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Macroinvertebrate community responses to river impoundment at multiple spatial scales

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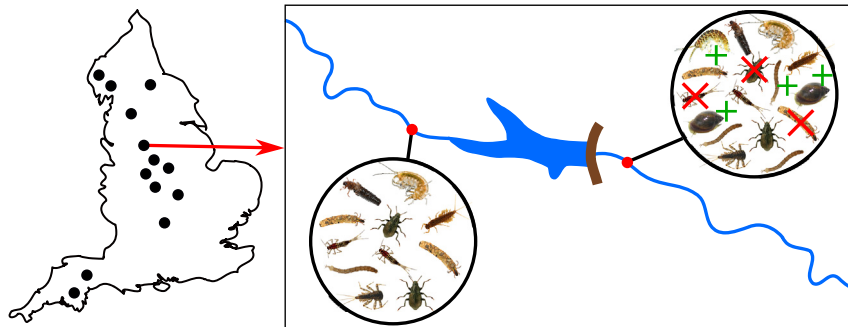
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HIGHLIGHTS

- Macroinvertebrate communities downstream of reservoirs differed from control sites.
- Community differences were detected at both the national and regional scales.
- Taxonomic richness was higher at impounded sites than control sites.
- Proportion of sensitive macroinvertebrate groups was lower downstream of reservoirs.
- Community differences were detected by macroinvertebrate biomonitoring indices.

GRAPHICAL ABSTRACT



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ABSTRACT

River impoundment by the construction of dams potentially modifies a wide range of abiotic and biotic factors in lotic ecosystems and is considered one of the most significant anthropogenic impacts on rivers globally. The past two decades have witnessed a growing body of research centred on quantifying the effects of river impoundment, with a focus on mitigating and managing the effects of individual large dams. This study presents a novel multi-scale comparison of paired downstream and control sites associated with multiple water supply reservoirs ($n = 80$) using a spatially extensive multi-year dataset. Macroinvertebrate community structure and indices were analysed in direct association with spatial (e.g. region) and temporal variables (e.g. season) to identify consistent patterns in ecological responses to impoundment. Macroinvertebrate communities at monitoring sites downstream of water supply reservoirs differed significantly from those at control sites at larger spatial scales, both in terms of community structure and taxa richness. The effect was most significant at the regional scale, while biogeographical factors appeared to be important drivers of community differences at the national scale. Water supply reservoirs dampened natural seasonal patterns in community structure at sites downstream of impoundments. Generally, taxonomic richness was higher and %EPT richness lower at downstream sites. Biomonitoring indices used for river management purposes were able to detect community differences, demonstrating their sensitivity to river regulation activities. The results presented improve our understanding of the spatially extensive and long-term effects of water supply reservoirs on instream communities and provide a basis for the future implementation of mitigation measures on impounded rivers and heavily modified waterbodies.

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1. Introduction

Streams and rivers are among the world's most threatened ecosystems (Malmqvist and Rundle, 2002; Vörösmarty et al., 2010; WWF, 2016), mainly as a result of increased anthropogenic management and modification on a global scale (Nilsson et al., 2005). The worldwide alteration of the terrestrial water cycle has been described as a global issue alongside climate change (Vörösmarty and Sahagian, 2000). River impoundment by the construction of dams and the creation of reservoirs is considered one of the most significant forms of river regulation (Petts, 1984; Zarfl et al., 2015). Today, there are an estimated 58,500 large dams (higher than 15 m) worldwide (ICOLD, 2017).

The physical and chemical impact of river impoundment has been extensively documented (e.g. Webb and Walling, 1993; Gilvear, 2004; Yang et al., 2014; Maavara et al., 2015). Modification of the discharge regime affects all critical components of the natural flow regime (Poff et al., 1997; Magilligan and Nislow, 2005), is regarded as a major cause of stream degradation (Gordon et al., 2004; Tonkin et al., 2018) and is one of the most important factors influencing instream communities (Rosenberg et al., 2000). River impoundment has a profound effect on the instream ecology of lotic environments by affecting flow-ecology relationships (Bunn and Arthington, 2002). Benthic macroinvertebrate communities in particular have been intensively studied in relation to the effect of impoundment, with research examining community structure (Lessard and Hayes, 2003; Ladrera et al., 2015; Santos et al., 2017) and species diversity and richness (García de Jalón et al., 1994; Grown and Grown, 2001; Bredenhand and Samways, 2009). Both flow and thermal regime have been linked to changes to downstream macroinvertebrate communities (Petts, 1984; Martínez et al., 2013; White et al., 2017a). Since direct comparison of pre- and post-dam macroinvertebrate communities is often not possible, due to an absence of pre-impoundment baseline monitoring data (but see Armitage, 1978; Maynard and Lane, 2012), most studies have compared sites downstream of impoundments with control sites (i.e. sites assumed to represent unregulated conditions at the downstream sites - e.g. Grown and Grown, 2001; Holt et al., 2015).

