

Working title: Temporal effects of enhanced fine sediment loading on
macroinvertebrate community structure and functional traits

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Temporal effects of enhanced fine sediment loading on macroinvertebrate community structure and functional traits

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Abstract

Deposition of fine sediment that fills interstitial spaces in streambed substrates is widely acknowledged to have significant negative effects on macroinvertebrate communities, but the temporal consistency of clogging effects is less well known. In this study the effects of experimentally enhanced fine sediment content on aquatic invertebrates were examined over 126 days in two lowland UK streams. Taxonomic approaches indicated significant differences in macroinvertebrate community structure associated with sediment treatment (clean or sedimented substrates), although the effects were variable on some occasions. The degree of separation between clean and sedimented communities was strong within 7 of the 9 sampling periods with significant differences in community composition being evident. EPT taxa and taxon characterised as sensitive to fine sediment demonstrated strong responses to enhanced fine sediment loading. In marked contrast, faunal traits did not facilitate the detection of enhanced fine sediment loading. More widely, the study highlights the temporal dynamics of sedimentation effects upon macroinvertebrate communities and the need to consider faunal life histories when examining the effects of fine sediment loading pressures on lotic ecosystems.

Keywords: colmation, sedimentation, sediment clogging, community composition, life-history traits, colonisation.

1. Introduction

Increased instream fine sediment loading is widely regarded as a global threat to ecological integrity and lotic ecosystem health, often leading to reduced macroinvertebrate diversity through direct exclusion of taxa, enhanced drift or reductions in the availability of suitable trophic resources and habitat (Larsen and Ormerod, 2010; Jones et al., 2012; Wood et al., 2016). The infiltration of fine sediment into the river (colmation / clogging) has been reported to modify benthic macroinvertebrate community structure and functioning (Descloux et al., 2013). Substrates characterised by a high proportion of fine sediment are frequently dominated by taxa with low dissolved oxygen requirements (Angradi, 1999; Zweig and Rabeini, 2001) and exhibit an absence of taxa vulnerable to fine sediment due to impairment or damage of filter-feeding apparatus or delicate gills (Wood and Armitage, 1997; Larson et al., 2009). In addition, some taxa may be excluded and unable to colonise habitats where excessive fine sediment is present, for example due to the absence of suitable materials for case building by caddisfly larvae (Higler, 1975; Urbanič et al., 2005). Some functional feeding groups may also be disadvantaged by enhanced fine sediment loading, due to reduced food quality or impaired access to food resources, notably for algal scrapers and filter feeders (Rabeni et al., 2005; Kreutzweiser et al., 2005). This may lead to shifts in community structure towards those dominated by deposit feeders (Relyea et al., 2000).

Some fauna respond to fine sediment deposition pressures as a function of their morphological characteristics and functional traits (Lamouroux et al., 2004; Bona et al., 2016; Doretto et al., 2017). Recently there has been a growing focus on the incorporation of faunal traits within biomonitoring tools to elucidate on the changes that occur to invertebrate community structure in freshwater ecosystems (Menezes et al., 2010; Göthe et al., 2016; Pilière et al., 2016). Biological traits are based on the habitat model concept (Southwood, 1977), and therefore community traits may reflect spatial and temporal variations in environmental factors (Townsend and Hildrew, 1994). Trait composition can also be used to identify sources of environmental impairment associated with anthropogenic and natural stressors which act as 'filters', selecting taxa with relevant adaptive traits. Consequently, some traits may be particularly sensitive to environmental pressures and it is this possibility that has led to the increasing application of biological traits within biomonitoring tools

(Statzner et al., 2004; Friberg. 2014; Turley et al., 2016). However, relatively little information exists regarding how macroinvertebrate faunal traits respond to instream fine sediment loading and the limited studies in this area to date have yielded variable results (e.g. Buendia et al., 2013; Descloux et al., 2014).

The majority of studies conducted on sedimentation to date have focussed on artificial enhanced fine sediment loads (Suren and Jowett, 2001; Larsen et al., 2011) or have been associated with heavily sedimented river beds (Matthaei et al., 2010; Wagenhoff et al., 2012). A small number of studies have experimentally manipulated the volume of fine sediment within the substrate directly through the application of faunal colonisation devices, but these studies have typically examined the effects at a single point in time (Bo et al., 2007; Larsen et al., 2011; Pacioglu et al., 2012; Descloux et al., 2013; 2014). There is an absence of research that considers the temporal variability of fine sediment effects on macroinvertebrate communities and the value of life history traits for understanding and monitoring these effects.

Species phenology within a community affects the composition of macroinvertebrates observed at differing times of the year (Delucchi and Peckarsky, 1989; Murphy and Giller, 2000), and may confound biomonitoring assessments if not acknowledged (Clarke, 2013; Carlson et al., 2013). Temporal and spatial heterogeneity of hydrological regimes is also a fundamental process in shaping riverine macroinvertebrate communities (Dewson et al., 2007; Monk et al., 2008). Natural streams are typically characterised by stable baseflow conditions punctuated periodically by flow disturbances. These flow disturbances have important implications for fine sediment dynamics, initiating entrainment of fine material stored in the channel and increasing suspended sediment concentrations (Leopold et al., 1964; Bond and Downes, 2003). The interaction between flow and fine sediment dynamics (entrainment, suspension and depositional processes) has been identified as a primary factor which influences the turnover of taxa within macroinvertebrate communities (Rempel et al., 2000; Buendia et al., 2014; Jones et al., 2015). Consequently, as a result of temporal variability in flow and species assemblages, it follows that it is important to consider the effects of sediment loading over time.

This study is the first to specifically consider the temporal variability of experimentally manipulated fine sediment loading on macroinvertebrate communities at a fine temporal resolution (weeks). The following research questions were addressed:

- (i) Is the effect of increased fine sediment loading on macroinvertebrate communities consistent temporally?
- (ii) Which taxa and functional traits are associated with enhanced fine sediment loading?
- (iii) Are the observed effects of enhanced fine sediment loading on macroinvertebrate communities evident and consistent for both taxonomic and faunal trait compositions?

2. Materials and methods

2.1 Field sites

The study took place on two small lowland rivers in Rutland, UK; the River Gwash (52°38' N, 00°44'W) and the River Chater (52°37' N, 00° 44'W). Sites were selected to be as broadly comparable in physical characteristics (channel size, water chemistry, altitude and geology) as possible. Both river channels were characterised by a riffle – pool morphology (channel width 2.9 – 6.5m). Catchment geology was dominated by Jurassic mudstones and sandstones (British Geological Survey, 2008) and study sites were located in arable farmland. Close to the catchment outlets, mean daily flows were $0.18 \text{ m}^3 \text{ s}^{-1}$ and $0.52 \text{ m}^3 \text{ s}^{-1}$ for the River Gwash and Chater respectively (record 1978-2015; NRFA, 2017). Subsurface bed material (based on four pooled individual McNeil samples from two riffles per site, average sample weight 20.01kg [McNeil and Ahnell, 1964]) indicated similar grain size distributions (GSD) between sites; with both being naturally characterised by a moderate fine sediment content (mass < 2mm; Gwash 20% and Chater 28.8%). Hydrological data from local gauging stations indicated that the study coincided with periods of stable flow punctuated by increased river stage associated with summer rainfall events (Figure 1).

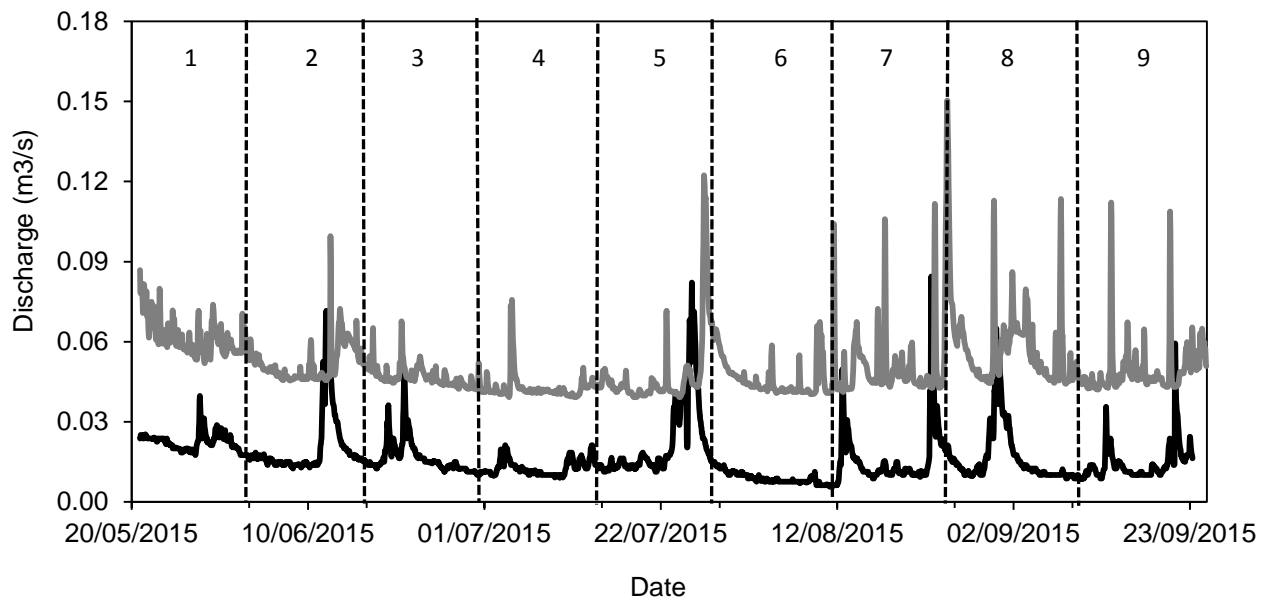


Figure 1. River discharge (hourly average $\text{m}^3 \text{s}^{-1}$) for the River Gwash (black) and River Chater (grey) Rutland, UK during the sampling campaign. Dashed lines indicate the two week sampling periods (21st June - 24th September 2015).

2.2 Colonisation columns

Macroinvertebrate colonisation columns were installed at the two sample sites. These comprised PVC cylinders (diameter 65 mm, height 200 mm) perforated with twelve horizontal holes (diameter 6 mm) to permit horizontal and vertical exchange of water and the free movement of macroinvertebrates and fine sediment (Fraser et al; 1996; Pacioglu et al., 2012; Descoux et al; 2013; Mathers and Wood, 2016). All columns were filled with a pre-washed gravel framework collected from each of the respective sample sites (truncated at 8 mm). This substrate was enclosed in a net bag (7 mm aperture) within each column. Columns were assigned to one of two treatments; a) clean substrates which were free from fines upon installation or; b) heavily sedimented substrates comprising gravel and 250g of fine sand (63 – 2000 μm). Preliminary tests indicated that this volume of sand filled 100% of interstitial volume. For the sedimented columns, a circular disk (64 mm diameter) was attached to the mesh bag to effectively seal the base of the column and reduce the loss of fine sediment vertically into the riverbed.

Columns were inserted into the river bed by placing the PVC cylinders onto a steel pipe (35 mm diameter) that was driven into the river bed sediments until a sufficient depth was obtained to insert it flush with the substrate surface (200 mm). The surrounding stream bed remained unchanged and consisted of non-uniform cobbles and gravel. Columns were left *in-situ* for the entire sampling campaign, but every 14 days the gravel netting bag was removed and replaced without disturbing the surrounding gravel framework. At the end of each 14-day sampling period, the net bag (containing the substrate and macroinvertebrates) was carefully removed, placed in a sample bag and preserved in 10% formaldehyde for subsequent processing in the laboratory. Empty columns were then replaced immediately with the corresponding gravel bag treatment (clean or sedimented).

Colonisation columns were installed every 14 days between 21st May and 24th September 2015 providing a 126 day record (9 sample sets). A time period of 14 days was adopted because preliminary tests indicated that this represented sufficient time to allow for colonisation by macroinvertebrates whilst minimising the amount of fine sediment lost during occasional high flows (See Supplementary Material and Figure S1). At each riffle site (three on the Gwash and two on the Chater; one until the fourth sampling set), four columns of each type (clean or sedimented) were installed providing a total of 20 replicates (16 initially for three sample sets) for each 14-day sampling period. In total 162 clean and 163 sedimented substrate samples were examined (6 clean and 5 sedimented samples were lost or not retrieved during the field campaign). Two additional sampling timeframes (ca one month: 28 days and ca two months: 56 days) were examined to capture potential temporal variability in environmental conditions (i.e. rising or falling discharge or suspended sediment concentrations) and to confirm the most appropriate time-frame to consider in the main study and are presented in Supplementary material (Figure S1).

2.3 Laboratory procedures and statistical analysis

Within the laboratory, the contents of the column bags were passed through a sieve nest (4 and 2 mm sieves) to remove larger gravel clasts. The remaining material was passed through a 250 µm sieve and processed for invertebrates. All macroinvertebrates were identified to the lowest taxonomic level possible usually species or genus with the exception of Oligiochetea (order), Diptera families

218 (including Ephydriidae, Ptychopteridae, Chironomidae, Psychodidae, Simuliidae,
219 Ceraptogonidae and Stratiomyidae), Sphaeriidae and Zonitidae (family) and
220 Ostracoda, Hydracarina and Collembola which were recorded as such.

221 Compositional differences in communities between the two sediment treatments
222 were examined via non-metric multidimensional scaling (NMDS) using Bray-Curtis
223 similarity coefficients for the entire data set and for each individual sampling period.
224 This approach enabled an examination consistency in the community effects or if
225 they varied over time as a function of environmental conditions (i.e. discharge over
226 the 14-day period). A One way ANOSIM (Analysis of Similarities) was used to
227 examine differences in the communities amongst sediment treatments for the overall
228 data set and for each individual sample set (1-9) using a random Monte Carlo
229 permutations test (999 permutations). Both P and R ANOSIM values were examined,
230 with R values >0.75 indicating strong separation amongst groups, $R = 0.75-0.25$
231 indicating separate groups with overlapping values and $R < 0.25$ as barely
232 distinguishable groups (Clarke and Gorley, 2006). Taxa contributing to the
233 divergence of communities were identified through the application of the similarity
234 percentage (SIMPER). The top six taxa identified as driving dissimilarity between
235 clean and sedimented communities were selected for further detailed analysis of
236 their sensitivity to fine sediment.

237 The functional composition of macroinvertebrate communities was determined
238 through the assignment of fauna into 6 categories which were comprised of 44
239 biological traits from the Tachet et al., (2010) database (Table 1). Categories
240 represent grouping features including 'maximum body size' and 'functional feeding
241 group', whilst traits signify modalities residing within these such as 'shredder' or
242 'filter-feeder'. Traits were assigned based on a fuzzy-coding approach with scores
243 ranging from zero (indicating no affinity) to three or five (the strongest affinity based
244 on available literature; Chevene et al., 1994). Affinity scores were subsequently
245 rescaled as proportions for each category (sum = 1) for each taxon. Chironomidae
246 and all taxa recorded at a coarser resolution than family-level were excluded due to
247 the large species diversity within the groups. To produce a trait abundance matrix,
248 taxon-trait categories were multiplied by $\log(x+1)$ transformed abundances (Larsen
249 and Ormerod, 2010; Descloux et al., 2014; White et al., 2017).. Functional
250 compositional differences for each sampling set were visualised via NMDS plots. All

ordination analyses were performed in PRIMER Version 7.0.11 (PRIMER-E Ltd, Plymouth, UK).

The macroinvertebrate communities of the two study streams represent distinct community structures as a function of signal crayfish invasion within the River Gwash in 1996 (global ANOSIM $p < 0.001$; Mathers et al. 2016). Following invasion, signal crayfish typically have significant, long-term and persistent effects on macroinvertebrate communities (McCarthy et al., 2006; Twardochleb et al., 2013). As a result, preliminary analyses were conducted on the individual rivers to determine whether the gross effects of sediment loading were comparable for the communities. This analysis took the form of temporal group centroid (clean and sedimented) NMDS plots using Bray-Curtis similarity coefficients. These results indicated that the temporal trajectory of community change and sedimentation effects were comparable for both community composition and biological traits. Taxonomic plots determined a significant sediment treatment effect for both rivers (ANOSIM Gwash $p = 0.035$; Chater $p = 0.012$; Figure S2) whilst biological traits indicated no divergence in trait composition (ANOSIM Gwash $p = 0.143$; Chater $p = 0.104$). Consequently, as both river communities reacted in a similar manner to sediment loading, the final analyses outlined above were conducted on the combined datasets.

Community abundance, taxa richness and richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa were derived from the raw data. Abundances of taxa characterised as sensitive to sediment according to sensitivity weights provided in the Empirically-weighted Proportion of Sediment-sensitive Invertebrates index (E-PSI; Turley et al., 2016) were also calculated for each sample. To examine statistical differences associated with sediment treatment for individual taxon abundances (as previously selected from the global SIMPER), generalised linear mixed effects models were employed (GLMMs). Models were fitted using the '*lme4*' package in R version 3.2.2 using the '*glmer*' function (R development Core Team, 2015). To examine differences associated with the volume of fine sediment, sediment treatment was specified as a fixed factor and riffle was nested within site as a random factor (based on columns at individual riffles and sites being less independent of each other). Models were fitted using a Poisson error distribution and log link structure. Linear mixed models were fitted to the functional traits and community metrics using the '*nlme*' package and '*lme*' function. The same model

284 structure (outlined above) was employed and the models were fitted using the
 285 restricted maximum likelihood (REML) estimation function. A Bonferroni correction
 286 was applied to all models to account for the large number of models constructed.

287

Table 1. Macroinvertebrate functional traits examined within this study (taken from Tachet et al., 2010).

Category	Trait
Maximal potential size	< 0.25 cm
	> 0.25 - 0.5 cm
	> 0.5 - 1 cm
	> 1 - 2 cm
	> 2 - 4 cm
	> 4 - 8 cm
	> 8 cm
Reproduction	Ovoviviparity
	Isolated, free eggs
	Isolated eggs, cemented
	Clutches, cemented eggs
	Clutches, free
	Clutches, in vegetation
	Asexual
Respiration	Gill
	Plastron
	Spiracle
	Hydrostatic vesicle
	Tegument
Locomotion	Flier
	Surface swimmer
	Full water swimmer
	Crawler
	Burrower
	Interstitial
	Temporarily attached
	Permanently attached
Feeding group	Absorber
	Deposit feeder
	Shredder
	Scraper
	Filter-feeder
	Piercer
	Predator
	Parasite
Substrate preference	Coarse substrates
	Gravel
	Sand
	Silt
	Macrophytes
	Microphytes
	Twigs / roots
	Organic detritus
	Mud

3. Results

3.1 Community composition associated with sediment treatment

63 taxa were recorded in the clean sediment treatment (mean 6.79 taxa per sample, range 2-13) and 58 taxa in the sedimented treatment (mean 6.94 taxa per sample, range 1- 16). A total of 9,656 individuals were recorded in the clean sediment samples (mean 59.98 individuals per sample, range 14-136) and 8,078 in the sedimented samples (mean 49.86 individuals per sample, range 9-168).

Communities in the clean sediments were dominated by *Gammarus pulex* (67.68% of total abundance), Chironomidae (9.67%) and *Potamopyrgus antipodarum* (6.73%). The most abundant taxa within the sedimented substrates were *G. pulex* (53.50%), Chironomidae (12.17%) and Oligochaeta (10.84%). A total of 11 taxa were unique to clean sediments (3 Gastropoda, 2 Trichoptera, 2 Diptera, 1 Ephemeroptera, 1 Hirudinea, 1 Coleoptera and 1 Ostrocodia) and 2 to the sedimented substrates (1 Tricladida, 1 Trichoptera) although these occurred at low abundances (constituting 29 and 2 individuals respectively).

Non-metric Multi-Dimensional Scaling (NMDS) ordination diagrams indicated distinct clusters of macroinvertebrate communities associated with sediment treatment on seven out of the nine sampling occasions (Figure 2). The degree of separation between the groups varied over time with highly significant divergence in sets 2, 4, 5 and 7 (ANOSIM $p < 0.005$; Figure 2b,d,e & g), and moderate separation in set 1 (ANOSIM $p = 0.041$; Figure 2a), whilst a number of sets were less significantly dispersed; sets 6 and 8 (ANOSIM $P < 0.05$; Figures 2f & h; Table 2). Two 14-day periods, sets 3 and 9 (Figure 2c & i), demonstrated no significant differences in the macroinvertebrate communities inhabiting the two substrate types. The global dataset indicated some divergence of communities when all timeframes were considered ($p < 0.0001$; ANOSIM) although analysis of the R value ($R = 0.083$), indicated that the groups were barely distinguishable from each other (Figure 2j). This low degree of separation reflects the varying stability of these patterns between the individual sample sets. The top six taxa driving dissimilarity were Oligochaeta (5.75% dissimilarity), Chironomidae (5.42%), *P. antipodarum* (5.12%), *G. pulex* (4.49%), *Dicranata* sp. (3.10%) and *Habrophlebia fusca* (2.70%).

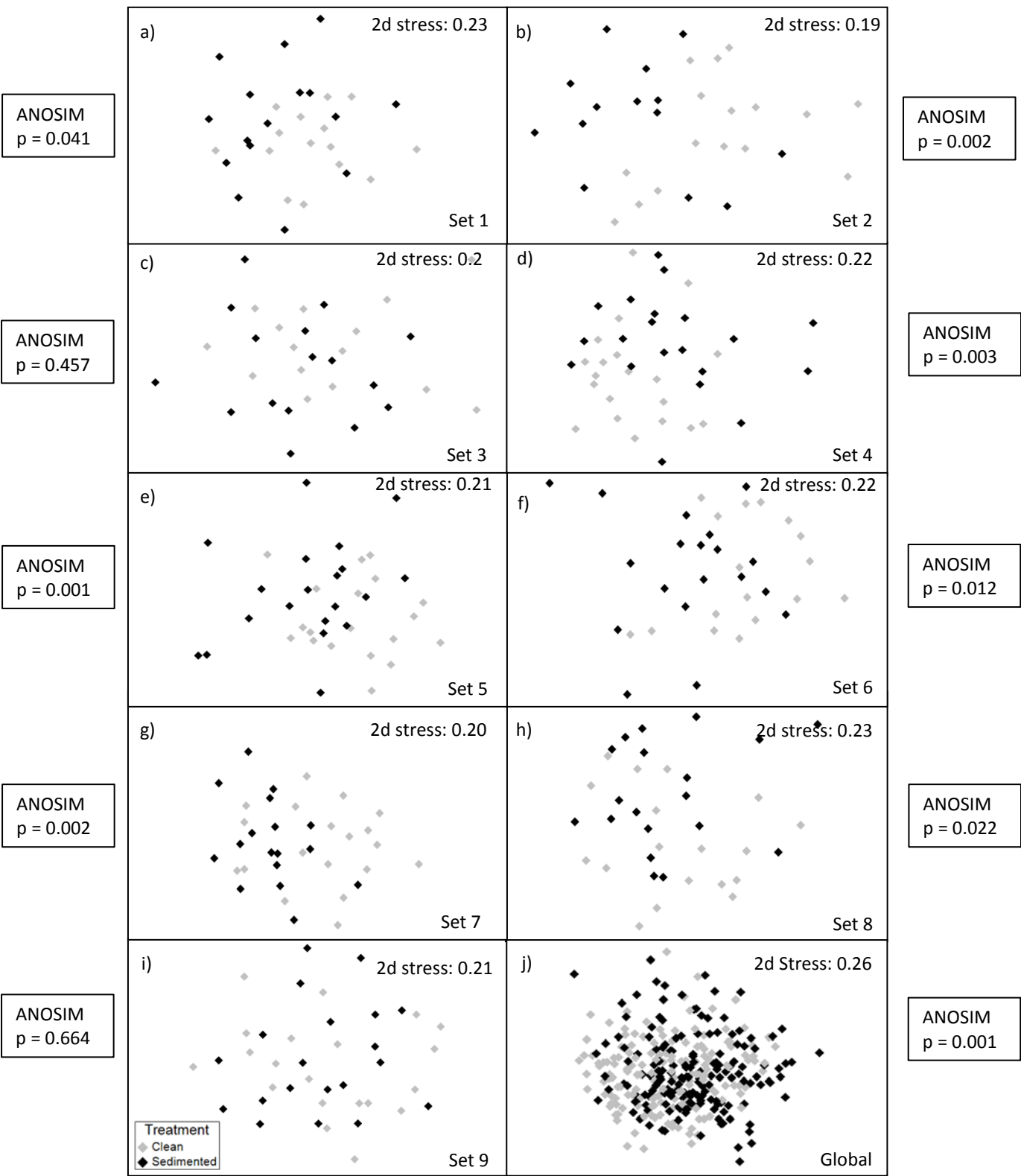


Figure 2. Non-metric multidimensional scaling (NMDS) of macroinvertebrate community data from the River Gwash and River Chater by sediment treatment using the Bray-Curtis similarities coefficients for cylinder sets 1 - 9 (panes a-i) and global dataset (pane j). Grey rhombus = clean cylinders and black rhombus = sedimented communities.

Table 2. Summary of ANOSIM values over time by sediment treatment .

Set	r value	p value
1	0.078	0.041
2	0.231	0.002
3	-0.003	0.457
4	0.107	0.003
5	0.127	0.001
6	0.096	0.012
7	0.166	0.002
8	0.082	0.022
9	-0.018	0.664

3.2 Biological traits associated with sediment treatment

NMDS ordination analysis indicated no clear and consistent differentiation between sediment treatments over time when trait community composition was examined (Figure 3). Trait based community composition demonstrated some degree of separation in a number of instances (i.e. sample sets 3, 4, 6; Figures 3c, d & f), but this was not consistent or clear for all sample sets (i.e. sample sets 1, 5; Figures 3a & e). Divergence in communities was most marked during sample set 6 which also corresponds to the only statistically significant difference in trait community composition (ANOSIM $p = 0.037$; Figure 3f). When individual traits were considered, eight trait modalities varied significantly as a function of sediment treatment. The trait profile of locomotion was the most significant with individuals characterised as being full water swimmers ($t_{10,320} = -4.53$, $p < 0.001$; LME), crawlers ($t_{20,310} = -3.224$, $p = 0.001$) or interstitial dwellers ($t_{10,320} = -4.93$, $p = < 0.001$) demonstrating significant reductions for the sedimented treatment. Species demonstrating ovoviviparity ($t_{10,320} = -4.51$, $p = < 0.001$), respiring via plastron ($t_{6,320} = -4.90$, $p = < 0.001$) or spiracles ($t_{10,320} = -3.12$, $p = < 0.001$) and / or demonstrating shredder affinities ($t_{10,320} = -3.43$, $p = < 0.001$) all demonstrated a reduction within sedimented substrates. Maximum potential size of individuals also varied between treatments with a decline in larger taxon characterised with a body size of 1-2 cm within the sedimented columns ($t_{10,320} = -3.59$, $p = < 0.001$).

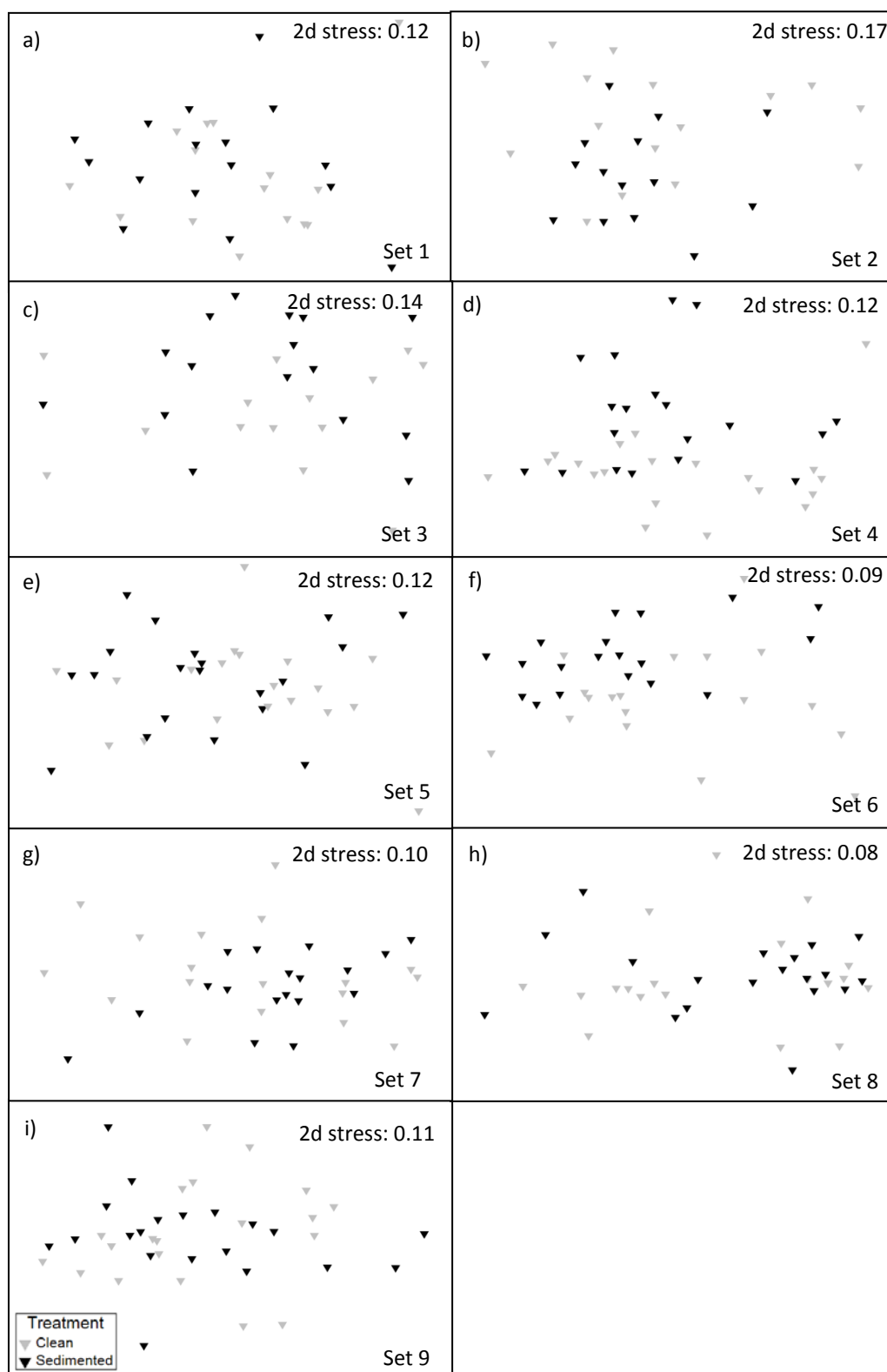


Figure 3. Non-metric multidimensional scaling (NMDS) of macroinvertebrate community functional traits from the River Gwash and River Chater by sediment treatment using the Bray-Curtis similarities coefficients for cylinder sets 1 - 9 (panes a-i). Grey rhombus = clean cylinders and black rhombus = clogged communities.

3.3 Community metrics and individual taxon abundances associated with sediment treatment

Community abundance, taxa richness and EPT richness did not vary by sediment treatment (LME $p > 0.05$). Sediment sensitive taxa (as defined under E-PSI metric) were recorded in significantly greater abundances in the clean sediments ($t_{10,310} = -2.94$, $p < 0.001$). The divergence of clean and sedimented substrates was not apparent during Set 1, 3 and 9 with similar abundances of sensitive taxa in both treatments whilst the greatest distinction between sediment treatments was during sets 4-8 (Figure 4). When individual taxon abundances were considered, *Dicranota* sp. and Oligochaeta were found in significantly greater abundances in sedimented columns ($Z_{6,320} = 8.76$, $p < 0.001$ and $Z_{6,320} = 15.84$, $p < 0.001$; GLMM). Clean sediment treatments were found to support greater abundances of the ephemeropteran *H. fusca* ($z_{6,320} = -6.76$, $p < 0.001$) and the amphipod *G. pulex* ($Z_{6,320} = -20.03$, $p < 0.001$). No significant sediment treatment differences were determined for any other taxa ($p > 0.05$) although EPT richness demonstrated significant variability over time within this study ($t_{10,320} = -3.45$, $p < 0.001$; LME; Figure 5).

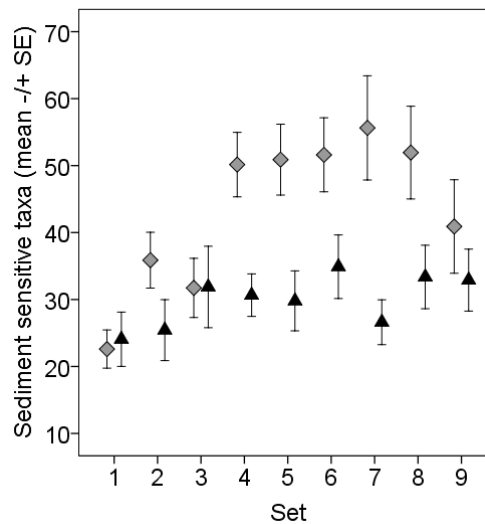


Figure 4. Mean abundances (± 1 SE) of sediment sensitive taxa (as defined under the E-PSI index) over the nine sampling sets. Grey rhombus = clean substrates and; black triangle = sedimented substrates.

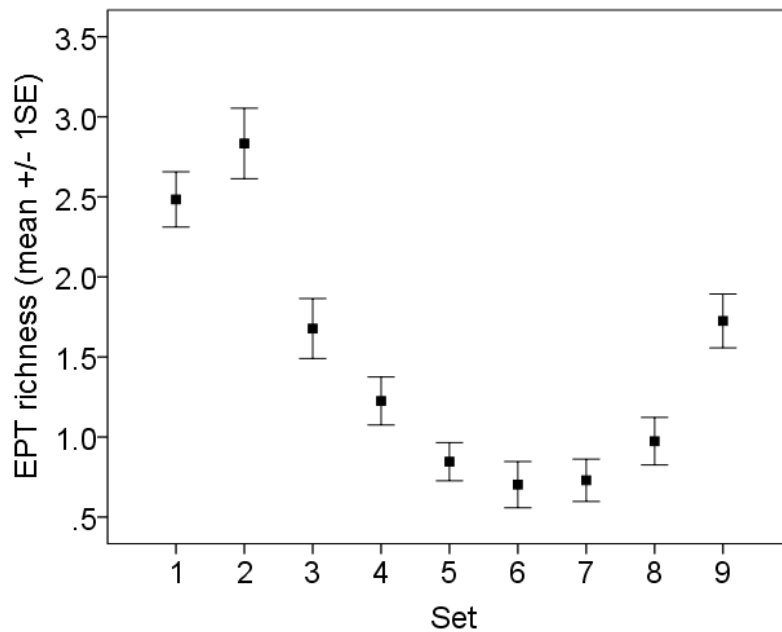


Figure 5. Mean abundances (± 1 SE) of EPT taxa over the nine sampling sets.

4. Discussion

4.1 Macroinvertebrate community composition

This study sought to examine the temporal variability of experimentally enhanced fine sediment loading on macroinvertebrates communities. The results indicate colonisation by macroinvertebrates may be impeded as a result of enhanced fine sediment loading but that the effects vary temporally. Analysis demonstrated a significant difference in macroinvertebrate community composition associated with sediment treatment during seven of the nine 14-day sampling periods. However, the effects of sedimentation were not temporally consistent with differences between community composition being stronger in some periods and breaking down completely in others.

No evidence was found to suggest that spate periods affected the degree of separation between communities within sedimented and clean substrates. A number of sample sets experienced periods with high flows (e.g. sets 6 and 8) but this did not appear to have any effect on the colonisation of the sediments. Similarly, sample sets which demonstrated little separation did not correspond with periods of high flow (i.e. sample set 3). It is likely that the variable responses to sedimentation reflects

the different life cycle characteristics and stages present in the river during the study and therefore reflects natural temporal variability in the macroinvertebrate community structure. The abundance of sediment sensitive taxa demonstrated a similar pattern to that recorded for the taxonomic NMDS plots, with no differences in abundances recorded for sets 1, 3 and 9. These changes in sediment sensitive taxa may be driven by the life cycle of EPT taxa, which are particularly sensitive to fine sediment within the substrate (Conroy et al . 2016) and which were temporally variable abundance in richness during this study. EPT richness below a threshold of 2 taxa in this study coincided with clear differences in community structure associated with the sediment treatment.

Given the study took place during summer; discharges were naturally low and favoured the deposition of fine sediments (Wood and Armitage, 1999). Consequently, the dominant taxa recorded during this period are more likely to display affinities to fine sediment such as the families of Caenidae and Chironomidae (Jowett, 1997; Dewson et al., 2007). The presence of later instars of EPT taxa during the summer months may be limited due to emergence patterns, but the majority (excluding Caenidae) probably display a greater affinity for clean substrates (Sutherland et al., 2012) and may account for the community patterns recorded in this study. As such, the implications of fine sediment deposition will be most pronounced during summer months. It is therefore vital to consider within-year temporal variation and taxon life stages when assessing the implications of fine sediment deposition on aquatic communities (Johnson et al., 2012).

Overall significant differences were recorded for the abundances of taxa classified as sensitive to fine sediment (Turley et al., 2016). These results indicate that at the patch scale, removal of fine sediments may enhance habitat complexity and thereby increase the heterogeneity of instream communities. Micro-scale habitat characteristics are critical in the regulation of macroinvertebrate diversity (Pardo and Armitage, 1997; Lamouroux et al., 2004; Laini et al., 2014). Despite this, the majority of studies conducted on fine sedimentation impacts often take a reach-scale approach (e.g. Downes et al., 2006; Burdon et al., 2013) and therefore understanding the importance of variable micro-scale habitat dynamics is limited. Within this study clean substrates supported a greater number of unique taxa (11)

compared to sedimented substrates (2), highlighting the importance of micro-scale habitat differences for biodiversity.

Taxa richness, community abundance and EPT richness did not demonstrate any significant differences between sediment treatments. The documented effects of fine sediment on taxa richness and community abundance are not consistent in the literature with some studies documenting a reduction in taxa richness (Cline et al., 1982; Rabeni et al., 2005) or community abundance (Armstrong et al., 2005; Larsen et al., 2011) while others recorded no modification (Lenat et al., 1981; Kaller et al., 2004; Downes et al., 2006); and in some instances abundances have been reported to increase (Matthaei et al., 2006). Streams that are characterised by low fine sediment content and support a greater proportion of fine sediment sensitive taxa, are likely to be more heavily affected. In contrast, rivers that are species poor may not display a marked response to an increase in fine sediment.

4.2 Taxon specific responses to fine sedimentation

A small number of associations were observed between individual taxa and fine sediment treatments. Sedimented substrates were characterised by significantly greater abundances of two taxa that typically burrow into fine substrates; *Dicranota* sp. and Oligochaeta (Lenat et al., 1979; Fitter and Manuel, 1986). Even at the order level, Oligochaeta are widely documented to be positively correlated with fine sediment (Richards et al., 1993; Waters, 1995; Angradi, 1999; Descloux et al., 2013); however, the experimental effects of fine sediment for *Dicranota* sp. have not been widely documented. The reduction of pore space in heavily sedimented and clogged substrates potentially favours taxa with small body sizes (Gayraud and Phillipe, 2001; Duan et al., 2009; Xu et al., 2012). In marked contrast, two species demonstrated strong affinities for clean substrates; the Ephemeropteran species, *Habrophlebia fusca* which may be vulnerable to gill damage within fine bed material (Jones et al., 2012) and *Gammarus pulex*, which although common in rivers with fine sediment patches is a highly mobile taxon and may have actively sought clean sediments (Wood et al., 2010; Mathers and Wood, 2016).

4.3 Biological traits

Several previous studies have suggested that macroinvertebrate community trait profiles may alter as a function of habitat modifications; reflecting a filtering effect of

taxa with traits sensitive to fine sediment deposition (Usseglio-Polatera et al, 2000; Larsen et al., 2011; Bona et al., 2016; Doretto et al., 2017). However, when the functional composition of macroinvertebrate communities was examined in this study, the effects of fine sediment were not as marked as those obtained using taxonomic community composition data. Differences between functional trait composition associated with sediment treatment were only observed on a very limited number of sampling occasions. Despite the absence of a clear community effect, a number of individual traits showed a significant response to fine sediment content.

Locomotion modalities were the most responsive to increased fine sediment loading with crawlers, swimmers and interstitial dwellers all demonstrating a reduction in occurrence within sedimented substrates. Habitat trait groups have been reported to display significant responses to sedimentation, with fine sediment having the potential to limit access to preferred habitats (Gayraud and Philippe, 2001; Rabeni et al., 2005). Interstitial pore space is an important determinant in macroinvertebrate colonisation and diversity, with fine sediment clogging limiting the ability of many taxa to access subsurface habitats, in particular larger organisms that require larger interstitial space (Larsen and Ormerod, 2010; Mathers et al., 2014). It is therefore not surprising that the number of interstitial dwellers in combination with the maximal size of organisms reduced within the sedimented columns (Buendia et al., 2013; Descloux et al., 2014; Milesi et al., 2016). Similarly, crawlers have been widely documented to be affected by increasing fine sediment content with some studies citing their reduced locomotion as a factor in their reduced abundance (Bo et al. 2007; Buendia et al., 2013) whilst others link their decline to negative effects on respiration modalities (Rabeni et al., 2005). In contrast, the habitat group of swimmers demonstrated variable responses to enhanced sediment loading, with some studies documenting a decrease in richness but no effect on density (Rabeni et al., 2005), whilst others saw a reduction in abundance (Larsen et al., 2011) or even a positive correlation (Buendia et al., 2013). Habitat complexity prior to sedimentation probably influences the magnitude of the effects recorded on the invertebrate assemblage. Rivers which are naturally more heterogeneous are likely to display greater effects in response to instream stressors such as fine sediment deposition.

Feeding modalities are often associated with fine sediment content, with increasing fine sediment loads affecting the quality of trophic resources and thereby affecting feeding activities (Jones et al., 2012). In contrast to the expectations of the wider literature, the only taxa that demonstrated a reduction in abundance to increased fine sediment content were those that displayed shredder feeding characteristics (Descoux et al., 2014; Doretto et al., 2016). Similarly, respiration modalities are often particularly sensitive to fine sediment with some respiratory structures being significantly impaired or damaged by fine particles (Lemley, 1982; Townsend et al., 2008). This study documented no significant associations with fine sediment content and respiratory structures which were supported by the wider sedimentation literature. Taxa which respire via plastron and spiracles demonstrated a reduction in abundance in marked contrast to results reported by Logan (2007) and Archaimbault et al., (2005). This biological response is primarily a function of increasing numbers of the Diptera within the genus *Dicranota* sp. and may highlight a limitation of biological trait analyses that only consider individual traits.

The application of biological traits in evaluating the effect of stressors has seen increasing recognition, with many studies proposing that the application of trait compositions may provide a better or comparable indicator for different types and combinations of instream stressors than traditional taxonomic based metrics (Menezes et al., 2010; White et al., 2016; Göthe et al., 2016). However, from the results reported here and in a number of other studies, it is clear that further research is required around the assignment of biological traits and caution should therefore be applied when undertaking such analyses (Buendia et al., 2013; Descoux et al., 2014). Further research is required to develop trait databases that have greater applicability to the ecosystems being assessed. Currently the only database available to European researchers is that by Tachet et al. (2010) developed in French streams. Although applicable to other European streams, the low taxonomic resolution of the database (family / genus) raises some questions regarding the wider application of such an approach without some local modifications as many families with multiple genus (e.g. Baetidae and Chironomidae) support highly variable taxonomic responses (Monk et al., 2008). Traits are also unlikely to act in isolation but rather a combination of traits will determine the response of an individual species to a stressor (Pilière et al., 2016). Consequently, in future research,

traits should be assessed as interacting factors within a more fully developed mechanistic understanding of the observed effects of fine sediment for macroinvertebrates.

5. Conclusion

Understanding the mechanistic implications of fine sediment upon macroinvertebrate communities still remains a significant challenge. This study indicates that the effect of increased fine sediment loading upon macroinvertebrate assemblages is not temporally consistent with a number of sampling periods displaying no discernible effects of fine sediment loading. The implications of increased fine sediment loading are likely to be heavily dependent on the timing of sedimentation events relative to taxon life cycles. Future studies concerned with investigating the effects of fine sediment should do so with a greater awareness of the temporal dynamics of the communities they are studying. Despite the increasing application of biological trait composition within biomonitoring efforts, community trait profiles displayed no consistent effect to fine sediment on community structure in this study. Patch scale responses to fine sediment were however evident, with the two substrate treatments supporting distinct communities when taxonomic composition and individual trait modalities were considered. The results from this study indicate the importance of recognising micro-scale habitats within the context of maximising aquatic biodiversity. Further research is required to fully understand the seasonal effects of fine sediment deposition and dynamics on aquatic macroinvertebrate assemblage structure and function.

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Figure 2. Non-metric multidimensional scaling (NMDS) of macroinvertebrate community data from the River Gwash and River Chater by sediment treatment using the Bray-Curtis similarities coefficients for cylinder sets 1 - 9 (panes a-i) and global dataset (pane j). Grey rhombus = clean cylinders and black rhombus = sedimented communities.

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Figure 5. Mean abundances (± 1 SE) of EPT taxa over the nine sampling sets.

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