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Limited impacts of experimental flow releases on water quality and macroinvertebrate community composition in an upland regulated river

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Running title: Impacts of experimental flow releases

Abstract

River regulation following the construction of dams has affected the hydrology, water quality and biology of watercourses across the globe. The term 'environmental flows' has been used to describe measures which can be employed to return some lost elements of the natural flow regime. Their introduction has been suggested as a way to mitigate the impacts of river regulation throughout the world but understanding of the effects of artificial high flows on water quality and biota is limited for many different river types. We report a field study which manipulated compensation flows from reservoirs in the Pennine uplands of northern England, and measured changes in water quality and benthic macroinvertebrates using a before-after-control-impact approach. These resulted in minor short-term changes in water quality but there was no evidence of immediate (within 48 hours) responses by the macroinvertebrate community to individual flow releases. However, a shift in macroinvertebrate community composition was found after multiple releases, characterised by reductions in *Amphinemura sulcicollis* (Plecoptera) and *Baetis rhodani* (Ephemeroptera) and changes in the density of all Diptera. The introduction of short-term flow pulses in flashy regulated river systems is unlikely to yield significant changes in water quality and biota. Nevertheless, cumulative rather than single environmental flow events show promise for mitigating some of the impacts of river regulation. More widely, our findings indicate that environmental flow releases from reservoirs may have to go beyond occasional experimental high flow releases if these rivers are to more closely mimic unregulated river systems.

Keywords: water quality; macroinvertebrates; reservoir; regulated rivers; LIFE scores; Water Framework Directive (WFD); environmental flows.

1. Introduction

River regulation is globally ubiquitous (Nillson et al., 2005; Lehner et al., 2011) and it has been estimated that >60% of the world's freshwater flows are obstructed by dams (Petts, 1985; McCully, 1996; Grill et al., 2019). Furthermore, 3,700 dams are either planned or under construction, which will result in a further reduction in the occurrence of free-flowing rivers c. 21% (Zarfl, 2015). Considerable evidence demonstrating the impacts of damming of rivers on downstream hydrological, water quality and ecological characteristics is available (Petts, 1985; Poff & Zimmerman, 2010; Maavara et al., 2017). A major focus now is in understanding how to mitigate such impacts, both to avoid further/ ongoing environmental degradation and to meet legislative targets such as those embedded in the EU Water Framework Directive (WFD) (EC, 2000) or the US Clean Water Act (1972) (Acreman and Ferguson, 2010; Arthington et al., 2018).

Contemporary environmental legislation requires that regulated rivers meet targets based on abiotic and biotic aspects of river ecosystems. A reconsideration of how regulated flow regimes are managed can potentially mitigate impacts associated with dams, thereby meeting these targets (Acreman & Ferguson, 2010; Acreman et al., 2014). However, before management practices can be implemented, an understanding of the relationship between regulated river flow management and ecosystem response must be established (Gillespie et al., 2015). Flow experiments (FEs) are one tool which can be used to establish such relationships (Konrad et al., 2011; Olden et al., 2014; Gillespie et al., 2015). An accepted definition of FEs is yet to emerge in the literature, but we define FEs as any prescribed modification of the flow regime of a regulated river system for which river ecosystem responses are measured. This definition can encapsulate such terms as environmental flows and artificial floods, and includes modifications such as increases or decreases in flow magnitude/ duration and change in reservoir draw off valve height.

There is currently no consensus on the effects of FEs on water quality variables in rivers (Gillespie et al., 2015), with equivocal change in river dissolved oxygen (DO), temperature (T) and electrical conductivity (EC) observed during FEs (Table 1). Water quality changes can impact benthic macroinvertebrate communities, which play important functional roles (nutrient cycling, productivity, decomposition rates and movement of materials) in rivers (Wallace & Webster, 1996). They also serve as a crucial food web link between basal resources and higher aquatic organisms such as birds and mammals, and are an important component of river ecology monitoring programmes as they respond differentially to environmental pressures (Metcalfe, 1989). The monitoring of macroinvertebrate responses to FEs is therefore undertaken regularly and a general consensus in response is emerging from the global literature: macroinvertebrate abundance, richness, diversity and the abundance of Ephemeroptera typically decrease post-FE (e.g. Pardo et al., 1998; Harby et al., 2001; Cereghino et al., 2004; Robinson et al., 2004a; Mannes et al., 2008). Despite this, impacts in regulated streams in the UK uplands, where many reservoirs exist, remain poorly understood.

Many UK upland catchments are dominated by moorland, relatively low temperatures and high precipitation, resulting in hydrologically 'flashy' streams (Hope et al., 1997; Neal et al., 2010; Ramchunder et al., 2011). Where dammed, they also tend to exhibit antiquated infrastructure unsuitable for meeting the demands of contemporary legislation (e.g. reservoirs have manually operated outflows and physical and safety restraints on release flow characteristics (e.g. magnitude). Some reservoirs are also now far below their original capacities due to sedimentation (Labadz et al., 1991) resulting in frequent overspill events (Gustard, 1989). The combination of these hydrological factors is likely to mean that macroinvertebrate communities in these systems are resilient to dynamic flow regimes and already exposed to them. The introduction of environmental flows truncated in magnitude due to infrastructure limitations and similar to normal compensation flows are unlikely to result in major shifts in macroinvertebrate community composition. However, whilst it may be logistically difficult to generate individual flow events of a large enough magnitude to elicit ecosystem change, multiple disturbances may provide cumulative effects on river ecosystems (Robinson et al., 2004, 2018). These hypotheses need to be tested given the emphasis of current legislation on introducing environmental flows in regulated river systems, and the large financial investments being made in compliance with such legislation (e.g. £7.6m between 2015 and 2020 by Yorkshire Water (Yorkshire Water, 2013)).

This paper addresses the research gaps outlined above by reporting responses of river EC, DO, pH, temperature and macroinvertebrates to FEs in upland regulated rivers. The aims of the study were to: (i) identify any impacts of these FEs on downstream water quality and macroinvertebrates and, (ii) assess the potential for the use of FEs for managing water quality and macroinvertebrate communities.

2. Materials and Methods

2.1 Experimental Design

The study area was located within the south Pennines, UK (Figure 1) and was characterised predominantly by peat surface geology (BGS, 2012) and low forest and semi-natural land cover (CORINE, 2010) (Table 2). Average annual rainfall for the study area is approximately 1,200mm (Evans et al., 2006) and four reservoirs are located here. Widdop reservoir was constructed in the late 19th century whilst building of the chain of three Walshaw Dean reservoirs was finalised in 1907 (Tedd & Hoton, 1994). The dams of the Walshaw Dean reservoirs are tallest at 24m although Widdop reservoir has the greatest maximum capacity (c. 2.9 million m^3). The smallest capacity is at Walshaw Dean Lower reservoir (c. 0.7 million m^3) (Tedd & Hoton, 1994). Both Widdop and Walshaw Dean Lower reservoirs are used exclusively for water supply and no hydroelectric or recreational activities are associated with either. Typically, both reservoirs provide seasonally variable deep-release (i.e. hypolimnetic) compensation flows (Widdop: 0.04 & 0.15 m^3s^{-1}; Figure 2; Walshaw Dean Lower: 0.04 & 0.17 m^3s^{-1}, between January 1st - October 31st and November 1st - December 31st, respectively). The seasonally variable element of these compensation flow regimes was introduced in 2006 to better replicate a natural flow regime. To enable objective assessments of ecosystem response to each FE, a paired site approach was taken whereby experimental 'impact' (I) sites were paired with 'control' (C) sites. Sites were located downstream of Widdop (impact) and Walshaw Dean Lower (control) reservoir, at between 253 and 307 m aod. FEs were made from Widdop reservoir, and so sites *Iu*, *Im* and *Il* (Impact upper, middle and lower, respectively) were established downstream of this reservoir to record ecosystem response during FEs (Figure 1). These sites were paired with three *C* sites: *Cu*, *Cm* and *Cl* downstream of Walshaw Dean Lower reservoir where typical reservoir operation remained unchanged for the duration of the study. Water quality data were collected from all six sites whilst macroinvertebrate sampling was undertaken at *Im* and *Cm* only. Geological and land cover characteristics of the drainage basins of paired *I* and *C* sites were approximately similar (Table 2). Long-term flow data recorded at *Iu* demonstrated the generally dynamic nature of the flow regime (Figure 2) which was driven by regular overspill events. Long-term flow data for comparable sites downstream of Walshaw Dean Lower reservoir were not available.

