

1 **The effects of altered flow and bed sediment on macroinvertebrates in stream mesocosms.**

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6 **Abstract**

7 River regulation and altered land use are common anthropogenic disturbances resulting in ecological  
8 impacts through siltation or altered hydrology. We tested the separate and combined effects of  
9 increased flow and fine particles (colmation) on macroinvertebrates in flume mesocosms. We  
10 hypothesised that increased flow would reduce any effects of colmation. We tested two bed types:  
11 clean and colmated sediment where fines were 10% by weight. Two flow rates were initially  
12 established, a turbulent flow in six mesocosms and a lower rate to create a transitional flow between  
13 turbulent and laminar flows in the remaining six mesocosms. After 30 days macroinvertebrates were  
14 sampled and the flow in three turbulent flow mesocosms and three transitional flow mesocosms  
15 switched to the lower and higher flow rates, respectively, thus creating four flow scenarios. The  
16 experiment was concluded after sampling macroinvertebrates again at day 70. We demonstrated that  
17 colmation and decreased flows individually result in decreased density and richness of  
18 macroinvertebrates and altered assemblage and trait structure. However, our hypothesis that higher  
19 flows would ameliorate any effects of fines was not supported. Further research is required to evaluate  
20 if lower thresholds of colmation have ecological impacts and determine the velocities required to  
21 ameliorate those impacts.

22

23 *Keywords: river regulation, colmation, sedimentation, flume mesocosms, benthos*

24

## 25 **Introduction**

26 Modification of flows in regulated rivers is arguably the greatest source of human alteration of  
27 riverine ecosystems, with nearly 80% of the discharge of rivers being affected (Nilsson *et al.* 2005;  
28 Carlisle *et al.* 2010). There are four ways in which flow modification is likely to cause ecological  
29 effects (Ward and Stanford 1979). First, rivers with reduced flow will have decreased local current  
30 velocities, decreased overall stream habitat and increased siltation of the stream bed. Second, streams  
31 with constant seasonal flows will have uniform currents, which may enhance riparian and aquatic  
32 vegetation through bed stability. Third, increased discharge may lead to higher current velocities  
33 leading to bed scour, resulting in a change to a coarse substratum. Fourth, short-term fluctuations in  
34 flow created during the generation of hydro-electricity can cause current and depth fluctuations,  
35 turbidity and bed and bank instability. There are two main physical impacts from river regulation:  
36 alteration of flow and, as a consequence, changed sediment dynamics (Buendia *et al.* 2014).

37         The flow of water in a river determines many critical physicochemical characteristics such as  
38 channel geomorphology, sediment dynamics and habitat diversity, and limits the distribution and  
39 abundance of riverine species (Biggs *et al.* 2005; Larned *et al.* 2010). Alteration of the natural flow  
40 regime alters many of the naturally occurring ecological and physical processes and properties (e.g.  
41 Menéndez *et al.* 2012; Araujo *et al.* 2013; Ruiz-Gonzalez *et al.* 2013; Grownns *et al.* 2014).  
42 Specifically, changes in flow regimes and near-bed hydraulics can modify sediment retention (Palmer  
43 *et al.* 2014), macroinvertebrate assemblage and trait structure (Brooks *et al.* 2005; Brooks *et al.* 2011),  
44 periphyton assemblages (Hart *et al.* 2013), benthic metabolism (Reid *et al.* 2006), carbon uptake by  
45 algae (Finlay and Sinsabaugh, 1999), insect larval sizes (Sagnes *et al.* 2008) and feeding efficiency  
46 rates in filter-feeding invertebrates (Lancaster and Downes 2010). It is not surprising then that river  
47 regulation leads to ecological change and that the risk of ecological change increases with increasing  
48 magnitude of flow alteration (Bunn and Arthington 2002; Poff and Zimmerman 2010; Cortez *et al.*  
49 2012).

50         Changes in natural sediment dynamics can cause increased deposition of fine sediment  
51 (colmation), which results in the clogging of river bed interstices that may form a seal, disconnecting

52 surface water from the hyporheic zone (Brunke 1999). Colmation can occur either under low flows  
53 where the settling of particles can cause external colmation or following flooding which can cause silt  
54 to deposit within the stream bed (Olsen *et al.* 2010). Increased amounts of fine-grained sediment in  
55 the river bed can affect benthic macroinvertebrate assemblage structure and trait characteristics  
56 through clogging of gills and other body parts (Kefford *et al.* 2010; Descloux *et al.* 2014), mortality  
57 through burial (Wood *et al.* 2005), removal of habitat through filling of interstitial spaces (Vadher *et*  
58 *al.* 2015) and decreased bed stability (Kaufmann *et al.* 2009). The relationship between  
59 macroinvertebrates and fine-grained sediments is poorly defined (Jones *et al.* 2012), however,  
60 negative ecological responses can occur with small additions of surface sediment (Bryce *et al.* 2010;  
61 Wagenhoff *et al.* 2012)

62         The relationship between flow and colmation of substrata is not straightforward. Whilst peak  
63 flows can be associated with the delivery of large quantities of fine-grained sediment from the  
64 catchment, in areas of the river bed experiencing high flow, frequently occurring flood events tend to  
65 clear fine-grained sediments allowing an exchange of oxygen-rich surface water with the pore water  
66 of hyporheic interstices (Gibson, 2002; Mürle *et al.* 2003). In simple terms, the behaviour of fine-  
67 grained sediment within rivers is influenced by hydrologic conditions, whereas the load of fine-  
68 grained sediments entering rivers is largely dependent on landscape erosion within the catchment  
69 (Boulton *et al.* 1997; Collins and Anthony 2008), with both factors interacting to govern the rate of  
70 colmation. As drivers such as forestry and agricultural intensification tend to be associated with  
71 changes to both flow and fine-grained sediment load (i.e. hydromorphological changes to increase  
72 drainage and increased tillage) there is considerable advantage to understanding the separate and  
73 combined influence of sediment and flow on benthic conditions. To date, experimental investigations  
74 of the combined effects of colmation and altered flow on benthic macroinvertebrates are rare.

75         Here we present an experimental investigation where we artificially manipulated the amount  
76 of fine-grained sediment in the stream bed and flow rates in the channel and examined their individual  
77 and joint effects on benthic macroinvertebrate assemblages. We hypothesised that, in addition to  
78 individual treatment effects, there would be a strong interaction effect of stream flow and colmation,

79 specifically that high flow rates would reduce the ecological effects of colmation through increased  
80 inter-gravel flows and potentially flushing of fine-grained sediments from the stream bed. Further, we  
81 tested the hypothesis that low flows would have a lasting effect on invertebrate assemblages even  
82 after flows had been increased. Such legacy effects of changes in hydrology have been noted before  
83 (Ledger *et al.* 2006; Ledger and Hildrew 2001), and are a consequence prior effects on the species  
84 present. Our objective here was to establish if the invertebrate assemblage was resilient to changes in  
85 hydrology, and thus to establish the implications of periods of low flow.

## 86 **Methods**

### 87 *Study area*

88 The River Frome has a catchment area of 414 km<sup>2</sup>, which is underlain mainly by Cretaceous Chalk  
89 bedrock. The land use is primarily agricultural and Dorchester is the only significant urban area in the  
90 catchment, with a population of 19,000 in 2013 (Office of National Statistics, 2014). For the period  
91 1965 to 2005, the mean annual rainfall at East Stoke was 1020 mm and the mean annual discharge  
92 was 6.38 m<sup>3</sup> s<sup>-1</sup> (Marsh and Hannaford 2008).

### 93 *Experimental design*

94 The experiment was carried out between May and August 2012 in twelve open-air, flow-through  
95 flume mesocosms located at the Freshwater Biological Association's River Laboratory (50°40'49"N,  
96 2°11'05"W) in Dorset, U.K. Four blocks of mesocosms were sited adjacent to, and fed from, the Mill  
97 Stream, a side channel of the River Frome. Each block consisted of three parallel linear steel flumes  
98 (0.33 m width, 12.4 m length and 0.30 cm depth) positioned at approximately 140° to the riverbank.

