the 12 reaches where invertebrates were collected in subsequent years by both kick-samples and aggregated Surber samples, axis 1 DCA scores were highly inter-correlated between the two methods (r = 0.86, n = 12; P < 0.001) implying that both collected near-identical assemblages. Moreover, besides a decrease in the proportion of Coleoptera (r_s = −0.7; P < 0.01), there were no other significant correlations between reach-wide metrics based on aggregated Surber

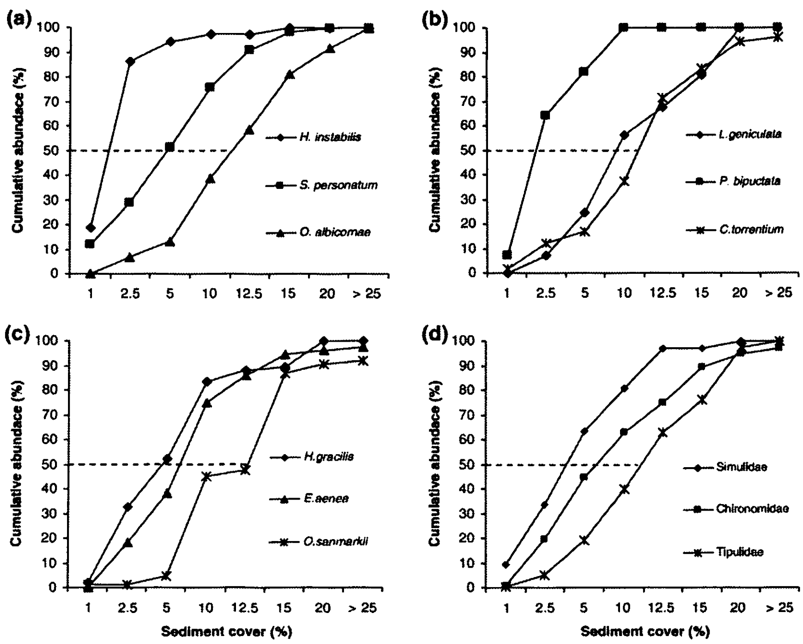

Fig. 6 Examples of cumulative abundance curves for three species of Trichoptera (a), Plecoptera (b), Coleoptera (c) and three dipteran families (d) in relation to sediment cover. Tolerance values (Table 4) were estimated where 50% cumulative abundance occurred (dotted line).

samples and sediment features averaged at the reach-scale. In other words, when using fine-scale methods at the same sampling resolution as the reach-scale survey, sediment effects were far less detectable. This result confirms that differences in survey outcome between the patch and reach-scale survey were not due to differences in the timing or method of invertebrate collection.

In a second methodological evaluation, we assessed whether patch-scale effects of sediments were still apparent within those streams with sufficient variation in sediment cover. In the Afon Cynrig (sediment cover 2.5–35%) and Ysgir Fechan (10–27%) EPT richness declined consistently with increasing suspendable sediments or sediment cover ($r_s = -0.81$ to -0.88, $n = 6$–7; $P = 0.02$–0.01). In the Afon Honndu (9.5–28.7%) %EPT declined with increasing suspendable sediments ($r_s = -0.76$; $n = 8$; $P = 0.02$). However, in the Bran (6.5–31%) no effects were evident on community metrics. Also, in the Cynrig, total taxon richness also declined with increasing sediments ($r_s = -0.84$; $P = 0.01$, $n = 7$) and in the Ysgir Fechan the relative abundance of Oligochaeta increased ($r_s = 0.81$; $P = 0.04$; $n = 6$). Therefore, the responses of invertebrates to sediments were generally consistent within streams and even with reduced sample size.

Discussion

Linkages among riparian or catchment land-use, erosion and sediment behaviour in streams are increasingly well established (Rabeni & Smale, 1995; Riley *et al.*, 2003; Opperman *et al.*, 2005). Awareness of the ecological significance of suspended and bedload sediments is growing, particularly in anthropogenically modified catchments and where there are important resources such as salmonids or other organisms of high conservation value (Walling, Collins & Mcmellin, 2003; Owens *et al.*, 2005). Understanding the factors controlling the spatial variability of sediments and their effects is therefore an important management requirement. Although derived from an extensive, correlative survey across locations, our data offer some support for these needs in upland, temperate streams.

In support of the first of our hypotheses, more than 59% of the variation in deposited sediments in the Usk was explained by local (500 m) bank erosion. Catchment woodland cover was also an important correlate, supporting its role in preventing the release of fine sediments into the channel (Zimmerman, Vondracek & Westra, 2003; Opperman *et al.*, 2005). In turn, bank erosion appeared to be mediated by riparian land use, with wooded vegetation likely to

Table 4 Ranking of 27 common taxa based on their 50% abundance in relation to cumulative sediment cover (see Fig. 6)

Taxon	Order	Sediment cover (%) for 50% abundance
Hydropsyche instabilis	Trichoptera	1.5
Perla bipunctata	Plecoptera	2.5
Helodidae	Coleoptera	3.1
Simulidae	Diptera	3.5
Caenis rivulorum	Ephemeroptera	4.5
Sericostoma personatum	Trichoptera	4.7
Hydraena gracilis	Coleoptera	4.7
Hydropsyche siltalai	Trichoptera	5.3
Baetis scambus	Ephemeroptera	6
Elmis aenea	Coleoptera	6.3
Rhyacophila spp.	Trichoptera	6.3
Chironomidae	Diptera	6.3
Esolus parallelepipedus	Coleoptera	6.6
Heptagenia lateralis	Ephemeroptera	8.3
Rhithrogena semicolorata	Ephemeroptera	8.9
Ephemerella ignita	Ephemeroptera	9.1
Limnius volkmari	Coleoptera	9.1
Baetis rhodani	Ephemeroptera	9.5
Leuctra geniculata	Plecoptera	9.8
Baetis muticus	Ephemeroptera	10
Leuctra moselyi	Plecoptera	10
Ecdyonurus sp.	Ephemeroptera	10.6
Chloroperla torrentium	Plecoptera	11.2
Odontocerum albicorne	Trichoptera	12
Tipulidae	Diptera	12
Oligochaeta	Anellida	12.7
Oreodytes sanmarkii	Coleoptera	13.1

limit sediment release by stabilizing stream banks. This finding accords with the general pattern of sediment sources for other rivers in this region, as assessed by fingerprinting methodologies, where channel and sub-surface sources are the major contributors to in-stream sediments (Walling *et al.*, 2003). Also, fine sediments collected in our streams were mostly composed of coarser sand fractions likely to originate from the channel (Knighton, 1998). However, other factors beside woodland cover must affect sediment supply in the study area, since relatively low sedimentation was also observed in some grassland reaches with eroded banks. Although Townsend *et al.* (2004) suggested that marginal pastures margins could increase stock trampling and bank instability, there is evidence that grassland buffers can be effective sediment filters, especially of the coarse fraction (Le Bissonnais, Lecomte & Cerdan, 2004; Dosskey, Hoagland & Brandle, 2007; Mankin *et al.*, 2007). Temporal variability and seasonality in bed sediment cover and direct livestock access to streams might also be involved (Walling *et al.*, 2003; Mciver & Mcinnis, 2007). In these instances, destabilization of stream banks due to over-grazing coupled with footpaths and roads running across steep slopes can be responsible for disproportionately large increases in sediment delivery – even very locally – but no such occurrences were apparent in our data.

Scale-dependent effects

Our second hypothesis, that relationships between invertebrates and sediments should be scale dependent, was also supported strongly, and this result raises some methodological and management issues. Few other studies have addressed this hypothesis (e.g. Townsend, Scarsbrook & Doledec, 1997; Smiley & Dibble, 2008), and in all cases significant effects were observed mostly at the finest spatial resolution.

At broader, reach-scales, neither assemblage nor invertebrate metrics revealed any large effects of sediments, with most invertebrate variations instead tracking land-use change from upland to improved grassland. Such significant land-use effects on stream biota occur often where native vegetation changes to pasture or agriculture (Braccia & Voshell, 2007; Niyogi *et al.*, 2007), and mechanisms include altered hydrology (Allan *et al.* 1997, Davies-Colley 1992), nutrient release and allochthonous or solar energy flux (Osborne & Kovacic, 1993; Harding *et al.*, 1999). Reduced invertebrate diversity observed in pasture reaches in the Usk is likely to have reflected changes in water quality as both nitrates and BOD were higher in grassland. Even small changes in these variables, similar to those detected here, were sufficient to affect invertebrates in the adjacent Wye (Clews & Ormerod, 2008). Most of the remaining reach-scale variation in invertebrate composition remained unexplained, as is common in surveys, and largely depends on the number of sites and taxa (Leps & Smilauer, 2003). Nevertheless, the increased abundance of oligochaetes in sediment-enriched reaches showed that some localized effects were detectable even at this scale.

Apparent sediment effects on organisms became far clearer at increased sampling resolution, i.e. in units of decreased sample size that captured within-reach variation. Overall composition and associated invertebrate metrics responded predictably to increasing fine sediments measured as both bed cover and suspendable material, with overall taxon richness and EPT taxon richness respectively 20% and 25% lower at the most sediment-impacted sites than in locations free of sediments. Besides the proportion of Oligochaeta, none of the invertebrate metrics related to sediments correlated with other micro-habitat features, such as current velocity or water depth, implying that the correlations were not spurious. However, one interesting methodological point to emerge was that estimates of sediment cover differed between surveys at reach- and patch-scales. Although the values were correlated with each other ($r_s = 0.62$; $P = 0.03$) and with measures of bank erosion, the latter produced lower estimates (1–35% cover) than the former (1–75%). A further corollary is the patch-scale measurements evidently detected sedimentation effects on organisms at substantially lower values of cover than could occur at the reach scale without such effects. Almost certainly, these differences reflect the gain in measurement accuracy at the finer scale, when 10 observations were made immediately around each Surber sampler as opposed to 12 estimates spread sparsely in two transects over entire reaches. Not only there were more measurements per unit area at the finer scale, but also they were taken directly adjacent to the point of biological sampling. At the same time, there is a potential sampling bias in that Surber sampling is constrained to operate in substrata of finer particle sizes (i.e. avoiding boulders and bedrock) where sediment deposition effects could be greatest.

The net outcome from the patch-scale survey was that variations in composition, invertebrate diversity and EPT richness could be related to sediment cover, with results supporting previous work. Generally consistent effects of sedimentation on overall diversity and EPT taxa in North America (Fossati *et al.*, 2001; Zweig & Rabeni, 2001; Kreutzweiser *et al.*, 2005), Australia and New Zealand (Quinn *et al.*, 1992; Downes *et al.*, 2006; Matthaei *et al.*, 2006) imply that the same general processes must be involved, linked also with shared biological traits among sensitive organisms. Similarly, Braccia & Voshell (2006) found relative abundance of Coleoptera to be consistently related to fine sediment in cattle impacted streams. In some cases, where sediment cover reaches 100%, effects can be even stronger than those we detected (Zweig & Rabeni, 2001). In our example, those taxa most sensitive to sediments, as identified from the cumulative abundance curves, were *H. instabilis* and *P. bipunctata*, both species normally associated with fast-flowing and sediment-free habitats. For hydropsychids, previous data suggest that sensitivity can arise due to the effects of suspended sediments on feeding nets (e.g. Strand & Merritt, 1997), and similar mechanisms might be responsible for the decreased abundance among filter-feeding simuliids. With some authors calling for the development of more pressure-specific metrics through which stream organisms can be used to diagnose reasons for stream impairment, rather than just detecting it (Clews & Ormerod, 2008), further data ranking the specific sensitivities of invertebrates to fine sediments would be valuable.

Interestingly, the patch-scale data revealed that some effects of varying sediment occurred only within land-use types. Invertebrate assemblages in upland locations showed the stronger response to sediments, with almost all invertebrate metrics highly significantly affected by sedimentation. The response of Chironomidae to sedimentation must, however, be interpreted with caution considering their wide ranging habitat and feeding strategies. Even at the sub-family level, Orthocladiinae and Chironominae respond respectively negatively and positively to sediment accumulation, so that family level identification is inadequate to appraise response (Angradi, 1999). Increased invertebrate abundance in upland locations with increasing sediment cover is somewhat contrary to expectation but linked to the increased abundance of sediment tolerant oligochaetes as well as the stonefly, *Leutra moselyi*.

By contrast, sediment effects on invertebrates in grassland locations were weaker, even though this is where the largest sediment accumulations occurred. One possibility is that effects were masked here because invertebrate diversity was already lower than in upland locations, linked possibly to nutrient concentrations. These results support those from experiments by Matthaei *et al.*(2006), who showed that sediments affect streams with the greatest invertebrate diversity where previous sediment effects have been small. As in our upland sites, these workers also observed a moderate increase in invertebrate density with increasing sediment cover. In combination, this previous study and ours suggest that sediment effects on macroinvertebrate communities might depend on the diversity and sensitivity of organisms present, with streams in semi-natural catchments at greatest risk of impairment.

Overview

Overall, we conclude that sediment deposition in this upland, temperate river system mostly reflects local bank erosion, particularly interacting with riparian and catchment woodland cover. Ecological effects on organisms occured mostly in upland locations, where reductions in richness at the most sediment-affected sites were substantial, and there are three general implications.

First, the interaction between woodland, sediment release and ecological effects is important in this British river catchment where many riparian trees have been removed for agriculture, and only now are being restored through a range of agri-environment and riparian management schemes. Sediment controls are only one such benefit from carefully riparian-zone maintenance (Petersen *et al.*, 2004).

Secondly, ecological effects in the Usk occurred even though most of the fine sediments involved were coarser, non-flocculating sand rather than silt and clay. Elsewhere, these finer fractions substantially alter substratum quality, reduce interstitial flow, alter oxygen exchange and increase ion-exchange capacity (Schalchli, 1992; Brunke & Gonser, 1997), and are considered to be responsible for many of the negative effects on stream organisms (Waters, 1995). This fraction was a minor substratum component in our study streams, yet some effects were still detectable.

Finally, the detection of such effects was scale-dependent. This implies that sediment effects may be influenced by larger catchment controls, while requiring also a finer-scale approach that might have been more accurate for sediment effects in the Usk. We suggest that the assessment of the effects of diffuse anthropogenic sediment can benefit from a scale-specific approach, in which local (i.e. reach-based) effects can be separated from broader (i.e. whole-stream, catchment) influences. Of more direct management importance, sediment effects could go undetected without appropriately scaled investigation.

Acknowledgments

The funding for this study was provided by the Wye and Usk Foundation, Wales, and we thank Dr Stephen Marsh-Smith and Simon Evans. We also thank Federica Pinto for assistance in the field. Numerous landowners allowed access to study sites. We are grateful to two anonymous reviewers and Dr Richard Johnson for their valuable comments on the manuscript.

References

Allan J.D., Erickson D.L. & Fay J. (1997) The influence of catchment land use on stream integrity across multiple spatial scales. *Freswater Biology*, **37**, 149–161.

Angradi T.R. (1999) Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications. *Journal of the North American Benthological Society*, **18**, 49–66.

Ankers C., Walling D.E. & Smith R.P. (2003) The influence of catchment characteristics on suspended sediment properties. *Hydrobiologia*, **494**, 159–167.

Bond N.R. (2004) Spatial variation in fine sediment transport in small upland streams: the effects of flow regulation and catchment geology. *River Research and Applications*, **20**, 705–717.

Braccia A. & Voshell J.R. (2006) Environmental factors accounting for benthic macroinvertebrate assemblage structure at the sample scale in streams subjected to a gradient of cattle grazing. *Hydrobiologia*, **573**, 55–73.