To mitigate the perceived deleterious effects of impoundments, the implementation of environmental flows or e-flows (Acreman et al., 2009; Poff et al., 2010; Horne et al., 2017) has been proposed, referring to the quantity, timing and quality of river flow that is required to sustain lotic ecosystems and the services they provide (Dyson et al., 2003; Acreman et al., 2014; Overton et al., 2014). A range of studies have investigated reservoir outflow modification to enhance downstream ecosystems (for a review, see Gillespie et al., 2015b). Research centred on the effects of river impoundment has typically taken place on the site-specific scale involving single or several reservoirs (e.g. Greenwood et al., 1999; Holt et al., 2015), with a focus on the effects of large hydropower dams with rapidly changing discharge regimes (Alfredsen et al., 2012; Yang et al., 2014; Phillips et al., 2015). Moreover, most studies cover short time periods (Jackson et al., 2007; Gillespie et al., 2015a), generally restricted by the availability of appropriate ecological datasets.

The use of long-term observation datasets has recently been deployed in related ecological studies, for instance to demonstrate the effect of climate change on benthic macroinvertebrate communities on a large spatial scale (Jourdan et al., 2018). However, transferable flow-ecology relationships beyond the site scale remain elusive (Poff and Zimmerman, 2010). Moreover, the impact of reduced flow variability downstream of water supply reservoirs is not yet fully understood. Most dams of water supply reservoirs release water to the downstream river via a managed discharge regime that bears little resemblance to the natural hydrograph (historically termed 'compensation flows' in the UK - Gustard, 1989; Acreman and Dunbar, 2004), often reducing peak flows and increasing low flows (Higgs and Petts, 1988; McManamay et al., 2012; Stewardson et al., 2017).

This paper presents a large-scale comparison between the macroinvertebrate communities of monitoring sites downstream of multiple water supply reservoirs operating fixed flow releases and control sites. The overarching research aim was to identify consistent downstream patterns in ecological responses to water supply reservoirs beyond the site-specific scale. To address this, a multi-year (covering 2012–2016) national-scale biomonitoring dataset associated with 37 reservoir clusters (80 reservoirs) in England was used. The study aimed to assess the following hypotheses: 1) Consistent differences exist between macroinvertebrate communities at sampling sites downstream of water supply reservoirs and at control sites at the regional and national scales; 2) Patterns in ecological responses can be detected by existing macroinvertebrate biomonitoring tools employed to assess environmental variability.

2. Methods

2.1. Study area

The current study used data from the monitoring network SHEBAM (Setting the Hydro-Ecological Basis for Adaptive Management), which was established in 2012 by the Environment Agency of England (the statutory environmental regulatory agency in England, UK) to improve understanding of the ecological response to river flow alteration downstream of water supply reservoirs. This is to support assessments for the EU Water Framework Directive, particularly the ecological basis for adaptive management trials. The key feature of the network is the pairing of monitoring sites downstream of water supply reservoirs subject to compensation flow release schemes (called 'downstream sites' hereafter) and control sites, predominantly located in upland areas of England. As only limited pre-impoundment biomonitoring took place, control sites were selected to reflect the conditions that would occur at the downstream sites without the presence of the impoundment. These control sites were located either on the river reach upstream of the reservoir or on an unregulated tributary. The total network comprised 37 clusters (Fig. 1) of either individual or serial impoundments, involving a total of 105 monitoring sites associated with 80 reservoirs (1–6 reservoirs per cluster). From each cluster, 1 downstream and 1 control site closest to the impoundment were selected, resulting in a total of 74 sample sites (37 downstream-control site pairs). From the 37 control sites examined, 28 sites were upstream of the impoundment and 9 sites were located on tributaries.

2.2. Sampling

All monitoring sites were sampled biannually (spring and autumn) 2012–2016, yielding a maximum of ten samples per site, with the exception of sites that were introduced or replaced in 2015 after a network revision ($n = 20$; mainly control sites). For these sites, samples were only available for 2015 and 2016 (maximum of 4 samples). Spring samples were collected March–May and autumn samples were collected September–November. Benthic macroinvertebrates were collected by means of a standardised 3-minute kick-sampling method with an additional 1-minute hand search (Murray-Bligh, 1999). All samples were preserved using denatured alcohol (70% ethanol) in the field (ISO, 2012) and were returned to the laboratory for processing and identification. Macroinvertebrate taxa were identified to a consistent mixed taxonomic level (species level where possible, but some taxa at genus level or family level - see Davy-Bowker et al., 2010), with abundances being recorded. For a number of samples, faunal identifications were independently verified following Environment Agency quality assurance protocols.

The total number of samples available for analysis was 615 (315 downstream site samples, 300 control site samples), initially comprising >500 taxonomic entries (called 'taxa' hereafter). Pre-analysis was undertaken to ensure a consistent taxonomy across all samples by merging overlapping family, genus and species entries occurring in