2.2 Flow Experiments

Four FEs were carried out by reservoir operational staff (FE 1-4 respectively, Table 3). The peak magnitude of each FE was maximised within the practical restrictions placed on the reservoir operator (Yorkshire Water Services Limited (YWSL) by the Environment Agency (EA), local stakeholders, water resource availability and the capability of reservoir infrastructure. However, in comparison to reservoir overspill events, peak magnitudes of FEs were unexceptional and this may actually negate the need for flow releases in flashy upland catchments or limit their ability to bring about ecological change (Figure 2).

2.3 Water Level and River Discharge

To characterise the water quality dynamics of rivers during each FE, discharge data (recording frequency: 15 min.) were provided by YWSL for *Iu* (Flow meter: Warren Jones Ultra Sonic, WJ440).

At *Cu*, YWSL did not record discharge and a SEBA Hydrometrie MDS Dipper-3(T3) vented water level data logger (recording frequency: 15 min.) was therefore installed in a stilling basin at a permanent weir located ~20 m upstream of *Cu*. Ratings ($y = 15.45\ x^{1.49}$; $R^2 = 1$) were obtained from a water level-discharge rating curve constructed from a rating table for water level and discharge at *Cu* (YWSL, unpublished data). These coefficients were then used to calculate discharge from logged water level. Water level was also recorded at sites *Im* and *Il* (using SEBA loggers as above), but discharge data were not collected.

2.4 Water Quality

To examine river water quality responses to FEs, EC, pH and DO (% saturation) were recorded at 15 min intervals using a YSI 6560 probe (accuracy: ±0.5 % of reading + 1 $\mu S\ cm^{-1}$ (YSI, 2005)), a 6-series pH probe (accuracy: ±0.2 units (YSI, 2011)) and a 6150 ROX ® Optical Dissolved Oxygen 6-series probe (accuracy: ±1 % of reading or 1 % air saturation (whichever is greatest) (YSI, 2008)), respectively. Probes were installed on YSI 6600 V2-2 sondes fitted with a protective shield and automated wiping brush to reduce fouling, and installed at *Iu* and *Cu* for each FE (±24 hours). Prior to each deployment, each probe was calibrated by the EA against known standards and sound functioning checked once deployed. Each sonde was located in a well-mixed location of the river to enable comparison between sites and data were transmitted using GRPS to a dedicated website maintained by Meteor Communications (Europe) Limited. River temperature was recorded at 15 min intervals before (>12 hours) and during each FE using a combination of Gemini Tinytag Aquatic 2 data loggers and a SEBA Hydrometrie MDS Dipper-3(T3) (manufacturer stated accuracies ± 0.5 and ± 0.1 ºC, respectively). During deployment, cross-calibration of the latter probe to Gemini Tinytag Aquatic 2 data loggers was undertaken across a range of temperatures to ensure comparability ($y = 1\ x + 0.04$; $R^2 = 1$). Each sensor was shielded from direct sunlight and internal clocks synchronised prior to deployment. T sensors were secured in well-mixed locations within the rivers.

2.5 Benthic Macroinvertebrate Response

To assess the impact of FEs on macroinvertebrate populations, five replicate 0.05 m^2 Surber samples (250 µm mesh) were collected randomly from riffle habitat at *Im* and *Cm* within 48 hours before and after each FE. Riffles were sampled to ensure directly comparable responses between impacted and control rivers using common sampling methods, although it is acknowledged that responses in other types of mesohabitats may differ from those studied here. Sampling was undertaken relatively soon after each FE to detect any immediate changes as result of increased hydraulic stresses, bed movement and invertebrate drift, and before significant levels of recovery could potentially occur, although our design also enabled longer-term responses to be assessed across the full FE programme. All samples were preserved immediately in 70 % methanol and were then sieved, removing fine particles to aid sorting, employing Protocol P3 (full count) without subsampling as described by Stark et al. (2001). Individuals were counted and identified to species level using a light microscope (x50 magnification) with the exception of Chironomidae (family); Oligochaeta (sub-class) and Sphaeriidae (genus).

2.6 Data Analysis

2.6.1 Quality control procedures

Data quality was first ensured using a similar approach to Jones & Graziano (2013) whereby removal of data occurred if any of the following standards were met (which were assumed to indicate probe/ logger malfunction): EC: < 10 or > 300 µS cm^{-1}; doubled or halved in a 15 min period; pH: < 3 or > 8; doubled or halved in a 15 min period ; DO: < 20 or > 150 % saturation; doubled or halved in a 15 min period; T: < -1 or > 35 ºC; air temperature: < -10 or > 35 ºC; discharge and water level: doubled or halved within a 15 min period. Data were also assessed visually for drift and probe failure/malfunction and neither approach resulted in data removal.

2.6.2 Statistical testing

R Studio was used for all statistical analyses. To assess the impact of each FE on river water quality properties, a modified paired Before-After-Control-Impact (BACIP) (Stewart-Oaten et al., 1986; Smith, 2002) analysis was undertaken which replaced 'After' with 'During' (e.g. Dinger & Marks, 2007) to allow the during-FE impact to be assessed statistically through interrogation of a modelled interaction term (Smith, 2002). For each FE, response variables (raw water quality data) were modelled using GAMM (Wood, 2011) with Gaussian distribution specified, as a function of *time* (fitted as a smoother), *site* (two levels: experimental (*Iu*, *Im* & *Il*) and paired control (*Cu*, *Cm* & *Cl* respectively)) and *period* (two levels: ‘before’ and ‘during’) and the interaction between these two factors ($site * period$). ‘Before’ was defined as all data from 00:00:00 until the start of each FE and ‘during’ was defined by the start and end times of each FE. Significance of the $site * period$ interaction term was assessed using t-statistics and associated p-values.

Prior to macroinvertebrate data analysis, the commonly used biomonitoring indices taxonomic richness, dominance and 1/Simpson's diversity index (e.g. Ramchunder et al., 2012), BMWP, ASPT and LIFE (AQEM, 2011), species level PSI (Extence et al., 2013) and the recently adopted WHPT system (Paisley et al., 2007) were calculated for each Surber sample. Additionally, 'global' β-diversity (Whittaker, 1972) was calculated following Brown et al. (2007) to allow for a novel assessment of the response of β-diversity to FEs. Furthermore, total number of individuals, Coleoptera, Diptera, Ephemeroptera, Plecoptera and Trichoptera were estimated per m^2 for comparison with previous studies which suggested that these taxa show responses to river regulation (e.g. Armitage, 1978; Gillespie et al., 2015a).

To assess macroinvertebrate response to FEs (both individual and cumulative), indices for Surber samples at *Im* and *Cm* for each sampling date before and after each FE were modelled using GLMM (Wood, 2013), model selection being made by minimising Akaike's An Information Criterion. Modelling used the formula: $bi = \alpha + \beta\ site * period + \ \varepsilon$ where *bi* = biotic index, α = regression intercept, β = regression coefficient, $site * period$ was the interaction term between factors *site* (replicate coded for each site) and *period* (before or after each FE (to test the effect of individual FEs) or before or after the first and last FE respectively (to test the effect of cumulative FEs)) and ε = model error. Replicate sample number (for macroinvertebrate analyses) was incorporated into models as a random effect. Negative binomial distribution was specified for all count data, and Gaussian distributions for all other metrics. Significance of the $site * period$ interaction term was examined using t-statistics and p-values to provide an indication of whether an impact had occurred.

To further assess macroinvertebrate response, composition of macroinvertebrate assemblages before and after each FE were visualised using the results of a 2-dimensional NMDS undertaken on means of replicates taken before and after each FE at each site. The analysis was based on Bray-Curtis dissimilarities of $Log_{10}(n+1)$ taxa abundance (Oksansen et al., 2013). Moreover, to test similarity of macroinvertebrate community composition before and after each individual FE and all FEs, $site * period$ interaction terms were tested using multivariate analysis of variance (MANOVA) on taxon abundance matrices of replicates from each site using 999 permutations and Bray-Curtis dissimilarities (Oksansen et al., 2013). All statistical tests were deemed significant at $p < 0.05$ and all plot creation and statistical analyses were undertaken using R v 3.2.3 (2016).

3. Results

3.1 Water quality response

The largest range in EC was observed during FEs 3 and 4 but was very small (6 µS cm^{-1}), mean EC decreased at *Iu* during all FEs, but statistically significant impacts were observed only for FEs 2 and 4 (Table 4; Figure 3). Mean DO response to each FE varied: statistically significant impacts were only observed during FEs 2 and 4 (Table 4), where small (<10 % saturation) reductions in DO occurred at *Iu* (Figure 3). Statistically significant reductions in pH were observed during FE 2 and 4, but the largest range in pH during either of these FEs was small at 0.41 during FE2 (Table 4; Figure 3).