Braccia A. & Voshell J.R. (2007) Benthic macroinvertebrate responses to increasing levels of cattle grazing in Blue Ridge Mountain streams, Virginia, USA. *Environmental Monitoring and Assessment*, **131**, 185–200.

Bradley D.C. & Ormerod S.J. (2002) Evaluating the precision of kick-sampling in upland streams for assessments of long-term change: the effects of sampling effort, habitat and rarity. *Archiv fur Hydrobiologie*, **155**, 199–221.

Broekenhuizen N., Parkyn S. & Miller D. (2001) Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). *Hydrobiologia*, **457**, 125–132.

Brunke M. & Gonser T. (1997) The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology*, **37**, 1–33.

Bruns D.A. (2005) Macroinvertebrate response to land cover, habitat, and water chemistry in a mining-impacted river ecosystem: a GIS watershed analysis. *Aquatic Sciences*, **67**, 403–423.

Bunn S.E. & Davies P.M. (2000) Biological processes in running waters and their implications for the assessment of ecological integrity. *Hydrobiologia*, **422–423**, 61–70.

Ciesielka I.K. & Bailey R.C. (2007) Hierarchical structure of stream ecosystems: consequences for bioassessment. *Hydrobiologia*, **586**, 57–67.

Clews E. & Ormerod S.J. (2008) Improving bio-diagnostic monitoring using simple combinations of standard biotic indices. *River Research and Applications*, in press.

Collins A.L. & Walling D.E. (2007) Fine-grained bed sediment storage within the main channel systems of the Frome and Piddle catchments, Dorset, UK. *Hydrological Processes*, **21**, 1448–1459.

Countryside Council for Wales (2002) *Phase 1 Survey From the Countryside Council for Wales*. CCW Geographic Information Unit, Bangor, Gwynedd.

Davies-Colley R.J., Hickey C.W., Quinn M.J. & Ryan P.A. (1992) Effects of clay discharges on streams. Optical properties and epilithon. *Hydrobiologia*, **248**, 215–234.

Dosskey M.G., Hoagland K.D. & Brandle J.R. (2007) Change in filter strip performance over ten years. *Journal of Soil and Water Conservation*, **62**, 21–32.

Downes B.J., Lake P.S., Glaister A. & Bond N.R. (2006) Effects of sand sedimentation on the macroinvertebrate fauna of lowland streams: are the effects consistent? *Freshwater Biology*, **50**, 144–160.

Edington J.M. & Hildrew A.G. (1981) *A Key to the Caseless Caddis Larvae of the British Isles with Notes on their Ecology*. Freshwater Biological Association, Ambleside, Cumbria.

Elliott J., Humpesch U. & Macan T. (1988) *Larvae of the British Ephemeroptera: A Key with Ecological Notes. Scientific Publication 49*. Freshwater Biological Association, Ambleside.

Emery J.C. & Hill C.T. (2005) *Fluvial Audit of the Upper Usk Tributaries*. GeoData Institute, Southampton.

Environment Agency (1998) *Rural Usk LEAP Consultation Report*. Environment Agency Wales, Cardiff, Wales.

Environment Agency (1999) *Procedures for Collecting and Analysing Macroinvertebrate Samples. Quality Management Systems for Environmental Monitoring: Biological Techniques*. Environment Agency, Bristol.

Environment Agency (2003) *River Habitat Survey in Britain and Ireland, Field Survey Guidance Manual*. Environment Agency, Bristol.

ESRI (2004) *ArcGIS 9.1. E.S.R.I. Inc.* Environmental System Research Institute Inc., Redlands.

Feld C.K. (2004) Identification and measure of hydromorphological degradation in Central European lowland streams. *Hydrobiologia*, **516**, 69–90.

Fossati O., Wasson J.G., Hery C., Salinas G. & Marin R. (2001) Impact of sediment releases on water chemistry and mocroinvertebrate communities in clear water Andean stream (Bolivia). *Archiv fur Hydrobiologie*, **151**, 33–50.

Friday L. (1988) *A Key to the Adults of British Water Beetles*. Field Studies Council, Preston Montford.

Gard M.F. (2002) Effects of sediment loads on the fish and invertebrates of Sierra Nevada river, California. *Journal of Aquatic Ecosystem Stress and Recovery*, **9**, 227–238.

Gayraud S., Herouin E. & Philippe M. (2002) The clogging of stream beds: a review of mechanisms and consequences on habitats and macroinvertebrate communities. *Bulletin Francais de le Peche et se la Pisciculture*, **365**, 339–355.

Gray J.L. & Ward J.V. (1982) Effects of sediment releases from a reservoir on stream macroinvertebrates. *Hydrobiologia*, **96**, 177–184.

Greig S.M., Sear D.A. & Carling P.A. (2005) The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. *Science of the Total Environment*, **344**, 241–258.

Halekoh U., Hojsgaard S. & Yan J. (2006) The R Package geepack for generalized estimating equations. *Journal of Statistical Software*, **15**, 1–9.

Harding J.S., Young R.G., Hayes J.W., Shearer K.A. & Stark J.D. (1999) Changes in agricultural intensity and river health along a river continuum. *Freshwater Biology*, **42**, 345–357.

Ihaka R. & Gentleman R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.

Imhof J.G., Fitzgibbon J. & Annable W.K. (1996) A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 312–326.

Jones K.B., Neale A.C., Nash M.S., Van Remortel R.D., Wickham J.D., Riitters K.H. & O'neill R.V. (2001) Predicting nutrient and sediment loadings to streams from landscape metrics: a multiple watershed study from the United States Mid-Atlantic Region. *Landscape Ecology*, **16**, 301–312.

Jongman R.H.G., Ter Braak C.J.F. & Van Tongeren O.F.R. (1995) *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge.

Knighton D. (1998) *Fluvial Forms and Processes: A New Perspective*. Hodder Arnold, London.

Kreutzweiser D.P., Capell S.S. & Good K.P. (2005) Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology*, **39**, 55–66.

Le Bissonnais Y., Lecomte V. & Cerdan O. (2004) Grass strip effects on runoff and soil loss. *Agronomie*, **24**, 129–136.

Leps J. & Smilauer P. (2003) *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge.

Luedtke R.J. & Brusven M.A. (1976) Effects of sand sedimentation on colonization of stream insects. *Journal of the Fisheries Research Board of Canada*, **33**, 1881–1886.

Mankin K.R., Ngandu D.M., Barden C.J., Hutchinson S.L. & Geyer W.A. (2007) Grass-shrub riparian buffer removal of sediment, phosphorus, and nitrogen from simulated runoff. *Journal of the American Water Resources Association*, **43**, 1108–1116.

Matthaei C.D., Weller F., Kelly D.W. & Townsend C.R. (2006) Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology*, **51**, 2154–2172.

Mciver J.D. & Mcinnis M.L. (2007) Cattle grazing effects on macroinvertebrates in an Oregon mountain stream. *Rangeland Ecology & Management*, **60**, 293–303.

Moran M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100**, 403–405.

Mykra H., Heino J. & Muotka T. (2007) Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. *Global Ecology and Biogeography*, **16**, 149–159.

Newcombe C.P. & Macdonald D.D. (1991) Effects of suspended sediments on aquatic ecosystems. *North American Journal of Fisheries Management*, **11**, 72–82.

Niyogi D.K., Koren M., Arbuckle C.J. & Townsend C.R. (2007) Stream communities along a catchment land-use gradient: subsidy-stress responses to pastoral development. *Environmental Management*, **39**, 213–225.

Opperman J.J., Lohse K.A., Brooks C., Kelly N.M. & Merenlender A.M. (2005) Influence of land use on fine sediment in salmonid spawning gravels within the Russian River Basin, California. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2740–2751.

Ormerod S.J. & Edwards R.W. (1987) The ordination and classification of macroinvertebrate assemblages in the catchment of the River Wye in relation to environmental factors. *Freshwater Biology*, **17**, 533–546.

Osborne L.L. & Kovacic D.A. (1993) Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology*, **29**, 243–258.

Owens P.N., Batalla R.J., Collins A.J. *et al.* (2005) Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications*, **21**, 693–717.

Parkhill K.L. & Gulliver J.S. (2002) Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia*, **472**, 5–17.

Petersen I., Master Z., Hildrew A.G. & Ormerod S.J. (2004) Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology*, **41**, 934–950.

Platts W.S., Megaham W.F. & Minshall G.W. (1983) *Mehods for Evaluating Stream, Riparian, and Biotic Conditions*. General Technical Report INT-138. Intermountain Forest Range Experiment Station, United States Department of Agriculture, Ogden, UT.

Quinn M.J., Davies-Colley R.J., Hickey C.W., Vickers M.L. & Ryan P.A. (1992) Effects of clay discharge on streams. Benthic invertebrates. *Hydrobiologia*, **248**, 235–247.

Rabeni C.F. & Smale M.A. (1995) Effects of siltation on stream fishes and the potential mitigating role of the buffering riparian zone. *Hydrobiologia*, **303**, 211–219.

Rabeni C.F., Doisy K.E. & Zweig L.D. (2005) Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences*, **67**, 395–402.

Rier S.T. & King D.K. (1996) Effects of inorganic sedimentation and riparian clearing on benthic community metabolism in an agriculturally-disturbed stream. *Hydrobiologia*, **339**, 111–121.

Riley R.H., Townsend C.R., Niyogi D.K., Arbuckle C.A. & Peacock K.A. (2003) Headwater stream response to grassland agricultural development in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **37**, 389–403.

Roth N.E., Allan J.D. & Erickson D.L. (1996) Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology*, **11**, 141–156.

Sable K.A. & Wohl E. (2006) The relationship of lithology and watershed characteristics to fine sediment deposition in streams of the Oregon Coast Range. *Environmental Management*, **37**, 659–670.

Schalchli U. (1992) The clogging of coarse gravel river beds by fine sediment. *Hydrobiologia*, **235**, 189–197.

Smiley P.C. & Dibble E.D. (2008) Influence of spatial resolution on assessing channelization impacts on fish and macroinvertebrate communities in a warm water stream in the southeastern United States. *Environmental Monitoring and Assessment*, **138**, 17–29.

Standing Committee of Analysts (1979) *Dissolved Oxygen in Natural and Waste Waters*. HMSO, London.

Standing Committee of Analysts (1981) *Biological Oxygen Demand*. HMSO, London.

Standing Committee of Analysts (1987) *Kjeldahl Nitrogen in Waters*. HSMO, London.

Standing Committee of Analysts (1992) *Phosphorus and Silicon in Waters, Effluents and Sludges*. HMSO, London.

Strand M.R. & Merritt R.W. (1997) Effects of episodic sedimentation on the netspinning caddisflies *Hydropsyche betteni* and *Ceratopsyche sparna* (Trichoptera: Hydropsychidae). *Environmental Pollution*, **98**, 129–134.

Townsend C.R., Scarsbrook M.R. & Doledec S. (1997) The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography*, **42**, 938–949.

Townsend C.R., Doledec S., Norris R., Peacock K. & Arbuckle C. (2003) The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology*, **48**, 768–785.

Townsend C.R., Downes B.J., Peacock K. & Arbuckle C.J. (2004) Scale and the detection of land-use effects on morphology, vegetation and macroinvertebrate communities of grassland streams. *Freshwater Biology*, **49**, 448–462.

Vaughan I.P., Noble D.G. & Ormerod S.J. (2007) Combining surveys of river habitats and river birds to appraise riverine hydromorphology. *Freshwater Biology*, **52**, 2270–2284.

Wallace I., Wallace B. & Philipson G. (2003) *Keys to the Case-Bearing Caddis Larvae of Britain and Ireland. Scientific Publication 61*. Freshwater Biological Association, Ambleside.

Walling D.E. & Amos M. (1999) Source, storage and mobilisation of fine sediment in a chalk stream system. *Hydrological Processes*, **13**, 323–340.

Walling D.E., Collins A.L., Sichingabula H.M. & Leeks G.J.L. (2001) Integrated assessment of catchment suspended sediment budgets: a Zambian example. *Land Degradation and Development*, **12**, 387–415.

Walling D.E., Collins A.L. & Mcmellin K.G. (2003) A reconnaissance survey of the source of interstitial fine sediment recovered from salmonid spawning gravels in England and Wales. *Hydrobiologia*, **497**, 91–108.

Ward P. & Myers R.A. (2007) Bait loss and its potential effects on fishing power in pelagic longline fisheries. *Fisheries Research*, **86**, 69–76.

Waters T.F. (1995) *Sediments in Streams: Sources, Biological Effects, and Control*. AFS Monographs, Bethesda, MD.

Wright J.F., Furse M.T. & Moss D. (1998) River classification using invertebrates: RIVPACS applications. *Aquatic Conservation – Marine and Freshwater Ecosystems*, **8**, 617–631.

Zimmerman J.K.H., Vondracek B. & Westra J. (2003) Agricultural land use effects on sediment loading and fish assemblages in two Minnesota (USA) watersheds. *Environmental Management*, **32**, 93–105.

Zorn C.J.W. (2001) Generalized estimating equation models for correlated data: a review with applications. *American Journal of Political Science*, **45**, 470–490.

Zweig L.D. & Rabeni C.F. (2001) Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society*, **20**, 643–657.

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Complete list of taxa collected in the 2006 and 2007 surveys.

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(Manuscript accepted 21 July 2008)

Freshwater Biology

Freshwater Biology (2010) **55**, 476–486 doi:10.1111/j.1365-2427.2009.02282.x

APPLIED ISSUES

Low-level effects of inert sediments on temperate stream invertebrates

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SUMMARY

1. The delivery, entrainment and deposition of inert fine sediments are among the most significant contributors to stream and river impairment worldwide. Associated ecological effects have been observed frequently, but specific experiments to identify sensitivity and avoidance behaviour in stream organisms are few, particularly in headwaters.

2. In a field-experiment, we added fine sand at low levels (*c.* 4–5 kg m^{-2}) to 10 m reaches of two replicate headwater streams in the Usk catchment (Wales, U.K.) over two periods (autumn and summer). Upstream reaches were used as control in a classic before-after-control-impact design. Invertebrate drift and benthic composition were measured for 2 days before and 1 day after sediment impact.

3. Sediment addition significantly increased overall drift density (by 45%) and propensity (by 200%), with effects largest on the night following addition rather than immediately (i.e. within 9 h). The mayflies *Baetis rhodani*, *B. muticus* and *Ecdyonurus* spp., simuliid and chironomid dipterans, and helodid beetles were the strongest contributors.

4. There were no marked effects on benthic composition, but density declined in treated reaches by 30–60%, particularly in *B. rhodani*, *Ecdyonurus* spp. and *Leuctra hippopus* + *L. moselyi*.

5. All effects were consistent between both seasons and streams.

6. These data show how even low-level, short-term, increases in fine sediment loading to upland, stony streams can reduce overall benthic density through increased drift. We suggest that the likely cause of the delayed drift response was a change in habitat quality which prompted avoidance behaviour. Longer-term experiments are required to assess whether these effects reduce fitness or explain the losses of some types of organisms observed recently in sediment-impaired reaches of this and other catchments.