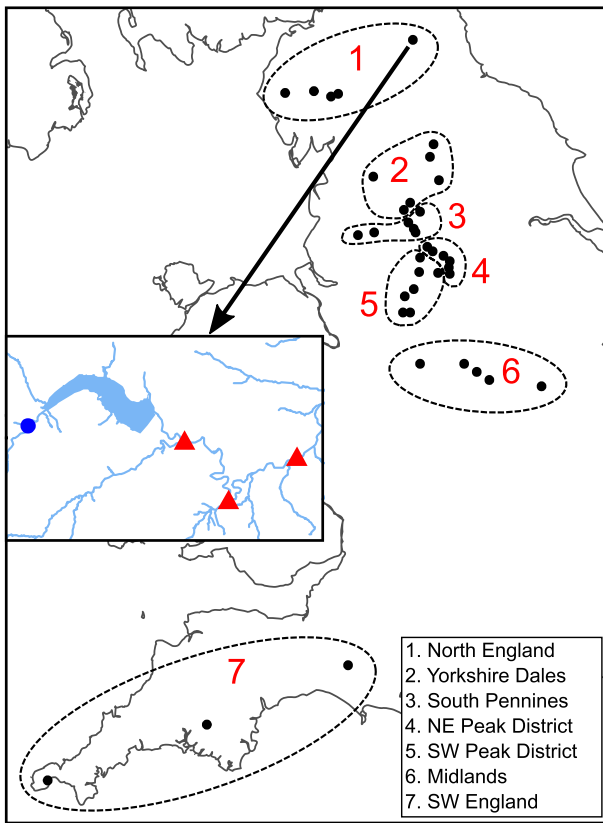


Fig. 1. Location of the 37 SHEBAM reservoir groups. The dash-lined circles indicate regions. INSET: close-up of the Derwent reservoir in Northumberland, comprising one control site (blue dot) and 3 downstream sites (red triangles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

separate samples to ensure consistency. In addition, some taxa at order, family or genus level were removed; a number taxa of were resolved to genus (mainly insect taxa), family (e.g. most Diptera taxa), order (e.g. Cladocera, Odonata) or higher taxonomic levels (e.g. Hydracarina, Oligochaeta). This process resulted in a final macroinvertebrate dataset comprising 236 taxa.

3. Data analysis

Macroinvertebrate communities at downstream and control sites were analysed at different spatial scales. At the national scale, all 37 downstream- control site pairs (615 samples) were analysed together. For the regional- scale analysis, the 37 pairs were divided into seven regions (see Fig. 1), based on the geographical proximity of the reservoir clusters while also aiming for a balanced design as to the number of clusters and sample sites per region. Each region comprised 3–7 pairs, with most regions comprising 5 or 6 pairs. Differences in macroinvertebrate community structure were tested against three spatial and two temporal variables, all treated as multi-level factors: 'Site type' (2 levels: 'Downstream' and 'Control'); 'Region' (7); 'Downstream-Control site pair' ('DC pair'; 37); 'Season' (2: 'spring' and 'autumn'); 'Year' (5: 2012–2016).

3.1. Community structure

Prior to analysis, macroinvertebrate abundances (absolute counts) were transformed into proportions by dividing individual taxa counts by the total count per sample. Community structure was analysed using a three-step approach: 1) The influence of 'Site type' (downstream or control site) on macroinvertebrate communities was examined by analysing spring and autumn samples separately, in common

with other studies involving macroinvertebrate samples (e.g. Monk et al., 2008); 2) The impact of impoundment on seasonal patterns in macroinvertebrate community structure was examined by dividing samples into 'Downstream' and 'Control' site groups and testing both groups in association with 'Season' (spring or autumn); 3) The influence of the other spatio-temporal variables 'Region', 'Year' and 'DC pair' was tested by analysing both seasons and site types individually, thus dividing samples into four groups.

In all three steps, differences in community structure between levels of individual variables were tested with a non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA; see Anderson, 2001) using the 'adonis' function from the R package 'Vegan' (Oksanen et al., 2017). This function partitions the total statistical variation (sums of squares) for the different sources of variation (i.e. the analysed variable(s)). This way, we determined the amount of total statistical variation that is explained by the spatio-temporal variable analysed and the amount that was unexplained. The 'adonis' function outputs the partitioned statistical variation as *partial R-squared* values or R^2 -values, which will be presented throughout the text and alongside the standard *pseudo-F* and *p*-value output in the relevant tables. The significance of the partitions were inspected using 999 permutations. Multivariate patterns in community structure were visualised using Non-metric Multi-dimensional Scaling (NMDS) ordination, using the 'metaMDS' function in 'Vegan'. Both techniques were applied using Bray-Curtis dissimilarity matrices.

3.2. Taxonomic richness and biomonitoring indices

For every macroinvertebrate sample, total taxonomic richness (the number of taxa recorded in a sample), total EPT richness (the number of Ephemeroptera, Plecoptera and Trichoptera taxa in a sample) and relative EPT richness (%EPT - the number of EPT taxa in proportion to the total number of sampled taxa) were calculated. In addition, four macroinvertebrate community biomonitoring indices were derived, each developed for assessing the impact of different abiotic factors: i) Lotic-invertebrate Index for Flow Evaluation (LIFE) - flow variability (Extence et al., 1999); ii) Walley-Hawkes-Paisley-Triggs (WHPT) - environmental quality (Paisley et al., 2014); iii) Proportion of Sediment-sensitive Invertebrates (PSI) - instream fine sediment loading (Extence et al., 2013); and iv) Community Conservation Index (CCI) - community richness and relative rarity of taxa (Chadd and Extence, 2004). Differences in taxonomic richness and biomonitoring indices between different site types (downstream or control sites) were tested by means of a non-parametric one-way Analysis of Variance test (Kruskal-Wallis), analysing spring and autumn samples separately.

4. Results

4.1. Community structure

National-scale analysis on separate spring and autumn samples (Step 1 of analysis) indicated that community structure differed significantly between downstream sites and control sites, both for spring and autumn samples. Results from the PERMANOVA analysis indicated that the proportion of the total statistical variation (R^2 ; see Section 3.1) explained by variable 'Site type' (downstream or control) was <5% (Table 1). Ordination plots (NMDS) indicated that the clusters of downstream and control site samples largely overlap, but density and distribution of both point clouds differ (autumn samples in Fig. 2, panel a; see Fig. S1 for spring samples). Regional-scale analysis identified a similar pattern to the national scale analysis (Table 1). Macroinvertebrate community structure differed significantly between downstream and control sites for all regions except the Midlands region (see Fig. 1). The R^2 for 'Site type' was higher at the regional scale than at the national scale (7–26%), being highest for the North East Peak District region. Clusters of downstream and control site samples were distinct for most

Table 1

Results from PERMANOVA testing the significance of ‘Site type’ on community structure for separate spring and autumn samples (Step 1). NS = non-significant; *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$.

Region	Season	Pseudo-F	R ²	p
National scale	Spring	12.30	0.039	0.001***
	Autumn	13.44	0.042	0.001***
North England	Spring	5.56	0.122	0.001***
	Autumn	6.46	0.145	0.001***
Yorkshire Dales	Spring	3.39	0.078	0.002**
	Autumn	3.21	0.073	0.004**
South Pennines	Spring	5.44	0.108	0.001***
	Autumn	5.08	0.099	0.001***
North East Peak District	Spring	20.27	0.262	0.001***
	Autumn	13.21	0.191	0.001***
South West Peak District	Spring	3.58	0.068	0.001***
	Autumn	5.13	0.093	0.001***
Midlands	Spring	1.54	0.034	0.101 (NS)
	Autumn	1.74	0.038	0.067 (NS)
South West England	Spring	4.78	0.201	0.001***
	Autumn	3.85	0.176	0.002**

regions (autumn samples in Fig. 2, panels b–h; see Fig. S1 for spring samples).

Macroinvertebrate community structure differed significantly between spring and autumn at the national scale (Step 2). The proportion of the total statistical variation explained by ‘Season’ was slightly lower for downstream (4.4%) than for control sites (5.6%) (Table S1). At the regional scale, the seasonal effect was significant for all regions except for downstream sites in South West England (Table S1). The R² for ‘Season’ was typically less for downstream sites (5–11%) than for control sites (6–25%).

Community composition differed significantly between regions (Step 3). The R² for ‘Region’ was higher for control than for downstream site samples and highest for spring samples at control sites (30%, versus 22% for control site autumn samples - see Table S2–S3). At downstream sites, the R² was 15–16% with no apparent difference between seasons. Samples from individual regions were largely separated (Fig. 3). ‘Year’ was typically not significant at the regional scale, but was significant

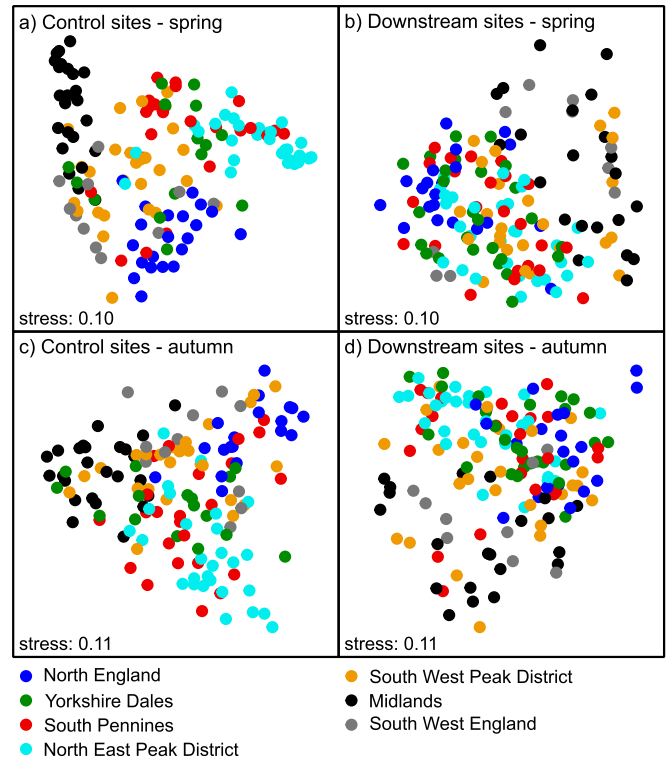


Fig. 3. National-scale NMDS ordination results involving sample subsets based on ‘Site type’ and ‘Season’, labelled according to ‘Region’ (Step 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for autumn downstream site samples at the national scale. The variable ‘DC pair’ (Downstream- Control site pairs) tested significantly and resulted in a high R² at the national scale, around 60% for individual seasons and site types. At control sites, the R² was higher for spring

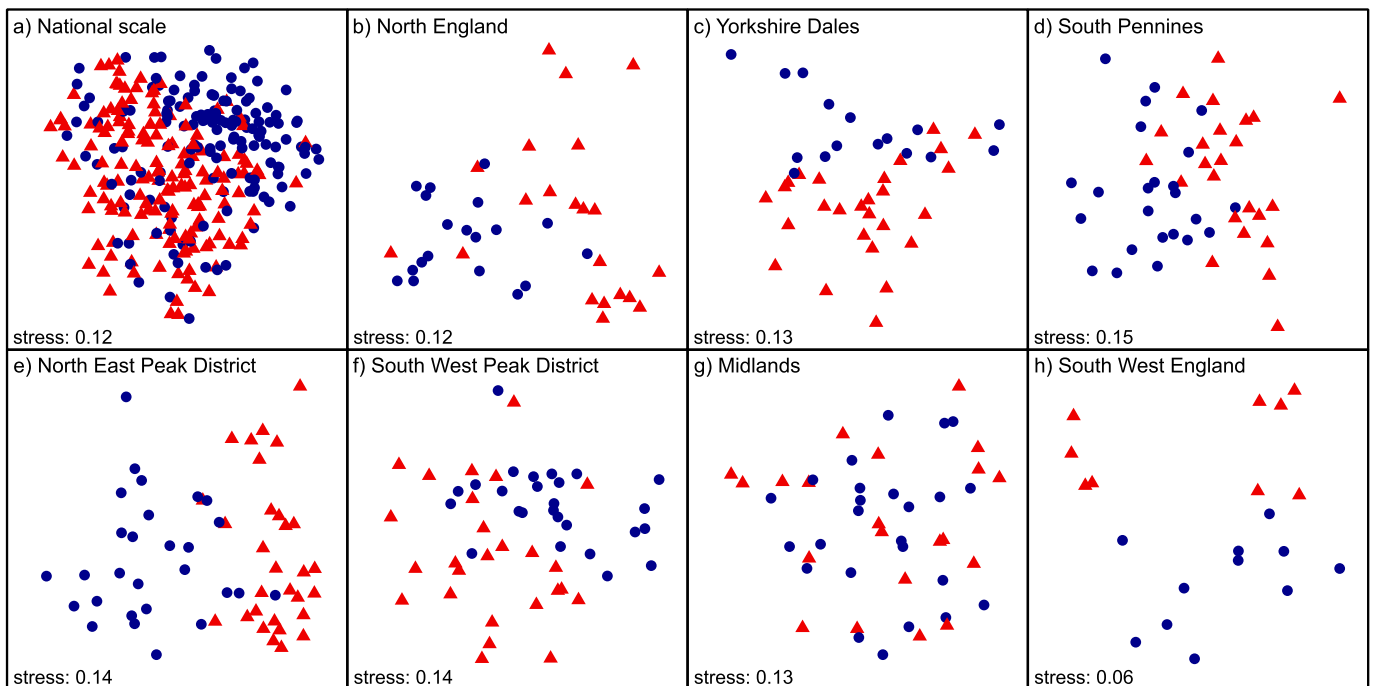


Fig. 2. NMDS ordination results including all autumn samples on national (panel a) and region scale (panels b–h), labelled according to ‘Site type’ (Step 1). Blue dots = control sites, red triangles = downstream sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

samples than for autumn samples, similar to the 'Region' variable. No clear differences were recorded at downstream sites. The variable 'DC pair' was also statistically significant at the regional scale, although the proportions of total variation explained varied markedly between regions.

4.2. Taxonomic richness

Taxonomic richness indices all differed significantly between downstream and control sites at the national scale (Table 2 and Table S4). Taxonomic richness was significantly higher at downstream sites than control sites, with on average higher values in spring than in autumn. There was a similar pattern for total EPT richness, although the difference between downstream and control sites was small. The proportion of EPT was significantly lower at downstream sites than control sites.

At the regional scale, taxa richness was typically higher at downstream sites than at control sites (autumn samples in Fig. 4; spring samples in Fig. S2). This difference was significant for three regions in spring and five regions in autumn (Table 2 and Table S4). On average, total EPT richness was higher at downstream sites in most regions, although results were not statistically significant in most instances. The proportion of EPT was typically lower at downstream sites than control sites, although this difference was significant in only 2 regions in autumn and 4 regions in spring. In addition, values for %EPT were markedly lower for the Midlands compared to the other regions.

4.3. Biomonitoring indices

All biomonitoring indices studied differed significantly between downstream and control sites at the national scale (Table 3 and Table S5). Scores for all indices were lower at downstream sites, although differences in LIFE and CCI scores were limited. Values were on average higher in spring than in autumn.

Values for LIFE, WHPT and PSI were significantly lower at downstream sites than control sites in the majority of regions (Table 3 and Table S5) and generally displayed a greater spread of scores at downstream sites than at control sites (autumn samples in Fig. 5; spring samples in Fig. S3). Values for LIFE, WHPT and PSI were markedly lower for the Midlands than for other regions, similar to values for %EPT (Section 4.2). Scores for CCI did not differ significantly between downstream and control sites for most regions and did not show a clear trend.

Table 2

Results from Kruskal-Wallis testing the significance of variable 'Site type' on taxonomic richness indices for separate spring and autumn samples. NS = non-significant; *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$.

Region	Season	Kruskal-Wallis p-value		
		Taxa richness	EPT richness	%EPT
National scale	Spring	0.001***	0.003**	0.001***
	Autumn	0.001***	0.014*	0.001***
North England	Spring	0.001***	0.066 (NS)	0.001***
	Autumn	0.001***	0.179 (NS)	0.001***
Yorkshire Dales	Spring	0.467 (NS)	0.221 (NS)	0.370 (NS)
	Autumn	0.001***	0.003**	0.538 (NS)
South Pennines	Spring	0.001***	0.003**	0.418 (NS)
	Autumn	0.009**	0.085 (NS)	0.137 (NS)
North East Peak District	Spring	0.001***	0.032*	0.014*
	Autumn	0.010**	0.317 (NS)	0.004**
South West Peak District	Spring	0.220 (NS)	0.657 (NS)	0.172 (NS)
	Autumn	0.103 (NS)	0.317 (NS)	0.374 (NS)
Midlands	Spring	0.758 (NS)	0.190 (NS)	0.028*
	Autumn	0.480 (NS)	0.138 (NS)	0.158 (NS)
South West England	Spring	0.723 (NS)	0.190 (NS)	0.041*
	Autumn	0.012*	0.818 (NS)	0.053 (NS)

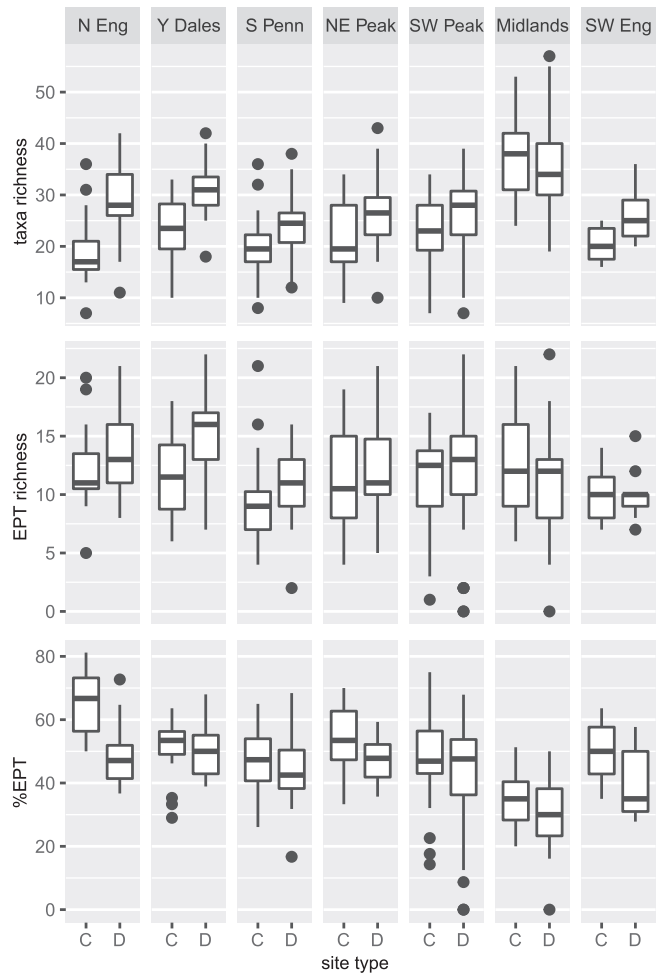


Fig. 4. Regional-scale taxonomic richness values calculated on autumn samples, per site type (C = control, D = downstream sites).

5. Discussion

5.1. Changes in community structure

The results of this study clearly indicate significant differences in macroinvertebrate community structure between monitoring sites downstream of impounding water supply reservoirs and unregulated control sites. This supports observations from the wider literature (e.g. Inverarity et al., 1983; Boon, 1988; Lessard and Hayes, 2003; Nichols et al., 2006; Katano et al., 2009; Ladrera et al., 2015) indicating that river impoundment leads to shifts in community structure. However, the majority of previous research (e.g. Jackson et al., 2007; Grownns et al., 2009; Maynard and Lane, 2012) has examined the effect of impoundment at the scale of individual rivers or reservoirs and only a limited number of studies have demonstrated an effect over larger spatial scales. In the current study, this effect was apparent at both the regional and national scale. Our study is consistent with a regional-scale study in Australia by Grownns and Grownns (2001), who reported significant differences in macroinvertebrate communities from regulated streams downstream of water supply reservoirs compared to control sites upstream of reservoirs and unregulated neighbouring rivers. Gillespie et al. (2015a) also reported modified macroinvertebrate community structure at regulated sites in a regional study of upland areas in Yorkshire, England.

The proportion of the total statistical variation explained by 'Site type' (R^2) at the national scale was small (4%) and only moderately larger at the regional scale (7–26%). This highlights the influence of other

Table 3

Results from Kruskal-Wallis testing the significance of variable 'Site type' on biomonitoring indices for separate spring and autumn samples. NS = non-significant; *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$.

Region	Season	Kruskal-Wallis p-value			
		LIFE	WHPT	PSI	CCI
National scale	Spring	0.001***	0.001***	0.001***	0.023*
	Autumn	0.001***	0.001***	0.001***	0.037*
North England	Spring	0.001***	0.001***	0.001***	0.187 (NS)
	Autumn	0.001***	0.001***	0.001***	0.116 (NS)
Yorkshire Dales	Spring	0.238 (NS)	0.300 (NS)	0.126 (NS)	0.154 (NS)
	Autumn	0.513 (NS)	0.175 (NS)	0.018*	0.200 (NS)
South Pennines	Spring	0.148 (NS)	0.008**	0.015*	0.524 (NS)
	Autumn	0.256 (NS)	0.004**	0.002**	0.005**
North East Peak District	Spring	0.001***	0.001***	0.001***	0.005**
	Autumn	0.001***	0.001***	0.001***	0.004**
South West Peak District	Spring	0.001***	0.011*	0.001***	0.474 (NS)
	Autumn	0.001***	0.007**	0.001***	0.770 (NS)
Midlands	Spring	0.012*	0.026*	0.019*	0.073 (NS)
	Autumn	0.045*	0.041*	0.120 (NS)	0.559 (NS)
South West England	Spring	0.001***	0.006*	0.001***	0.218 (NS)
	Autumn	0.003**	0.003*	0.003**	0.676 (NS)

spatial variables and stressors on macroinvertebrate communities (Leps et al., 2015; Villeneuve et al., 2018) and partly reflects the fact that the analysis comprised multiple sampling years. Although the temporal variable 'Year' was not significant in most instances, part of the total statistical variation will comprise temporal variation. Our results point to the influence of biogeography as an important control on community structure. The spatial variables 'Region' and 'DC pair' (the reservoir group a sample site belongs to) yielded relatively high R^2 values, indicating that biogeographical signals likely confound the effect of river impoundment on macroinvertebrate communities.

5.2. Impact on seasonal patterns

The results of this study demonstrate that impoundment by water supply reservoirs dampens the natural season patterns at downstream sites in two ways. First, the temporal variable 'Season' was found to explain a smaller proportion of the total variation at downstream sites than at control sites. Second, the seasonal pattern in sensitivity to biogeographical variables, which was apparent at control sites, was largely absent at downstream sites. At control sites, macroinvertebrate community responses to biogeographical variables appeared stronger in spring than in autumn. This highlights the potential influence of fauna life-cycles on the temporal community structure. The spring samples represent the community that has overwintered, whereas autumn samples reflect the effect of baseflow conditions coinciding with the sampling period. We hypothesise that this dampening effect on natural seasonal patterns downstream of the reservoirs is the result of modification of the flow and temperature regime by water supply reservoirs. A similar effect on seasonal variation in phytoplankton communities in regulated rivers was observed by Tornés et al. (2014) and was attributed to changes in hydrodynamics downstream of reservoirs.

5.3. Changes in taxa richness

Changes in community structure were reflected in a significantly greater number of macroinvertebrate taxa recorded at downstream sites than at control sites at both the national scale and for a number of regions. This is in line with some published research on individual water supply reservoirs (e.g. Petts and Greenwood, 1985; Petts et al., 1993; Maynard and Lane, 2012) but in marked contrast to others (e.g. Scullion et al., 1982; Grown and Grown, 2001; Nichols et al., 2006; Benítez-Mora and Camargo, 2014; Ladrera et al., 2015) and literature centred on hydropower dams (e.g. García de Jalón et al., 1994; Vinson, 2001; Jackson et al., 2007).

Our results further indicate a moderate increase of EPT taxa richness at the national scale and a mixed response at the regional scale. The reported responses of sensitive macroinvertebrate groups including Ephemeroptera, Plecoptera and Trichoptera downstream of impoundment are not uniform in the wider literature. Some studies, often involving HEP dams, have reported an absolute reduction of some or all of these groups (Boon, 1988; Jackson et al., 2007; Holt et al., 2015), while others have observed increases (Armitage, 2006; Maynard and Lane, 2012; Gillespie et al., 2015a). We also found a lower percentage of EPT taxa (%EPT) comprising communities at downstream sites, as reported in other studies (Lessard and Hayes, 2003; Phillips et al., 2015), which indicates an increase of less-sensitive non-EPT taxa. The increase of more ubiquitous macroinvertebrate orders including.

Diptera or Oligochaeta are often reported downstream of impoundments (Ogbeibu and Oribhabor, 2002; Jackson et al., 2007; Phillips et al., 2016).

We hypothesise that the proportional reduction of EPT taxa and increase of less-sensitive taxa at downstream sites are linked to post-impoundment flow regime and water quality modifications (Armitage et al., 1987; Phillips et al., 2015; White et al., 2017a). Further research should aim to quantify the various environmental drivers of community changes downstream of impoundments. For example, Maynard and Lane (2012) reported that flow regime changes following impoundment on a UK river had only limited effects on macroinvertebrate communities and linked this to the strict compensation flow scheme with a relatively high minimum flows.

5.4. Biomonitoring indices

The analysis of macroinvertebrate biomonitoring indices yielded similar results to those observed in the analyses on community structure and taxonomic richness, underscoring their value in impounded river research. Values for the Lotic-invertebrate Index for Flow Evaluation (LIFE), Walley- Hawkes-Paisley-Triggs (WHPT) index, Proportion of Sediment-sensitive Invertebrates (PSI), and Community Conservation Index (CCI) were significantly lower at downstream sites compared to control sites at the national scale. Scores for LIFE, WHPT and PSI at downstream sites were also typically lower at the regional scale, but CCI turned out to be less responsive.

The results suggest that a combination of abiotic changes related to impoundment affected the macroinvertebrate communities at downstream sites. Lower LIFE scores point to a reduction of taxa that favour moderate to high flow velocity conditions (Extence et al., 1999), lower PSI scores indicate an increase of taxa tolerant of increased fine

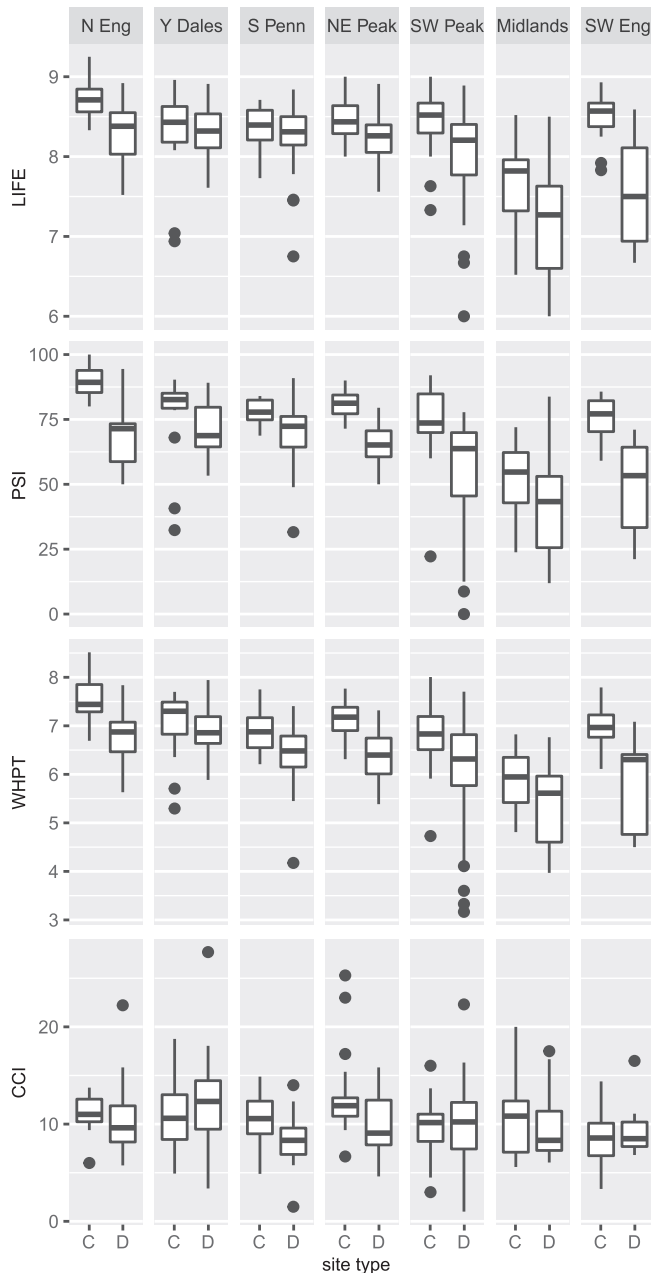


Fig. 5. Regional-scale biomonitoring indices values calculated on autumn samples, per site type (C = control, D = downstream sites).

sediment deposition (Extence et al., 2013), and lower WHPT scores indicate an increase of pollution-tolerant taxa (Paisley et al., 2014). Flow regulation and fine sediment accumulation often occur downstream of impoundment (Petts, 1984; Magilligan and Nislow, 2005; Yang et al., 2014), and releases from reservoirs can modify water quality in downstream river reaches (Growth et al., 2009; Casado et al., 2013). Given that the CCI index did not show obvious differences between downstream and control sites in most regions, it suggests no difference in overall conservation value, despite clear differences in community composition.

Relatively few studies have used biomonitoring indices to examine the effect of river impoundment. White et al. (2017a) reported that LIFE and PSI differed significantly between sites downstream of impoundments and control sites, whereas Gillespie et al. (2015a) found that only LIFE scores displayed a significant reduction due to regulation and PSI scores did not. In marked contrast, Bilotta et al. (2017) reported

that small-scale run-of-river hydroelectric power schemes did not have a significant effect on LIFE, PSI or WHPT scores at downstream sites. These variable results may reflect differences in impoundment characteristics and management.

6. Conclusion and study implications

This study represents one of the first large-scale multi-year comparisons between macroinvertebrate community structure and biomonitoring indices at monitoring sites downstream of water supply reservoirs and paired control sites. We used an extensive dataset derived from a national-scale routine biomonitoring network. Results demonstrated consistent differences in macroinvertebrate community structure between site types across spatial scales beyond individual reservoirs (hypothesis 1), highlighting generalisable effects over space and time that can be used by scientists and environmental regulators and managers in future research and management activities. The influence of other spatio-temporal variables including biogeography as key factors explaining differences at larger spatial scales was demonstrated. Water supply reservoirs were found to dampen natural seasonal patterns in downstream communities. In addition, the impact of water supply reservoirs was observed using existing biomonitoring indices used for river management purposes (hypothesis 2). This demonstrates that univariate biomonitoring indices are a valuable tool for quantifying the effects of river impoundment on instream macroinvertebrate communities.

The need for transferable flow-ecology relationships to underpin large-scale studies has been increasingly advocated (Zimmerman et al., 2010; Webb et al., 2013). Our results highlighted a consistent response to water supply reservoirs across different regions in England, but also indicated a relatively lower predictive power at larger spatial scales due to the associations of instream communities with other spatial and temporal factors. Recent studies centred on macroinvertebrate community responses to external drivers have applied the concept of functional diversity alongside taxonomic community composition (Tupinambás et al., 2014; White et al., 2017b). The use of functional traits was beyond the scope of the current study, but may have the potential to overcome the influence of confounding biogeographical factors in ecohydrological studies at larger spatial scales (Menezes et al., 2010; Stutzner and Bêche, 2010). However, we believe that by using biomonitoring indices we have presented a promising alternative to be applied in large-scale river impoundment research.

Further research using additional hydrology and water temperature data, combined with information on reservoir operation characteristics may help quantify the effects of flow and thermal alteration on macroinvertebrate communities and enable the translation of regional results into environmental flow prescriptions for individual reservoirs. Ultimately, this research improves our understanding of the impact of river impoundment on instream communities and provides guidance for the implementation of more natural flow regimes downstream of water supply reservoirs.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.09.264>.

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