Mean river temperature before and during each FE was highest for FE1 and lowest for FE4 for all sites (Table 4). A general diurnal trend in T was observed on each FE day at all sites, although this trend appeared to be suppressed at sites *Iu* and *Cu* (immediately downstream of Widdop and Walshaw Dean Lower reservoirs respectively) (Figure 3). During FEs, minor increases (< 0.5 °C) in T were observed at experimental cf. control sites, resulting in statistically significant impacts at sites closest and furthest from the reservoir during FEs 2 and 4, respectively (Table 4).

3.2 Response of benthic macroinvertebrates

Non-significant interaction terms were identified for the majority of statistical tests (Table 5). Where tests indicated that an impact had occurred to macroinvertebrate indices at *Im*, mean changes were generally small: 1/ S (-1.5 during FE 2), D: (+0.1 during FE 2), Ephemeroptera (-140 individuals/m^2 during FE 2 and +16 during FE 4). For comparison, mean total density across all samples was 738 individuals/m^2 (Figures 4 and 5).

Throughout the period of FE implementation, NMDS axis 1 and 2 scores for site *Im* were generally lower and higher, respectively, than for site *Cm*, although the direction of change was not the same after each FE (Figure 6). Temporally, NMDS scores at both sites were characterised by generally increasing axis 1 scores throughout the series of FEs, but this increase was delayed at site *Im* until after FE 3. The magnitude of changes in composition after each FE were similar at both sites (Figure 6). Changes in NMDS scores at site C*m* represented shifts from populations characterised by taxa such as *Rhyacophila dorsalis* and *Amphinemura sulcicollis* to *Isoperla grammatica* and *Plectrocnemia conspersa*. At *Im* the macroinvertebrate assemblage was initially characterised by taxa such as Simuliidae and *Leuctra* sp. Subsequently, species such as *Elmis aenea* and *Leuctra inermis* became increasingly prevalent (Figure 6). A significant effect of cumulative FEs was observed for *Baetis rhodani* and *A. sulcicollis* as well as the density of all Diptera (Table 5).

4. Discussion

In response to legislative pressures (e.g. the EU WFD, Australian Water Resources Act (2007)) environmental flows (manipulation of reservoir releases to the downstream channel to more closely resemble natural flows) are being used widely in attempts to improve or restore river water quality and ecological properties (Gillespie et al., 2015; Stein et al., 2017; Arthington et al., 2018). However, the evidence for impacts of such flow modification is limited and remains largely equivocal (Gillespie et al., 2015b; Robinson et al., 2018). This paper has provided novel information on ecosystem responses to a series of FEs in an upland UK catchment. Some impacts on downstream EC, DO, pH and macroinvertebrates were identified, but responses were not consistent between FEs, limited in magnitude and likely to be of little ecological significance.

4.1 Water quality response to flow experiments

There is currently a requirement to understand the potential for FEs to be used to mitigate impacts associated with regulated systems to meet legislative goals (Acreman & Ferguson, 2010), for example, Good Ecological Potential under the EU WFD (European Commission, 2015). Evidence that minor changes in water quality occurred was found, but, none of the changes were large enough in magnitude, or sustained post FE, to suggest that FEs in the UK uplands would be useful as management tools with the aim of invoking a major ecosystem response.

EC was found to have a broadly inverse relationship with discharge during each FE, but the largest fall in EC was only 6 $\mu S\ cm^{-1}$ and pre-FE concentrations were returned to immediately after each FE. In contrast, previous studies have observed complex, spatially and temporally variable impacts of FEs on EC. For example, Petts et al. (1985) observed an initial reduction (prior to peak discharge) followed by a rise in EC after peak discharge on a larger river in the UK. This relationship was thought to depend on in-channel sources of solutes. Foulger & Petts (1984) also highlighted the potential importance of in-channel sources in determining EC response to FEs. The most upstream site in the impact stream (*Iu)* in this study was relatively close to the outlet of the reservoir and therefore sources of solutes were limited and unlikely to be a major influence on EC during FEs.

This potentially explains the apparent simple, minor dilution effect observed in the majority of the FEs. Under normal compensation flow conditions EC is likely to increase due to factors such as increased water residence time and exposure to mineral substrate in the river channel. It is hypothesised that during FEs the influence of such processes was reduced due to faster travel time between the reservoir outflow and *Iu*, resulting in lower EC. Future work could aim to determine whether biogeochemical processes (e.g. suppressed groundwater interaction) are drivers of such responses.

In contrast to the findings of most other studies which noted increased DO during FEs (e.g. Shannon et al., 2001; Bednarek & Hart, 2005, Naliato et al., 2009), this study found evidence of minor (<10 % saturation) reductions in DO. Naliato et al. (2009) also observed reductions in DO during FEs and linked these instances to reservoir stratification. Stratification of a reservoir can result in the development of a hypolimnetic layer of relatively low DO water (Petts, 1985). If water is drawn from this layer during an FE but from higher in the water column before, DO may decline. Water prior to and during each FE reported on in this study was drawn from the same valve (which was located at the bottom of the dam wall of Widdop reservoir) and therefore a modification in valves during reservoir stratification cannot explain the observations noted. The changes in DO observed are likely to be either due to modification of physical-chemical processes such as aeration rates (e.g. Butts et al., 1989) or biotic processes such as production/respiration in the reservoir water column as hypothesised by Chung et al. (2008) or a combination of factors. However, given that DO did not change to within a range where biological effects would be expected (e.g. Kramer, 1987) and was not consistent between FEs, any mechanisms were clearly minor in influence and temporally variable. A more in-depth assessment of physical-chemical and biological processes (e.g. respiration), extended both temporally and longitudinally, may shed more light on the processes involved.

The impact of FEs on pH had not previously been assessed prior to this study (Gillespie et al., 2015), and therefore the observations of reduced pH in each FE, albeit minor, give this observation particular importance. The observed reductions in pH may be either due to a reduction in stilling basin residence time (and therefore interaction with buffering substrate), increased carbonic acid formation due to increased aeration during FEs, disruption of biological processes, or a combination of the aforementioned (Glaser et al., 1990; Morrison et al., 2001). However, given the minimal changes in pH and lack of increased solute concentration during FEs (see McCahon and Pascoe, 1989 for discussion of importance of solute concentrations in determining ecological impact during reduced river pH), ecological impacts would be unlikely.

This study found very little evidence of impacts of FEs on river water temperature at any of three sites within 2 km downstream of the experimental reservoir. Where statistically significant effects were identified, temperature change at the impact site was not outside of the accuracy of the probes and can therefore be disregarded. In agreement with the findings of this study, King et al. (1998) (South Africa) and Robinson et al. (2004) (Switzerland) both reported no change in river temperature during FEs. Both studies suggested that this was due to pre-FE and FE water being hypolimnetic in origin and this likely explains the observations in our study. It is therefore plausible that, for FEs to have a notable impact on river water temperature in the study area, the draw off level of water from the water column must be modified from pre-FE conditions. Dickson et al. (2012) showed that water derived from the upper water column raised water temperature in cold alpine rivers, although these findings were due to unplanned flow magnitude increases linked to reservoir overspill effects rather than FEs. Further research may enable comparison of pre-FE and FE relationships between river temperature response and hydrological indices which was not possible in the current study.

Our findings are useful in a river management context as they challenge the paradigm that increasing flows can always be an effective technique for restoring the ecological quality of regulated rivers, but some key research questions remain. For example, we know little about how these regulated systems respond to FEs of alternative characteristics (e.g. at alternative times of year, different hydrological characteristics) or how river EC, DO and pH respond longitudinally during FEs. Echoing the recommendations of Gillespie et al. (2015b), such questions should be prioritised for future research to enable informed management decisions to be made.

4.2 Benthic Macroinvertebrate Response to Flow Experiments

FEs have been shown to invoke change in downstream biotic assemblages in several studies from around the world (Gillespie et al., 2015b). This study is the first to assess specifically the impact of FEs on macroinvertebrate assemblage in an upland regulated river in the UK. In contrast with various published studies (e.g. Pardo et al., 1998; Harby et al., 2001; Cereghino et al., 2004; Robinson et al., 2004a; Mannes et al., 2008; Benítez-Mora & Camargo, 2014), this research did not reveal any major change in either traditional or recently adopted macroinvertebrate biomonitoring indices or in specific taxa as a result of individual FEs or all FEs combined. Some statistically significant impacts were identified, but effect sizes were typically small, suggesting that FEs had limited impact on the macroinvertebrate assemblage assessed, at least during the first 48 hours after FEs when effects were measured in the current study. In contrast, assessments of macroinvertebrate response to FEs globally have all revealed significant shifts in such measures (e.g. reduced total abundance (Robinson et al., 2003, 2018), taxonomic richness (Bednareck & Hart, 2005; Mannes et al., 2008), Ephemeroptera (Lauters et al., 1996; Harby et al., 2001) and Chironomidae (Robinson et al., 2004b)).