Keywords: drift, habitat quality, insects, macroinvertebrates, water quality

Introduction

Catchment agriculture, urbanisation, forestry and mining not only alter energy fluxes, hydrology, thermal regimes and habitat availability in rivers (Osborne & Kovacic, 1993; Roth, Allan & Erickson, 1996; Manel, Buckton & Ormerod, 2000), but can also increase fine sediment delivery and alter sediment quality with profound consequences for aquatic organisms (reviewed by Ryan, 1991; Waters, 1995; Wood *et al.*, 2005). These ecological effects depend on sediment character, size-distribution, particle shape and associated pollutants (Lemly, 1982; Wood *et al.*, 2005), as well as catchment and stream characteristics (Culp, Wrona & Davies, 1985; Collins, Walling & Leeks, 1997; Kreutzweiser, Capell & Good, 2005; Larsen, Vaughan & Ormerod, 2009). Organisms at all trophic levels are affected, for example through a reduction of available light for primary producers and visual predators (Rowe & Dean, 1998; Parkhill &

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Gulliver, 2002), alteration of substratum structure and habitat quality for benthic organisms (Chutter, 1968; Turnpenny & Williams, 1980), decline in feeding efficiency of filter-feeders and grazers (Graham, 1990; Broekenhuizen, Parkyn & Miller, 2001) and reduced oxygen supply to salmonids eggs via interstitial occlusion (Argent & Flebbe, 1999; Greig, Sear & Carling, 2005). Shorter-term effects are also possible through the displacement or avoidance behaviour of organisms affected by suspended, saltating or deposited particles (Gibbins *et al.*, 2007).

However, identifying sediment effects on stream organisms, and the processes involved, is hindered by two major problems. First, sediments occur often alongside other stressors which might exacerbate or mask effects (Matthaei *et al.*, 2006). In agricultural catchments, such confounds include nutrients, pesticides, alteration in runoff pattern and habitat modification. Secondly, sediments in any one location can arise from a diverse array of catchment sources. For example, point-sources associated with the effects of livestock on bank erosion might be locally important, but small by comparison with larger-scale releases from tillage, from the wider conversion of catchment forests to grassland or even from large-scale natural release. In these circumstances, experimental investigations can have major advantages over observational approaches, with sediment additions, artificial substrates of varying grain-size, flumes or experimental streams all used in the past (Doeg & Milledge, 1991; Angradi, 1999; Bond & Downes, 2003; Connolly & Pearson, 2007).

In the Upper Usk catchment, in south-central Wales (U.K.), recent surveys have suggested that local sediment deposition is associated with decreased woodland cover and increased bank erosion (S. Larsen and S.J. Ormerod, unpubl. data). Apparent effects on stream invertebrates include altered assemblage composition, reduced richness, reductions in the density of sensitive species and an overall reduction in trait diversity (S. Larsen & S.J. Ormerod unpublished data). However, the exact mechanisms are unclear. There are a range of possibilities (see above), but here we turn our attention to the possibility that sediment deposition and sediment movement might cause short-term invertebrate losses and redistribution through drift.

While the drift of invertebrates is a natural process in streams, representing emigration and immigration between patches of different quality, changes in substratum character can alter drift behaviour (e.g. Holomuzki & Biggs, 2003). Evidence from several studies has shown that sediment transport and increased turbidity can promote invertebrate drift causing a reduction in benthic density and richness (Rosenberg & Wiens, 1978; Culp *et al.*, 1985; Suren & Jowett, 2001). Laboratory data suggest that such effects can also arise due to small changes in bedload or saltating particles (Gibbins *et al.*, 2007). However, not all results have been consistent (Connolly & Pearson, 2007). Moreover, early experiments on the effects of sediments on drift were characterised by limited replication (Rosenberg & Wiens, 1978; Culp *et al.*, 1985), while those carried out in artificial channels might not scale-up to represent real stream ecosystems (Suren & Jowett, 2001; Bond & Downes, 2003). Most of all, considering the sensitivity of streams and stream organisms to sediments (Matthaei *et al.*, 2006; Connolly & Pearson, 2007), realistic experiments to investigate the effects of sediments on invertebrate drift have been surprisingly few.

Following experimental approaches used previously (Rosenberg & Wiens, 1978; Culp *et al.*, 1985), we describe a replicated field-experiment in which we manipulated fine sediment supply to two second to third streams to test the hypothesis that relatively small increases in sediment deposition and transport can increase the short-term drift of sensitive benthic invertebrates. Specifically, we expected that any invertebrates showing an immediate avoidance or displacement reaction to sediment addition might occur rapidly in the drift. Alternatively, alterations in habitat quality for invertebrates would be reflected in increased behavioural drift as part of the normal nocturnal drift pattern. Both responses could reduce benthic density and we evaluated this possibility. A secondary aim of the experiment was to compare the apparent sensitivity of individual species to sediments as shown by their short-term drift with apparent tolerance to longer-term sediment effects indicated by our previous surveys (Larsen *et al.*, 2009).

Methods

Study area

The Senni and Grwyne Fawr are two small, third-order tributaries (3–5 m wide) of the Usk River in Wales at 290–300 m above sea level (National Grid

Reference: SN925207 and SO266251, respectively) and these upland locations have been shown previously to be sensitive to sediment deposition (Larsen *et al.*, 2009). One of the largest rivers in Wales, the Usk is dominantly rural, sparsely populated and one of the most important game fisheries in Britain (see Larsen *et al.*, 2009 for more details). The reaches selected for the experiment drained semi-natural rough pasture and woodland, and had substrata of bedrock, boulders and cobbles, moderately shaded by deciduous or conifer trees. The streams have similar ionic composition, rich in carbonates with high pH (*c.* pH 7.8–8) but low in nutrients (average nitrate 0.9 mg L^{-1}; phosphate 0.02 mg L^{-1}), and invertebrate communities are diverse and dominated by Ephemeroptera, Plecoptera and Trichoptera. The local geology of Devonian Old-red Sandstone has given rise to relatively sandy soils and alluvial deposits that, in the upper catchment, enter streams through bank-face erosion in locations where broadleaf trees have been removed. There are also point sediment sources where livestock trampling or local bank manipulations have caused sediment release. We wished to mimic the effects of such low-level sediment additions experimentally under controlled conditions.

Experimental design

In each of the two replicate streams we selected one downstream reach for sediment addition ('impact') and one upstream control reach to be as similar physiographically as possible within the same 40 m section. Invertebrate drift patterns were measured simultaneously in both reaches for two × 24 h periods before sediment addition ('Before 1', 'Before 2') and for 24 h after sediment addition ('After'), thus following a classic before-after-control-impact (BACIP) design (Stewart-Oaten & Bence, 2001). Experiments were carried on in autumn 2007 (21 September–10 October) and repeated in entirety at each site in summer 2008 (26 June–19 July), giving a total 12 days (288 h) of drift sampling.

In each case (i.e. each season and each stream), at the beginning of the 'After' period (*t.* 24:00 hours), clean childrens' play-sand (0.25–0.125 mm = ~60% in dry weight and 2–0.5 mm = ~30%) was added as evenly as possible to the 10 m impact reaches at a concentration of c 4–5 kg m^{-2} (corresponding to *c.* 25–35% bed cover). We chose this material because it was unaffected by contaminants or nutrients that would confound sedimentation effects and it had a size-distribution near-identical to naturally occurring sediments in the Usk (0.25–2 mm; Larsen *et al.*, 2009). Additions were made mostly from the banks to limit substratum disturbance, and we aimed to cover up to 35% of the benthos to mimic values at which longer-term effects occur (Larsen *et al.*, 2009). Water temperature, pH and conductivity were measured on each day of the experiment.

Invertebrate sampling

Throughout all experiments, steel poles fixed to the streambed held two adjacent rectangular drift nets (40 × 24 cm) in both impact and control reaches, respectively of two mesh sizes (0.9 and 0.44 mm) thereby attempting to capture differently sized organisms. The twin control nets were positioned at least 6 m from the upstream end of the sand-impacted reaches. Net contents were collected at 3 h intervals for 24 h starting at 12:00 on each sample day, with all drift samples combined from the contents from the two nets in each reach. The volumes of water filtered were estimated from three measurements of current velocity and water depth at the beginning, middle and end of each 3 h sampling session.

In addition to drift samples, four pooled Surber samples (30 × 30 cm; 0.44 mm mesh) were collected in both impact and control reaches at the end of each drift sampling day. Invertebrates were immediately preserved in 70% ethanol and then sorted and identified as far as possible in the laboratory (Edington & Hildrew, 1981; Friday, 1988; Elliott, 2003; Wallace, Wallace & Philipson, 2003).

Data analysis

Analyses were carried out to assess variations in both drift density (N/100 m^3) and drift propensity (drift density/benthic density), thereby accounting for differences in discharge and benthic composition among times and locations. Invertebrate abundances were log $(x + 1)$ transformed when necessary. Although invertebrate composition differed slightly between the streams (see Results), dominant taxa were the same and could be included in the same analyses.

Drift variations were assessed using mixed-effects models because we had longitudinal data (repeated measures). Season and stream were included as random factors, while experimental period (before and after) was treated as a fixed factor to assess differences in drift response. Analyses were run on R (Ihaka & Gentleman, 1996), using the 'nlme' extension (Pinheiro & Bates, 2000).

The BACIP design used allowed us to derive the main variables for analysis form the differences between impact and control locations; H_0 was that the impact-control difference before treatment was equal to the impact-control difference after treatment. This is equivalent to measuring the interaction term between reach type (control, impact) and time (before, after) in a classic ANOVA (Weiss & Reice, 2005; James, Dewson & Death, 2008). Response variables thus described the total drift densities and propensity, drift densities and propensities of each dominant taxon and benthic densities. No correction for multiple tests was performed and we give exact *P*-values in each case.

We used detrended correspondence analysis (DCA; Hill & Gauch, 1980) to assess whether sand addition had any gross effects on either benthic or drift composition. This exploratory method is a well-known, simple approach to indirect gradient ordination that uses reciprocal averaging to order samples objectively according to the frequency of co-occurrence of their constituent taxa. Sample scores reflect turnover in taxonomic composition along orthogonal axes, and these can be related to sample attributes or environmental conditions, in this case before and after sediment addition, and benthic versus drift samples. Although DCA has received some criticism associated with the detrending algorithm used to remove any curvilinear relationships between axes (i.e. 'the arch effect') (Wartenberg, Ferson & Rohlf, 1987), in our case identical ordination patterns were produced by DCA and non-metric multidimensional scaling based on Bray-Curtis similarity.

Results

Autumn and summer water temperatures during the experiment ranged were 9–12 and 12–17 °C, respectively, while conductivities during both seasons was *c.* 150 $\mu s\ cm^{-1}$ and pH 7.2–8. Current velocities in the study streams over the two seasons typically ranged over 20–60 $cm\ s^{-1}$

Seventy-two macroinvertebrate taxa occurred in the drift, but most were at low abundance. *Baetis rhodani* (Pictet), *Ecdyonurus* spp., chironomids and simuliids accounted for more than 60% of total drift abundance, with aquatic drift densities peaking at *c.* 60–80 individuals m^{-3} prior to any treatment. The contribution of terrestrial invertebrates to total drift in any single 24 h reached 50% in the summer, but fell to <10% throughout the autumn experiments. Overall, terrestrial invertebrates, mostly dipterans, accounted for up to 16% of total drift.

Drift response to sediments

Sediment addition increased both drift density and drift propensity (Table 1, Fig. 1). Sand additions, on average, resulted in 15 more individuals drifting per 100 m^3 and drift density in the impact reach increased by 35% in autumn, 60% in summer and 45% overall. Although there was a slight increase in drift in the autumn experiment immediately after sediment input, significantly increased drift was not immediate (i.e. within the first 9 h after addition). Instead, drift patterns maintained the expected diel variation, with densities increasing after sunset (*c.* 19:00 hours in autumn and 21:00 hours in summer; Fig. 2). Invertebrate response to treatment therefore appeared to be delayed and contributed to night-time drift in the impacted reaches compare to control (Fig. 2).

Table 1 Mixed effect model ($N = 12$) BACIP *F* and *P*-values of the effect of sand addition to drift and benthic variables for the two streams and seasons combined

	F (2, 6)	*P*-value	% change in Impact reach
Drift variables			
Total density	15.9	0.004	+45
Total propensity	66.7	0.0001	+200
Baetis rhodani density	15.8	0.004	+63
Ecdyonurus spp. density	47.7	0.0002	+26
Simulidae density	10.4	0.01	+81
Baetis rhodani propensity	12.2	0.007	+155
Ecdyonurus sp. propensity	15.8	0.004	+422
Baetis muticus propensity	6.0	0.03	+437
Helodidae propensity	4.5	0.05	+121
Chironomidae propensity	7.2	0.02	+433
Benthic variables			
Total density	14.0	0.005	−30
Baetis rhodani	4.75	0.05	−63
Ecdyonurus sp.	11.0	0.009	−26
Leuctra (hippopus + moselyi)	29.5	0.0008	−50

See text for details.

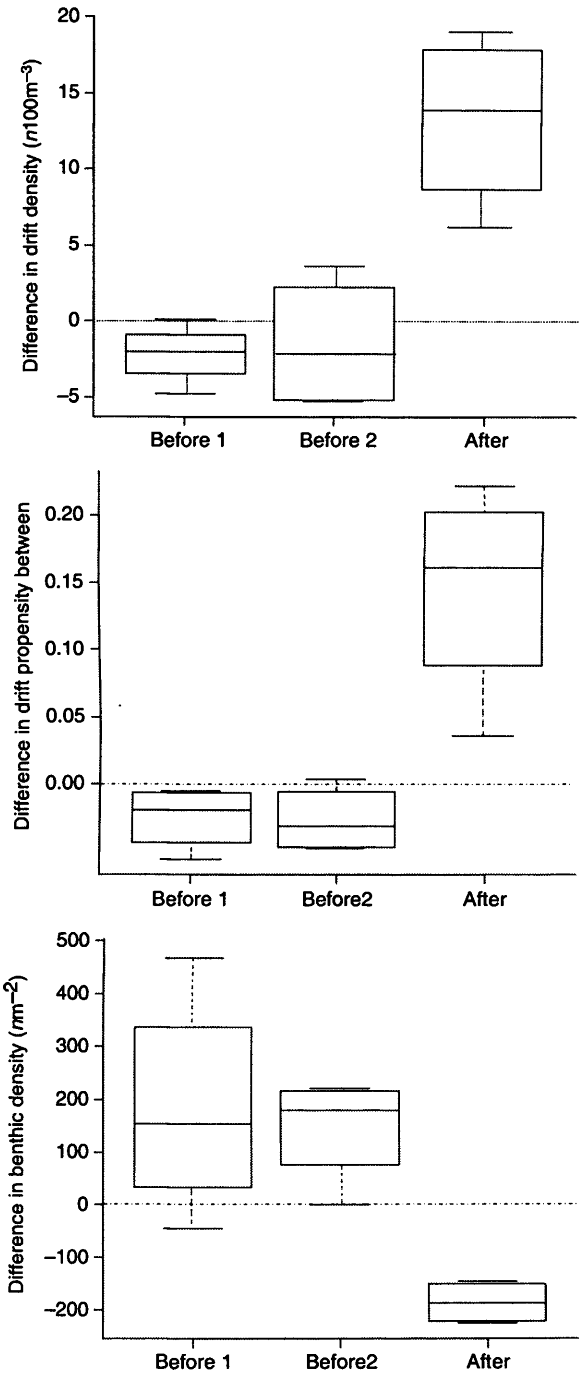

Fig. 1 Box-Whisker plots, showing mean and interquartile range to illustrate the differences in drift and benthic measures between impact and control reaches before and after sediment addition. Drift propensity = drift density/benthic density. Note that transformed abundances were used in analyses.