99         Mesocosms were filled to a depth of 20 cm with sediment sourced from a local quarry to  
100 replicate the sediment-size distribution of the Mill Stream (volumetric proportions of particle sizes,  
101 85% 11–25 mm, 5% 2–11 mm, 5% 0.35–2 mm, 5% 0–0.35 mm (Armitage, 1995; Ledger *et al.* 2008).  
102 Sediments were mechanically mixed to ensure homogeneity prior to use. To mimic internal  
103 colmation, fine-grained river sediment (< 2 mm size fraction, obtained from dredged river bed  
104 material) was added to the sediment placed in the downstream 4 m stretch of each mesocosm. In these

105 sections total fine-grained sediment represented 10% of the total sediment by weight. We chose 10%  
106 as ecological impairment potentially occurs when fine sediment reaches this level (see Kemp *et al.*  
107 2011). Therefore, each mesocosm contained two bed sediment types: “clean” sediment in the  
108 upstream most 4 m section and experimentally colmated sediment in the downstream most 4 m  
109 section. The intervening 4 m was treated in the same way (upstream 2 m filled with clean sediment,  
110 downstream 2 m filled with experimentally colmated sediment) but treated as a buffer region between  
111 the sediment treatments (i.e. not sampled), in case there was migration of fine-grained sediment  
112 between treatments. Three replicate five litre sediment samples were taken randomly from the clean  
113 and experimentally colmated bed sediments. These samples of bed sediment were dried and sieved  
114 into <0.125, 0.25, 0.5, 1.0, 2.0, 4.0, 8.0 and 16 mm or greater size fractions and the dry mass of each  
115 determined. For each size fraction the percentage organic matter was calculated from loss on ignition  
116 following combustion at 450 °C in a muffle furnace.

117 Unfiltered river water was delivered at the head of each block through an upstream inflow  
118 pipe (110 mm diameter) into a reservoir, approximately 2 m long, 1 m wide and 35 cm deep. From  
119 this reservoir, water flowed by gravity over a low weir into the upper end of each channel, creating a  
120 localised affect in the first 100 mm of the upstream section in each mesocosm; flow rates in the  
121 individual mesocosms were controlled by adjusting the height of the weir. Macroinvertebrates  
122 colonised the mesocosms by drift from the Mill Stream or aurally (Harris, 2006).

123 Two flow rates were initially established in the twelve mesocosms. The higher flow rate  
124 (mean  $5.3 \times 10^{-3} \text{ m}^3 \text{ s}^{-1}$  range  $4.7 \times 10^{-3}$  to  $6.1 \times 10^{-3}$ ) was chosen to create turbulent flow (Reynolds  
125 number  $>2000$ ) and the lower flow rate ( $3.2 \times 10^{-4} \text{ m}^3 \text{ s}^{-1}$  range  $2.7 \times 10^{-3}$  to  $3.9 \times 10^{-3}$ ) was chosen to  
126 create a transitional flow between turbulent and laminar flows (Reynolds number between 500 and  
127 2000). The higher and lower flow rates were assigned to each mesocosm alternately along the east-  
128 west direction. Flow was started in each mesocosm in May 2012. After 40 days, flow rates in six out  
129 of twelve of the mesocosms were switched; three of the higher flow flumes were altered to the low  
130 flow rate and three of the slower flow mesocosms were increased to the high flow rate. Therefore, we  
131 had four flow scenarios: fast flow throughout the experiment (FF flow scenario), slow flow

132 throughout (SS), fast flow for 40 days and then changed to slow flow (FS) and slow flow for 40 days  
133 changed to fast flow (SF). The experiment was concluded at day 70.

#### 134 *Macroinvertebrate and physico-chemical sampling*

135 Electrical conductivity, pH and temperature were measured with a regularly calibrated hand-  
136 held electronic meter (Hanna Instruments HI98129) in each of the experimental sections at the start of  
137 the experiment, at four day intervals until the end of day 40 when the flows in some channels were  
138 changed, then at 8 day intervals and at the termination of the experiment on day 70.

139 Macroinvertebrates were sampled using 25 x 25 cm Surber sampler (300 µm mesh), with the substrate  
140 disturbed to a depth of approximately 3 cm, at day 30 and day 70. Six randomly placed samples were  
141 taken from of each 4 m sediment-type section in each mesocosm. Samples were preserved with 4%  
142 formaldehyde for subsequent identification and quantification to family level, with the exceptions that  
143 chironomid larvae were identified to subfamily and mites, nematodes and ostracods to order.

#### 144 *Macroinvertebrate traits*

145 Data describing freshwater macroinvertebrate traits were obtained from Tachet *et al.* (2000)  
146 with additional information from [www.freshwaterecology.info](http://www.freshwaterecology.info) and Descloux *et al.* (2014) for those  
147 taxa or traits that were not included in Tachet *et al.* (2000). Each biological trait, e.g. mode of  
148 respiration, was described by several trait-classes, e.g. respiring via tegument, gill, spiracle or  
149 plastron. The trait characteristics of each taxon were scored by assigning a value to each trait-class  
150 reflecting the affinity of the taxon to the trait-class (Table 2). Scores ranged from 0 to 5, indicating no  
151 to high affinity, respectively (Chevenet *et al.* 1994). Fuzzy coding was used where taxa were not  
152 exclusive to a single trait-class. The trait assemblage data was presented as a matrix of the relative  
153 prevalence of each trait-class (within each trait) in each of the 24 experimental sections on both  
154 sampling occasions. This matrix was created by first log-transforming the mean abundance of each  
155 recorded taxon from the six Surber samples taken in each experimental section on each sampling  
156 occasion. The trait-class scores for each recorded taxon were then multiplied by its log-transformed  
157 mean abundance to provide weighted trait-class scores. These were summed across recorded taxa

158 within a trait class and then expressed as a proportion of the total sum of weighted trait-class scores  
159 within a trait to give the relative prevalence of each trait-class (within each trait) in each of the 24  
160 experimental sections on both sampling occasions.

161 *Statistical analyses*

162 Differences in water quality, macroinvertebrate richness, density, community assemblage  
163 structure and trait assemblage structure between the fixed factors sampling occasion, flow scenario  
164 and bed sediment type were tested using Permutational Analysis of Variance (PERMANOVA)  
165 (Anderson 2001). The main factors sediment type and flow scenario were used as tests of the  
166 independent effects of sediment and flow, and their interaction to test for any ameliorative effect of  
167 increased flow on the effect of experimental colmation. The interaction between flow scenario and  
168 sampling occasion was also of interest, to test the effects of reversing flow on day 30 in the FS and SF  
169 flow scenarios (see Table 1). The random factor mesocosm was nested in the sediment type and flow  
170 scenario. Given there were twelve mesocosms, there were three replicates of each combination of the  
171 main factors. Individual samples, six taken from each experimental section on each sampling  
172 occasion, were pooled to give a single sample for each replicate channel.

173 To address our hypotheses we used planned contrasts to compare physicochemical variables  
174 and the macroinvertebrate assemblage among flow scenarios. To test for the immediate effects of  
175 flow, the fast-flow scenarios were compared with the slow-flow scenarios in place at the time of the  
176 first sampling occasion (FF and FS with SS and SF) and second sampling occasion (FF and SF with  
177 SS and FS). To test for legacy effects of historical flow, planned contrasts were used to compare  
178 within the fast-flow and slow-flow scenarios on both sampling occasions, i.e. FF with FS and SS with  
179 SF on the first sampling occasion and, FF with SF and SS with FS on the second sampling occasion.  
180 Planned contrasts allowed us to examine pairs of flow scenarios in specific comparisons rather  
181 examining all possible post-hoc pairwise comparisons. Planned contrasts were only conducted when  
182 the flow scenario main factor was significant in the main model.

183 Prior to analysis, water quality data were normalised and macroinvertebrate density data were  
184 log-transformed to minimise skewed distributions. Euclidean distance was used to form similarity  
185 matrices as input for the PERMANOVA analysis for water chemistry, and macroinvertebrate density,  
186 richness and trait assemblage structure. Bray-Curtis distance was used to form similarity matrices for  
187 the macroinvertebrate community assemblage data following range standardisation by dividing each  
188 taxon by its maximum density to ensure equal weighting of each taxon in the dissimilarity value.  
189 Significant relationships among the main factors and interactions were tested using a Monte Carlo  
190 procedure with 9999 randomisations. Patterns of differences in macroinvertebrate community and  
191 trait assemblages identified by PERMANOVA were presented diagrammatically using non-metric  
192 multidimensional scaling ordination (nMDS). The algorithm similarity percentages (SIMPER) was  
193 used to identify macroinvertebrate taxa or traits contributing to differences in main factors identified  
194 by PERMANOVA.

195

## 196 **Results**

### 197 *Effects on the physico-chemical environment*

198 The experimental manipulation of the sediment in the mesocosm produced a significant difference in  
199 substrate particle size (as percentage by weight) between the experimental sediment treatments  
200 (pseudo- $F = 314$ ;  $df = 8,1$ ;  $P = 0.0001$ ; Figure 1). The mean percentage (all means  $\pm$  1 standard error)  
201 of particles smaller than 2 mm was greater ( $9.8 \pm 1.0\%$  w/w) in experimentally colmated sediment  
202 than the clean sediment ( $6.2 \pm 0.6\%$  w/w). The mean organic content of the experimentally colmated  
203 sediment was also greater ( $4.8 \pm 0.4\%$  w/w) when compared with the clean sediment ( $0.0 \pm 0.0\%$   
204 w/w).

205 Time had a significant effect on the electrical conductivity, temperature and pH of the water in the  
206 mesocosms (Table 1), most likely a consequence of temporal changes in the source of the water, the  
207 River Frome. A slight but statistically significant difference in temperature and pH was found  
208 between the sediment treatments. Mean temperature in the experimental colmated substrate sections



209 (15.9 ± 0.06°C) was slightly greater than in the clean sediment sections (15.7 ± 0.05°C). Mean pH  
210 was also slightly greater in the experimental colmated substrate sections (8.6 ± 0.04) compared with  
211 the clean sediment sections (8.5 ± 0.03). There was no significant difference in water quality between  
212 the different flow scenarios.

### 213 *Response of macroinvertebrates – immediate effects and their interactions*

214 Macroinvertebrate richness, density and community and trait assemblage structure were all  
215 significantly influenced by the sediment experimental treatment (Table 1). Richness, community and  
216 trait assemblage structure were also influenced by sampling occasion and flow scenario (Table 1).  
217 One of the terms of interest, the sediment by flow scenario interaction was not significant for any of  
218 the four biological measures, suggesting that flow regimes did not greatly influence the effects of the  
219 added fine-grained sediment on macroinvertebrate richness, density, community or trait assemblage  
220 structure (Table 1). In addition, the sediment by sampling occasion interaction was not significant for  
221 any of the biological measures, suggesting that any effects of the fine-grained sediment addition were  
222 constant through time (Table 1).

223 Overall, the mean richness was 26.4 ± 1.0 taxa in clean sediment compared with 23 ± 0.7 taxa  
224 in experimentally colmated sediment, and the mean number of taxa increased from 23 ± 1.0 at day 30  
225 to 26 ± 0.8 at day 70 (Figure 2). Clean sediment in the FF flow scenario had a significantly greater  
226 number of taxa than the experimentally colmated sediments, but this did not occur for the other flow  
227 scenarios. Macroinvertebrate richness was significantly greater when the flow was fast, i.e. in flow  
228 scenarios FF and FS on day 30 and SF and FF on day 70 (Table 1). The increased richness in the SF  
229 flow scenario from day 30 to day 70 and decrease in the FS flow scenario from day 30 to day 70  
230 (Figure 2), probably explain the significant interaction between flow scenario and sampling occasion.

231 Macroinvertebrate density was generally greater in the clean versus the experimentally  
232 colmated sediment type in all flow scenarios and on both sampling occasions (Figure 2). Mean  
233 density in clean sediments declined from 3930 ± 218 to 2885 ± 191 animals per m<sup>2</sup> from day 30 to

234 day 70. While, in experimentally colmated sediments mean density remained the same, varying from  
235  $2293 \pm 198$  to  $2320 \pm 49$  animals per  $m^2$  over the same time.

236 There was a significant interaction between flow scenario and sampling occasion for both  
237 macroinvertebrate community and trait assemblage structure, indicating that the influence of flow  
238 regime changed through time. For both assemblage measures, on day 30 the two fast flow scenarios  
239 (FF and FS) were not significantly different to each other but were significantly different to  
240 assemblages from the slow flow scenarios (SS and SF: Table 1). These results are illustrated in the  
241 nMDS ordination plots where for both community and trait assemblages a similar pattern is evident  
242 (Figure 3). The fast flow scenarios (FF and FS) and slow flow scenarios (SS and SF), respectively,  
243 occupy similar positions in the ordination space on day 30, indicating that they support similar  
244 assemblages (Figure 3). In contrast, on day 70, while the fast (FF and SF) scenarios were significantly  
245 different to each other, they were more distinctly different to the slow (SS and FS) flow scenarios,  
246 explaining the interactions between sampling occasion and flow scenario (Table 1). These results  
247 confirm that the macroinvertebrate community and trait assemblages responded to flow within the  
248 mesocosms; switching the flow from fast to slow or from slow to fast at day 40 resulted in the faunal  
249 assemblage changing to become more similar to the slow controls (SS) or fast controls (FF),  
250 respectively, at day 70 (Figure 3).

251 Four macroinvertebrate taxa contributed up to 20% of the significant differences between fast  
252 and slow flow scenarios on day 30 (Table S2). Athericidae, Baetidae and Ephemerellidae were more  
253 abundant in the faster flowing mesocosms and Dytiscidae more abundant in the slower flow scenarios.  
254 Five taxa including, Hydropsychidae, Baetidae, Hydroptilidae, Polycentropodidae and Leuctridae,  
255 contributed up to 20% to the significant differences between the fast and slow flow scenarios on day  
256 70. With the exception of Leuctridae, all these taxa were more abundant in the faster flow scenarios.

257 Seven taxa contributed up to 20% of the difference in macroinvertebrate assemblages  
258 between sediment types (Table S3). Leuctridae, Ephemeridae and Baetidae were more abundant in the

259 experimentally colmated sediment type, whilst Dytiscidae, Hirudinea, Hydracarina and Caenidae were  
260 more abundant in the clean sediments.

261 The prevalence of three traits: potential number of life cycles per year, maximal potential  
262 size, and reproduction were significantly affected by the experimental treatments (Tables S2 and S3).  
263 The prevalence of animals with more than one life cycle per year was greater in slow flowing  
264 experimental areas and in colmated sediments (Figure 3). The prevalence of macroinvertebrates with  
265 a maximum potential size of 0.5-1 cm was also greater in colmated than clean sediment but in fast  
266 rather than slow flowing experimental areas. The prevalence of laying fixed clutches of eggs was less  
267 in colmated than clean sediments and greater in slow flows after 70 days. . After 30 days the  
268 prevalence of laying unattached clutches of eggs was greater in slow flow treatments than fast flow  
269 treatments (Tables S.2 and S3; Figure 3).

#### 270 *Response of macroinvertebrates – legacy effects*

271 At the end of the experiment the planned contrasts identified differences in macroinvertebrate  
272 community structure between the two slow flow (SS v FS) treatments and between the two fast flow  
273 (FF v SF) treatments (Table 1: Figure 3a), indicating that prior flow conditions had a lasting influence  
274 on the invertebrate community. The effect size (pseudo- $F$ ) was larger for the difference between slow  
275 flow (SS v FS) treatments than between the fast flow (FF v SF) treatments (Table 1), suggesting that  
276 the flow switching had a more pronounced effect on prior fast flow than prior slow flow. The  
277 positions of the centroids in the nMDS ordination plot indicate that FS treatment was more distinct  
278 (further from the origin) than the SS treatment (Figure 3a), suggesting increased sensitivity to flow  
279 reduction in the prior fast flow community. The planned contrasts also identified an effect of previous  
280 flows on the trait assemblage, but here the effect size suggested the opposite pattern to the community  
281 response, with the difference between the fast flow (FF v SF) treatments returning a larger pseudo- $F$   
282 than the slow flow (SS v FS) treatments (Table 1). In contrast to community composition (Figure 3a),  
283 the position of centroids suggest that prior flow conditions did not have a substantial differential effect  
284 on trait composition (Figure 3b).

285 **Discussion**

286 *Effects of flow and colmation, and their interaction*

287 We have demonstrated that colmation and decreased flows individually result in decreased density  
288 and richness of macroinvertebrates and altered assemblage structure. However, our hypothesis that  
289 higher flows would ameliorate any effects of added fine sediment was not supported; there was no  
290 interaction between flow type and sediment treatment. These results are in contrast with the  
291 observation that increased flow can reduce the effects of sedimentation on macroinvertebrates  
292 (Matthaei *et al.* 2010). It is possible that the differences between the turbulent and transitional flow  
293 regimes (and their alteration) in our mesocosms was not sufficient to create enough shear stress or  
294 power to remove fine sediment or substantially alter sediment dynamics. However, Boulton *et al.*  
295 (2004) showed that artificial floods, which created a three-fold increase in discharge, only caused  
296 limited change in sediment dynamics within bed sediment. Whilst it may be hard to draw any  
297 generalities from individual studies, as local hydraulic conditions will influence fine-grained sediment  
298 dynamics, Jones *et al.* (2015) demonstrated that the increased flow used in the mesocosms resulted in  
299 increased penetration of oxygen into the stream bed and affected the distribution of hyporheic  
300 invertebrates, with a significant interaction between the flow and sediment treatments. Yet flow had  
301 no apparent ameliorating effect on the benthic macroinvertebrate assemblage, indicating that the  
302 macroinvertebrates living at the surface of the stream bed were not affected by conditions deeper  
303 within the hyporheos and suggesting that any difference in assemblage was due to the physical effects  
304 of the added fine-grained sediment at the surface.

305 Flow had a significant effect on the trait assemblage. Furthermore, the alteration in flow after  
306 day 40 led to a shift in prevalent traits to a condition most closely resembling the corresponding  
307 unaltered flow treatments. After 70 days, larger sized, ovoviviparous and asexually reproducing  
308 macroinvertebrates tended to be more prevalent in slow flows, whereas intermediately-sized  
309 macroinvertebrates that laid isolated cemented eggs or clutches of cemented eggs tended to be  
310 associated with high flows. These results indicate that the macroinvertebrate community rapidly  
311 responded in a predictable way to the changes in flow.

312           The difference between the macroinvertebrates in the experimentally colmated and clean  
313 sediments was primarily driven by the differences in abundances of seven taxa. Higher densities of  
314 four taxa, Caenidae, Dytiscidae, Hirudinea and Hydracarina, were found in clean sediment whereas  
315 three families, Baetidae, Ephemeridae and Leuctridae, were found at higher densities in the  
316 experimentally colmated sediment, suggesting that colmation can have both positive and negative  
317 impacts, depending on individual taxa. Correspondingly, we found a significant effect of fine-grained  
318 sediment addition on the benthic macroinvertebrate trait assemblage; with relatively small size  
319 (maximum size between 0.5-1 cm) and animals with more than one life cycle per year associated  
320 with the experimental addition of fine-grained sediment. We set up our experimentally colmated  
321 sediments to mimic changes to bed composition resulting from increased inputs of fine-grained  
322 sediment from catchments, where the mean size of particles becomes smaller, interstices between  
323 larger particles become filled and a surface drape of deposited sediment occurs (Kaufmann *et al.*  
324 2009). Most macroinvertebrate species have specific requirements of the substrate they occupy and  
325 tend to avoid patches that fail to meet their requirements (Peckarsky, 1991; Williams and Smith,  
326 1996; Sarriquet *et al.* 2007). For example, blackfly larvae tether themselves by means of a posterior  
327 circlet of hooks onto strands of silk which they attach to comparatively clean substrate, and they avoid  
328 substrates covered by a surface drape of loose sediments (Bass, 1998). Several species of crawling  
329 mayfly larvae avoid finer, less stable substrates as they cannot grip them effectively (Ciborowski *et al.*  
330 1977; Corkum *et al.* 1977). However, other species, for example, certain Chironomidae and  
331 Ephemeridae, select finer sediments into which they build tunnels. Along with physical changes to  
332 bed sediments, colmation can also impact the chemical environment, particularly to decrease oxygen  
333 levels (Jones *et al.* 2012). Although we noted small changes to in pH and temperature in our  
334 mesocosms, oxygen penetration in the bed was always greater than the sampling depth of 3 cm (Jones  
335 *et al.* 2015), suggesting that altered bed particle size structure was the main mechanism affecting  
336 macroinvertebrates.

337 *Legacy effects of past flow conditions*

338 We used planned contrasts to test the hypothesis that low flows would have a lasting effect on  
339 invertebrate assemblages even after flows had been increased due to prior effects on the species  
340 present (Ledger *et al.* 2006; Ledger and Hildrew 2001). We identified legacy effects of prior flow  
341 conditions but contrary to our assumptions, found that prior high flows had a larger influence on  
342 assemblage structure after flow switching than prior low flows: the difference between the SS and FS  
343 treatments was larger than that between the FF and SF treatments. It appears that the invertebrate  
344 community established during prior high flows was more susceptible to the impact of reduced flow.  
345 Legacy effects were also apparent on trait composition, but here we found less of a differential effect  
346 of the flow switching treatments, leading to a conclusion that the trait assemblage was robust to  
347 changes in flow.

348 Differences in susceptibility to variation flow among invertebrate communities have been  
349 identified previously and attributed to differences in within-site heterogeneity (Dunbar *et al.* 2010).  
350 Here we highlight the importance of prior flows: both within-site heterogeneity and flow history will  
351 mold the habitat template that defines the community and its response to disturbance (Gjerløv *et al.*  
352 2003).

353 *Effects on taxonomic composition* The influence of substrate composition on invertebrate taxa  
354 has been known for a long time (e.g. Ellis 1936). More recently, river managers have attempted to use  
355 the specific substrate requirements of taxa to develop indices to assess the impact of sediment run-off,  
356 such as the proportion of sediment-sensitive invertebrates (PSI: Extence *et al.* 2013). The PSI purports  
357 to provide a proxy to describe the extent to which the surface of river beds are composed of, or  
358 covered by, fine sediments. Yet, these indices have rarely been tested experimentally. Somewhat  
359 surprisingly, the taxa that responded to the experimental addition of fine-grained sediment appeared to  
360 contradict the PSI system. The taxa that were more abundant in the clean sediment (Caenidae,  
361 Dytiscidae and Hirudinea), have PSI scores that indicate they are tolerant of fine-grained sediment,  
362 whereas two of the taxa that were more abundant in the experimentally colmated sediment (Baetidae  
363 and Leuctridae) have PSI scores that indicate they are sensitive to sediment additions. Only  
364 Ephemeridae responded to the experimental addition of fine-grained sediment in the way predicted by

365 the PSI system (Hydracarina are not scored). It is apparent that the PSI system does not accurately  
366 reflect the response of these macroinvertebrate taxa to additions of fine-grained sediment, and we  
367 suggest that diagnostic indices should be based on empirical data rather than expert opinion (e.g.  
368 Murphy *et al.* 2013).

369         The responses of the macroinvertebrates to the altered flows was consistent with Dewson *et*  
370 *al.* (2007), who indicated that overall macroinvertebrate abundance can increase or decrease in  
371 response to decreased flow, whereas macroinvertebrate richness commonly decreases because habitat  
372 diversity decreases. The differences in assemblage structure between the fast and slow flows were  
373 primarily driven by eight taxa, six of which were more abundant in the fast flows. The increased  
374 abundance of three of the six taxa (Baetidae, Ephemerellidae and Hydropsychidae) is consistent with  
375 Extence *et al.* (1999), who indicated these taxa are primarily associated with moderate to fast flows.  
376 In contrast, Extence *et al.* (1999) also included Leuctridae as typical of fast flows, but this family was  
377 more abundant in our slow flow mesocosms. In addition, although Hydroptilidae and  
378 Polycentropodidae were more abundant in our fast flow mesocosms, Extence *et al.* (1999) lists these  
379 taxa as primarily associated with slow flowing and standing waters. Only one taxon, Dytiscidae, was  
380 more abundant in the slow flow mesocosms and was listed by Extence *et al.* (1999) as associated with  
381 slow flowing waters. The contrasting results from the mesocosms and the classification of Extence *et*  
382 *al.* (1999) suggest that many taxa may have more flexible hydraulic requirements than previously  
383 thought.

#### 384 *Conclusion*

385         Our study suggested that sediment accumulation associated with low flows (an increase in the  
386 proportion of bed fine sediment to 10% by weight) had detrimental ecological effects and the  
387 difference in flows in our mesocosms was not enough to ameliorate those effects. We found no  
388 interaction between our flow and sediment treatments. Our study also suggested that different faunas  
389 are associated with different flow rates or near-bed hydraulics. Taken together, these results suggest  
390 that to preserve or enhance ecosystems in regulated rivers, levels of minimal flows need to be

391 maintained and that previous fast flow conditions can have lasting effects on the assemblage  
392 characteristics of the community present during periods of low flow. However, further research is  
393 required to evaluate if there are lower thresholds of fine sediment levels that result in ecological  
394 impairment and to determine what flow thresholds are required to ameliorate colmation impacts. It  
395 would also be an advantage to the management of regulated rivers to determine if the timing of high  
396 flow conditions can be optimized to promote any long term, legacy effects.

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408



409 **References**

- 410 Anderson, M.J. (2001) Permutation tests for univariate or multivariate analysis of variance and  
411 regression. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 626-639.
- 412
- 413 Araujo, E.S., Marques, E.E., Freitas, I.S., Neuberger, A.L., Fernandes, R., and Pelicice, F.M. (2013)  
414 Changes in distance decay relationships after river regulation: similarity among fish  
415 assemblages in a large Amazonian river. *Ecology of Freshwater Fish* **22**(4), 543-552.
- 416
- 417 Armitage, P.D. (1995) Faunal community change in response to flow manipulation. In Ecological  
418 basis for river management (Eds. D Harper and A Ferguson) pp. 59-78. (John Wiley & Sons  
419 Ltd: Chichester)
- 420
- 421 Bass, J.A.B. (1998) 'Last-instar larvae and pupae of the Simuliidae of Britain and Ireland: a key with  
422 brief ecological notes.' (Freshwater Biological Association: Ambleside)
- 423
- 424 Biggs, B.J.F., Nikora, V.I., and Snelder, T.H. (2005) Linking scales of flow variability to lotic  
425 ecosystem structure and function. *River Research and Applications* **21**(2-3), 283-298.
- 426
- 427 Boulton, A., Harvey, M., and Proctor, H. (2004) Of spates and species: responses by interstitial water  
428 mites to simulated spates in a subtropical Australian river. *Experimental and Applied Acarology*  
429 **34**, 149-169.
- 430
- 431 Boulton, A.J., Scarsbrook, M.R., Quinn, J.M., and Burrell, G.P. (1997) Land-use effects on the  
432 hyporheic ecology of five small streams near Hamilton, New Zealand. *New Zealand Journal of*  
433 *Marine and Freshwater Research* **31**, 609-622.
- 434
- 435 Brooks, A.J., Haeusler, T., Reinfelds, I., and Williams, S. (2005) Hydraulic microhabitats and the

436 distribution of macroinvertebrate assemblages in riffles. *Freshwater Biology* **50**, 331-344.

437

438 Brooks, A.J., Russell, M., Bevitt, R., and Dasey, M. (2011) Constraints on the recovery of

439 invertebrate assemblages in a regulated snowmelt river during a tributary-sourced

440 environmental flow regime. *Marine and Freshwater Research* **62**(12), 1407-1420.

441

442 Brunke, M. (1999) Colmation and depth filtration within streambeds: Retention of particles in

443 hyporheic interstices. *International Review Of Hydrobiology* **84**, 99-117.

444

445 Bryce, S.A., Lomnický, G.A., and Kaufmann, P.R. (2010) Protecting sediment-sensitive aquatic

446 species in mountain streams through the application of biologically based streambed sediment

447 criteria. *Journal of the North American Benthological Society* **29**(2), 657-672.

448

449 Buendia, C., Gibbins, C.N., Vericat, D., and Batalla, R.J. (2014) Effects of flow and fine sediment

450 dynamics on the turnover of stream invertebrate assemblages. *Ecohydrology* **7**(4), 1105-1123.

451

452 Bunn, S.E., and Arthington, A.H. (2002) Basic Principles and Ecological Consequences of Altered

453 Flow Regimes for Aquatic Biodiversity. *Environmental Management* **30**(4), 492-507.

454

455 Carlisle, D.M., Wolock, D.M., and Meador, M.R. (2010) Alteration of streamflow magnitudes and

456 potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the*

457 *Environment* **9**(5), 264-270.

458

459 Chevene, F., Doledec, S., and Chessel, D. (1994) A fuzzy coding approach for the analysis of long-

460 term ecological data. *Freshwater Biology* **31**(3), 295-309.

461

462 Ciborowski, J.J.H., Pointing, P.J., and Corkum, L.D. (1977) The effect of current velocity and

463 sediment on the drift of the mayfly *Ephemerella subvaria* McDunnough. *Freshwater Biology*

464 7(6), 567-572.

465

466 Collins, A., and Anthony, S. (2008) Predicting sediment inputs to aquatic ecosystems across England  
467 and Wales under current environmental conditions. *Applied Geography* **28**(4), 281-294.

468

469 Corkum, L.D., Pointing, P.J., and Ciborowski, J.J.H. (1977) The influence of current velocity and  
470 substrate on the distribution and drift of two species of mayflies (Ephemeroptera). *Can. J. Zool.*  
471 **55**, 1970-1977.

472

473 Cortez, D.P., Grown, I.O., Mitrovic, S.M., and Lim, R.P. (2012) Effects of a gradient in river  
474 regulation on the longitudinal trends in water quality and benthic algal and macroinvertebrate  
475 assemblages in the Hunter River, Australia. *Marine and Freshwater Research* **63**(6), 494-504.

476

477 Descloux, S., Datry, T., and Usseglio-Polatera, P. (2014) Trait-based structure of invertebrates along a  
478 gradient of sediment colmation: Benthos versus hyporheos responses. *Science of The Total*  
479 *Environment* **466**, 265-276.

480

481 Dewson, Z.S., James, A.B.W., and Death, R.G. (2007) A review of the consequences of decreased  
482 flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological*  
483 *Society* **26**(3), 401-415.

484

485 Dunbar, M.J., Pedersen, M.L., Cadman, D., Extence, C., Waddingham, J., Chadd, R., and Larsen, S.E.  
486 (2010) River discharge and local-scale physical habitat influence macroinvertebrate LIFE  
487 scores. *Freshwater Biology* **55**(1), 226-242.

488

489 Ellis, M.M. (1936) Erosion Silt as a Factor in Aquatic Environments. *Ecology* **17**(1), 29-42.

490

491 Extence, C.A., Balbi, D.M., and Chadd, R.P. (1999) River flow indexing using British benthic

492 macroinvertebrates: a framework for setting hydroecological objectives. *Regulated Rivers:*  
493 *Research & Management* **15**, 543-574.

494

495 Extence, C.A., Chadd, R.P., England, J., Dunbar, M.J., Wood, P.J., and Taylor, E.D. (2013) The  
496 assessment of fine sediment accumulation in rivers using macroinvertebrate community  
497 response. *River Research and Applications* **29**(1), 17-55.

498

499 Findlay, S., and Sinsabaugh, R.L. (1999) Unravelling the sources and bioavailability of dissolved  
500 organic matter in lotic aquatic ecosystems. *Marine and Freshwater Research* **50**(8), 781-790.

501

502 Gibson, R.J. (2002) The effects of fluvial processes and habitat heterogeneity on distribution, growth  
503 and densities of juvenile Atlantic salmon (*Salmo salar* L.), with consequences on abundance of  
504 the adult fish. *Ecology of Freshwater Fish* **11**(4), 207-222.

505

506 Gjerløv, C., Hildrew, A.G., and Iwan Jones, J. (2003) Mobility of stream invertebrates in relation to  
507 disturbance and refugia: a test of habitat templet theory. *Journal of the North American*  
508 *Benthological Society* **22**(2), 207-223.

509

510 Growns, I., Chessman, B., Mitrovic, S., and Westhorpe, D. (2014) The effects of dams on longitudinal  
511 variation in river food webs. *Journal of Freshwater Ecology* **29**(1), 69-83.

512

513 Harris, R.M.L. (2006) The Effect of Experimental Drought Disturbance on Macroinvertebrate  
514 Assemblages in Stream Mesocosms. University of Birmingham, Birmingham, U.K.

515

516 Hart, D.D., Biggs, B.J.F., Nikora, V.I., and Flinders, C.A. (2013) Flow effects on periphyton patches  
517 and their ecological consequences in a New Zealand river. *Freshwater Biology* **58**(8), 1588-  
518 1602.

519

520 Jones, I., Grown, I., Arnold, A., McCall, S., and Bowes, M. (2015) The effects of increased flow and  
521 fine sediment on hyporheic invertebrates and nutrients in stream mesocosms. *Freshwater*  
522 *Biology* **60**(4), 813-826.

523

524 Jones, J.I., Murphy, J.F., Collins, A.L., Sear, D.A., Naden, P.S., and Armitage, P.D. (2012) The  
525 Impact of Fine Sediment on Macro-Invertebrates. *River Research and Applications* **28**(8),  
526 1055-1071.

527

528 Kaufmann, P.R., Larsen, D.P., and Faustini, J.M. (2009) Bed Stability and Sedimentation Associated  
529 With Human Disturbances in Pacific Northwest Streams<sup>1</sup>. *JAWRA Journal of the American*  
530 *Water Resources Association* **45**(2), 434-459.

531

532 Kefford, B.J., Zaluzniak, L., Dunlop, J.E., Nuggeoda, D., and Choy, S.C. (2010) How are  
533 macroinvertebrates of slow flowing lotic systems directly affected by suspended and deposited  
534 sediments? *Environmental pollution (Barking, Essex : 1987)* **158**(2), 543-550.

535

536 Kemp, P., Sear, D., Collins, A., Naden, P., and Jones, I. (2011) The impacts of fine sediment on  
537 riverine fish. *Hydrological Processes* **25**(11), 1800-1821.

538

539 Lancaster, J., and Downes, B.J. (2010) Linking the hydraulic world of individual organisms to  
540 ecological processes: Putting ecology into ecohydraulics. *River Research and Applications*  
541 **26**(4), 385-403.

542

543 Larned, S.T., Arscott, D.B., Schmidt, J., and Diettrich, J.C. (2010) A Framework for Analyzing  
544 Longitudinal and Temporal Variation in River Flow and Developing Flow-Ecology  
545 Relationships<sup>1</sup>. *Journal of the American Water Resources Association* **46**(3), 541-553.

546

547 Ledger, M.E., Harris, R.M., Milner, A.M., and Armitage, P.D. (2006) Disturbance, biological legacies

548 and community development in stream mesocosms. *Oecologia* **148**(4), 682-691.

549

550 Ledger, M.E., Harris, R.M.L., Armitage, P.D., and Milner, A.M. (2008) Realism of model  
551 ecosystems: an evaluation of physicochemistry and macroinvertebrate assemblages in artificial  
552 streams. *Hydrobiologia* **617**(1), 91-99.

553

554 Ledger, M.E., and Hildrew, A.G. (2001) Recolonization by the benthos of an acid stream following a  
555 drought. *Archiv für Hydrobiologie* **152**(1), 1-17.

556

557 Marsh, T., and Hannaford, J. (2008) UK hydrometric register. *Hydrological data UK series. Centre*  
558 *for Ecology and Hydrology, Wallingford, UK*, 1-210.

559

560 Matthaei, C.D., Piggott, J.J., and Townsend, C.R. (2010) Multiple stressors in agricultural streams:  
561 interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of*  
562 *Applied Ecology* **47**(3), 639-649.

563

564 Menéndez, M., Descals, E., Riera, T., and Moya, O. (2012) Effect of small reservoirs on leaf litter  
565 decomposition in Mediterranean headwater streams. *Hydrobiologia* **691**(1), 135-146.

566

567 Mürle, U., Ortlepp, J., and Zahner, M. (2003) Effects of experimental flooding on riverine  
568 morphology, structure and riparian vegetation: The River Spöl, Swiss National Park. *Aquatic*  
569 *Sciences* **65**(3), 191-198.

570

571 Murphy, J.F., Davy-Bowker, J., McFarland, B., and Ormerod, S.J. (2013) A diagnostic biotic index  
572 for assessing acidity in sensitive streams in Britain. *Ecological Indicators* **24**(0), 562-572.

573

574 Nilsson, C., Reidy, C.A., Dynesius, M., and Revenga, C. (2005) Fragmentation and Flow Regulation  
575 of the World's Large River Systems. *Science* **308**(5720), 405-408.

576

577 Office of National Statistics (2014) Annual mid-year population estimates, 2013. In: Statistical  
578 Bulletin. Office of National Statistics, Newport UK.

579

580 Olsen, D.A., Matthaei, C.D., and Townsend, C.R. (2010) Effects of a depositional flood event on the  
581 hyporheos of a New Zealand stream. *Fundamental and Applied Limnology / Archiv für*  
582 *Hydrobiologie* **176**(4), 337-348.

583

584 Palmer, M.A., Filoso, S., and Fanelli, R.M. (2014) From ecosystems to ecosystem services: Stream  
585 restoration as ecological engineering. *Ecological Engineering* **65**, 62-70.

586

587 Peckarsky, B.L. (1991) Habitat selection by stream-dwelling predatory stoneflies. *Canadian Journal*  
588 *of Fisheries and Aquatic Sciences* **48**, 1069-1076.

589

590 Poff, N.L., and Zimmerman, J.K.H. (2010) Ecological responses to altered flow regimes: a literature  
591 review to inform the science and management of environmental flows. *Freshwater Biology*  
592 **55**(1), 194-205.

593

594 Reid, M.A., Thoms, M.C., and Dyer, F.J. (2006) Effects of spatial and temporal variation in hydraulic  
595 conditions on metabolism in cobble biofilm communities in an Australian upland stream.  
596 *Journal of the North American Benthological Society* **25**(4), 756-767.

597

598 Ruiz-Gonzalez, C., Proia, L., Ferrera, I., Gasol, J.M., and Sabater, S. (2013) Effects of large river dam  
599 regulation on bacterioplankton community structure. *Fems Microbiology Ecology* **84**(2), 316-  
600 331.

601

602 Sagnes, P., Merigoux, S., and Peru, N. (2008) Hydraulic habitat use with respect to body size of  
603 aquatic insect larvae: Case of six species from a French Mediterranean type stream.

604 *Limnologica* **38**(1), 23-33.

605

606 Sarriquet, P.E., Bordenave, P., and Marmonier, P. (2007) Effects of bottom sediment restoration on  
607 interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater  
608 stream. *River Research and Applications* **23**(8), 815-828.

609

610 Tachet, H., Bournaud, M., Richoux, P., and Usseglio-Polatera, P. (2000) 'Invertébrés d'eau douce :  
611 systématique, biologie, écologie.' (CNRS Editions: Paris)

612

613 Vadher, A.N., Stubbington, R., and Wood, P.J. (2015) Fine sediment reduces vertical migrations of  
614 *Gammarus pulex* (Crustacea: Amphipoda) in response to surface water loss. *Hydrobiologia*, 1-  
615 11.

616

617 Wagenhoff, A., Townsend, C.R., and Matthaei, C.D. (2012) Macroinvertebrate responses along broad  
618 stressor gradients of deposited fine sediment and dissolved nutrients: a stream mesocosm  
619 experiment. *Journal of Applied Ecology* **49**(4), 892-902.

620

621 Ward, J.V., and Stanford, J.A. (1979) Ecological factors controlling stream zoobenthos with emphasis  
622 on thermal modification of regulated streams. In *The ecology of regulated streams*. (Eds. JV  
623 Ward and JA Stanford) pp. 35-55. (Plenum Press: New York)

624

625 Williams, D., and Smith, M. (1996) Colonization dynamics of river benthos in response to local  
626 changes in bed characteristics. *Freshwater Biology* **36**(2), 237-248.

627

628 Wood, P.J., Toone, J., Greenwood, M.T., and Armitage, P.D. (2005) The response of four lotic  
629 macroinvertebrate taxa to burial by sediments. *Archiv für Hydrobiologie - Hauptbände* **163**(2),  
630 145-162.

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Table 1. Effect of experimental treatments on physico-chemical variables and macroinvertebrate richness, density, community and trait assemblage structure. Pseudo-*F* values and probability levels given for each source of variance in PERMANOVA models. The percent variance explained by each significant term is given in parentheses after the significance level. Degrees of freedom for biotic variables are given in parentheses.

Source of variation	Degrees of freedom	Electrical conductivity	pH	Temperature	Richness	Density	Community assemblage structure	Trait assemblage structure
Sediment type (ST)	1 (1)	ns	48 <sup>***</sup> (5%)	ns	14.6 <sup>***</sup> (14%)	19.7 <sup>***</sup> (29%)	3.5 <sup>***</sup> (4%)	4.7 <sup>***</sup> (4%)
Sampling occasion (SO)	13 (1)	1218 <sup>***</sup> (90%)	54 <sup>***</sup> (46%)	221 <sup>***</sup> (93%)	15.0 <sup>***</sup> (12%)	ns	33.3 <sup>***</sup> (35%)	49.7 <sup>***</sup> (49%)
Flow scenario (FS)	3 (3)	ns	ns	ns	6.8 <sup>***</sup> (12%)	ns	4.7 <sup>***</sup> (11%)	13.7 <sup>***</sup> (13.8%)
ST x SO	13 (1)	ns	18 <sup>***</sup> (29%)	ns	ns	ns	ns	ns
ST x FS	3 (3)	ns	ns	ns	ns	ns	ns	ns
SO x FS	39 (3)	ns	ns	ns	7.9 <sup>***</sup> (25%)	ns	4.4 <sup>***</sup> (15%)	3.8 <sup>***</sup> (11%)
SO x ST x FS	39 (3)	ns	ns	ns	ns	ns	ns	ns
Channel(FS x ST)	16 (16)	ns	ns	ns	ns	ns	ns	ns
Planned contrasts								
Time 1								
(FF,FS) vs (SS,SF)	1				31.7 <sup>***</sup>		18.0 <sup>***</sup>	13.1 <sup>***</sup>
(SS) v (SF)	1				ns		ns	ns
(FF) v (FS)	1				ns		ns	ns
Time 2								
(FF,SF) vs (SS,FS)	1				9.1 <sup>**</sup>		11.1 <sup>***</sup>	9.4 <sup>***</sup>
(SS) v (FS)	1				ns		2.9 <sup>*</sup>	3.3 <sup>*</sup>
(FF) v (SF)	1				ns		1.9 <sup>*</sup>	4.5 <sup>*</sup>

ns – not significant, \*\*\* -  $p < 0.001$ , \*\* -  $p < 0.01$ , \* -  $p < 0.05$ , FF – Fast/fast flow scenario, FS – Fast/slow, SS – Slow/slow, SF – Slow/fact.

Table 2 Macroinvertebrate biological traits used with their associated trait classes.

Trait	Trait-Class	Abbreviation
Maximal potential size	≤ .25 cm	MaxS_25cm
	> .25-.5 cm	MaxS_5cm
	> .5-1 cm	MaxS_1cm
	> 1-2 cm	MaxS_2cm
	> 2-4 cm	MaxS_4cm
	> 4-8 cm	MaxS_8cm
	> 8 cm	MaxSm8cm
Potential number of cycles per year	< 1	Pcyc_lt1
	1	Pcyc_1
	> 1	Pcyc_gt1
Reproduction	ovoviviparity	Repr_ovo
	isolated eggs, free	Repr_ief
	isolated eggs, cemented	Repr_iec
	clutches, cemented or fixed	Repr_ccf
	clutches, free	Repr_cfr
	clutches, in vegetation	Repr_cvg
	clutches, terrestrial	Repr_ctr
	asexual reproduction	Repr_asr
	parthenogenesis	Repr_par
Resistance forms	eggs, statoblasts	Rest_egg
	cocoons	Rest_coc
	housings against desiccation	Rest_hou
	diapause or dormancy	Rest_dia
	none	Rest_non
Respiration	tegument	Resp_teg
	gill	Resp_gil
	plastron	Resp_pla
	spiracle	Resp_spi
Locomotion and substrate relation	flier	Loco_fli
	surface swimmer	Loco_ssw
	full water swimmer	Loco_swi
	crawler	Loco_crw
	burrower	Loco_bur
	interstitial	Loco_int
	temporarily attached	Loco_tpa
	permanently attached	Loco_pat
Food	microorganisms	Food_mio
	detritus (< 1mm)	Food_det
	dead plant (>= 1mm)	Food_dep
	living microphytes	Food_mip
	living macrophytes	Food_map
	dead animal (>= 1mm)	Food_dea
	living microinvertebrates	Food_mii
	living macroinvertebrates	Food_mai
	vertebrates	Food_vrt

## Supporting Information

Table S1. Pseudo- $F$  values and probability levels for pairwise PERMANOVA comparisons of flow scenarios at Day 30 and Day 70.

Flow scenarios	Day 30	Day 70
FF vs. SS	2.5**	2.4**
FF vs. FS	ns	2.8**
FF vs. SF	2.4**	ns
SS vs. FS	2.5**	1.7**
SS vs. SF	ns	1.9**
FS vs. SF	2.5**	2.9**

FF – Fast/fast flow scenario, FS – Fast/slow, SS – Slow/slow, SF – Slow/fact.

Table S2. SIMPER results of macroinvertebrate taxa and trait-classes contributing to differences (Bray-Curtis distance) between flow scenarios. . Codes for trait-classes are explained in Table 2.

Variable	Mean density in fast flows	Mean density in slow flows	Dissimilarity ratio	Cumulative percentage
<u>Taxon</u>				
Day 30				
Athericidae	0.64	0.03	3.12	4.85
Baetidae	0.65	0.06	2.23	9.60
Dytiscidae	0.14	0.62	1.63	13.69
EphemereIIDae	0.69	0.20	3.36	17.54
Day 70				
Hydropsychidae	0.65	0.03	2.10	4.99
Baetidae	0.56	0.10	2.08	8.75
Hydroptilidae	0.45	0.00	1.09	12.45
Polycentropodidae	0.47	0.04	1.29	15.94
Leuctridae	0.52	0.61	1.24	19.38
<u>Trait</u>				
	Mean prevalence in fast flows	Mean prevalence in slow flows		
Day 30				
MaxS_1cm	0.40	0.34	1.04	8.39
Pcyc_gt1	0.51	0.56	0.99	15.61
Repr_cfr	0.19	0.23	1.06	22.36
Day 70				
Repr_ccf	0.32	0.26	1.04	13.78
MaxS_1cm	0.36	0.29	1.32	24.99

Table S3. SIMPER results of macroinvertebrate taxa and trait-classes contributing to differences (Bray-Curtis distance) between sediment types. Codes for trait-classes are explained in Table 2.

Variable	Mean density in clean sediment	Mean density in experimentally colmated sediment	Dissimilarity ratio	Cumulative percentage
<b>Taxon</b>				
Leuctridae	0.37	0.49	1.27	3.1
Ephemeraidae	0.31	0.34	1.20	6.0
Dytiscidae	0.36	0.24	1.14	8.9
Baetidae	0.26	0.42	1.28	11.6
Hirudinea	0.32	0.15	1.00	14.3
Hydracarina	0.46	0.26	1.40	17.0
Caenidae	0.33	0.27	1.20	19.6
<b>Trait</b>				
	Mean prevalence in clean sediment	Mean prevalence in experimentally colmated sediment		
Pcyc_gt1	0.483	0.502	0.84	11.05
Repr_ccf	0.295	0.265	0.80	18.09
MaxS_1cm	0.34	0.359	0.78	24.58

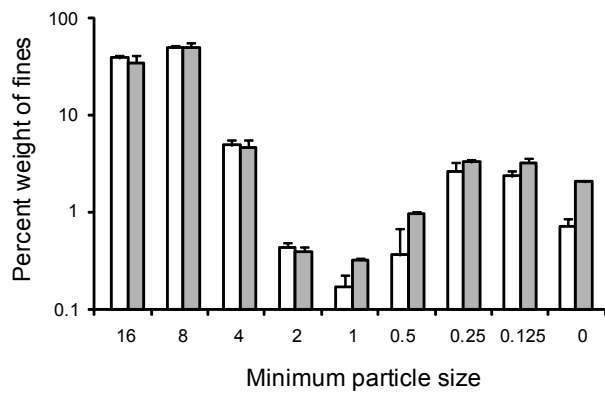


Figure 1. Mean percentage weight ( $\pm 1$  S.E.) of bed sediment particles among sizes classes for sediment loaded into mesocosms at Day 0. White columns indicate clean sediment and grey columns sediment with fine sediment added.

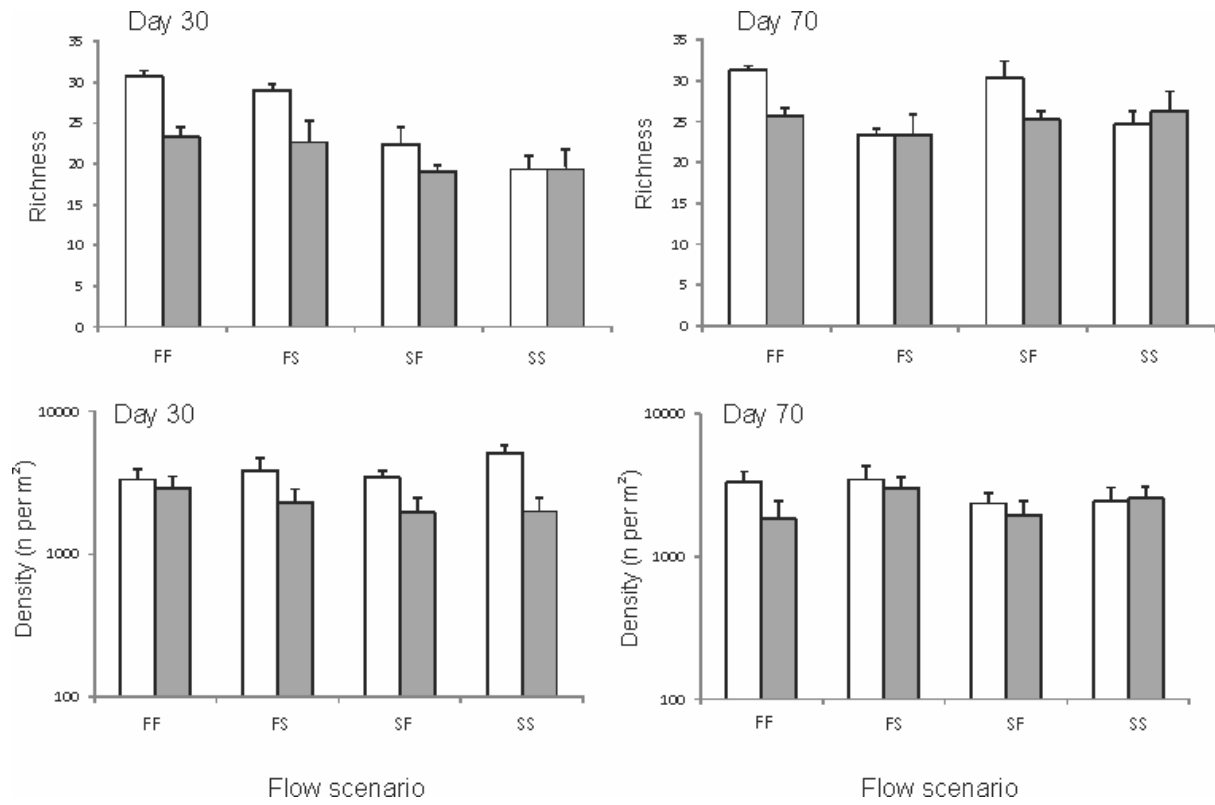


Figure 2. Mean macroinvertebrate richness and density ( $\pm 1$  S.E.) at Day 30 and 70 in four flow scenarios. White columns indicate clean sediment and grey columns experimentally colmated sediment.



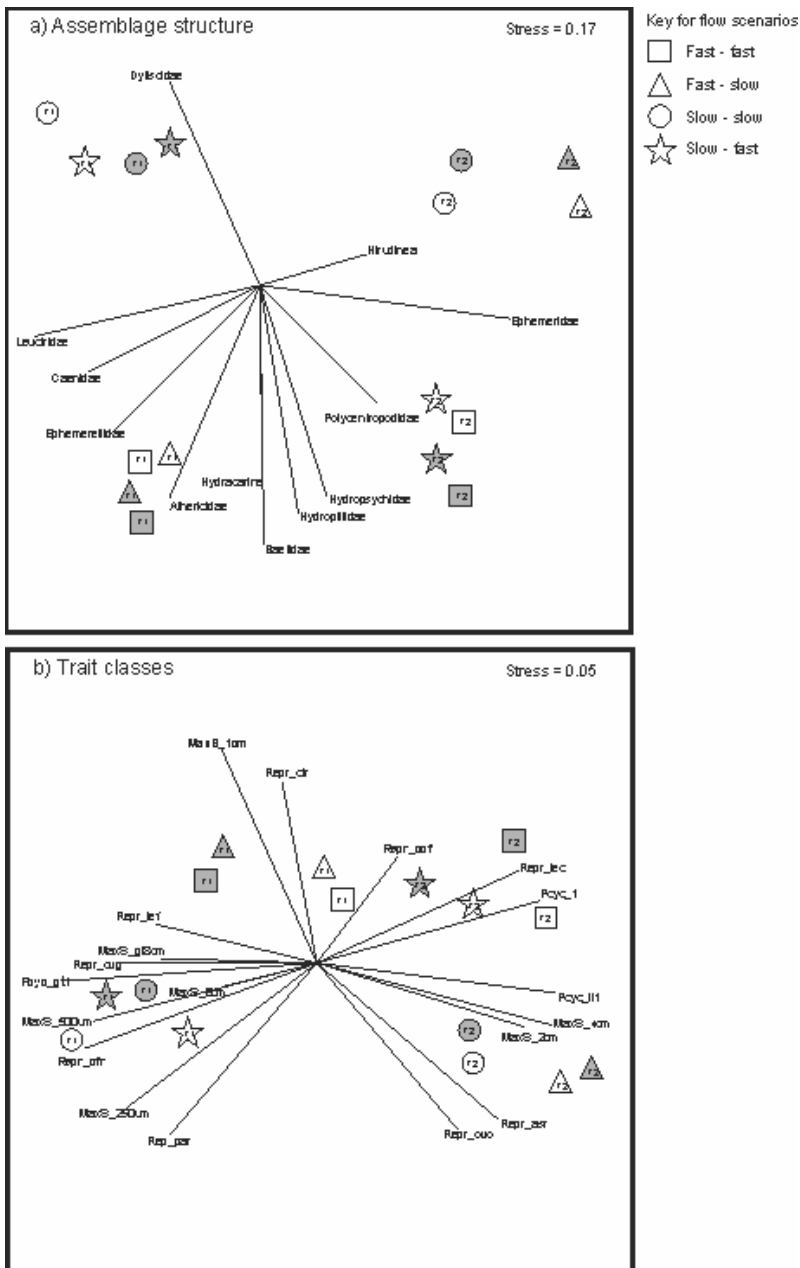


Figure 3. Ordination of centroids of (a) macroinvertebrate community assemblages and (b) trait assemblages from different flow scenarios at day 30 (T1) and day 70 (T2). White symbols indicate clean sediment and grey symbols experimentally colmated sediment. Macroinvertebrate (a) taxa and (b) trait-classes that best discriminated between the different experimental treatments are included with the direction and relative length from the origin of each line indicating its association with each of the treatment centroids.