The macroinvertebrate response identified by this study may be a reflection of the characteristics of the macroinvertebrate assemblage (e.g. behaviour) within the study river cf. others where dramatic responses have been observed. Dynamic antecedent hydrological conditions in the study river may contribute to the presence of predominantly disturbance resistant/resilient assemblages (Monk et al., 2006; Durance & Ormerod, 2007; Gillespie et al., 2015a; White et al., 2017). These upland systems are characterised by relatively low pH, flashy flows and low productivity

(Ramchunder et al., 2009; Aspray et al., 2017), thus biological communities are necessarily adapted to these conditions. Combined with the fact that flow releases greater than those experienced due to reservoir overspill could not be achieved, these factors can explain the minor response in macroinvertebrates. If further evidence is found to support this theory, it will contribute towards management decisions for other regulated rivers where the implementation of extreme FEs is restricted, for example, in urban catchments where flooding is a concern, or where water resource availability is low.

Analyses of the overall taxonomic composition of the macroinvertebrate assemblage at the impact site revealed no statistically significant change as a result of individual FEs. Again, this finding is in contrast to published literature (e.g. Robinson et al., 2003) where individual FEs have resulted in clear shifts in taxonomic composition. However, of particular note was a statistically significant effect of the four FEs cumulatively, an effect which has been noted over multiple years for example in the Spöl river system in Switzerland (Robinson et al., 2018). This effect was driven primarily by reductions (relative to the control site) in *B. rhodani* and *A. sulcicollis* abundance and changes in the abundance of all Diptera at the impact site relative to the control site (Figure 7). This finding is particularly important as both taxa were highlighted as being associated with river regulation in a recent study on upland UK regulated rivers (Gillespie et al., 2014), suggesting that cumulative FEs may have the potential to mitigate for this association.

Given the very limited water quality impacts of the FEs in this study, we deduce that the response in *B. rhodani*, *A. sulcicollis* and Diptera was hydraulically driven. Mean density of *A. sulcicollis* remained approximately constant at the impact site, whereas it increased by c. 500% at the control site. Conversely, a decrease in *B. rhodani* mean density was observed at the impact site, whereas it remained approximately constant at the control site (Figure 7). For *Amphinemura,* this finding suggests that the FEs either had the ability to suppress population increasing behaviour (e.g. reproduction) of the extant population, or that they eliminated individuals at approximately the same rate as net increases to the population were being made (taking into account natural death, recruitment and migration rates for example). This seems unlikely as *Amphinemura* are typically well adapted to moderate-fast flow velocities that would be encountered during flow experiments (Extence et al., 1999), although bed sediments were entrained during the high flows likely causing additional stress. For *Baetis,* the reduction in abundance due to FEs most likely occurred because they are typically stone-surface-dwelling collector-gatherers, and will have involuntarily entered the drift during FEs despite being strong swimmers. Similar decreases for B. rhodani have been reported from rivers post-flooding in Spain (Pupilli and Puig, 2003). An alternative explanation is that these species are both largely detritivorous, and FEs are likely to have depleted standing stocks of particulate matter from the riverbed. Further studies that explicitly monitor population dynamics, behavioural responses and food availability would be needed to examine these hypotheses in more detail.

Our evidence suggests that *cumulative* rather than *single* FEs at study sites such as ours are the management tool with most promise. Further research to identify macroinvertebrate, other biological group (e.g. algae, macrophytes, fish) and geomorphological responses to both single and cumulative FEs in similar upland rivers is required to assess the validity and generality of this theory. A shift in taxonomic composition following several FEs is consistent with the literature (e.g. Robinson et al., 2004, 2018; Mannes et al., 2008), but it is important to note that the statistical design used in this study assumes that both control and impact sites are identical apart from the FE implementation (see Underwood (1994) and Conquest (2000) for discussion). Of course, in reality this is not true and other factors may play a role and these could change with time. We therefore suggest that further studies look to see whether this finding can be replicated at other similar sites.

Invertebrate response to these FEs was observed, although, importantly, we have provided evidence that *cumulative*, rather than *single* FEs may invoke invertebrate assemblage response.

Interestingly, widely used biomonitoring indices (i.e. taxonomic richness, BMWP, ASPT and WHPT which has now been adopted by UK regulatory agencies) failed to pick up on any invertebrate response. These findings support other regulated river studies that have suggested these indices may be unsuitable for use in these upland river environments (e.g. Gillespie et al., 2015a). The generality of our findings for water quality and invertebrate responses to FEs needs to be tested across other upland river systems.

5. Conclusions

The current study has indicated that managed high flow releases from reservoirs in flashy upland catchments are unlikely to bring about substantial changes in water quality and benthic macroinvertebrate communities. It was found that, despite being impounded, these streams experienced great variation in flow due to frequent overspill events and were already subject to regular disturbance. Moreover, environmental peak flows that could be released from these reservoirs were small in comparison to some prior overspill events. Whilst it is logistically impossible to conduct e-flow trials on all rivers, our suggestion that multiple small flow events may be more effective in bringing about ecological change than single releases should at least be verified in a handful of other locations to determine if Pennine region rivers can be assumed to show similar behaviours.

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Tables

Table 1: Publications evidencing increases, decreases or no change in electrical conductivity (EC), dissolved oxygen (DO) or water temperature (T) during Flow Experiments from reservoirs.

Table 2: Percentage surface geology and land cover composition of upper, middle and lower (u, m and l, respectively) impact (I) and control (C) sites and study area drainage basins (sources: BGS, 2012 & CORINE, 2010 respectively); altitude and catchment (source: OS, 2012).

Table 3: Hydrological characteristics of each Flow Experiment (FE) (measured at Iu). ROC = rate of change; statistics based on 15-min records from site Iu.

Table 4: Mean (& St. dev.) and test statistics (t) for electrical conductivity (EC) ($\mu S\ cm^{-1}$), dissolved oxygen (DO) (%), pH and river temperature (T) (°C) indices before and during FEs 1-4 for each site where measurements were taken. *$p < 0.05$, **$p < 0.01$.

Table 5: GLMM test statistics for impact of Flow Experiments (FEs) 1-4 on macroinvertebrate indices and community composition respectively. *$p < 0.05$, **$p < 0.01$. For FE1-4 we tested directly before vs after these experiments. For the overall response, data from before FE1 were compared to data collected after FE4. High resolution (e.g. sub-family) statistics are only shown where significant effects were identified. Mean and standard deviation of each taxon before and after each FE at Im and Cm are included in Table 1 *of the supplementary information.*

Table 1:

Parameter	Increase	Decrease	No change
EC	Foulger & Petts, 1984; Shannon et al., 2001; Bruno et al., 2010	Petts et al., 1985; Jakob et al., 2003; Cánovas et al., 2012	Cambray et al., 1997
DO	Shannon et al., 2001; Bednarek & Hart, 2005, Naliato et al., 2009	Chung et al., 2008; Naliato et al., 2009	
T	Cambray et al., 1997; King et al., 1998; Ashby et al., 1999; Lagarrigue et al., 2002; Chung et al., 2008; Naliato et al 2009	Foulger & Petts, 1984; Lagarrigue et al., 2002; Bruno et al., 2010	King et al., 1998; Robinson et al., 2004a

Table 2:

	Surface geology (%)	Land cover (%)				Altitude (m aod)	Catchment size (km^2)
	Mud/ silt/ sand-stone	Agricultural	Forests/semi-natural	Wetland	Waterbody		
Study area	42.90	16.10	41.20	40.70	2.00	n/a	40.66
Iu	48.00	0.00	62.30	25.90	11.80	307	3.09
Cu	20.2	1.80	26.00	67.30	4.90	289	9.05
Im	56.00	0.00	66.10	23.80	10.10	292	3.63
Cm	27.80	8.20	27.90	59.50	4.30	264	10.32
Il	34.90	4.40	40.50	51.70	3.50	271	10.50
Cl	31.20	11.60	28.30	56.10	4.00	253	11.09
Overall study area	42.90	16.10	41.20	40.70	2.00	n/a	40.66

Table 3:

FE	Duration (h)	Magnitude (% increase)	ROC (rising limb) ($m^3s^{-1}d^{-1}$)	ROC (falling limb) ($m^3s^{-1}d^{-1}$)	Max. discharge ($m^3 s^{-1}$)
1	4.8	287.10	1.61	1.07	0.17
2	2.64	424.39	8.39	3.15	0.31
3	2.88	294.02	9.95	7.13	0.67
4	3.12	423.85	11.39	13.24	0.99

N.B. water was drawn from valves at the bottom of the reservoir water column during all FEs.