Much of the additional drift was explained by commonly drifting taxa; drift density in the mayflies *B. rhodani*, and *Ecdyonurus* spp., as well as simuliid dipterans, all increased after sediment input (Table 1). Overall changes in drift propensity in the impact reach were large (200%), particularly in the aforementioned taxa, and in *Baetis muticus* (Linnaeus), chironomids and larval Helodidae. There was no effect on some other taxa that were relatively common in the drift, such as the mayflies *Baetis scambus* Eaton, *Heptagenia lateralis* (Curtis) and the coleopterans *Elmis aenea* (Muller), *Limnius volkmarii* (Panzer) or *Oulimnius tuberculatus* (Muller).

Visual inspection of DCA plots for both seasons illustrated that sediment addition had no marked effects on the taxonomic composition of the drift (Fig. 3), and drifting invertebrates formed assemblages that were equally distinct from the benthos both before and after sediment addition. Even though general assemblage composition apparently differed between the two streams according to ordination, drift responses to sediments were highly consistent across both streams and seasons (Fig. 4).

Benthic response to sediments

Benthic samples produced 56 taxa, with *B. rhodani*, *Ephemerella ignita* (Poda), *Ecdyunurus* spp. and chironomids the most abundant. Average densities in the treated reaches were slightly higher than control reaches before sediment input (Fig. 1), but sediment addition reversed this position, resulting in a significant reduction in overall benthic density of >300 individual m^{-2} (Fig. 1). In particular, densities of *B. rhodani*, *Ecdyonurus* sp. and *Leuctra hippopus* (Kempny) + *L. moselyi* Morton were significantly reduced in impacted reaches after sand addition by 26–63% (Table 1). Ordination showed that there were no changes in overall taxonomic composition (Fig. 3). As with the drift, benthic invertebrate in the two study streams formed distinct groups in DCA plots for both seasons, but sediment effects on density were consistent across sites and seasons (Fig. 4).

Discussion

These results support the hypothesis that small increases in sediment loads to stony streams increase invertebrate drift and reduce benthic density, at least

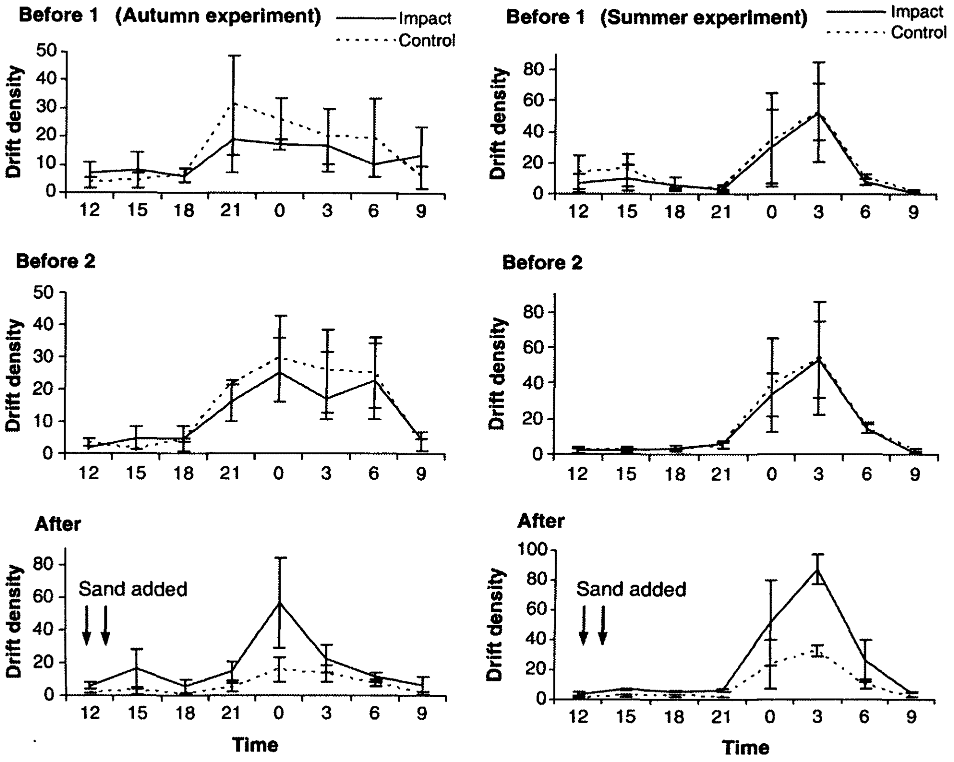

Fig. 2 Diel drift density (N/100 m^3) profiles of aquatic invertebrates autumn and summer experiments for the two days before and immediately after sediment addition. The X-axis represents actual time of day. Note changes in Y-axis.

over short-time periods. Sediment additions of just 4–5 kg m^{-2}, covering the benthos to levels typically seen at the lower range of deposition of this same catchment, increased drift density or propensity in simuliids, chironomids and several mayflies, with the latter also declining consistently in benthic numbers. Drift responses were not immediate (Rosenberg & Wiens, 1978; Culp *et al.*, 1985; Doeg & Milledge, 1991), but delayed into the first period of darkness following sediment addition, suggesting avoidance of apparently impaired habitat rather than immediate behavioural displacement (Fairchild *et al.*, 1987; Matthaei *et al.*, 2006). This form of behavioural drift and redistribution is well-known as a response to local carrying capacity and habitat conditions, particularly where reduced food quality or availability prompts individuals to seek new patches (Hildebrand, 1974). However, because drift carries a predation risk, it is mostly nocturnal in locations occupied by drift-feeding fishes and it is interesting that drift from sediment-impacted patches here was deferred into darkness. Diel activity patterns in epilithic grazers such as mayflies also mean that surface-deposited sediments might not be encountered until darkness (Glozier & Culp, 1989). Interestingly, leuctrid stoneflies also declined in the benthos following sediment addition despite showing no change in drift suggesting that other avoidance behaviours might also have occurred, such as movement into the hyporheos.

Despite apparently straightforward support for the hypothesis under test, several aspects of our results require cautious interpretation. As well as water quality or temperature, biotic factors such as food scarcity, competition and the presence of predators can influence drift densities (e.g. James *et al.*, 2008). Drift can therefore vary significantly not only through the diel cycle, but even between days in the same week (Brittain & Eikeland, 1988). Variations also occur among streams, as well as vertically and horizontally within streams, potentially affecting estimates based on small numbers of observations (Neale *et al.*, 2008). Variations around the drift profiles during our

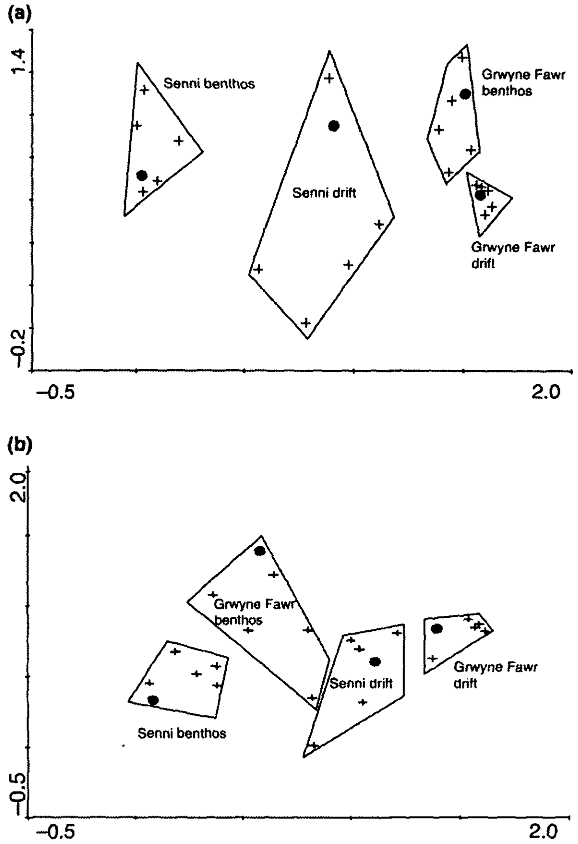

Fig. 3 DCA plots of summer (a) and autumn (b) experiments. Each group has six samples corresponding to either drift or benthic samples taken twice before and once after sediment addition in both control and impact reaches. Black circles represent impact locations after sediment addition. Drift and benthic assemblages formed distinct groups for both streams. Note that the axes are in units of standard deviation such that 4 SD represents *c.* 100% turnover in species composition.

experiment reflect some of these differences between sampling sessions and streams after accounting for varying discharge. However, our experimental BACIP design, with matched control with impact reaches and analysis focused on the differences between them, meant that any confounds were unlikely (Stewart-Oaten & Bence, 2001). Moreover, despite some variability, the direction of all results was consistent between seasons and study streams, allowing a more confident interpretation of observed effects.

Three particular methodological aspects of our study were not controlled by our design and require particular attention. First, the possibility exists that extreme invertebrate drift distances might have exceeded the length of our experimental reaches, so that not all invertebrates captured in the drift had necessarily originated from the treated areas (Brittain & Eikeland, 1988). However, changes in such effects during the experiment would be an unlikely explanation for apparently enhanced drift in both treated reaches and on both experimental occasions. Moreover, typical drift distances are much less than our experimental reaches and typically <2–20 m (Allan, 1995). Secondly, and linked to the previous point, upstream drift nets in the reference reaches might have intercepted drifting invertebrates and therefore contributed to the reduction in treatment-reach density over the course of the experiment. We rule out this possibility because any such effects should already have been apparent before sediment addition (i.e. on the second 'Before' day) rather than following sediment addition. Thirdly, the type of sediments we added, although formed from siliceous sand comparable in size and composition to the naturally occurring fine fraction in the Usk system, may have differed in other features, such as sphericity and angularity. These features can be relevant ecologically (Holomuzki & Biggs, 2003). However, any such effects would limit the application of the results to the Usk rather than their general relevance to other locations where sandy sediments enter streams.

Although not common, other studies have reported the effects of experimental sediment additions and turbidity on drift, but comparisons with our experiment are complicated by the differences in the methods, designs and sediment characteristics used. For example, Rosenberg & Wiens (1978) and Doeg & Milledge (1991) detected an immediate drift response to increased suspended clay and silt sediments in natural channels, but neither measured behavioural drift at night nor used a replicated or controlled design. Culp *et al.* (1985) added sand to two contrasting streams and recorded immediate and delayed drift only where sand particles were transported downstream by saltation, suggesting that sediment-flow interactions are important to invertebrate redistribution. Similarly, working in a flume, Gibbins *et al.* (2007) showed that fine sediment movement could trigger substantial drift, concluding that even low bed loads could denude stream patches of invertebrates. In this study, we did not measure the rate of sand displacement, but most of the material added was transported away from the treated reaches after 24 h

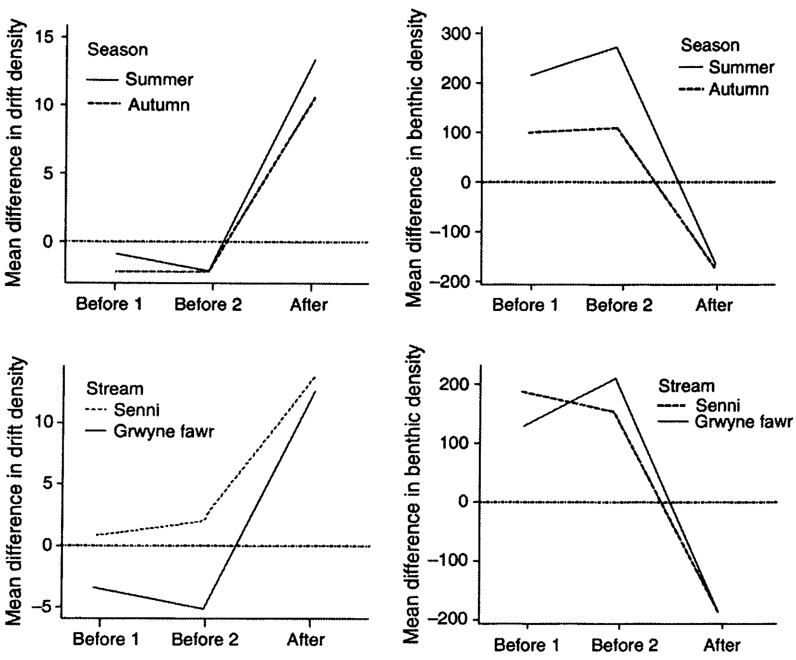

Fig. 4 Interaction plots showing the contribution of streams or seasons on the mean differences of drift and benthic density between impact and control reaches before and after sediment addition.

illustrating that saltation and/or suspension must have been occurring. However, Suren & Jowett (2001) demonstrated that even deposited, non-saltating, fine sediments (~12 kg m^{-2}) caused significant drift coupled with decreased benthic densities in some taxa. In complete contrast, Bond & Downes (2003) concluded from experimental manipulations that suspended sediment additions to experimental streams had no additional effects in displacing invertebrates over those caused by flow increase alone. The sediment size range was very similar to that in our study, although drift was recorded over a much shorter, diurnal period that, if used in our experiment, would have failed to detect the subsequent increase in nocturnal drift. With the exception of this last study, and notwithstanding some variations with respect to the timing and possible mechanisms involved, overall this study is consistent with previous data in confirming that invertebrates drift in response to sediments even at the low loadings used.

Despite their limitations, freshwater ecology has a long history of using experiments at small spatio-temporal extents to examine the potential effects of larger-scale phenomena. Examples include investigating the role of drift or refuge effects in large-scale disturbance and recolonisation (Townsend & Hildrew, 1976; Palmer, Bely & Berg, 1992), or assessing the short-term (<24 h) sensitivity of invertebrates to globally widespread pollutants (Ormerod *et al.*, 1987). In all these cases, there are difficulties in scaling-up, but equally there are major benefits in understanding whether effects observed at one support patterns observed at other scales. In keeping with these concepts, a secondary aim of this experiment was to examine how drift responses to sediments might corroborate previous survey work in the same river system that related invertebrate assemblages, trait composition and apparent species sensitivity to large-scale sediment cover (Larsen *et al.*, 2009; S. Larsen and S.J. Ormerod, unpubl. data). There are limitations here because the 24 h treatment period was apparently insufficient to reduce benthic richness or alter community composition. Moreover, the limited reach length in our experiment means also that drift responses will have represented local redistribution of organisms between patches rather than larger-scale impairment. Additionally, because experiments on drift are likely to capture a different set of taxa from benthic sampling (see Fig. 4), there are also difficulties in comparisons with taxa whose sensitivity to sediments was shown from benthic data. Nevertheless, substantially reduced density in treated reaches is an illustration of how longer-term sediment effects on benthic organisms might arise and develop where sediment delivery is sustained.

In our larger-scale surveys, the overall richness of Ephemeroptera, Plecoptera and Trichoptera was reduced at sediment-treated sites, to which a longer-term displacement of *B. rhodani, B muticus* and *Ecdyonurus* spp. could contribute. *Baetis* spp, generally avoid fine substrata (Wagner, 1989; Wood *et al.*, 2005) and also drift rapidly as bedload transport increases (Gibbins *et al.*, 2005). Simuliids, also, are intolerant to smothering in agreement with the increased drift densities in our impacted reaches (Minshall, 1984; Larsen *et al.*, 2009). Our previous study showed that taxa sensitive to sediments were characterised by particular feeding or behavioural traits (S. Larsen and S.J. Ormerod, unpubl. data), and this is again consistent with the drift and density data here. For example, simuliids are filter-feeders whose mouthparts can be impaired by fine particles (Strand & Merritt, 1997). *Baetis* and *Ecdyonurus* species are mostly scrapers in which feeding would be quickly impaired on smothered periphyton even if the short duration of the experiment will not have altered underlying periphyton quality.

Overall, even if the temporal and spatial scale of this experiment was limited, the data show how even small increases in fine sediment supply to upland streams can reduce benthic density by promoting drift. Many temperate river catchments are now characterised by land use practices that increase sediment delivery to streams, for example through the conversion of natural vegetation to pasture and the removal of riparian trees. Both appear to increase the risks of sediment release in the Usk (Larsen *et al.*, 2009). Small-scale effects like those observed here could, therefore, form part of a larger-scale attrition of stream integrity. We suggest that larger, longer-term experiments would be a valuable means of assessing this possibility.

Acknowledgments

The funding for this study was provided by the Wye and Usk Foundation, Wales and we thank Dr Stephen Marsh-Smith and Simon Evans. We thank Richard Johnson and two anonymous reviewers for their valuable comments and suggestions. We also thank Federica Pinto and Giorgio Pace for their valuable assistance in the field, Dr Ian Vaughan for statistical advice and landowners for allowing access to the sites. Two referees provided insightful comments on the manuscript.

References

Allan J.D. (1995) *Stream Ecology. The Structure and Function of Running Waters.* Chapman & Hall, London.

Angradi T.R. (1999) Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications. *Journal of the North American Benthological Society*, **18**, 49–66.

Argent D.G. & Flebbe P.A. (1999) Fine sediment effects on brook trout eggs in laboratory streams. *Fisheries Research*, **39**, 253–262.

Bond N.R. & Downes B.J. (2003) The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. *Freshwater Biology*, **48**, 455–465.

Brittain J.E. & Eikeland T.J. (1988) Invertebrate drift – a review. *Hydrobiologia*, **166**, 77–93.

Broekenhuizen N., Parkyn S. & Miller D. (2001) Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). *Hydrobiologia*, **457**, 125–132.

Chutter F.M. (1968) The effects of silt and sand on the invertebrate fauna of stream and rivers. *Hydrobiologia*, **34**, 57–76.

Collins A.L., Walling D.E. & Leeks G.J.L. (1997) Source type ascription for fluvial suspended sediment based on a quantitative composite fingerprinting technique. *Catena*, **29**, 1–27.

Connolly N.M. & Pearson R.G. (2007) The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: a comparison using flowthrough artificial stream channels and recirculating mesocosms. *Hydrobiologia*, **592**, 423–438.

Culp J.M., Wrona F.J. & Davies R.W. (1985) Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology*, **64**, 1345–1351.

Doeg T.J. & Milledge G.A. (1991) Effect of experimentally increasing concentrations of suspended sediment on macroinvertebrate drift. *Australian Journal of Marine and Freshwater Research*, **42**, 519–526.

Edington J.M. & Hildrew A.G. (1981) *A Key to the Caseless Caddis Larvae of the British Isles with Notes on Their Ecology*. Freshwater Biological Association, Ambleside.

Elliott J.M. (2003) A comparative study of the dispersal of 10 species of stream invertebrates. *Freshwater Biology*, **48**, 1652–1668.

Fairchild J.F., Boyle T., English W.R. & Rabeni C. (1987) Effects of sediment and contaminated sediment on structural and functional components of experimental stream ecosystems. *Water Air and Soil Pollution*, **36**, 271–293.

Friday L. (1988) *A Key to the Adults of British Water Beetles*. Field Studies Council, Preston Montford.

Gibbins C.N., Scott E., Soulsby C. & Mcewan I. (2005) The relationship between sediment mobilisation and the entry of Baetis mayflies into the water column in a laboratory flume. *Hydrobiologia*, **533**, 115–122.

Gibbins C., Vericat D., Batalla R.J. & Gomez C.M. (2007) Shaking and moving: low rates of sediment transport trigger mass drift of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 1–5.

Glozier N.E. & Culp J.M. (1989) Experimental investigations of diel vertical movements by lotic mayflies over substrate surfaces. *Freshwater Biology*, **21**, 253–260.

Graham C.K. (1990) Siltation of stone-surface periphyton in rivers by clay-sized particles from low concentration in suspension. *Hydrobiologia*, **199**, 107–115.

Greig S.M., Sear D.A. & Carling P.A. (2005) The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. *Science of the Total Environment*, **344**, 241–258.

Hildebrand S.G. (1974) Relation of drift to benthos density and food level in an artificial stream. *Limnology and Oceanography*, **19**, 951–957.

Hill M.O. & Gauch H.G. (1980) Detrended correspondence-analysis – an improved ordination technique. *Vegetatio*, **42**, 47–58.

Holomuzki J.R. & Biggs B.J.F. (2003) Sediment texture mediates high-flow effects on lotic macroinvertebrates. *Journal of the North American Benthological Society*, **22**, 542–553.

Ihaka R. & Gentleman R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.

James A.B.W., Dewson Z.S. & Death R.G. (2008) The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, **24**, 22–35.

Kreutzweiser D.P., Capell S.S. & Good K.P. (2005) Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology*, **39**, 55–66.

Larsen S., Vaughan I.P. & Ormerod S.J. (2009) Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology*, **54**, 203–219.

Lemly D. (1982) Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia*, **87**, 229–245.

Manel S., Buckton S.T. & Ormerod S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology*, **37**, 756–770.

Matthaei C.D., Weller F., Kelly D.W. & Townsend C.R. (2006) Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology*, **51**, 2154–2172.

Minshall G.W. (1984) Aquatic insect–substratum relationships. In: *The Ecology of Aquatic Insects* (Eds Resh V.H. & Rosenberg D.M.), pp. 358–400. Preager publishers, New York.

Neale M.W., Dunbar M.J., Jones J.I. & Ibbotson A.T. (2008) A comparison of the relative contributions of temporal and spatial variation in the density of drifting invertebrates in a Dorset (UK) chalk stream. *Freshwater Biology*, **53**, 1513–1523.

Ormerod S.J., Boole P., Mccahon C.P., Weatherley N.S., Pascoe D. & Edwards R.W. (1987) Short-term experimental acidification of a welsh stream – comparing the biological effects of hydrogen-ions and aluminum. *Freshwater Biology*, **17**, 341–356.

Osborne L.L. & Kovacic D.A. (1993) Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology*, **29**, 243–258.

Palmer M.A., Bely A.E. & Berg K.E. (1992) Response of invertebrates to lotic disturbance – a test of the hyporheic refuge hypothesis. *Oecologia*, **89**, 182–194.

Parkhill K.L. & Gulliver J.S. (2002) Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia*, **472**, 5–17.

Pinheiro J. & Bates D. (2000) *Mixed Effects Models in S and S-Plus*. Springer, New York.

Rosenberg D.M. & Wiens A.P. (1978) Effects of sediment addition on macrobenthic invertebrates in a Northern Canadian River. *Water Research*, **12**, 753–763.

Roth N.E., Allan J.D. & Erickson D.L. (1996) Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology*, **11**, 141–156.

Rowe D.K. & Dean T.L. (1998) Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New*

Zealand Journal of Marine and Freshwater Research, **32**, 21–29.

Ryan P.A. (1991) Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research*, **25**, 207–221.

Stewart-Oaten A. & Bence J.R. (2001) Temporal and spatial variation in environmental impact assessment. *Ecological Monographs*, **71**, 305–339.

Strand M.R. & Merritt R.W. (1997) Effects of episodic sedimentation on the netspinning caddisflies *Hydropsyche betteni* and *Ceratopsyche sparna* (trichoptera: hydropsychidae). *Environmental Pollution*, **98**, 129–134.

Suren A.M. & Jowett I.J. (2001) Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research*, **35**, 725–737.

Townsend C.R. & Hildrew A.G. (1976) Field experiments on drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology*, **45**, 759–772.

Turnpenny A.W.H. & Williams R. (1980) Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology*, **17**, 681–693.

Wagner R. (1989) The influence of artificial stream bottom siltation on Ephemeroptera in emergence traps. *Archiv fur Hydrobiologie*, **115**, 71–80.

Wallace I., Wallace B. & Philipson G. (2003) *Keys to the Case-Bearing Caddis Larvae of Britain and Ireland. Scientific Publication 61*. Freshwater Biological Association, Ambleside.

Wartenberg D., Ferson S. & Rohlf F.J. (1987) Putting things in order – a critique of detrended correspondence-analysis. *American Naturalist*, **129**, 434–448.

Waters T.F. (1995) *Sediments in Streams: Sources, Biological Effects, and Control*. AFS Monographs, Bethesda, MD.

Weiss J.M. & Reice S.R. (2005) The aggregation of impacts: using species-specific effects to infer community-level disturbances. *Ecological Applications*, **15**, 599–617.

Wood P.J., Toone J., Greenwood M.T. & Armitage P.D. (2005) The response of four lotic macroinvertebrate taxa to burial by sediments. *Archiv fur Hydrobiologie*, **163**, 145–162.

(Manuscript accepted 1 July 2009)

RIVER RESEARCH AND APPLICATIONS
River. Res. Applic. (2010)

(www.interscience.wiley.com) DOI: 10.1002/rra.1361

EXPERIMENTAL EFFECTS OF SEDIMENT DEPOSITION ON THE STRUCTURE AND FUNCTION OF MACROINVERTEBRATE ASSEMBLAGES IN TEMPERATE STREAMS

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ABSTRACT

Fine sediment in streams and rivers is one of the most globally widespread of all freshwater pollutants. However, the ecological implications are still poorly quantified, and field experiments to assess likely functional and structural effects are scarce.

We assessed the response of stream invertebrates to fine sediment (i.e. inert sand) added to trays ($n = 65$) containing otherwise natural substrata over a three-week period in three replicate streams in the Usk catchment, Wales.

Sediment addition to 0.6–18 $\mathrm{kg\,m^{-2}}$ affected both the structure and functional composition of invertebrate assemblages while also reducing overall abundance and in some common species (*Baetis rhodani*, *Ecdyonurus* sp. and *Leuctra geniculata*).

Sediment also reduced richness and overall trait diversity (TD), while different life-history traits were either favoured (polivoltinism, tegumental respiration and burrowing behaviour) or disfavoured (swimmers, attached taxa, gill respiration). Moreover, sediments appeared to promote a nested subset pattern in species composition, with generalists favoured at the expense of specialists either through exclusion or impaired colonization. Effects were due largely to the loss of five taxa that contributed to the significant nestedness across the sand gradient: *B. rhodani*, *Ecdyonurus* sp., *Leuctra geniculata*, Simuliidae and *Ephemerella ignita*.

This short-term experiment supports recent surveys in indicating how sedimentation can change the structural and functional composition of stream invertebrate assemblages even at low to moderate rates of deposition. In revealing direct effects on trait adversity, trait representation and nestedness, the data are also consistent with survey data in indicating that sediments have potentially important ramifications for conservation by removing organisms systematically according to life-history features.

KEY WORDS: conservation; insects; invertebrates; life-history traits; nestedness; rivers

Received 1 July 2009; Revised 8 December 2009; Accepted 22 December 2009

INTRODUCTION

The entrainment and deposition of inert fine particles, arising from catchment and riparian modification, is one of the most widespread of all pollution problems affecting freshwaters globally (Davies-Colley *et al.*, 1992; Waters, 1995; Wood and Armitage, 1997; Angradi, 1999; Broekenhuizen *et al.*, 2001; Connolly and Pearson, 2007). In United States, siltation is the principal source of impairment on the basis of stream distance impacted (USEPA 2000), while sediment fluxes throughout the world are increasing as catchments are progressively modified (Owens *et al.*, 2005). Consequent changes in water quality and habitat character affect aquatic organisms across all trophic levels through mechanisms that include (i) increasing turbidity, reducing primary production and available light for visual predators (Davies-Colley *et al.*, 1992; Davies-Colley and Smith, 2001); (ii) changing substratum structure and benthic habitat (Schalchli, 1992; Rehg *et al.*, 2005) (iii) filling interstices, thus altering hydrological exchange between surface and groundwater while decreasing nutrient and oxygen supply to the hyporheos and reducing salmonids eggs survival (Turnpenny and Williams, 1980; Richards and Bacon, 1994).

In agricultural catchments, sediments can arise from point-sources, such as livestock poaching and bank erosion, or from large-scale diffuse release, for example from tillage and deforestation (Kreutzweiser *et al.*, 2005; Larsen *et al.*, 2009). In these cases, increasing sedimentation is often associated with wider habitat modifications and other in-stream stressors resulting in complex synergistic or antagonistic ecological responses (Townsend *et al.*, 2008). For example, nutrients, pesticides and altered hydraulic and thermal regimes can potentially mask or exacerbate biological effects of sediments. Global climate change is also likely to modify precipitation and hydrologic regimes, therefore, altering soil erosion rates and sediment transport (Wilby *et al.*, 1997). Under all these circumstances, improved quantification of the ecological effects of sediments and improved understanding of the underlying mechanisms is a major requirement.

In the river Usk system, a temperate river system in Wales (UK), recent surveys have shown how localized sediment

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delivery and patch-to-patch variation in sediment deposition have been associated with reduced richness and densities of sensitive taxa, altered representation of certain life-history or behavioural traits, and reduced trait diversity (Larsen *et al.*, 2009; Larsen and Ormerod, in press). As is typical with large-scale surveys, however, these data were correlative rather than providing clear indications of cause and effect (Manel *et al.*, 2000). Here, and elsewhere, laboratory or field manipulations of sediment character or deposition rate offer a method of corroborating such larger-scale pattern (Angradi, 1999; Kreutzweiser *et al.*, 2005; Townsend *et al.*, 2008), investigating the possible mechanisms involved (Suren *et al.*, 2005; Wood *et al.*, 2005; Molinos and Donohue, 2009) or appraising directly the functional responses of impacted organisms (Rabeni *et al.*, 2005; Townsend *et al.*, 2008).

In this paper, we describe the results of field experiment in the Usk system, replicated at the stream scale, designed to mimic the effects of sediment deposition on stream patches. We increased the deposition of fine sand in trays filled with natural substrata held *in situ* to investigate effects on macroinvertebrate composition, abundance and functional characteristics. Based on previous findings from this catchment and elsewhere (Angradi, 1999; Doledec *et al.*, 2006; Matthaei *et al.*, 2006; Townsend *et al.*, 2008; Larsen *et al.*, 2009), we tested the following predictions:

(i) invertebrate density, diversity and richness should decline with increasing sediment deposition;
(ii) the representation of shorter life cycles, smaller sizes, tegumental respiration, detrital feeding and burrowing traits should be favoured in sediment-rich trays, while longer life cycles, larger size, gill respiration, filtering, grazing and temporary attachment should be disfavoured;
(iii) overall trait diversity should decline with increasing sediments.

The experiment also allowed us to test the hypothesis that local sedimentation can alter colonization patterns and promote nestedness in invertebrate community structure (Larsen and Ormerod, in press). Nested subset patterns occur where species present in depauperate locations constitute a subset of the species in richer locations. In perfectly nested systems, rare taxa only occur in the richest site and generalists at most sites. While nestedness analysis was initially developed as a mean of testing biogeographical theories (Atmar and Patterson, 1993; Hecnar *et al.*, 2002), applications to conservation and management are increasing (Fleishman *et al.*, 2007). This is because nested subsets in species composition can arise not only from extinction and colonization processes over broad spatio-temporal extents, but also from human disturbance, habitat alteration and even behavioural effects on patch use (Fernandez-Juricic, 2002; Summerville *et al.*, 2002; Hylander *et al.*, 2005). We examined the possibility that sediment deposition could promote a nested subset pattern in species occurrence across trays, for example, by impairing colonization by specialist and rare taxa during the experiment.

METHODS

Study area

The river Crai, Cynrig and Tarell are three, third-order tributaries (3–5 m wide) of the river Usk, which drain sandstone-rich catchments at 250–300 m above sea level (National Grid Reference: SN881235, SO048247, SO009269, respectively). The reaches selected for the experiment (*c.* 30 m) drained a blend of scattered deciduous woodland, improved grassland and rough pasture. Each was partially shaded by deciduous trees with substrata mainly of boulders, cobbles and pebbles and some gravel. Stream reaches were chosen for their relative similarity in geomorphology, faunal composition and riparian/catchment land-use as informed by previous surveys (Larsen *et al.*, 2009).

Stream waters were relatively clean, well oxygenated and rich in carbonates, with pH 7.2–8 and plant nutrients generally low (<2 mg nitrate L^{-1}). In some locations, where natural riparian vegetation has been removed and livestock have access to the stream banks, erosion has resulted in localized release and deposition of relatively coarse sediments (Larsen *et al.*, 2009). We attempted to recreate such patch-scale variation in deposited sediments under controlled conditions *in situ* in the three selected streams.

Experimental design

Following an approach similar to that of Angradi (1999), 22 plastic trays (18 cm × 12 cm × 5 cm), filled with natural substrata collected on site and composed of gravel, pebble and cobble, were deployed in each of the three streams on the 19th of July 2008 across a 30 m stretch within glide/run habitats with relatively homogeneous flow (c 20–30 cm s^{-1}). Each filled tray weighed *c.* 2 kg and was positioned in the stream bed so that the substratum surface in the tray was flush with the stream bed. In each stream, immediately after installation, trays were either covered with 1 kg of clean, childrens' play-sand (33% in weight, or *c.* 40 kg m^{-2}; $n = 6$), with 2 kg of sand (50% in weight, or *c.* 80 kg m^{-2}; $n = 6$) or left as controls (no sand added; $n = 6$). An open metal box was fitted around each treated tray to momentarily stop the flow prior to sand addition. To avoid excessive loss of sand, the sides of the trays were solid. Additionally, to maintain the intended sediment concentration over the experimental period and to simulate sediment re-supply, four additional

DOI: 10.1002/rra

trays in each stream were covered with 1 kg of sand on two occasions; at the beginning of the experiment and then again after a week, thus receiving 2 kg in total. Size distribution of sand used here (0.2–1 mm) was similar to natural occurring sediments in the catchment (Larsen *et al.*, 2009).

Trays were left in the streams for 19 days, with this interval determined by the risk and impact of high-flow events during this abnormally wet summer. Water velocity and depth immediately in front of each tray was monitored every 3 days for the duration of the experiment, while water temperature, conductivity and pH were also measured on three occasions. Although the experiment covered a relatively short period, associated work showed that sediment effects on stream invertebrates in the Usk and elsewhere can develop even within 24 h (Culp *et al.*, 1985; Suren and Jowett, 2001; Gibbins *et al.*, 2007; Larsen and Ormerod, in press). Moreover, a longer colonization period would have decreased the sediment gradient towards ambient conditions.

Trays were eventually retrieved paying attention not to lose any invertebrates or organic detritus by covering them with a net at the time of collection (mesh 0.2 mm). In addition, two pooled Surber samples (0.09 m^2; 0.44 mm) were taken at the time of tray collection to assess how closely assemblages in trays represented the faunal composition in each stream. The contents of each tray and Surber sample were sorted in the laboratory where invertebrates were separated from coarse particulate organic matter (CPOM), which was then dried and weighed. A sieve of 0.2 mm was used to retain the fine sediment fraction which was also dried and weighed to assess how closely sediment additions had produced the intended sediment cover. Invertebrates were identified, where practicable, to species.

Data analysis

Because background sediment accumulation in each tray would cause variations relative to the nominal additions, we used the exact mass of sand per-unit-area of tray substrate as a continuous variable to express sediment effects on the invertebrates. Data from all the three streams were combined in analysis in order to maximize sample size and decrease the risk that species occurred in individual trays by chance.

Prior to any further analysis, we used detrended correspondence analysis to parameterize variations in invertebrate assemblages among sample Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980). This ordination technique arranges samples with similar composition onto orthogonal axes that can be used in subsequent analyses. Preliminary investigation showed that species responded unimodally to sediment cover rather than rectilinearly suggesting that this technique was appropriate (Jongman *et al.*, 1995). After removing taxa that did not occur in all four streams, 18 were included in the ordination. Arithmetic and transformed abundances gave near-identical ordination results, and only analyses based on arithmetic abundances are presented.

To assess treatment effects on the taxonomic richness, diversity, individual abundances and community composition (i.e. sample ordination scores) of invertebrate, we used mixed-effects models, where stream identity was included as a random factor in analysis, while fine sediments and CPOM were considered fixed factors. Mixed models are appropriate for the data, providing flexibility in representing the covariance structure induced by data grouping (Pinheiro and Bates, 2000). In other words, the analysis takes into account the difference in species composition and biological response to treatment among the streams. We also assessed the influence of water flow on sediment levels, and measured the correlation between sediment and CPOM in trays.

Similarity in taxonomic composition among trays and adjacent Surber samples was assessed using the Bray-Curtis similarity index. Specifically, we plotted the similarity between control trays and treated trays, and between all trays and Surber samples, against sediment content. To allow direct comparison of richness between control trays and Surbers, we used EcoSim simulation software (Gotelli and Entsminger, 1997) to rarefy Surbers richness based on the average abundance in control trays.

To describe communities according to their functional trait representation, we defined 48 categories of 11 life-history and behavioural traits using available information (Richoux, 1994; Tachet *et al.*, 1994; Usseglio-Polatera, 1994; Usseglio-Polatera and Tachet, 1994; Tachet *et al.*, 2000). The affinity of each taxon for each trait category was described using fuzzy coding (Chevenet *et al.*, 1994). Information on trait coding was available only at the genus level, so we used this level of identification for all trait analysis. Each taxon was given an affinity score that ranged between 0 (no affinity) and 3, or 0 and 5 depending on the number of categories within each trait. When no exact information was available for a given taxon for a given trait, an affinity of 0 was applied so that the taxon was treated as though it had the average profile of the corresponding trait (Dolédec *et al.*, 1999). Affinity scores were rescaled as proportions (sum = 1) for each taxon, thus, representing the probability that any taxon belonged to a particular category. For each site, the resulting species × trait-category matrix was multiplied by the site × species-abundance matrix to give a site × trait abundance matrix. The abundance-weighted trait matrix were then defined as a frequency distribution of categories for each trait (Dolédec *et al.*, 2000; Archaimbault *et al.*, 2005). Fuzzy correspondence analysis (FCA) was used on the trait matrix to obtain scores of each tray based on overall trait composition (Chevenet *et al.*, 1994). The scores were then used to assess if sediment

DOI: 10.1002/rra

affected overall trait representation again using mixed modelling. Trait diversity in each tray was calculated as the average Simpson diversity (S) across all categories within each trait

$$\mathrm{TD} = \mathrm{S} = 1 - D_i, \text{ where } D_i = \sum \left(\frac{n_j}{N}\right)^2$$

with D_i = dominance index of trait i; n_j = relative abundance of trait category j; N = total abundance of all trait categories. The average of S across all traits was calculated to reduce lack of independence among traits (e.g. Bêche and Resh, 2007).

To assess if specific traits varied with sediment content, the proportion of trait categories describing maximal size, life cycles, numbers of generations per year, respiration, feeding and locomotion were analysed using mixed effect models as before. Proportions were arcsin $\sqrt{x}$ transformed before analysis to homogenize variances. For this particular test on trait categories, we corrected α values ($=0.05$) by dividing them by the number of categories within each trait (e.g. if a given trait has five categories, for significance $\alpha = 0.01$; Bêche *et al.*, 2006).

Nestedness across sites was calculated using the binary-matrix nestedness temperature calculator (BINMATNEST; Rodriguez-Girones and Santamaria, 2006), which is a recent improvement of the nested-temperature method of Atmar and Patterson (1993) in that it uses a more robust algorithm for matrix packing. The temperature method was chosen as it is relatively insensitive to matrix size and correlates well with other existing metrics (Wright *et al.*, 1998). Working on the species presence/absence matrix, BINMATNEST re-orders rows and columns maximizing matrix nestedness and then calculates a temperature (ranging over 0–100°C), which reflects the matrix deviation from an ideal nested structure; perfectly nested matrices with rare taxa in rich locations have $T = 0$°C while totally random matrices have $T = 100$°C. The temperatures of 400 simulated matrices using Monte Carlo randomization were used to calculate the statistical significance of the observed temperature against chance expectation. In the matrix simulations, we used the more conservative null-model III where the probability of a cell being occupied equals the average probabilities of occupancy of its row and column. This model is particularly reliable as it is less sensitive to species richness and occurrences (Rodriguez-Girones and Santamaria, 2006). The order with which the maximally packed matrix is sorted can then be compared with independent correlated to assess the likely drivers of nestedness. We used Spearman-rank correlation to evaluate the influence of sediment levels on the nested patterns of communities in trays (see Schouten *et al.*, 2007; Heino *et al.*, 2009 for a similar approach).

To examine which taxa contributed significantly to the overall nestedness we used the Mann–Whitney test on individual taxa. This is a two group test where presences (1) and absences (0) constitute the groups in the presence–absence matrix. For each taxon, the test gives the probability that the observed sequence of presences and absences differs from a random one (i.e. conforms to a nested pattern). To test specifically whether sediment treatment promoted 'nestedness' of individual taxa we first sorted the presence–absence matrix by increasing sediments. In this case, a perfectly 'nested' species would have no presences ('1') after the first absence ('0') along the sediment gradient. This approach has been used by Fernandez-Juricic (2002), Hecnar *et al.* (2002) and Summerville *et al.* (2002). Although this method assesses the 'nestedness' of individual taxa and it is useful to appraise specific contribution to the formation of nested subset patterns, real nestedness remains a property of assemblages since, by definition, it has a multi-species basis.

RESULTS

Physical conditions

Throughout the experiment, average current velocity in the steams ranged between 7 and 26 $\mathrm{cm\,s^{-1}}$ across trays, with water depths 6–18 cm. Average conductivity was *c.* 140 $\mu\mathrm{s\,cm^{-1}}$, pH *c.* 7.5, and stream temperature 14.5–17°C.Nitrate concentrations were similar across streams, averaging 1.3 $\mathrm{mg\,L^{-1}}$, while phosphates were very low (c. 0.01 $\mathrm{mg\,L^{-1}}$).

Upon retrieval, fine sediments accumulation in the trays ranged over 13–414 g (c 0.6–18 $\mathrm{kg\,m^{-2}}$), or *c.* 1–23% in proportional weight. In the untreated control trays (ambient substratum mixture), sediment weight ranged over 13–66 g (mean = 50 g ± 13 SD). One tray was lost so the final sample size was 65 trays. There was a tendency for lower sediment retention with increasing current velocity, but this trend was only marginally significant ($p = 0.07$). Compared to controls, CPOM content decreased by about 70% in the most sediment-affected trays (slope = -0.006; $p = 0.007$; Figure 1).

Invertebrate structure

Among the 34 taxa collected, *Baetis rhodani*, *Ecdyonurus* sp., *Leuctra moselyi*, *Ephemerella ignita* and Chironomidae were the most common. Taxon richness ranged between 4 and 14 (mean = 7 ± 2.16 SD) across trays, while abundances were 7–111 individuals per tray.

Mixed models showed that abundances and taxon richness were affected negatively by fine sediments, but not taxonomic diversity (Simpson index; Table I; Figure 2). Among individual taxa, the abundances of *B. rhodani*, *Ecdyonurus* sp., *Leuctra geniculata*, and *Gammarus pulex* were all affected by sediments (Table I).

DOI: 10.1002/rra

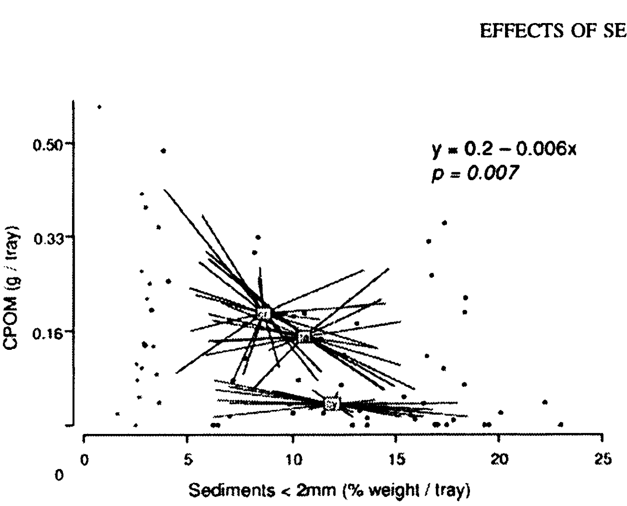

Figure 1. Relationship between CPOM (g/tray) and fine sediments in trays across the three replicate streams in the Usk catchment, Wales. Samples are grouped by stream; Cr = Crai; Cy = Cynrig; Ta = Tarell. Coefficients are based on mixed-effects model with streams as random factors. Experimental trays are shown with black symbols, and controls in grey

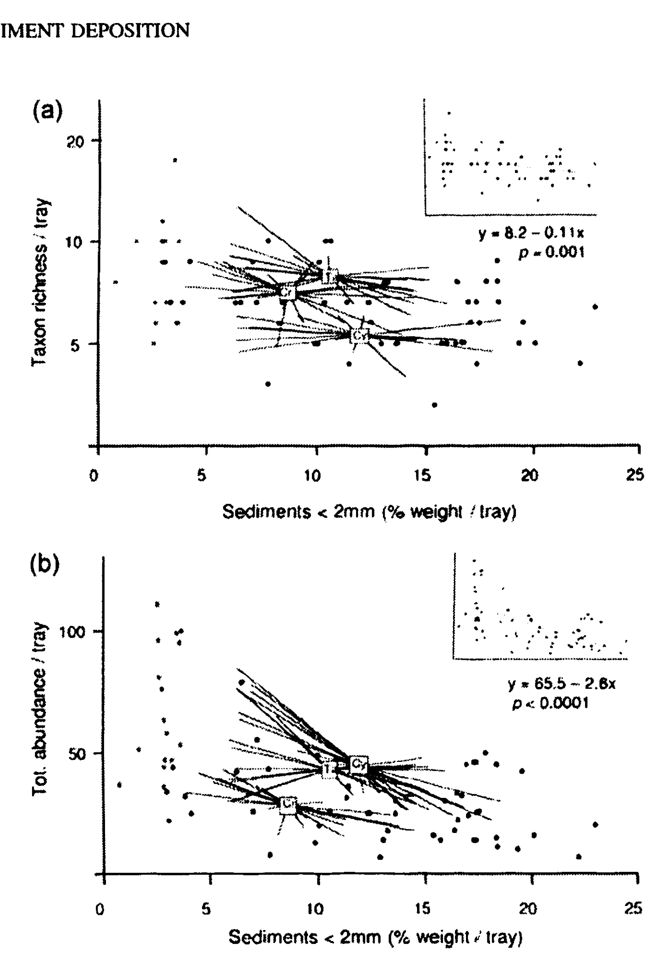

Figure 2. Relationship between taxon richness (a) and abundance (b) and fine sediment content in trays across the three replicate streams in the Usk catchment, Wales. Details as in Figure 1; experimental trays are shown with black symbols, and controls in grey

In community assessment, two DCA axes explained *c.* 50% of species variation across trays, with both axes showing significant relationships with sediment amount (Table I and Figure 3). Most species in the ordination appeared to prefer sediment-free conditions, being located mostly in the upper right quadrant of the factorial plane (Figure 3). Taxa apparently more common in sediment rich trays included chironomids, dytiscids and the mayfly *Habrophlebia fusca*. In contrast, the amount of CPOM in trays appeared to have no significant effects on species composition (DCA axes), richness or the abundance of individual taxa, implying that sediment affects were direct rather than being mediated through effects on organic detritus.

Comparison between Surber samples and control trays revealed some differences, and in particular average rarefied richness in Surber samples was 12–15 taxa, while the average richness in control trays was eight. *Hydropsyche siltalai*, *H. instabilis*, *Rithrogena semicolorata*, *Rhyacophila obliterata*, *Halesus* sp., *Perla bipunctata*, Tipulidae, Dytiscidae and *Oreodytes sanmarchii* were exclusive to Surber samples. Despite having reduced richness, 70% (i.e. 21) of the 30 taxa collected by Surber samplers were also present in control trays. Interestingly five taxa collected in control trays were not observed in Surbers: *Habrophlebia fusca*, *Odontocerum albicorne*, *Melampophylax mucoreus*, *Silo pallipes* and Psychodidae. With the exception of the first two, these were rare taxa, with only one occurrence in control trays.

Table I. The results of mixed-effects models showing the response of macroinvertebrate community variables and individual abundance to experimental sediment addition in the Usk catchment, Wales. Percentage change in each variable over the range of sediments accumulated is also shown

Response variable	Slope	% change	*p*
Richness	−0.11	−30%	0.001
EPT richness	−0.12	−46%	<0.0001
Abundance	−2.6	−90%	<0.0001
DCA axis 1	0.03		<0.0001
DCA axis 2	−0.03		0.0004
Baetis rhodani	−0.018	−42%	0.003
Ephemerella ignita	−0.014	−59%	0.018
Ecdyonurus sp.	−0.021	−71%	<0.0001
Leuctra moselyi	−0.016	−48%	0.011
Leuctra geniculata	−0.017	−90%	0.002
Gammarus pulex	−0.04	−70%	<0.0001
Trait diversity	−0.0003	−24%	0.001
FCA axis 1	0.016		<0.0001
FCA axis 2	−0.012		0.0004

Notes:
1. $N = 65$; d.f = 61.
2. Study streams (3) were included as random factors. Only significant models are shown.

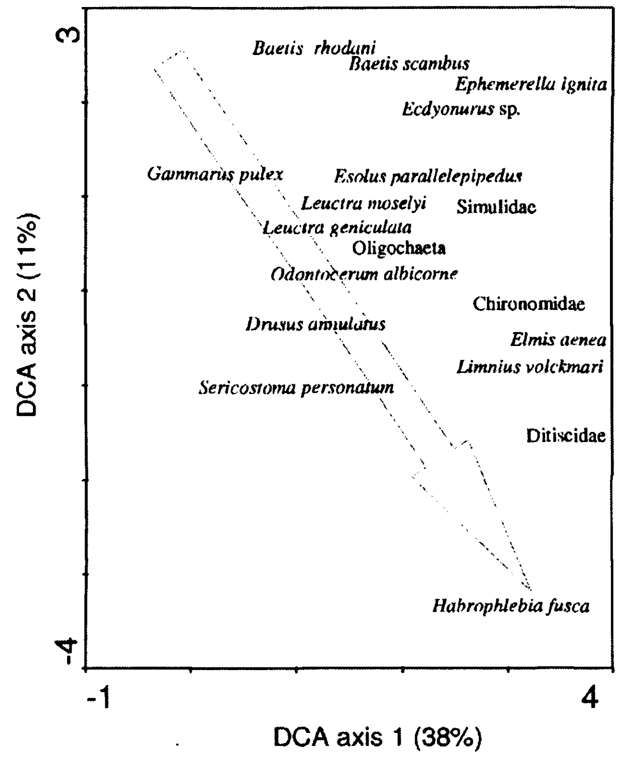

Figure 3. Plot of taxa collected during the experiment on the first DCA plane. Only taxa occurring more than four times were included. Arrow represents increasing fine sediments as reflected by correlation with both axes. Variation in species composition explained by each axis is reported in parenthesis

Average Bray–Curtis Similarity between Surber samples and trays (control + treatment) declined significantly with increasing sediment content, with control trays distinctively more similar to Surbers (Figure 4). Sediment addition also reduced the average similarity between treatment trays and controls (Figure 4).

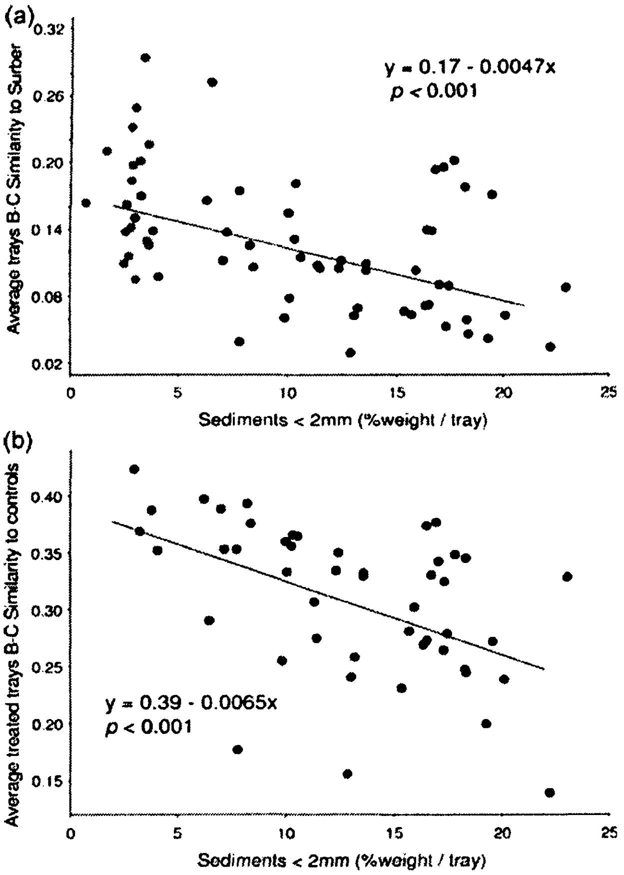

Figure 4. (a) Plot showing average similarity between trays (control + treatment) and Surber samples in relation to fine sediment content during an experiment involving sediment addition to three streams in the Usk catchment, Wales. Control trays are in grey, and experimental trays in black. (b) Average similarity of treated trays to control trays in relation to fine sediment content. Parameters are based on mixed-effects model

Functional response

The first factorial plane of the FCA explained >74% of the variation in biological traits across sites. Both axes were significantly related to fine sediment amount in trays implying that overall trait representation was affected by sediment addition (Table I).

Further effect of sediments on the trait structure was evident from the significant decline in overall trait diversity with increasing sediments (Table I). In other words, trays impacted by sand hosted a poorer array of reproductive, feeding and locomotion traits compared to controls. Mixed models showed that several trait categories responded to sediments (Table II). In particular, taxa characterized by shorter life cycles, detrital feeding and burrowing were all represented more in sediment-rich trays, while ovoviviparity, gill respiration, and temporarily attached taxa were disfavoured. There was no effect on the representation of different body sizes and number of generations per year.

Except for a proportional increase in shredder representation with increasing coarse organic matter ($p = 0.016$; not significant after correction based on number of categories), no effect of CPOM on trait representation was observed.

Nested subset pattern

Across the experimental trays, macroinvertebrate communities were significantly nested ($T = 16.4$; $p < 0.001$). Site ranking in the maximally-packed species-matrix (i.e. the matrix ordered by BINMATNEST to maximize nestedness) was significantly correlated with sediment

DOI: 10.1002/rra

Table II. The results of mixed effects models showing how the representation of individual trait category responded to experimental sediment addition in the Usk catchment, Wales. Percentage change over the range of accumulated sediment is also shown. Conventions as in Table I

Trait	Category	Slope	% change	p
Life-cycle duration	<1 year	0.47	+20	0.001
Reproduction	ovoviviparity	−1.01	−70	<0.001
	Clutches, free	0.7	+80	<0.001
Food	Detritus >1 mm	0.4	+40	<0.001
Respiration	Tegument	0.32	+24	0.012
	Gill	−0.4	−16	−0.005
Locomotion	Full swimmers	−0.52	−26	<0.001
	Interstitial	0.13	+14	0.008
	Burrower	0.41	+50	<0.001
	Temporarily attached	−0.14	−24	0.008

ranking across trays. In other words, there was a progressive loss of taxa with increasing sediment accumulation so that only common species persisted. The Mann–Whitney test showed that five taxa contributed to the significant nestedness along the sedimentation gradient (Table III): *B. rhodani*, *Ecdyonurus* sp., *Leuctra geniculata*, simuliids and, to a lesser extent, *Ephemerella ignita*, all decreased in frequency of occurrence with sedimentation more than would be expected by chance to create the nested pattern.

Table III. Mann–Whitney U test (z-scores) showing ‘nestedness[1]’ of individual taxa along the sediment gradient induced experimentally in three streams in the Usk catchment, Wales. See Methods for further details

Taxon	z-score	p
Baetis rhodani	−3.19	0.001*
Baetis scambus	−0.85	0.20
Ephemerella ignita	−1.68	0.04*
Ecdyonurus sp.	−2.86	0.002*
Habrophlebia fusca	−0.05	0.48
Leuctra moselyi	−0.6	0.27
Leuctra geniculata	−2.27	0.01*
Drusus annulatus	−1.13	0.13
Sericostoma personatum	−1.2	0.11
Odontocerum albicorne	−0.84	0.20
Simuliidae	−2.42	0.007*
Chironomidae	−1.6	0.06
Elims aenea	−0.92	0.18
Esolus parallelepipedus	−0.81	0.20
Limnius volckmari	−0.92	0.18
Dytiscidae	−1.14	0.13
Oligochaetes	−0.84	0.20
Gammarus pulex	−0.11	0.45

*$p < 0.05$; only taxa included in the ordination are shown

[1] This test assesses whether the sequence of taxon presence/absence along the sediment gradient conformed to a nested distribution pattern.

DISCUSSION

These experimental data confirm that even low to moderate amounts of sediment can alter the patch-scale richness, abundance, community composition, trait diversity and trait composition of invertebrates (Cardillo *et al.*, 2005; Downes *et al.*, 2005; Rabeni *et al.*, 2005; Suren *et al.*, 2005; Connolly and Pearson, 2007; Townsend *et al.*, 2008; Molinos and Donohue, 2009). In this experiment feeding, attachment, respiration and life-cycle traits all appeared to increase species' sensitivity to sediment addition. As with all experimental manipulations in ecology, there are some limitations in our approach, related mostly to the small-scale and short-term nature of the experiment. In large part, however, the data are consistent with other large-scale surveys and experiments in indicating how sediments can change benthic invertebrate assemblages. In particular, the results mirrored the effects of patch-scale (*c.* 1 m^2) variation in deposited sediments on invertebrates in the same catchments (Larsen *et al.*, 2009). We expand on these points in the discussion that follows.

Ecological experiments at small spatio-temporal scales are often used to investigate the mechanisms involved in larger-scale phenomena. However, care is needed in scaling-up biological responses to larger-scale patterns. Both the duration of the experiment and size of our sample units were particularly small, so that limited colonization time, patch-scale variability in invertebrate distribution, species-area effects, edge effects, local hydraulics, representativeness and chance could all limit realism (Angradi, 1999). The clearest evidence for the restricted realism of our experiment came from differences in invertebrate composition between the Surber samples and trays, with species such as *Hydropsiche siltalai*, *H. instabilis*, *Perla bipunctata* and Simuliidae absent or underrepresented in the experimental tray units. As observed by Angradi (1999), their absence may be linked to the absence of larger, stable substrata (e.g. boulders) in trays that are used by some of these taxa for anchorage or refuge (e.g. Hyrdopsychidae, Simuliidae). Species are also inherently variable in their ability to colonize newly created conditions—in this case those represented by introduced substrates (Boothroyd and Dickie, 1991; Olomukoro and Okologume, 2008). In addition to limits imposed by drift propensity among species, the enclosed nature of the trays could have altered interstitial flow and interstitial colonization routes. Notwithstanding such effects, the fact that trays held 70% of the 30 taxa collected by Surber samplers illustrates that they represented benthic assemblages reasonably well. Moreover, progressive dissimilarity between manipulated trays and controls or Surber samples with increasing sediment deposition shows that any limits on tray colonization did not mask sediment effects. Previous works on drift and changes in density in the

Usk and other catchments show that these effects can be generated very rapidly, and even within 24 h (Bond and Downes, 2003; Suren *et al.*, 2005; Gibbins *et al.*, 2007; Larsen *et al.*, 2009).

A further positive feature of our experimental approach is that it allowed relatively high power through replication within streams, and also replication at the stream scale. With this design, sediment addition clearly altered invertebrate assemblage composition, abundance and functional structure. Most of the observed responses were in-line with findings from previous surveys and experiments in the same catchment and elsewhere, thus reinforcing the validity and generalization of our results. The observed decline in overall macroinvertebrates richness with increasing fine sediments likely reflects the negative effect on Ephemeroptera, Plecoptera and Trichoptera (EPT), which are among the dominant taxa in the Usk system, and are reported to be sensitive to fine sediments: a linear decline of EPT taxon richness with increasing sediment cover has been observed frequently both in experimental studies (Angradi, 1999; Matthaei *et al.*, 2006) and in larger scale surveys (Zweig and Rabeni, 2001; Kaller and Hartman, 2004; Townsend *et al.*, 2008; Larsen *et al.*, 2009; Pollard and Yuan, 2009). Contrary to some studies (e.g. Lenat *et al.*, 1981), deposited sediments did not affect diversity indices of benthic communities in our trays possibly because the loss of rarer taxa at greater sediment cover led to fewer taxa that were more evenly distributed among individuals. This is a well recognized difficulty in interpreting diversity indices as opposed to richness.

Sediment treatments also reduced dramatically overall invertebrate abundance by up to 90% with six common taxa significantly affected at effect sizes of *c.* 40–90%. While this effects probably reflected reduced interstitial space (Bo *et al.*, 2007), it is possible that a longer-term experiment would have allowed invertebrates composition to adjust to the sediment conditions and even result in increased density of tolerant taxa (Lenat *et al.*, 1981). In grassland sites similar to those used here, the lower abundance we observed is consistent with previous data (Larsen *et al.*, 2009). Among the taxa affected, the mayflies *Baetis rhodani* and *Ecdyonurus* sp. are both grazers reportedly intolerant of sediment deposition (Rabeni *et al.*, 2005) and *Ecdyonurus* is also a clinger requiring clean interstitial spaces to maintain position in the substratum (Rabeni *et al.*, 2005; Pollard and Yuan, 2009). *Leuctra geniculata* appeared to be relatively sediment-intolerant in previous surveys and the abundance of both *L. geniculata* and *L. moselyi* was affected by a short-term experimental sediment addition in nearby streams (Larsen and Ormerod, in press). The amphipod *Gammarus pulex* was also negatively affected by sediment addition, although this trend was mostly due to one stream (Cynrig) where *Gammarus* dominated tray assemblages. Waters and Hokenstrom (1980) also reported reduced biomass of *Gammarus* in a small tributary of the upper Mississippi River after severe siltation.

In addition to changes in density and richness, we expected from previous findings that organisms with certain life-history traits would be affected by sediments (e.g. Rabeni and Smale, 1995; Doledec *et al.*, 2006; Townsend *et al.*, 2008). Typically, the representation of filter feeders and K-selected (i.e. larger, long-lived) taxa is affected negatively by fine-sediment deposition. Filterers are intolerant to sediments because fine particles impair filtering devices (Lemly, 1982), while K-selected taxa could be excluded by the unstable and transient environments that occur in fine sediments (Richards *et al.*, 1997; Townsend and Thompson, 2007). The reduced representation in the experimental trays of Hydropsychidae, Simuliidae and large stoneflies (e.g. *Perla*), prevented us from formally testing these hypotheses. Nevertheless, overall trait diversity declined with increasing sediment cover, and other life-history or behavioural traits responded as predicted to treatment. The observed reduction of invertebrate trait diversity with increasing fine sediments is in line with findings from previous surveys and reflects the specific selection (or filtering) of taxa according to their functional traits.

Evidence is increasingly clear that anthropogenic effects (e.g. land-use) can reduce functional diversity in ecological communities (Charvet *et al.*, 2000; Houghton, 2007; Schweiger *et al.*, 2007; Flynn *et al.*, 2009) Across the experimental trays in this study, the representation of shorter life cycles, burrowers, fine detritus feeders and tegumental respiration all increased with fine sediments. These traits reflect some adaptation to habitats dominated by fine substrata, and the taxa which possess them can be favoured in sediment-rich environments (Rabeni *et al.*, 2005; Doledec *et al.*, 2006; Townsend *et al.*, 2008). Groups with these traits in our experiment included chironomids, oligochaetes and, to a lesser extent, the trichopterans *Odontocerum albicorne* and *Sericostoma personatum*. Reproduction via free egg-clutches also appeared to be favoured by sedimentation, mostly due to the proportional increase of chironomids with increasing sediments. Similarly, reduced representation of ovoviviparity with sediment accumulation reflected negative effects on *Gammarus*, as no other taxon possessed this particular trait. Conversely, the decline in gill respiration, swimmers and taxa requiring attachment to the substratum appeared to be more community wide, consistent with previous observations (e.g. Townsend *et al.*, 2008). Organisms relying on gill respiration are particularly sensitive to fine particles that can impair their delicate respiratory structures (Lemly, 1982). In this instance, negative effects reflect the three common mayflies, *B. rhodani*, *Ecdyonurus* sp. and *E. ignita*. Also, particle-free surfaces are needed for those taxa requiring temporary

DOI: 10.1002/rra

attachment to the substratum and this could explain why simuliids colonized only untreated trays.

The consequences of alterations caused by sediments to the composition and diversity of trait representation in stream communities, for example for ecosystem function, are still poorly understood. This is also true of changes in the pattern of nestedness among stream species, where rarer taxa are lost in some locations where only commoner taxa persist. In this small-scale experiment, simuliids, *B. rhodani*, *Ecdyonurus* sp. and *L. geniculata* all contributed to the significant nestedness in species occurrences with increasing sedimentation. In other words, these taxa were absent more than expected by chance. Further evidence that experimental treatment promoted nestedness came from the significant rank-correlation between nestedness order of the presence/absence matrix (as calculated by BINMATNEST algorithm) and the amount of sediment in each tray. As with many other of the results from our experiment, similar patterns of nestedness have been shown at sediment-rich sites over larger areas (Larsen and Ormerod, in press), and it seems that trait-mediated sensitivity to sediments causes a non-random colonization—extinction pattern that transcends scale to cause a nested subset pattern in species composition. This is also consistent with the nested habitats hypothesis (Hylander *et al.*; 2005), where the sediment gradient could reflect changing heterogeneity or complexity where sediment-free trays or sites harboured a wider range of microhabitats (and thus a wider range of species from the available pool) than did sediment-impacted trays or locations. These results also suggest that nestedness can derive not only from large scale biogeographical processes, but also from variations in habitat quality and impairment (Fernandez-Juricic, 2002; Hylander *et al.*, 2005). Elsewhere, we have considered that alterations in both trait composition and nestedness caused by sediments may well have ramifications for conservation, by selectively removing not only key invertebrate traits and organism types, but also by changing the organization of assemblages (Larsen and Ormerod, in press): if sediment impacted location can support only a subset of pre-adapted generalist species, increasing sedimentation worldwide could lead to the selective loss of certain species types. This possibility requires wider examination.

ACKNOWLEDGEMENTS

Funding for this research was provided by the Wye and Usk Foundation, and the authors thank Dr Stephen Marsh-Smith and Simon Evans. They also thank Federica Pinto and Lorenzo Lemme for their valuable assistance in the field, Dr Ian Vaughan for statistical advice and landowners for allowing access to the sites. We also thank the reviewers for insightful and careful comments on the manuscript.

REFERENCES

Angradi TR. 1999. Fine sediment and macroinvertebrate assemblages in Appalachian streams: a field experiment with biomonitoring applications *Journal of the North American Benthological Society* **18**: 49–66.

Archaimbault V, Usseglio-Polatera P, Bossche JPV. 2005. Functional differences among benthic macroinvertebrate communities in reference streams of same order in a given biogeographic area. *Hydrobiologia* **551**: 171–182.

Atmar W, Patterson BD. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **96**: 373–382.

Bêche LA, McElravy EP, Resh VH. 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. *Freshwater Biology* **51**: 56–75.

Bêche LA, Resh VH. 2007. Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Fundamental and Applied Limnology* **169**: 1–23.

Bo T, Fenoglio S, Malacarne G, Pessino M, Sgariboldi F. 2007. Effects of clogging on stream macroinvertebrates: an experimental approach. *Limnologica* **37**: 186–192.

Bond NR, Downes BJ. 2003. The independent and interactive effects of fine sediment and flow on benthic invertebrate communities characteristic of small upland streams. *Freshwater Biology* **48**: 455–465.

Boothroyd IKG, Dickie BN. 1991. Macroinvertebrate drift and community colonization on perspex artificial substrates in the Ohinemuri River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **25**: 167–176.

Broekenhuizen N, Parkyn S, Miller D. 2001. Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). *Hydrobiologia* **457**: 125–132.

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005. Multiple causes of high extinction risk in large mammal species. *Science* **309**: 1239–1241.

Charvet S, Statzner B, Usseglio-Polatera P, Dumont B. 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology* **43**: 277–296.

Chevenet F, Doledec S, Chessel D. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* **31**: 295–309.

Connolly NM, Pearson RG. 2007. The effect of fine sedimentation on tropical stream macroinvertebrate assemblages: a comparison using flowthrough artificial stream channels and recirculating mesocosms. *Hydrobiologia* **592**: 423–438.

Culp JM, Wrona FJ, Davies RW. 1985. Response of stream benthos and drift to fine sediment deposition versus transport. *Canadian Journal of Zoology* **64**: 1345–1351.

Davies-Colley RJ, Hickey CW, Quinn MJ, Ryan PA. 1992. Effects of clay discharges on streams. Optical properties and ephilithon. *Hydrobiologia* **248**: 215–234.

Davies-Colley RJ, Smith DG. 2001. Turbidity, suspended sediment, and water clarity: a review. *Journal of the American Water Resources Association* **37**: 1085–1101.

Dolédec S, Olivier JM, Statzner B. 2000. Accurate description of the abundance of taxa and their biological traits in stream invertebrate communities: effects of taxonomic and spatial resolution. *Archiv Fur Hydrobiologie* **148**: 25–43.

Doledec S, Phillips N, Scarsbrook M, Riley RH, Townsend CR. 2006. Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. *Journal of the North American Benthological Society* **25**: 44–60.

Dolédec S, Statzner B, Bournard M. 1999. Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology* **42**: 737–758.

Downes BJ, Lake PS, Glaister A, Bond NR. 2005. Effects of sand sedimentation on the macroinvertebrate fauna of lowland streams: are the effects consistent? *Freshwater Biolology* 50.

Fernandez-Juricic E. 2002. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia* **131**: 269–278.

Fleishman E, Donnelly R, Fay JP, Reeves R. 2007. Applications of nestedness analyses to biodiversity conservation in developing landscapes. *Landscape and Urban Planning* **81**: 271–281.

Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* **12**: 22–33.

Gibbins C, Vericat D, Batalla RJ, Gomez CM. 2007. Shaking and moving: low rates of sediment transport trigger mass drift of stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 1–5.

Gotelli NJ, Entsminger GL. 1997. EcoSim: null models software for ecologists. *Bulletin of the Ecological Society of America* **78**: 96.

Hecnar SJ, Casper GS, Russell RW, Hecnar DR, Robinson JN. 2002. Nested species assemblages of amphibians and reptiles on islands in the Laurentian Great Lakes. *Journal of Biogeography* **29**: 475–489.

Heino J, Mykra H, Muotka T. 2009. Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. *Diversity and Distributions* **15**: 198–206.

Hill MO, Gauch HG. 1980. Detrended correspondence-analysis—an improved ordination technique. *Vegetation* **42**: 47–58.

Houghton DC. 2007. The effects of landscape-level disturbance on the composition of Minnesota caddisfly (Insecta : Trichoptera) trophic functional groups: evidence for ecosystem homogenization. *Environmental Monitoring and Assessment* **135**: 253–264.

Hylander K, Nilsson C, Jonsson BG, Gothner T. 2005. Differences in habitat quality explain nestedness in a land snail meta-community. *Oikos* **108**: 351–361.

Jongman RHG, Ter Braak CJF, Van Tongeren OFR. 1995. *Data analysis in community and landscape ecology*. Cambridge University Press: Cambridge.

Kaller MD, Hartman KJ. 2004. Evidence of a threshold level of fine sediment accumulation for altering benthic macroinvertebrate communities. *Hydrobiologia* **518**: 95–104.

Kreutzweiser DP, Capell SS, Good KP. 2005. Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology* **39**: 55–66.

Larsen S, Ormerod SJ. 2010. Low-level effects of inert sediments on temperate stream invertebrates. *Freshwater Biology* **55**: 476–486.

Larsen S, Vaughan IP, Ormerod SJ. 2009. Scale-dependent effect of fine sediments on temperate headwater invertebrates. *Freshwater Biology* **54**: 203–219.

Lemly D. 1982. Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. *Hydrobiologia* **87**: 229–245.

Lenat RD, Penrose DL, Eagleson WK. 1981. Variable effects of sediment addiction on stream benthos. *Hydrobiologia* **79**: 187–194.

Manel S, Buckton ST, Ormerod SJ. 2000. Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology* **37**: 756–770.

Matthaei CD, Weller F, Kelly DW, Townsend CR. 2006. Impacts of fine sediment addition to tussock, pasture, dairy and deer farming streams in New Zealand. *Freshwater Biology* **51**: 2154–2172.

Molinos JG, Donohue I. 2009. Differential contribution of concentration and exposure time to sediment dose effects on stream biota. *Journal of the North American Benthological Society* **28**: 110–121.

Olomukoro JO, Okologume U. 2008. Macroinvertebrate colonisation of artificial substrates in a Nigerian river I: gravel and leaf litter. *African Journal of Aquatic Science* **33**: 143–148.

Owens PN, Batalla RJ, Collins AJ, Gomez B, Hichs DM, Horowitz AJ, Kondolf GM, Marden M, Page MJ, Peacock DH, Petticrew EL, Salomons W, Trustrumi NA. 2005. Fine-grained sediment in river systems: environmental significance and management issues. *River Research and Applications* **21**: 693–717.

Pinheiro J, Bates D. 2000. *Mixed Effects Models in S and S-Plus*. Springer: New York.

Pollard AI, Yuan LL. Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity-based measures. *Freshwater Biology* (in press).

Rabeni CF, Doisy KE, Zweig LD. 2005. Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences* **67**: 395–402.

Rabeni CF, Smale MA. 1995. Effects of siltation on stream fishes and the potential mitigating role of the buffering riparian zone. *Hydrobiologia* **303**: 211–219.

Rehg JK, Packman AI, Ren J. 2005. Effects of suspended sediment characteristics and bed sediment transport on streambed clogging. *Hydrological Processes* **19**: 413–427.

Richards C, Bacon KL. 1994. Influence of fine sediment on macroinvertebrate colonization of surface and hyporheic stream substrates. *Great Basin Naturalist* **54**: 106–113.

Richards C, Haro RJ, Johnson LB, Host GE. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* **37**: 219–230.

Richoux P. 1994. Theoretical habitat templets, species traits, and species richness—aquatic Coleoptera in the upper Rhone River and its floodplain. *Freshwater Biology* **31**: 377–395.

Rodriguez-Girones MA, Santamaria L. 2006. A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography* **33**: 924–935.

Schalchli U. 1992. The clogging of coarse gravel river beds by fine sediment. *Hydrobiologia* **235**: 189–197.

Schouten MA, Verweij PA, Barendregt A, Kleukers RJM, de Ruiter PC. 2007. Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life-history traits. *Journal of Biogeography* **34**: 1938–1946 .

Schweiger O, Musche M, Bailey D, Billeter R, Diekotter T, Hendrickx F, Herzog F, Liira J, Maelfait JP, Speelmans M, Dziock F. 2007. Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos* **116**: 461–472.

Summerville KS, Veech JA, Crist TO. 2002. Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? *Oikos* **97**: 195–204.

Suren AM, Jowett IJ. 2001. Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research* **35**: 725–737.

Suren AM, Martin LM, Smith BJ. 2005. Short-term effects of high suspended sediments on six common New Zealand stream invertebrates. *Hydrobiologia* **548**: 67–74.

Tachet H, Richoux P, Bournaud M, Usseglio-polatera P. 2000. *Invertebres d'eau Douce. Systematique, Biologie, Ecologie*. CNRS Editions: Paris.

Tachet H, Usseglio-Polatera P, Roux C. 1994. Theoretical habitat templets, species traits, and species richness - Trichoptera in the upper Rhone River and its floodplain. *Freshwater Biology* **31**: 397–415.

Townsend CR, Thompson RM. 2007. Body size in streams: macroinvertebrate community size composition along natural and human-induced environmental gradients. In *Body Size: The Structure and Function of Aquatic Ecosystems*, Hildrew AG, Raffaelli D, Edmonds-Brown R (Eds). Cambridge University Press: Cambridge.

Townsend CR, Uhlmann SS, Matthaei CD. 2008. Individual and combined responses of stream ecosystems to multiple stressors. *Journal of Applied Ecology* **45**: 1810–1819.

Turnpenny AWH, Williams R. 1980. Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology* **17**: 681–693.

US Environmental Protection Agency. 2000. National water-quality inventory. Office of Water, US Environmental Protection Agency, Washington, DC.

Usseglio-Polatera P. 1994. Theoretical habitat templets, species traits, and species richness—aquatic insects in the upper Rhone River and its floodplain. *Freshwater Biology* **31**: 417–437.

Usseglio-Polatera P, Tachet H. 1994. Theoretical habitat templets, species traits, and species richness—plecoptera and ephemeroptera in the upper Rhone River and its floodplain. *Freshwater Biology* **31**: 357–375.

Waters TF. 1995. *Sediments in streams: sources, biological effects, and control*. AFS Monographs, Bethesda: Maryland.

Waters TF, Hokenstrom JC. 1980. Annual production and drift of the stream amphipod Gammarus-Pseudolimnaeus in valley Creek, Minnesota. *Limnology and Oceanography* **25**: 700–710.

Wilby RL, Dalgleish HY, Foster IDL. 1997. The impact of weather patterns on historic and contemporary catchment sediment yields. *Earth Surface Processes and Landforms* **22**: 353–363.

Wood PJ, Armitage PD. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* **21**: 203–217.

Wood PJ, Toone J, Greenwood MT, Armitage PD. 2005. The response of four lotic macroinvertebrate taxa to burial by sediments. *Archiv fur Hydrobiologie* **163**: 145–162.

Wright JF, Furse MT, Moss D. 1998. River classification using invertebrates: RIVPACS applications. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 617–631.

Zweig LD, Rabeni CF. 2001. Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society* **20**: 643–657.

DOI: 10.1002/rra