Table 4:

	FE 1		FE 2		FE 3		FE 4	
	Before	During	Before	During	Before	During	Before	During
<u>EC</u>								
Iu	53.90	52.63	57.90	52.91	57.90	57.30	59.76	58.00
	(0.32)	(0.50)	(0.74)	(1.30)	(2.18)	(1.83)	(0.99)	(1.63)
Cu	74.50	75.00	72.00	72.00	71.00	71.00	56.29	56.00
	(0.53)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.46)	(0.00)
T	-0.88		7.84 **		0.84		-3.51 **	
<u>DO</u>								
Iu	103.45	103.93	97.30	96.97	96.25	97.23	95.83	96.09
	(1.39)	(1.80)	(0.30)	(0.94)	(0.18)	(0.46)	(0.13)	(0.89)
Cu	93.92	98.65	91.99	94.07	93.80	94.71	92.19	92.44
	(1.02)	(0.66)	(0.24)	(0.33)	(0.12)	(0.22)	(0.18)	(0.13)
T	0.69		-2.95 **		-1.80		-2.39 *	
<u>pH</u>								
Iu	5.75	5.62	6.06	5.76	5.61	5.58	4.99	4.87
	(0.01)	(0.05)	(0.04)	(0.15)	(0.02)	(0.02)	(0.02)	(0.13)
Cu	6.91	7.02	6.91	6.97	6.65	6.72	5.67	5.69
	(0.02)	(0.02)	(0.01)	(0.01)	(0.02)	(0.01)	(0.01)	(0.01)
T	-1.28		6.31 **		-0.14		-2.08 *	
<u>T</u>								
Iu	15.86	16.13	10.41	10.95	11.80	11.85	7.36	7.47
	(0.04)	(0.05)	(0.07)	(0.18)	(0.02)	(0.02)	(0.02)	(0.05)
Cu	15.34	15.77	10.35	10.54	12.11	12.29	7.26	7.33
	(0.09)	(0.10)	(0.03)	(0.07)	(0.02)	(0.07)	(0.01)	(0.02)
T	-0.50		1.83		1.77		2.23 *	
Im	14.34	16.03	9.91	10.74	11.80	11.99	7.13	7.36
	(0.35)	(0.38)	(0.05)	(0.24)	(0.03)	(0.05)	(0.04)	(0.05)
Cm	14.23	15.95	10.00	10.50	12.16	12.58	7.28	7.63
	(0.50)	(0.54)	(0.07)	(0.17)	(0.05)	(0.09)	(0.08)	(0.04)
T	-1.13		0.05		0.20		-1.16	
Il	13.22	15.93	9.70	10.46	11.83	12.23	6.97	7.52
	(0.49)	(0.91)	(0.05)	(0.38)	(0.06)	(0.10)	(0.15)	(0.07)
Cl	13.76	14.56	10.06	10.12	12.06	12.23	7.37	7.61
	(0.13)	(0.30)	(0.04)	(0.07)	(0.01)	(0.09)	(0.06)	(0.01)
T	-0.50		-2.58 *		0.55		0.27	

Table 5

	FE1	FE2	FE3	FE4	Before – After all FEs
Total density (ind. / m^2)	1.30	0.91	1.05	-0.39	-0.74
Taxonomic richness	0.79	0.43	0.81	-1.57	-0.16
1/Simpson's diversity index (1/S)	-0.48	2.21 *	-0.81	-0.77	-1.7
β –diversity	0.62	0.41	0.08	-0.12	0.73
Taxonomic dominance (D)	1.08	-2.13 *	0.55	0.24	-1.78
BMWP	0.50	0.14	2.09	-1.55	0.05
ASPT	0.23	-0.46	1.74	-1.11	-1.40
LIFE	-0.99	0.57	1.32	1.14	0.45
WHPT	1.10	0.21	-1.24	-0.02	1.55
Coleoptera	-0.24	-0.43	2.23 *	-0.68	-1.29
Diptera	1.46	-1.12	0.14	0.52	2.31 *
Chironomidae	1.99 *	-0.10	1.96	-1.03	-1.90
Simuliidae	0.33	1.99 *	-	-60.3	-1.74
Ephemeroptera	-3.68***	4.09 ***	-1.13	-3.01 ***	-1.12
Baetis sp.	-2.03*	2.97 ***	-0.16	-1.36	--0.35
Baetis rhodani	0.49	-3.86 ***	-0.54	-	2.71 **
Plecoptera	1.99*	-1.31	0.41	0.78	-0.83
Amphinemura sulcicollis	-1.73	-0.22	-	-0.20	2.48 *
Leuctra sp.	2.36 *	-	-1.52	-	0.90
Leuctra hippopus	2.41 *	--0.35	2.25 *	0.30	-0/94
Trichoptera	0.83	0.42	0.31	-1.35	0.27
Oligochaeta	0.51	--1.87	-	-	-

Figures

Figure 1: Location of the study area within Great Britain (inset), detailing rivers and reservoirs in black, study sites (impact (I) and control (C), upper (u), middle (m) and lower (l)), altitude (m AOD), urban areas and roads. Map data: Ordnance Survey (2015). Produced using QGIS (2015) & Gimp (2014).

Figure 2: Maximum daily discharge measured immediately upstream of Iu (March 2000-December 2014) (left) and January – December 2013 (right). The period and timing of Flow Experiments (FEs) is denoted by grey shading and arrows respectively.

Figure 3: Discharge/ water level (grey shading) and water quality observations before and during each Flow Experiment (FE) at impact (full lines) and control (dashed lines) sites where measurements were taken. Site locations for each parameter are denoted to the right: u = upper, m = middle, l = Lower).

Figure 4: Boxplots, mean and standard deviation of macroinvertebrate indices before (grey boxes) and after each Flow Experiment at impact and control sites (left and right column, respectively).

Figure 5: Boxplots, mean and standard deviation of macroinvertebrate community composition indices before (grey boxes) and after each Flow Experiment at impact and control sites (left and right column, respectively).

Figure 6: Panel A: NMDS plot for mean macroinvertebrate samples. Arrows show the direction of change in population composition before and after each Flow Experiment (FE) and from before FE1 to after FE4 at each site. Panel B: species NMDS scores. Note: taxa labels are abbreviated; full names can be found in Supplementary information A.

Figure 7: Interaction plot displaying mean density of Amphinemura sulcicollis (top) and Baetis rhodani (bottom) before Flow Experiment (FE) 1 and after FE4 at impact (Im) (solid line) and control (Cm) (dashed line) sites. X-axis offset error bars of ±1 standard deviation are shown for each point.

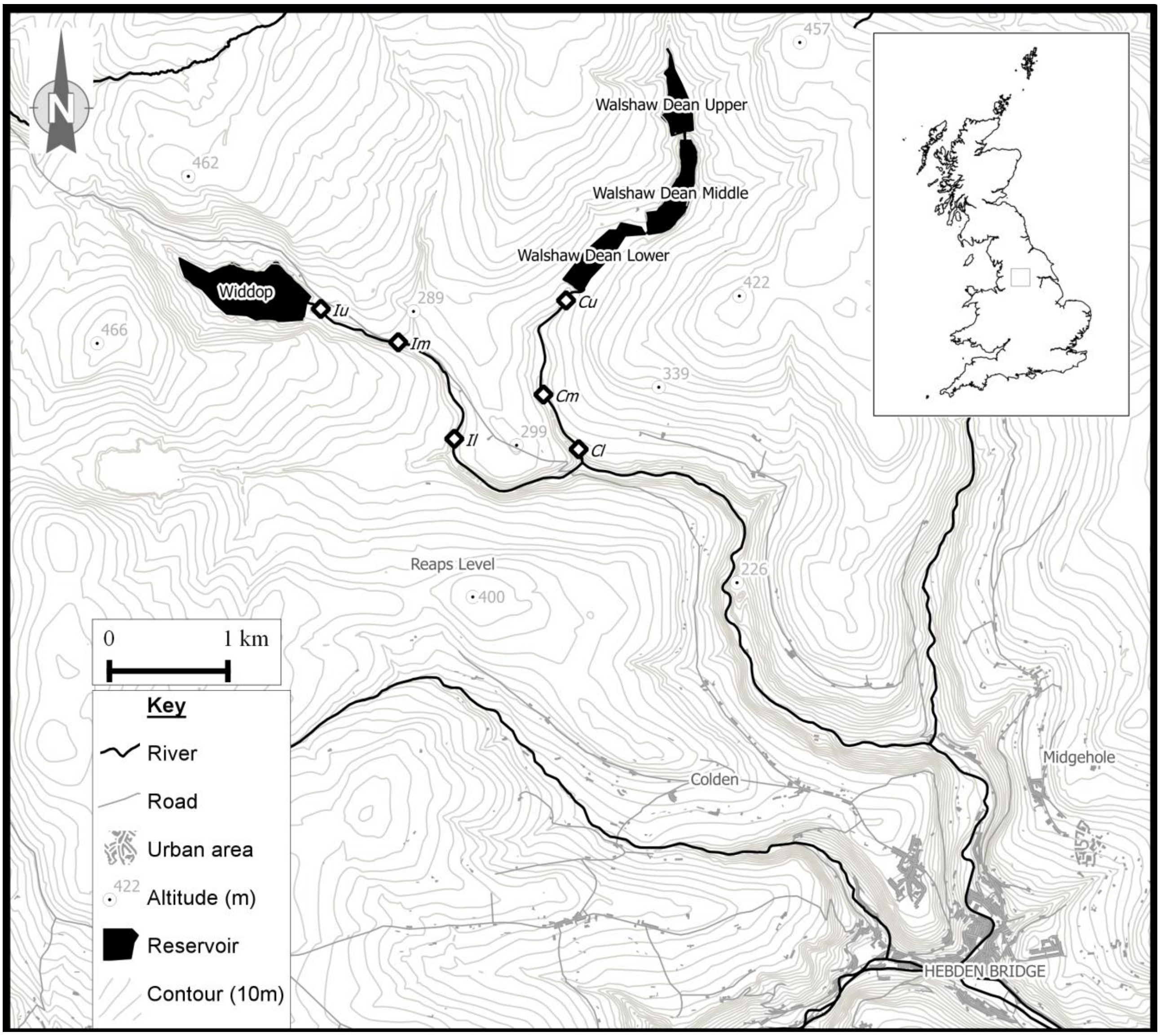

N
457
Walshaw Dean Upper
462
Walshaw Dean Middle
Walshaw Dean Lower
Widdop
Iu
Im
289
Cu
422
466
Cm
339
Il
299
Cl
Reaps Level
400
226
0
1 km
Key
River
Road
Urban area
422
Altitude (m)
Reservoir
Contour (10m)
Colden
Midgehole
HEBDEN BRIDGE

Figure 1:

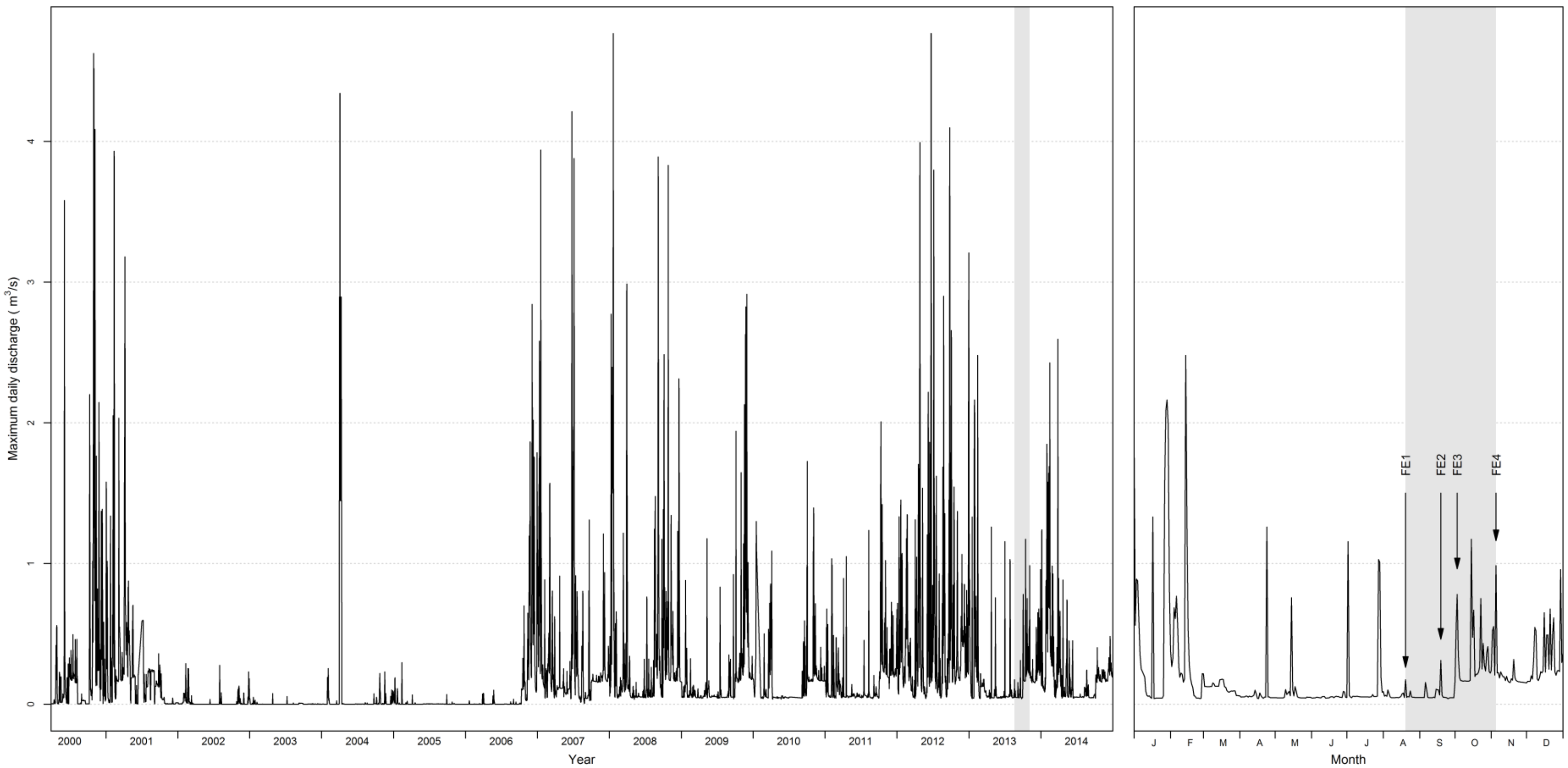

Maximum daily discharge (m³/s)
0
1
2
3
4
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
Year
FE1
FE2
FE3
FE4
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure 2:

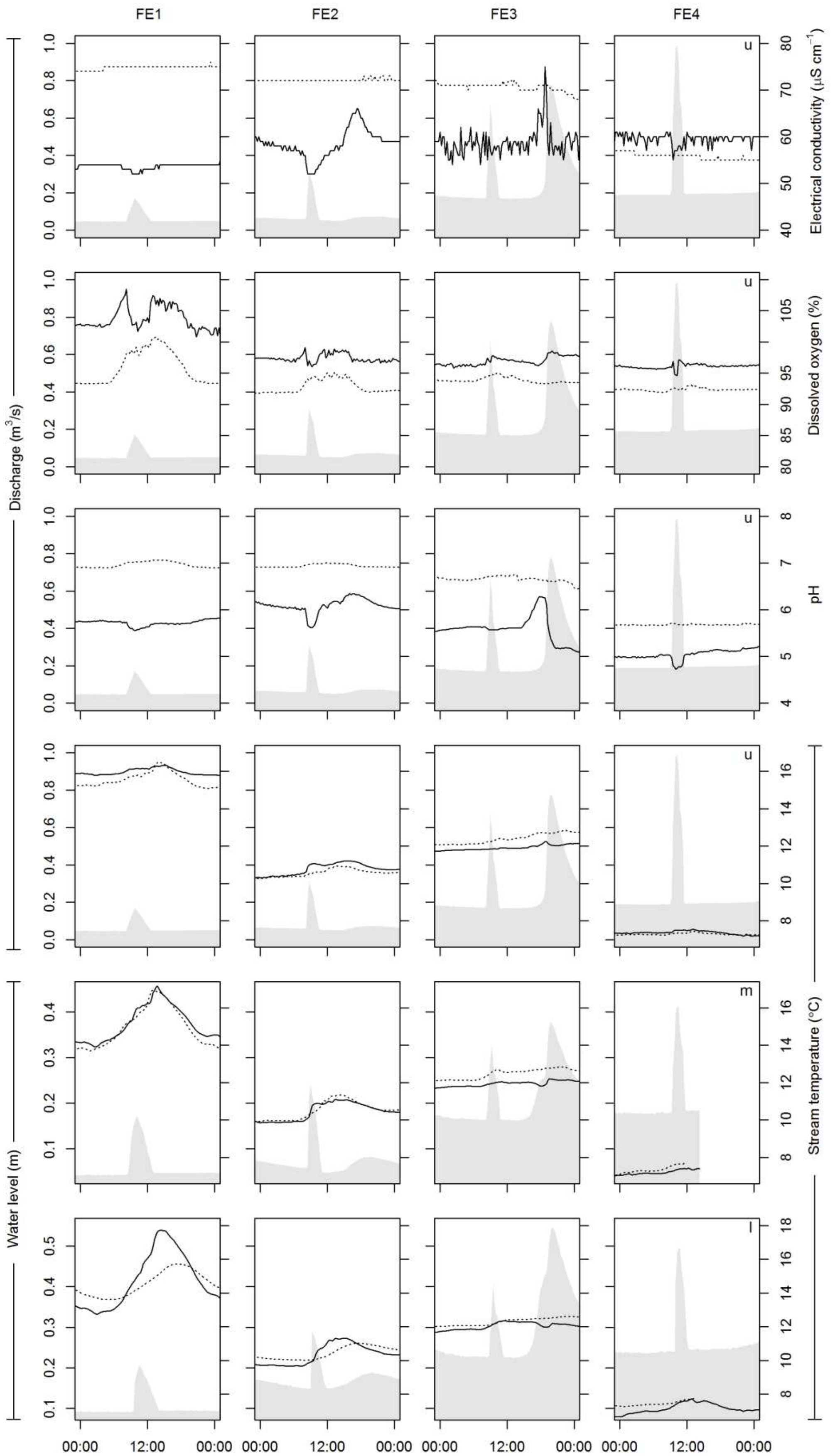

FE1
FE2
FE3
FE4
u
u
u
u
m
l
Discharge (m³/s)
Water level (m)
Electrical conductivity (µS cm⁻¹)
Dissolved oxygen (%)
pH
Stream temperature (°C)
00:00
12:00
00:00

Figure 3:

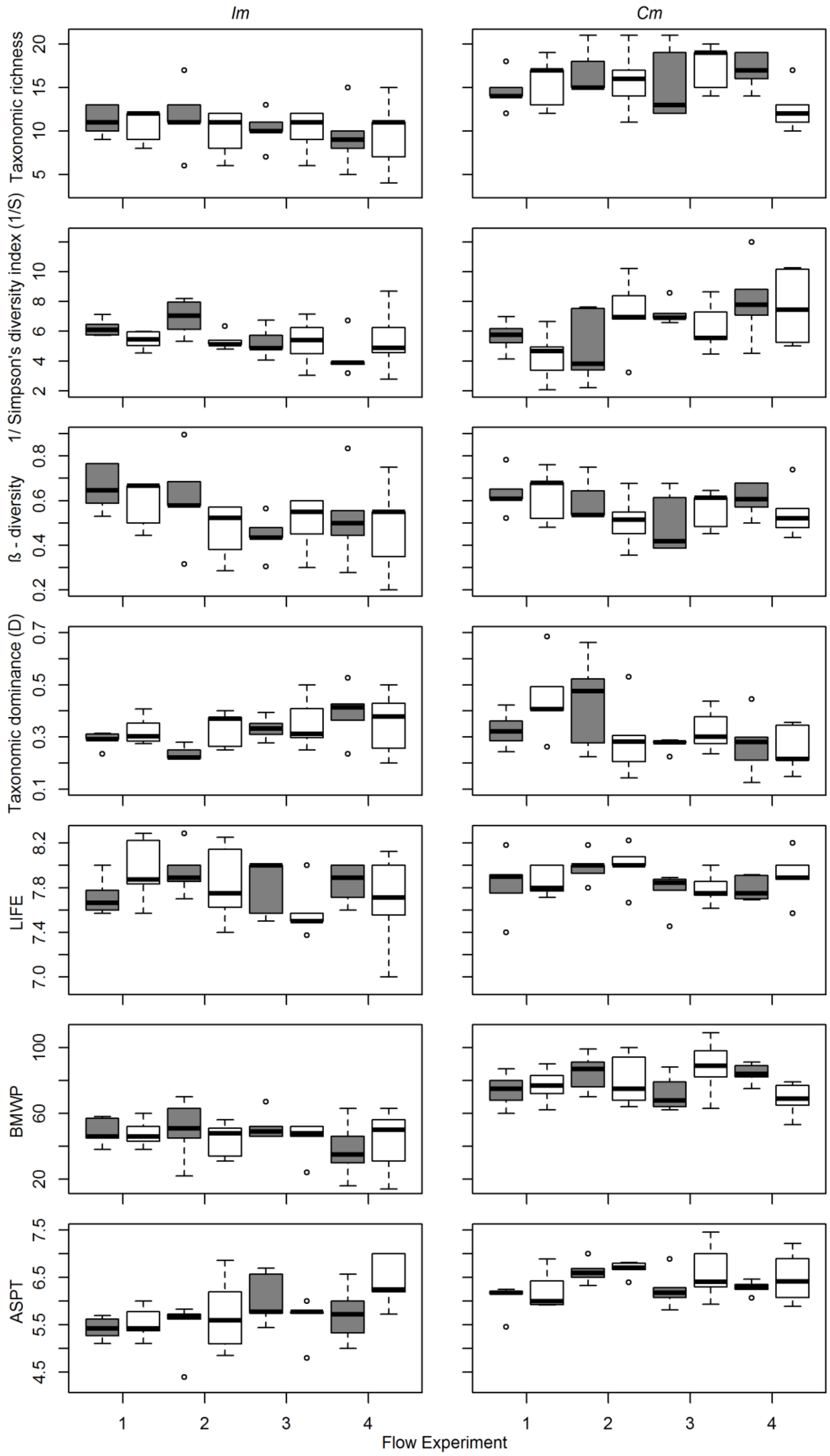

Im
Cm
Taxonomic richness
1/ Simpson's diversity index (1/S)
ß - diversity
Taxonomic dominance (D)
LIFE
BMWP
ASPT
Flow Experiment

Figure 4:

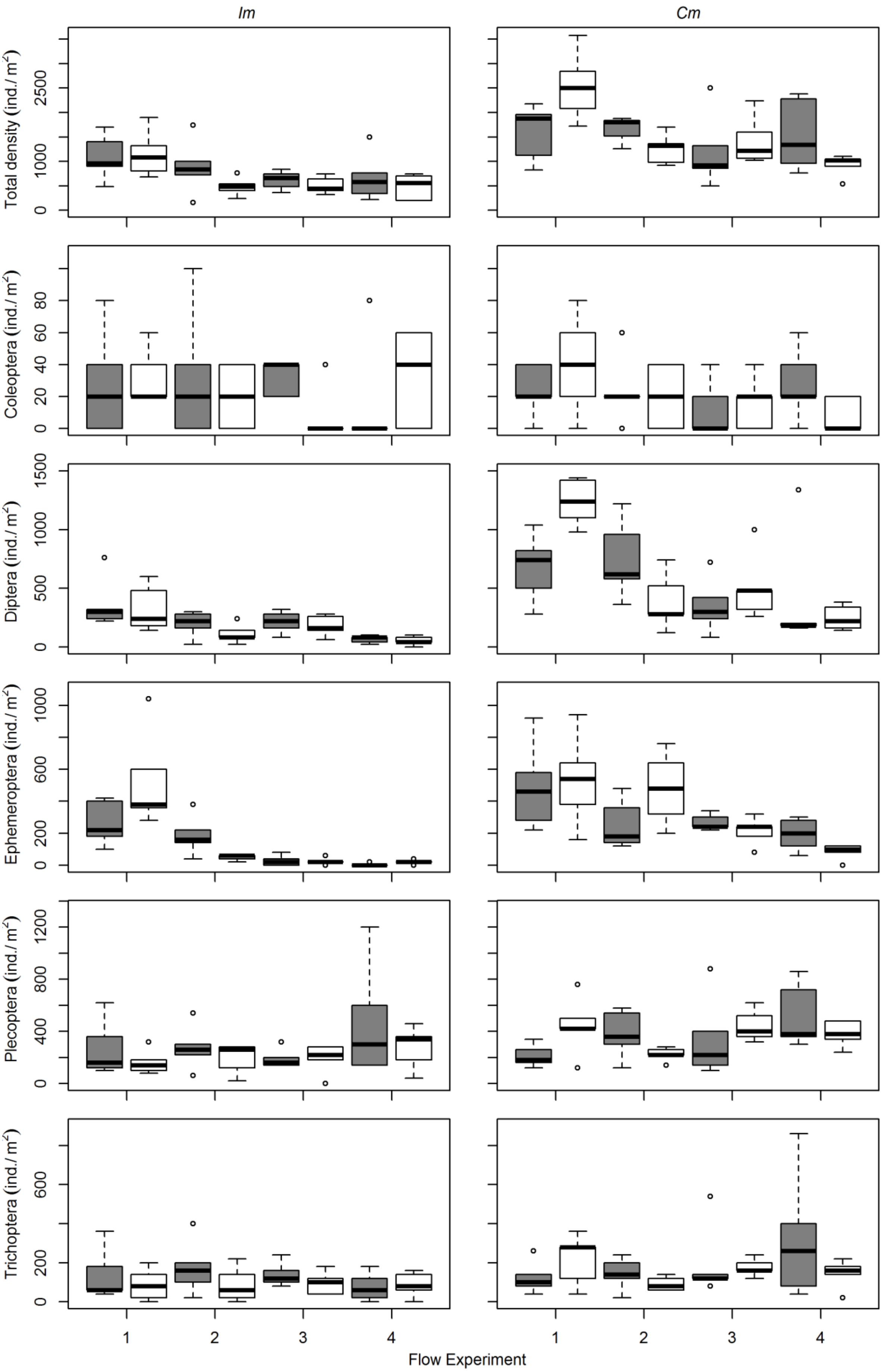
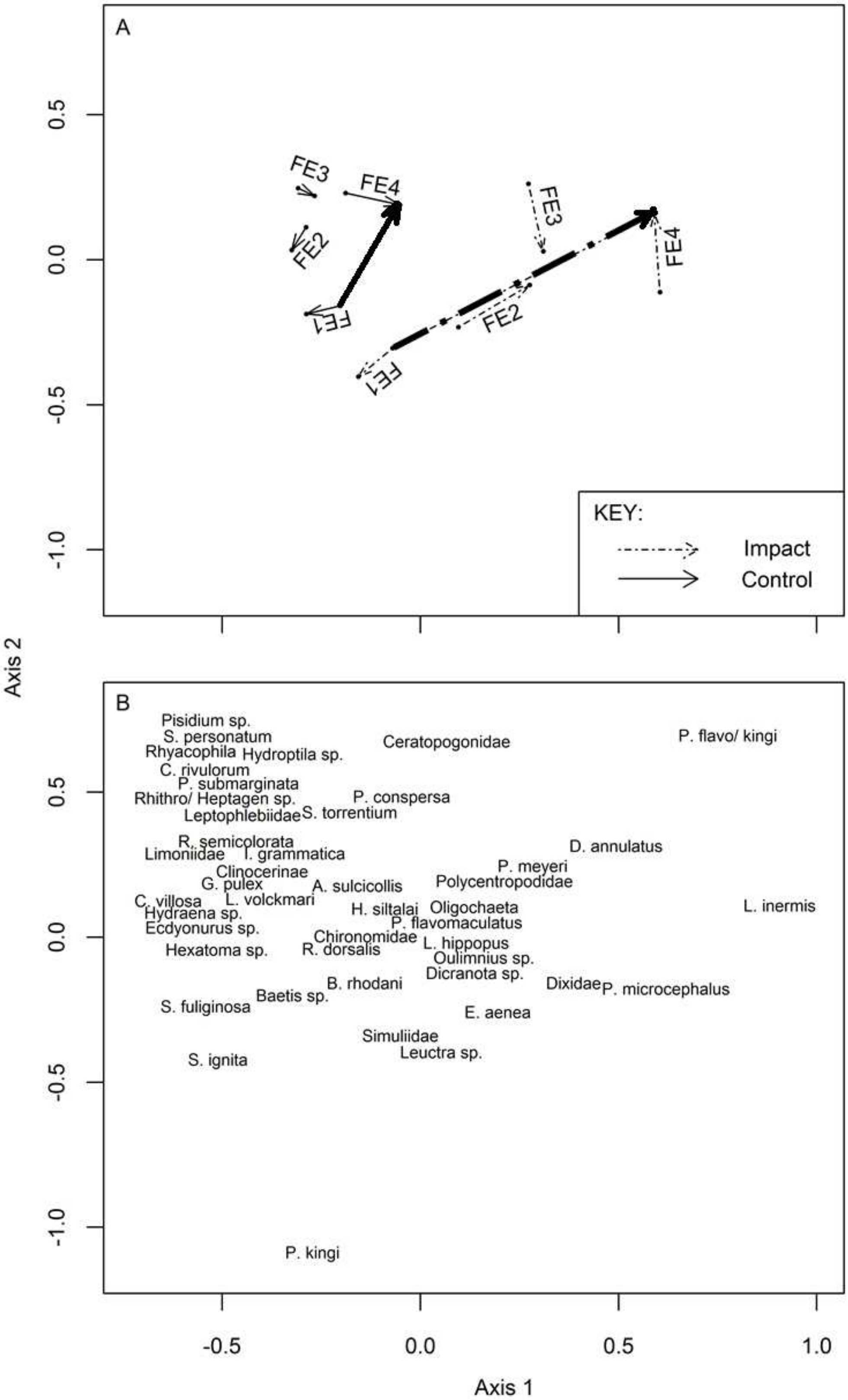

Im
Cm
Total density (ind./m²)
Coleoptera (ind./m²)
Diptera (ind./m²)
Ephemeroptera (ind./m²)
Plecoptera (ind./m²)
Trichoptera (ind./m²)
Flow Experiment
1
2
3
4

Figure 5:



754

755 Figure 6:

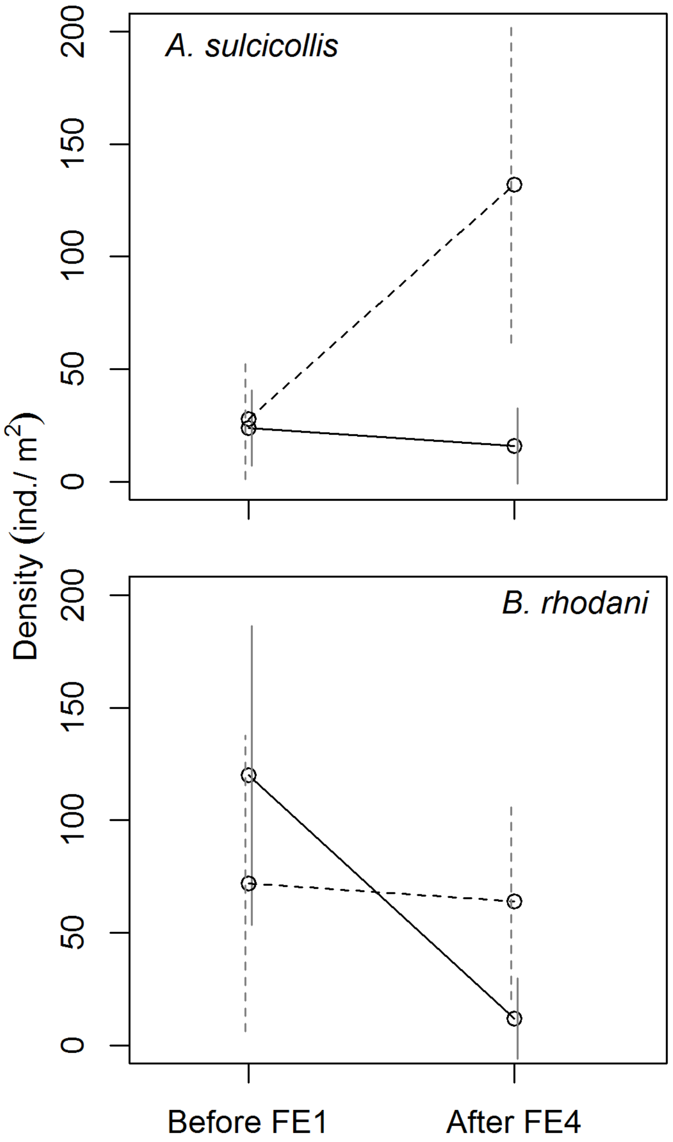

A. sulcicollis
B. rhodani
Density (ind./ m2)
0
50
100
150
200
Before FE1
After FE4

Figure 7: