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Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams

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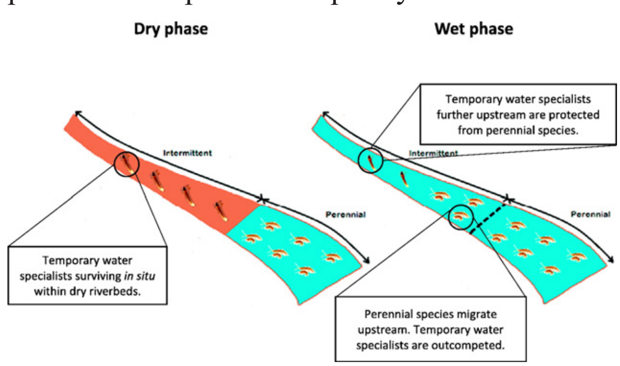
HIGHLIGHTS

- Macroinvertebrate communities differed between intermittent and perennial streams.
- Intermittent streams supported species of high conservation value.
- No negative ecological effects of groundwater abstraction were detected.
- Taxa richness was influenced by the geographical proximity to the perennial source along each watercourse.

GRAPHICAL ABSTRACT

Taxa migrating upstream from perennial to nearby intermittent reaches compete with and predate temporary water fauna.



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ABSTRACT

Intermittent rivers comprise a significant proportion of river networks globally and their spatial extent is predicted to increase with rising water abstraction pressures. Despite this, the ecological implications of hydrological modifications within intermittent rivers have received limited research attention. This paper examines macroinvertebrate assemblages across intermittent and perennial sections of headwater streams within the Hampshire Avon catchment (United Kingdom) over a five-year period. The composition of faunal assemblages was quantified in relation to four hydrological metrics: the duration of flowing conditions, the geographical proximity to the nearest perennial source along each watercourse (two observed flow parameters) and two modelled groundwater abstraction influences. The results highlight that macroinvertebrate communities inhabiting sites which dry periodically and are positioned at greater distances (>*c.* 2.5 km) above the perennial source (the most upstream point of permanent flow within a given year) possessed the highest conservation values. These sites supported species that are rare in many areas of Europe (e.g. Ephemeroptera: *Paraletophlebia werneri*) or with limited geographical distribution across the United Kingdom (e.g. Trichoptera: *Limnephilus bipunctatus*). A range of faunal community diversity indices were found to be more sensitive to the antecedent flow duration and distance

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from the perennial source, rather than any effects of groundwater abstraction. Taxonomic richness responded most strongly to these observed flow parameters and varied more markedly with the distance from the perennial source compared to the antecedent flow duration. Several taxa were significantly associated with the observed flow parameters, particularly those predominantly inhabiting perennially flowing systems. However, the distance that such fauna could migrate into intermittent reaches varied between taxa. This research demonstrates the overriding importance of antecedent flow durations and the geographical proximity to perennial sources on macroinvertebrate communities within intermittent and perennial headwater streams.

1. Introduction

It is estimated that over half the length of the global river network dries periodically (Datry et al., 2014b). Although these environments have historically received limited research attention, the number of studies on intermittent rivers has dramatically increased in recent years (Datry et al., 2016; Leigh et al., 2016), reflecting an increasing awareness of the landscape-scale biodiversity they support and ecosystem services they provide (Acuña et al., 2014; Boulton, 2014; Williams, 2006; Stubbington et al., 2017). The periodic drying of a channel may benefit some aquatic taxa exhibiting traits which make them resistant and/or resilient to flow cessation, including egg or larval diapause, rapid life-cycles and a high dispersal potential (e.g. Bonada et al., 2007; Cid et al., 2016; Garcia et al., 2017). Such taxa may thrive in intermittent rivers due to reduced biotic competition and predation they experience compared to perennial waterbodies (Arscott et al., 2010; Datry et al., 2014b; Fritz and Dodds, 2004; Wood et al., 2005). The spatial proximity and connectivity of intermittent waterbodies to adjacent perennial watercourses has been shown to influence faunal assemblages by controlling the ability of taxa to colonize from perennially flowing refuges and modify the nature of biotic interactions within temporary waterbodies (Bogan et al., 2013).

There have been recent calls for the wider conservation of intermittent rivers internationally (Acuña et al., 2014; Leigh et al., 2016), but the infrastructure and frameworks underpinning river management strategies have traditionally been focussed on perennial systems. For example, flow gauges are typically located on perennial waterbodies situated on lower regions of fluvial basins (Hannah et al., 2011) leading to a paucity of hydrological data on headwater temporary systems (e.g. Carlisle et al., 2010). In addition, intermittent rivers are grossly underrepresented within environmental policies, although they are beginning to receive wider consideration (Acuña et al., 2017; Leigh et al., 2016). The majority of existing biomonitoring indices used to assess the health of river ecosystems in accordance with environmental policy are based on the sensitivity of taxa to the degree of nutrient enrichment (such as within the EU Water Framework Directive - Birk et al., 2012). However, these water quality designations do not reflect the vulnerability of fauna to hydrological variability or drying events (Acuña et al., 2017) and there have been calls to adapt existing biological metrics or to develop new indices to more accurately represent the ecological status of intermittent rivers (e.g. Arthington et al., 2014; Prat et al., 2014). As such, there is a lack of baseline ecohydrological information on intermittent streams, which currently limits our scientific understanding of how lotic ecosystems respond to flow modifications, including groundwater abstraction practices.

Groundwater contributions to flow variability within fluvial environments has been acknowledged globally (e.g. Carlisle et al., 2010; Hannah et al., 2005; Sear et al., 1999) and is widely acknowledged as a key driver of biotic communities within lotic systems (e.g. Kath et al., 2016; Monk et al., 2006; Solans and García de Jalón, 2016). Despite this, the ecological implications of groundwater abstraction have been understudied relative to other forms of hydrological modification (e.g. impoundments – see Poff and Zimmerman, 2010). Studies centred on low flows and droughts have provided mechanistic insights into how ecosystems may respond to increased groundwater abstraction processes (Bogan and Lytle, 2011; Ledger et al., 2011; Wood and Armitage, 2004). However, limited empirical evidence exists regarding ecological responses to such hydrological alterations (but see Bradley et al., 2014; Kennen et al., 2014), in part due to logistical issues associated with establishing a gradient of groundwater abstraction pressures, as well as the presence of non-impacted (reference) sites (Acreman et al., 2014; Bickerton et al., 1993; Soley et al., 2012a). The development of groundwater models allows the influences that such subterranean pressures have on surface waters to be quantified. These can subsequently be used within water resource management strategies for the development of environmental flow frameworks (Soley et al., 2012b; Wilby et al., 2011).

Within the United Kingdom (UK), the chalk geology ($CaCO_3$), which underlies large areas of eastern and southern England, is subject to more groundwater abstraction than any other aquifer (Soley et al., 2012b). Headwater chalk streams are typically characterized by stable flow regimes and exhibit consistent wet/dry cycles on an inter-annual basis due to large seasonal fluctuations in the water table (Sear et al., 1999). These intermittent rivers are regionally referred to as ‘winterbournes’ and are of national scientific importance within the UK due to their unique hydrology which supports nationally rare flora and fauna (Armitage and Bass, 2013; Casey and Ladle, 1976; Punchard and House, 2009; Berrie and Wright, 1984). However, most ecological research on temporary rivers in the UK has predominantly focussed on the highly fissured karstic limestone systems in the English Midlands (e.g. Smith et al., 2003; Stubbington et al., 2016; Wood et al., 2005), which responds more rapidly to rainfall compared to the chalk and their remains a need to characterize the ecological and hydrological characteristics of winterbourne streams.

This paper examines macroinvertebrate community responses to observed hydrological parameters and modelled groundwater abstraction influences on intermittent and perennial reaches of chalk headwater streams in southern England (UK). The study aimed to: (i) characterize ecological and hydrological differences between ‘ecohydrological’ groupings used to guide river management strategies across intermittent and perennial headwater chalk streams (Punchard and House, 2009); (ii) quantify the sensitivity of various macroinvertebrate community diversity indices to the antecedent flow duration, distance from the closest perennial source along each watercourse and groundwater abstraction influences and (iii) examine the responses of selected widely occurring taxa to observed hydrological parameters.

2. Materials and methodology

2.1. Study area

A total of 62 sites situated along 12 streams in the Hampshire Avon catchment were examined (Hampshire, UK; Fig. 1). The catchment is primarily underlain by a chalk lithology (BGS, 2016) and the landuse is predominantly arable agriculture (NRFA, 2016), resulting in broadly comparable physico-chemical properties between streams (see Supplementary material, Appendix A). The Hampshire Avon is of international significance and has been designated as a Special Area of Conservation (SAC) under the EU Habitats Directives (92/43/EEC), with large areas of the catchment also being classified as a ‘Site of Special Scientific Interest’ (SSSI; Natural England, 1996). All of the rivers studied dry longitudinally downstream from the headwaters. The length of river subject

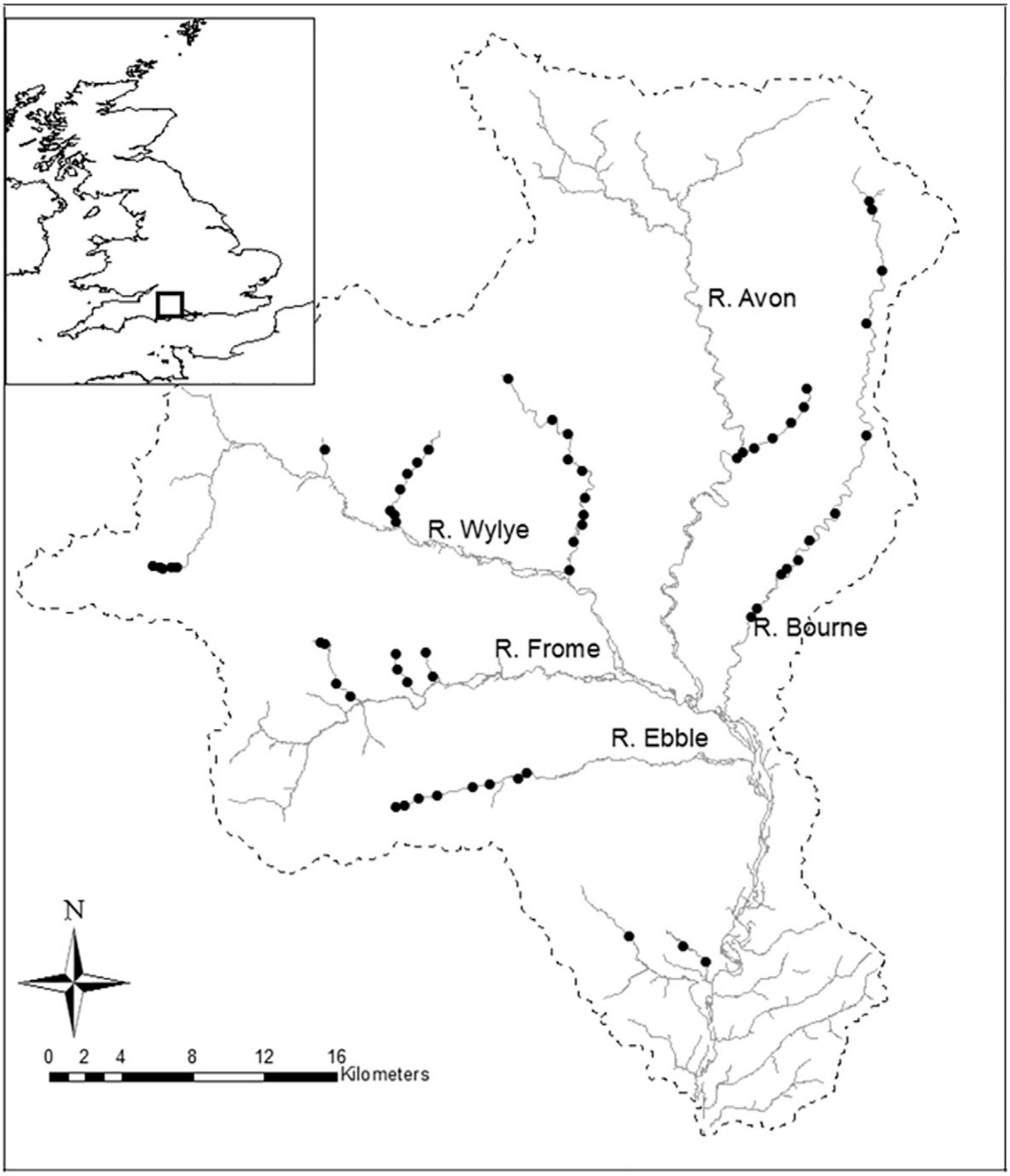

Fig. 1. The location of the study sites within the Hampshire Avon. Square = study region, dashed line = Hampshire Avon catchment boundary (Source: NRFA, 2016) and circles = sampling sites.

to drying events on an inter-annual basis varies from 4 km to 32 km between the watercourses studied. The regional water company (Wessex Water plc.) operates 21 groundwater public water sources across the study region, which collectively extracted ~63 Ml/d over the study period (2002–2007). Sampling sites were located along intermittent sections of each river and up to 5 km downstream of the source of permanent flows along each watercourse within a given year (the perennial source). Samples were collected across the study period during spring (March–May), when most intermittent systems across the catchment should typically be flowing.

2.2. Biological data

All macroinvertebrate samples were collected using a standardised 3-minute kick method, supplemented with a 1-minute hand search (Murray-Bligh, 1999). All samples were preserved using 70% ethanol in the field for subsequent processing and identification in the laboratory. Most samples (n = 116) were identified predominantly to species or genus level, but some taxa were resolved to family level (primarily Diptera larvae); while Nematoda (phylum), Hydracarina, Microturbelleria, Oligochaeta, Oribatei (class), Ostracoda (subclass), Cladocera, Collembola and Lepidoptera (order) were identified as such. Three datasets were derived from these samples to be used in subsequent analyses: (i) a 'presence/absence' matrix was constructed because a small number of taxa (notably the early instars of some aquatic insects) could not be consistently resolved to the lowest taxonomic resolution (a full list of taxa sampled within this study is presented in Supplementary material, Appendix B); (ii) a total abundance 'species/genera' level dataset was used to gain a greater understanding of the community structure and diversity (species or genus that could not be consistently resolved with confidence were

Table 1
Description of macroinvertebrate community clusters (EHC groups) reported by Punchard and House (2009) and used within this study.

Punchard and House (2009)	This study	Description
Perennial	Perennial	Permanent flows except during extreme drought and located ~2 km or more downstream of the perennial source.
Transitional A	Transitional	0–3 months dry and located within ~0.5 km of the perennial source.
Transitional B	Seasonal	6–9 months dry and located ~1 km upstream of the perennial source.
Winterbourne A	Winterbourne	6–9 months dry and located ~2.5 km upstream of the perennial source.
Winterbourne B		
Winterbourne C		
Intermittent	Intermittent	At least 9 months dry and located ~7.5 km upstream of the perennial source.

aggregated to a coarser taxonomic level; see Supplementary material, Appendix B); (iii) a 'family-level' dataset (total n = 171 - which included 55 historic samples that could not be included in ii).

2.3. Hydrological data

Four hydrological metrics were utilized within this study based on observed flow conditions and modelled groundwater abstraction influences. Drying patterns along each watercourse were observed on an inter-annual basis by surveyors monitoring the longitudinal extent of flowing conditions and dry reaches. All biological sampling sites along each stream were visited monthly for at least one year prior to sampling and the presence/absence of flow was recorded. This wet/dry mapping procedure (known as a 'winterbourne signature') allowed two 'observed flow parameters' to be quantified that characterized hydrological conditions in the year prior to each biological sample: the duration of

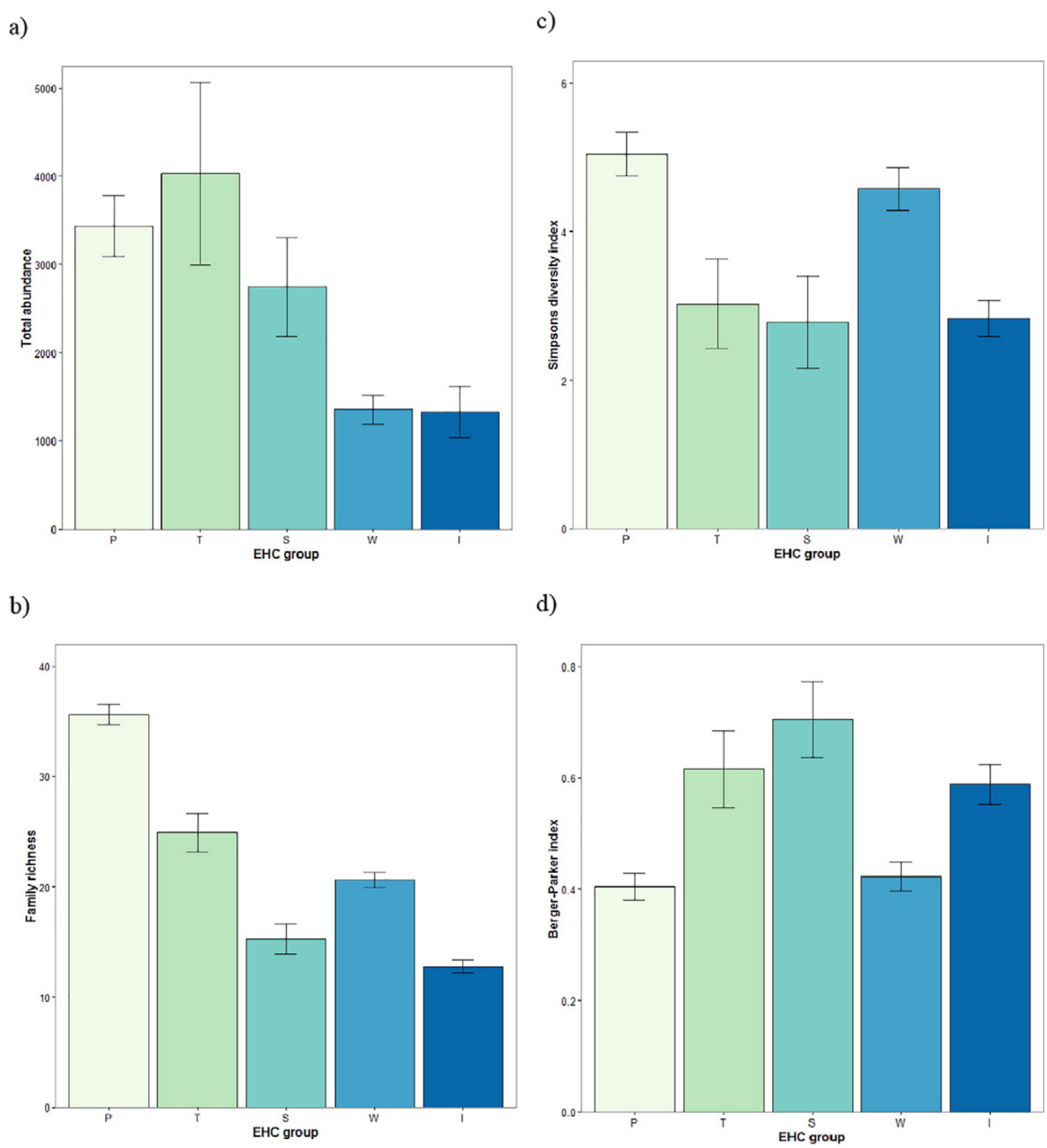

Fig. 2. Average (±1 standard error) values for various diversity indices and hydrological metrics exhibited by each EHC group. a) Total abundance; b) Taxonomic richness; c) Simpson's diversity index; d) Berger-Parker index; e) %EPT taxa; f) CCI; g) Antecedent flow durations and h) Distance from the perennial source. P = 'Perennial'; T = 'Transitional'; S = 'Seasonal'; W = 'Winterbourne' and I = 'Intermittent'.

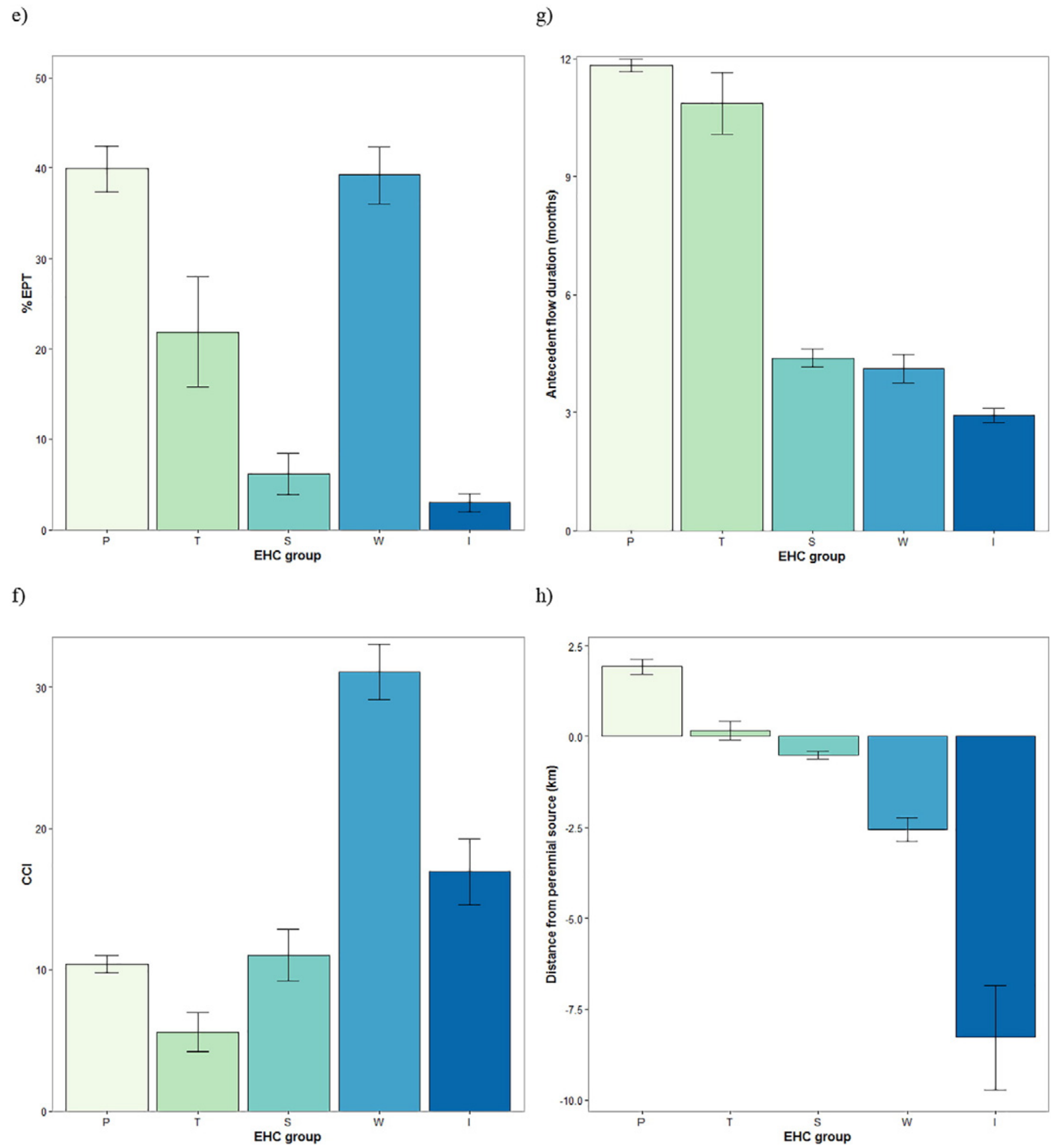

Fig. 2 (*continued*).

antecedent flow and the distance (km) of each macroinvertebrate sample site from the perennial source along each watercourse. These ranged from negative (upstream) to positive (downstream) values.

The 'Wessex Basin' regional groundwater model was utilized to quantify groundwater abstraction influences on macroinvertebrate communities in the year preceding each biological sample. The Wessex Basin model is a time variant numerical groundwater flow model. It combines representations of rainfall, routed runoff, evapotranspiration and recharge rates adapted from the 'MODFLOW' groundwater model (for full details, see ENTEC UK, 2010; Soley et al., 2012b). The model covers the Wessex Water plc. region overlaying Upper Greensand and chalk lithologies. The groundwater model divides the area into 250x250m grid cells which have been assigned specific geological properties (permeability and storage) and groundwater can leave (or enter) the aquifer via stream cells, which are located along perennial and winterbourne stream valleys. For each stream cell, the model outputs a historical (subject to water losses and abstraction) and naturalised (flows with no hydrological alterations) discharge time series at approximately 10-day intervals (3 modelled outputs per month). Model outputs have been calibrated against observed groundwater levels and river flow data (Soley et al., 2012b). The location of each biological sampling site was spatially joined to its respective stream cell using GIS software (ArcMap 10.1). Subsequently, historical and naturalised discharge time series were obtained from the model for up to 1-year prior to each macroinvertebrate sample collection date from each respective stream cell. Two measures of groundwater abstraction influences were derived from these time series: (i) the average difference between the historical and naturalised discharge time series when values were >0 (i.e. the reduction in total water volume due to groundwater abstraction when there was a modelled stream flow) and (ii) the number of model outputs when the historical and naturalised discharge time series equalled and exceeded 0, respectively (i.e. the reduction in the duration of flowing conditions due to groundwater abstraction); thus accounting for potential anthropogenic modifications to flow magnitude (i) and duration (ii - see Poff et al., 1997). Groundwater abstraction influences reduced discharge magnitudes by 0–67.03% (mean = 12.04%) and flow durations by 0–8 model outputs (~0–2.7 months; mean = 0.84 or ~0.3 months).

3. Data analysis

3.1. Characterising ecohydrological classification groups

Preliminary analyses were undertaken to examine the statistical variation accounted for by different hydrological groupings and clustering techniques on macroinvertebrate communities (for both family- and species/genus-level data). This demonstrated that the 'ecohydrological classification' (EHC) groups reported by Punchard and House (2009) accounted for the greatest amount of ecological variance (see Supplementary material, Appendix A). The authors established the EHC groups by clustering the composition of the 'family-level' macroinvertebrate dataset examined within this study into seven groups (see Table 1) using 'Two-Way Indicator Species Analysis' (Hill, 1979) and attributed ecological differences between these groups to variable hydrological characteristics (see Table 1). The nomenclature of these groups has been established in accordance with existing flow permanence classifications and denote specific hydrological conditions; although 'intermittent' and 'winterbourne' are used elsewhere in the manuscript as collective terms for rivers which periodically cease flows globally and within UK chalk regions, respectively (see Introduction). The 'Intermittent' EHC group displays a lower degree of flow permanence than

Table 2
Macroinvertebrate taxa significantly associated with different EHC groups based on IndVal analysis. IV = Indicator value. Stars indicate the degree of significance: * = p ≤ 0.05; ** = p ≤ 0.01; *** = p ≤ 0.001.

Taxa	IV	p-value	Taxa	IV	p-value
Perennial			Transitional		
Hydropsyche siltalai	0.885	0.001***	*Helobdella stagnalis*	0.619	0.001***
Ephemera danica	0.864	0.001***	*Bathyomphalus contortus*	0.424	0.005**
Limnius volckmari	0.827	0.001***	*Dendrocoelum lacteum*	0.375	0.023*
Leuctra sp.	0.824	0.001***	*Nebrioporus* sp.	0.374	0.01**
Rhyacophila sp.	0.794	0.001***	*Polycelis nigra*	0.342	0.025*
Sericostoma personatum	0.786	0.001***	*Gammarus pulex*	0.309	0.040*
Athripsodes sp.	0.756	0.001***			
Hydroptila sp.	0.756	0.001***			
Mystacides sp.	0.708	0.001***			
Sialis lutaria	0.678	0.001***			
Orectochilus villosus	0.663	0.001***			
Potamopyrgus antipodarum	0.655	0.001***			
Silo nigricornis	0.653	0.001***			
Chaetopteryx villosa	0.644	0.001***			
Lepidostoma hirtum	0.632	0.001***			
Caenis sp.	0.627	0.001***			
Elmis aenea	0.622	0.001***	Seasonal		
Polycelis felina	0.597	0.001***	*Dolichopodidae/Rhagionidae*	0.293	0.037*
Paraleptophlebia submarginata	0.594	0.001***			
Agapetus sp.	0.582	0.001***			
Glossiphonia complanata	0.579	0.001***			
Potamophylax cingulatus/latipennis	0.56	0.001***			
Dicranota sp.	0.559	0.001***			
Ancylus fluviatilis	0.536	0.001***			
Ecdyonurus sp.	0.532	0.001***			
Polycentropus flavomaculatus	0.508	0.002**			
Elodes sp.	0.502	0.001***			
Hydracarina	0.501	0.001***			
Anisus vortex	0.498	0.001***			
Oreodytes sanmarkii	0.497	0.002**	Winterbourne		
Riolus subviolaceus	0.48	0.001***	*Paraleptophlebia werneri*	0.717	0.001***
Oecetis testacea	0.48	0.001***	*Limnephilus bipunctatus*	0.629	0.001***
Valvata sp.	0.461	0.001***	*Nemoura cinerea/lacustris*	0.607	0.001***
Piscicola geometra	0.455	0.007**	*Isoperla grammatica*	0.515	0.001***
Oulimnius sp.	0.455	0.005**	*Aplexa hypnorum*	0.493	0.004**
Gyraulus crista	0.445	0.003**	*Dryops* sp.	0.491	0.002**
Asellus aquaticus	0.425	0.005**	*Anisus leucostoma*	0.474	0.001***
Bithynia tentaculata	0.421	0.004**	*Agabus* sp./*Ilybius* sp.	0.413	0.006**
Serratella ignita	0.416	0.008**	*Niphargus aquilex*	0.406	0.008**
Limoniidae	0.408	0.012*	*Limnephilus vittatus*	0.366	0.017*
Lype sp.	0.403	0.010**	*Radix balthica*	0.312	0.017*
Drusus annulatus	0.397	0.007**	*Hydroporus* sp.	0.296	0.041*
Baetidae	0.391	0.001***	*Galba truncatula*	0.294	0.046*
Physa fontinalis	0.382	0.011*			
Planorbis carinatus	0.354	0.028*			
Calopteryx splendens	0.354	0.03*			
Micronecta sp.	0.354	0.028*			
Ithytrichia sp.	0.354	0.033*			
Tinodes waeneri	0.354	0.031*			
Heptagenia sulphurea	0.343	0.027*			
Halesus digitatus	0.343	0.017*			
Sphaeriidae	0.332	0.018*			
Halesus radiatus	0.323	0.026*			
Empididae	0.322	0.027*	Intermittent		
Oxyethira sp.	0.315	0.043*	Microturbellaria	0.354	0.008**
Hydropsyche pellucidula	0.315	0.023*	Sciomyzidae	0.338	0.026*
Erpobdella octoculata	0.302	0.029*	Hydrophilidae	0.318	0.033*
Ceratopogonidae	0.294	0.023*	Ostracoda	0.264	0.038*

'Seasonal' flow regimes (see Williams, 2006). The three 'Winterbourne' EHC groups established by Punchard and House (2009) were combined in the statistical analyses presented within this study (see Table 1) and possess similar flow durations to the Seasonal group, but are typically positioned further upstream of the perennial source. The 'Transitional' EHC group only dries for short-term periods (sensu Stubbington et al., 2009) and is located within a close proximity to 'Perennial' reaches. All subsequent analyses were conducted using R studio version 3.3.1 (R Development Core Team, 2014). To comparatively examine structural differences in macroinvertebrate compositions between EHC groups, five community diversity indices were derived from the family-level community dataset: total abundance, taxonomic richness, inverse Simpson's diversity index (Oksanen, 2016), Berger-Parker index (Seaby and Henderson, 2007) and the percentage abundance of Ephemeroptera, Plecoptera and Trichoptera taxa (%EPT). Each of these diversity indices were then linearly modelled against the EHC groups (independent variable). Subsequently, model residuals were plotted against fixed values to assess the homogeneity of variances and Quantile-Quantile (QQ) plots were inspected to ensure that the data was normally distributed (which was conducted for all statistical models herein). Community abundances were log10(X + 1) transformed to ensure these assumptions were met. Differences in each of these community diversity indices between EHC groups were statistically analysed using a one-way 'Analysis of Variance' (ANOVA). The four hydrological metrics (i.e. two observed flow parameters and two modelled groundwater abstraction indices) were tested for collinearity by ensuring all 'Variance Inflation Factors' were below 3 (Zuur et al., 2010). Differences in each of these between the EHC groups were examined via a Kruskal-Wallis (KW) test (a non-parametric one-way ANOVA that approximates a X^2 distribution) given that the data was not normally distributed.

To test which taxa were significantly associated with a specific EHC group, a group-equalized 'Indicator Value' (IndVal) analysis was performed using Pearson's phi coefficient of association as a fidelity value (see Tichy and Chytry, 2006). This was conducted via the '*multipatt*' function in the 'indicspecies' package (De Caceres and Jansen, 2016), which iteratively measures the correlation between two binary vectors and was undertaken using the 'presence-absence' (species/genus-level) matrix. The same dataset was used to examine the conservation value of each EHC group via the Community Conservation Index (CCI) (sensu Chadd and Extence, 2004). The CCI reflects the national conservation status of aquatic macroinvertebrate communities based on the designated rarity of taxa and the community richness of samples. Differences in CCI values between each of the EHC groups was examined via a KW test. The multivariate composition of macroinvertebrate community abundances and contrasts between the EHC groups was visualized using an 'Non-metric Multidimensional Scaling' (NMDS). This was conducted via the '*metaMDS*' function within the 'Vegan' package (Oksanen et al., 2017), using the Bray-Curtis dissimilarity measure.

3.2. Hydrological controls on macroinvertebrate community diversity indices

The five macroinvertebrate community indices examined within this study (see above) were derived from both the family- and species/genus-level community datasets. These were used as fixed effects and modelled against the four hydrological metrics within mixed-effect models. Z-scores were derived for each hydrological metric to standardize the influences of each fixed effect between rivers. The year of sample collection and the identity of each watercourse were used as random effects to account for any potential lack of spatial or temporal independence between samples. Random slope models were fitted in all instances using a maximum-likelihood approximation.

The taxonomic richness was examined using a 'generalized linear mixed-effect model' (GLMM) modelled with a Poisson distribution, which was conducted via the '*glmer*' function in the lme4 package (Bates et al., 2016). The '*dispersion_glmer*' function within the 'blmeco' package (Korner-Nievergelt et al., 2015) was used to ensure that GLMM's were not under- or overdispersed (by ensuring values were between 0.75 and 1.4). To validate the assumptions of each GLMM, simulated residuals (which works comparably to parametric bootstrapping – see Hartig, 2016) were plotted using the '*simulateResiduals*' function in the 'DHARMa' package (Hartig, 2017). All other diversity indices were tested using linear mixed-effect models (LMM) via the '*lmer*' function in the lme4 package. Community abundances were log10(X + 1) transformed and %EPT was square-root transformed to normalize residuals and equalize variances. Subsequently, the '*dredge*' function within the 'MuMIn' package (Bartoń, 2017) was used to derive the optimal set of hydrological metrics influencing the diversity index tested within each LMM and GLMM. This function fits different models comprising all combinations of the fixed effects and ranks them by the corrected Akaike information criterion (AICc). The most parsimonious model within 2 AICc units of the model exhibiting the lowest AICc value was selected as the 'optimal' model. The significance of each optimal model was obtained via likelihood ratio tests (Winter, 2013). The explanatory power of the statistical models was derived from marginal pseudo r-squared values (r^2m; see Nakagawa and Schielzeth, 2013), which quantifies the variance explained by the fixed effects and were obtained using the '*rsquared.glmm*' function in MuMIn. Graphics for the GLMM outputs were prepared using raw hydrological values and confidence intervals were constructed using the framework outlined in Jamil et al. (2013).

3.3. The responses of specific taxa to observed hydrological parameters

The influence of the antecedent flow duration and distance from the perennial source were tested against specific taxa using 'generalized additive mixed-effect models' (GAMMs) via the '*gamm*' function in the 'mgcv' package (Wood, 2017). These were constructed to account for a potential lack of temporal and spatial independence (as above), as well as non-linear responses. GAMMs were derived for taxa which were: (i) consistently identified to species- or genus-level; (ii) present within at least 25% of samples; and (iii) found to be significantly associated with a specific EHC group (previously identified through IndVal).

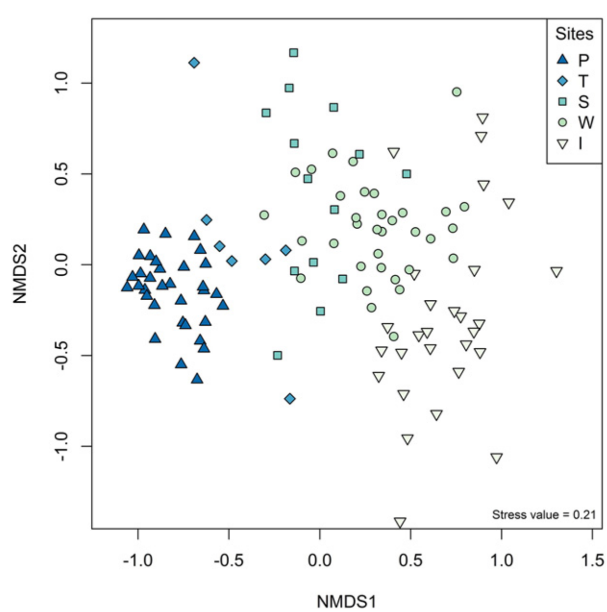

Fig. 3. NMDS plots of macroinvertebrates species-level community abundances between EHC groups. Triangles = 'Perennial'; Diamonds = 'Transitional'; Squares = 'Seasonal'; Circles = 'Winterbourne'; Inverted triangles = 'Intermittent'.

Table 3
Outputs from the mixed-effect models containing the optimal combinations of hydrological metrics influencing each macroinvertebrate community diversity index. Stars indicate the degree of significance: * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$.

Dataset	Response	Model	X^2	p-value	r^2m
Family	Total abundance	Antecedent flow duration	2721.93	<0.001***	0.29
	Taxonomic richness	Antecedent flow duration + Distance from perennial source	508.51	<0.001***	0.66
	Simpson's diversity	Distance from perennial source	16.55	<0.001***	0.08
	Berger-Parker	Distance from perennial source	10.50	0.001**	0.05
	%EPT taxa	Antecedent flow duration + Distance from perennial source	60.75	<0.001***	0.24
Species/genus	Taxonomic richness	Antecedent flow duration + Distance from perennial source	469.54	<0.001***	0.59
	Simpson's diversity	Antecedent flow duration + Distance from perennial source	37.53	<0.001***	0.21
	Berger-Parker	Distance from perennial source	8.84	0.002**	0.07
	%EPT taxa	Antecedent flow duration + Distance from perennial source	50.89	<0.001***	0.33

The raw abundances of these taxa were $\log10(X + 1)$ transformed and modelled against the additive effects of the antecedent flow duration and distance from the perennial source (fixed effects; with z-scores being obtained for these parameters), with the year of sample and watercourse identity being used as random effects. GAMMs were fitted using a maximum-likelihood approximation in all instances and plots were constructed using raw hydrological series.

4. Results

4.1. Biological and hydrological characteristics of EHC groups

Community abundances ($F = 128.77$, $p < 0.001$), family richness ($F = 122.70$, $p < 0.001$), Simpson's diversity ($F = 10.09$, $p < 0.001$), Berger-Parker ($F = 11.65$, $p < 0.001$) and %EPT ($F = 43.06$, $p <$

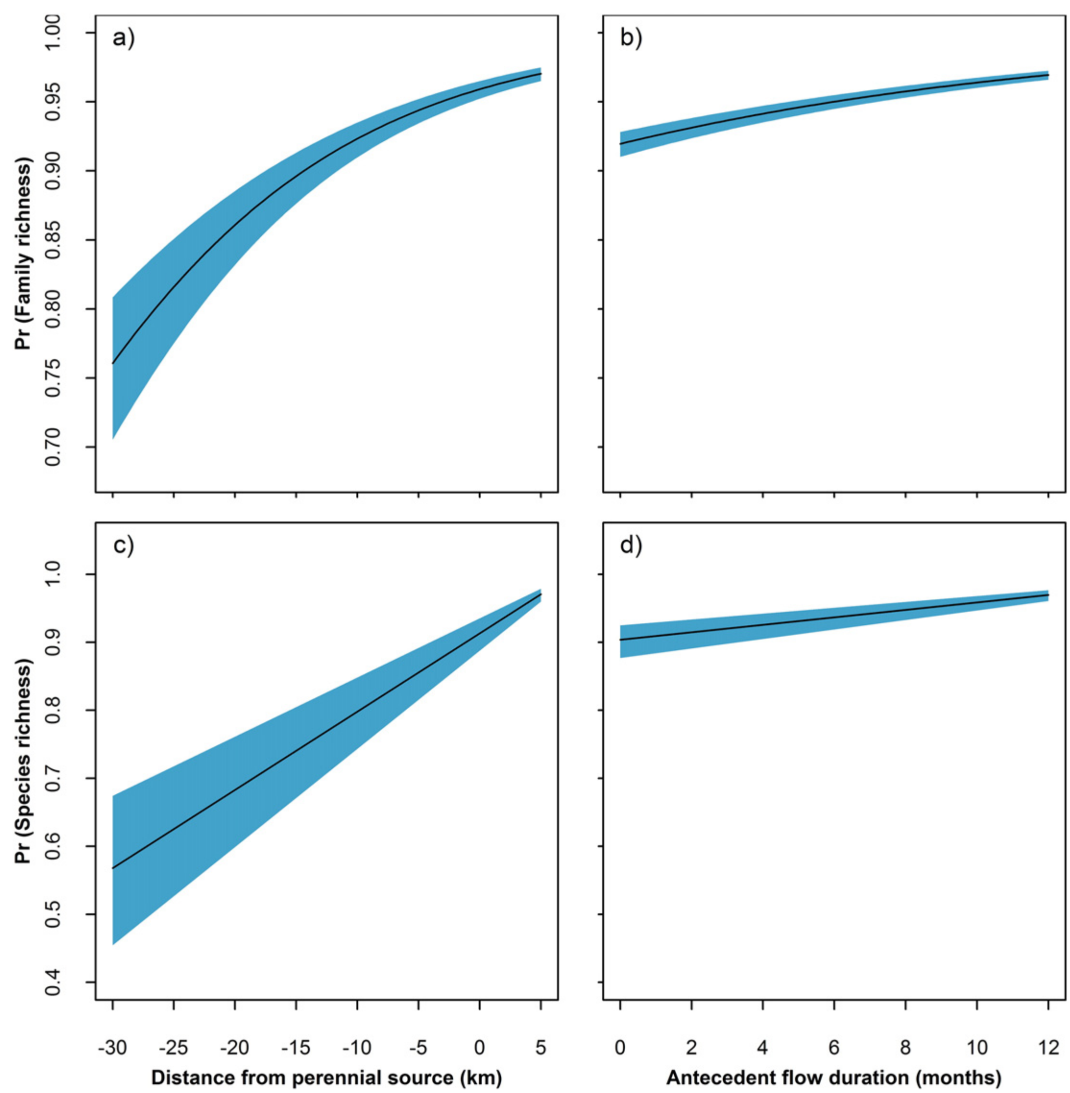

Fig. 4. Occurrence probability of taxonomic richness in relation to observed flow parameters obtained by mixed-effect models. a) Family richness versus the distance from the perennial source; b) Family richness versus the antecedent flow duration; c) Species richness versus the distance from the perennial source and d) Species richness versus the antecedent flow duration.

0.001) all differed significantly between EHC groups. The 'Transitional' group supported the highest number of individuals, followed by the 'Perennial' group (Fig. 2a). Perennial sites supported the greatest number of macroinvertebrate families (Fig. 2b) and along with the 'Winterbourne' group possessed a high community diversity (Fig. 2c) and a large percentage abundance of EPT taxa (Fig. 2e). The Perennial and Winterbourne groups were less influenced by dominant taxa compared to the Transitional and 'Seasonal' groups, which exhibited much higher Berger-Parker index values (Fig. 2d). The EHC groups exhibited contrasting hydrological characteristics, with the antecedent flow duration ($H = 124.39$, $p < 0.001$) and the distance from the perennial source ($H = 129.69$, $p < 0.001$) differing most markedly. Although some EHC groups displayed similar antecedent flow durations prior to biological sample collection (e.g. 'Perennial' versus 'Transitional' and 'Seasonal' versus 'Winterbourne'; see Fig. 2g), differences between the distance of each site from the perennial source were clear between all groups (see Fig. 2h). Reductions in flow magnitude ($H = 11.10$, $p = 0.025$) and duration ($H = 32.19$, $p < 0.001$) associated with groundwater abstraction influences also differed significantly between EHC groups, but there was less confidence in these models (as indicated by much lower H values relative to the outputs from KW tests analysing the observed hydrological parameters).

IndVal identified a range of macroinvertebrate taxa (across multiple taxonomic orders) which were significantly associated with different EHC groups (see Table 2). The Perennial group contained the largest number of taxa (n = 58 – see Table 2), while the Seasonal group was only significantly associated with the dipteran '*Dolichopodidae/Rhagionidae*'. The CCI values differed significantly between EHC groups ($H = 53.75$, $p < 0.001$), with those possessing shorter flow durations and located further upstream displaying the highest conservation scores (most notably the 'Winterbourne' group; see Fig. 2f). The degree to which specialist Winterbourne taxa were present within other EHC groups varied between species/genera, although those with higher conservation scores were most prevalent within the Winterbourne group (see Supplementary material, Appendix A). NMDS plots highlighted distinct shifts in macroinvertebrate community compositions with EHC groups distributed along the first axis in accordance with the duration of antecedent flow and the distance from the perennial source (perennial to intermittent – left to right on axis 1 – see Fig. 3).

4.2. Hydrological influences on macroinvertebrate community diversity parameters

The distance from the perennial source was included within 8 out of 9 optimal LMM's and GLMM's, while groundwater abstraction influences were not incorporated into any optimal model (see Table 3). The duration of antecedent flow was incorporated within 6 of the 9 optimal LMM's and GLMM's that accounted for the highest amount of the statistical variation (24%–66% – $r^2m = 0.24–0.66$, see Table 3). The observed hydrological parameters accounted for the greatest amount of statistical variation when modelled against taxonomic richness (for both family- and species/genus-level data). This diversity index was positively associated with both the duration of antecedent flow and the proximity to the perennial source; but the former exhibited a much shallower statistical gradient (see Fig. 4a and c) compared to the latter (see Fig. 4b and d).

4.3. Responses of individual taxa to observed hydrological parameters

Nineteen taxa and their responses to observed hydrological parameters were examined via a series of GAMMs (see Table 4). Taxa from the Perennial EHC group responded most strongly and were particularly sensitive to the duration of antecedent flow. Observed hydrological parameters accounted for the greatest amount of statistical variation when modelled against '*Elmis aenea*' (Coleoptera; adjusted $r^2 = 0.82$) and '*Caenis*' sp. (Ephemeroptera; adjusted $r^2 = 0.73$). These Perennial taxa were all significantly associated with the duration of antecedent flow and the distance from the perennial source. This was also observed for '*Gammarus pulex*' (Amphipoda; adjusted $r^2 = 0.69$) and '*Polycelis nigra/tenius*' (Tricladida; adjusted $r^2 = 0.21$), which were significantly associated with the Transitional EHC group (samples which were typically characterized by short-term drying events and located ~2 km further upstream of the 'Perennial' group; see Table 1 and Fig. 2g and h). GAMM outputs highlighted these species exhibited higher abundances further upstream of the perennial source compared to other taxa associated with the Perennial EHC group (see Fig. 5). Observed hydrological parameters accounted for the lowest amount of statistical variation when modelled against taxa associated with the Winterbourne EHC group, but '*Paraleptophlebia werneri*' (Ephemeroptera) and '*Nemoura cinerea/lacustris*' (Plecoptera) were both significantly associated with the duration of antecedent flow (see Table 4).

5. Discussion

5.1. Hydrological parameters and biotic compositions of the EHC groups

The results of this research demonstrate the importance of hydrological controls in structuring macroinvertebrate communities across intermittent and perennial headwater streams. The first aim of the study examined the 'ecohydrological classifications' (EHCs) reported by Punchard and House (2009) for use within a regional management context. The EHC groups accounted for a higher amount of statistical variance compared to alternative clustering techniques (see Supplementary material, Appendix A) and supported distinct macroinvertebrate communities. The results highlighted that the duration of antecedent flow and the distance of sample points from the closest perennial source along each watercourse differed more profoundly between EHC groups than groundwater abstraction influences. EHC groups characterized by a greater degree of flow permanence supported greater macroinvertebrate community abundances and a high taxonomic richness, as widely reported in other studies (e.g. Datry et al.,

Table 4
GAMM outputs examining the responses of select taxa to observed hydrological parameters. Stars indicate the degree of significance: NS = non-significant; * = p ≤ 0.05; ** = p ≤ 0.01; *** = p ≤ 0.001.

EHC group	Taxa	r^2	Antecedent flow duration		Distances from the perennial source	
			F	p-value	F	p-value
Perennial	*Elmis aenea*	0.82	34.00	<0.001***	4.98	<0.001***
	Caenis sp.	0.73	12.45	<0.001***	7.31	<0.001***
	Limnius volckmari	0.68	11.10	0.001**	7.46	<0.001***
	Sericostoma personatum	0.63	14.47	<0.001***	2.70	0.030*
	Seratella ignita	0.6	63.67	<0.001***	5.39	0.010**
	Agapetus sp.	0.49	8.29	0.005**	4.14	0.003**
	Glossiphonia complanata	0.48	61.84	<0.001***	1.42	0.236(NS)
	Hydroptila sp.	0.48	2.05	0.155(NS)	3.50	0.004**
	Asellus aquaticus	0.40	41.86	<0.001***	6.40	0.013*
	Valvata sp.	0.30	28.14	<0.001***	5.11	0.023*
	Erpobdella octoculata	0.18	11.51	<0.001***	0.83	0.364(NS)
Transitional	*Gammarus pulex*	0.69	25.27	<0.001***	4.54	0.002**
	Bathyomphalus contortus	0.23	15.69	<0.001***	3.10	0.081(NS)
	Polycelis nigra	0.21	6.12	0.008**	10.83	0.001**
Winterbourne	*Anisus leucostoma*	0.3	3.39	0.068(NS)	3.42	0.011*
	Nemoura lacustris	0.19	24.71	<0.001***	0.67	0.414(NS)
	Paraleptophlebia werneri	0.16	9.54	<0.001***	2.98	0.087(NS)
	Niphargus aquilex	0.15	0.11	0.745(NS)	2.23	0.064(NS)
	Isoperla grammatica	0.00	1.15	0.286(NS)	0.39	0.533(NS)

2014a; Garcia et al., 2017). Although the 'Perennial' EHC group was significantly associated with the highest number of taxa, sites characterized by shorter flow durations and located further upstream exhibited the highest conservation values, particularly the 'Winterbourne' EHC group. This was due to the presence of nationally rare taxa such as the ephemeropteran '*Paraleptophlebia werneri*', the trichopteran '*Limnephilus bipunctatus*' and the hypogean specialist amphipod '*Niphargus aquilex*' which occur in the benthos of headwater streams. While macroinvertebrate communities characterising the Winterbourne group were subject to comparable antecedent flow durations to the 'Seasonal' EHC group, sites belonging to the former were typically located approximately 2 km further upstream; suggesting that it is not only the degree of flow intermittency driving the composition of these biotic communities, but also their spatial proximity to perennial reaches (see below). This was probably a key factor driving low community diversity values exhibited by the Seasonal group, which were dominated by a small number of taxa and supported few EPT species. Sites within the 'Intermittent' EHC group were also characterized by low community diversity values, likely due to shorter flow durations precluding many temporary water specialists from completing their life-cycle, as reported elsewhere (e.g. Bonada et al., 2007; Stubbington et al., 2009; Garcia et al., 2017). However, macroinvertebrate communities residing within these sites displayed high conservation values, demonstrating how such environments can support specialist taxa with limited geographical distribution across the UK.

5.2. Macroinvertebrate community diversity responses to hydrological controls

Several authors have recently advocated the need to examine biotic metrics against continuous (as opposed to categorical) hydrological variables to provide a mechanistic understanding of ecological processes within intermittent rivers (e.g. Arscott et al., 2010; Datry, 2012). To address this, the present study modelled various macroinvertebrate community diversity indices against observed hydrological parameters and modelled groundwater abstraction influences. The duration of antecedent flow and the distance from the perennial source consistently yielded all optimal model outputs. The influence of flow intermittency on different macroinvertebrate alpha-diversity measures has been well documented and perennial environments have been consistently found to support a greater taxonomic richness (e.g. Arscott et al., 2010; Santos and Stevenson, 2011; Storey, 2016). Datry et al. (2014a) compiled results from various studies on intermittent rivers globally and highlighted that taxonomic richness and %EPT taxa were negatively correlated with flow intermittency. Results from this study demonstrated that

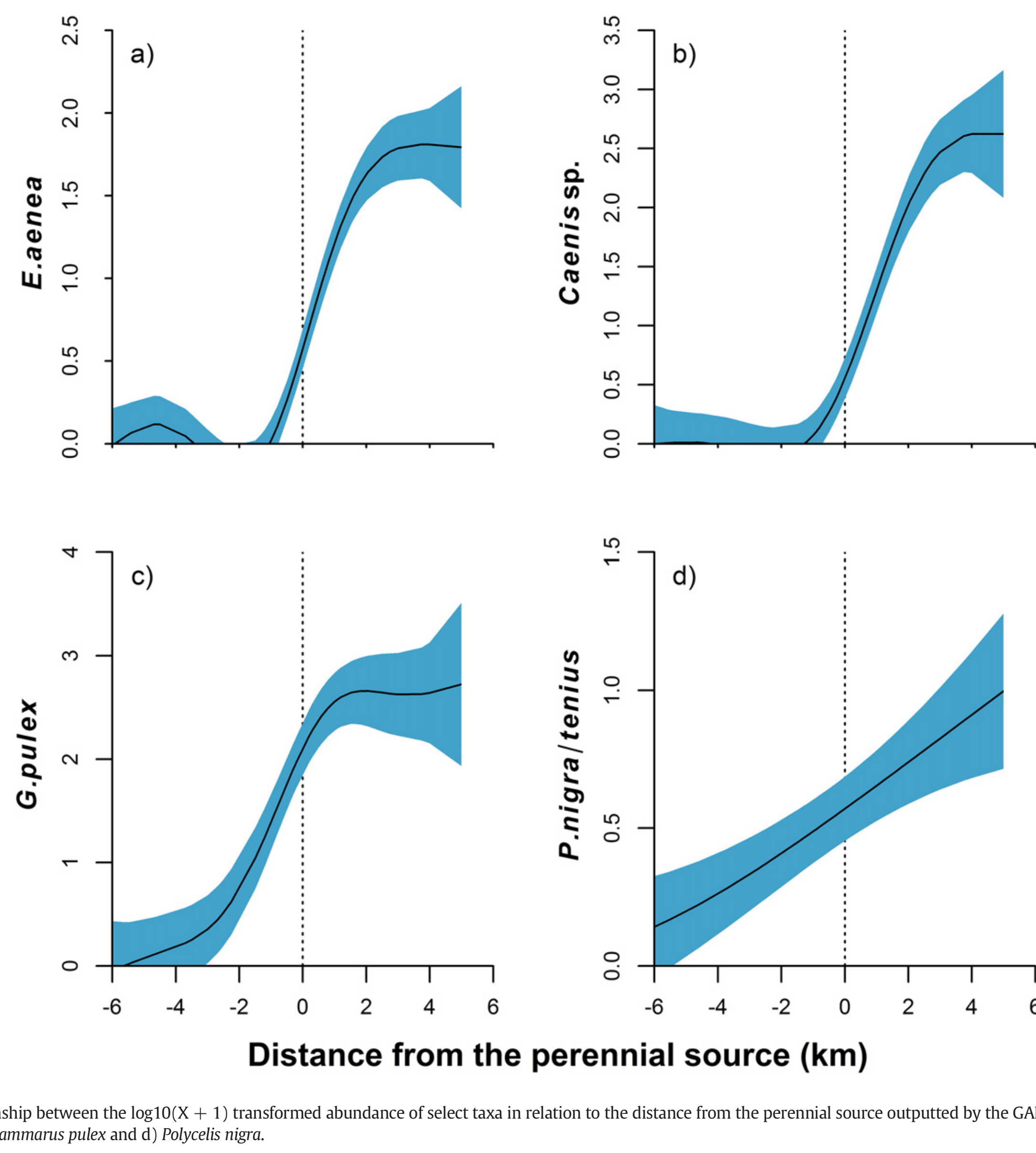

Fig. 5. The relationship between the log10(X + 1) transformed abundance of select taxa in relation to the distance from the perennial source outputted by the GAMM's. a) *Elmis aenea*; b) *Caenis*. sp.; c) *Gammarus pulex* and d) *Polycelis nigra*.

sites exhibiting longer antecedent flow durations supported a higher number of taxa, reflecting the known effects of the extirpation of aquatic taxa from sites which become dry (e.g. Cid et al., 2016; Garcia et al., 2017; Ledger et al., 2011).

The present study found that taxonomic richness was the most responsive diversity index to observed hydrological parameters and was particularly sensitive to the distance from the perennial source (for both family- and species/genus-level datasets). The geographical proximity of perennial and intermittent reaches in relation to sample site location has been reported as a key factor controlling macroinvertebrate community compositions due to is regulatory effect on the aerial and aquatic colonization of fauna into intermittent sites (Bogan and Boersma, 2012; Bogan et al., 2013; Cañedo-Argüelles et al., 2015; Gore, 1982).

5.3. The responses of individual taxa to observed hydrological parameters

Various macroinvertebrate taxa recorded in this study were strongly associated with the duration of antecedent flow and distance from the perennial source. Some species may flourish in intermittent streams that possess specific biological traits which allow them to complete their life-cycle in an environment with reduced biotic competition and predation (e.g. Arscott et al., 2010; Datry et al., 2014b). In this study, the univoltine mayfly larvae, *P. werneri* was significantly associated with the duration of antecedent flow and is known to be adapted to intermittent flows via the production of drought-resistant eggs (Wright et al., 1984). The stonefly larvae *N. cinerea*/*lacustris* (with the two species being grouped in this study due to their morphological similarity) was also significantly associated with the duration of antecedent flow. *N. cinerea* is widely recognized as a temporary stream specialist due to their eggs exhibiting a long diapause and possessing a gelatinous coat which protects them from drying events (Berrie and Wright, 1984). *N. lacustris* has only recently been discovered within the UK and have only been identified within winterbourne streams to date (Armitage and Bass, 2013; House and Tapia, 2014). Their persistence within intermittent streams is likely to be a function of their eggs experiencing a dormant phase after being deposited (Armitage and Bass, 2013).

The biological traits exhibited by macroinvertebrate taxa also govern their dispersal potential. For example, Bogan and Boersma (2012) highlighted that some taxa (e.g. Coleoptera: *Liodessus* sp) could widely colonize waterbodies at various distances from a source stream, while other fauna (e.g. Diptera: *Culex* sp.) were less likely to colonize isolated habitats. Results from this study demonstrated that the distance that select perennial fauna could migrate into intermittent reaches differed between taxa. Notably, the flatworm (Platyhelminth: *Polycelis nigra*/*tenuis*) and freshwater shrimp (Amphipoda: *Gammarus pulex*) were often sampled from sites upstream of the perennial source. Punchard and House (2009) proposed that the persistence of 'Winterbourne' communities is dependent on temporary stream sections being long enough to restrict the upstream migration of *G. pulex*, which would otherwise predate on specialist intermittent taxa and/or compete for their habitats and resources. Given the influence that *G. pulex* has been shown to have on macroinvertebrate community compositions within river systems (e.g. Kelly et al., 2006), the length of temporary reaches is likely to be highly influential in regulating the distance this fauna can migrate upstream. Various other studies have reported that although *G. pulex* can successfully colonize intermittent reaches, they have not been able to colonize the headwater reaches of winterbourne streams positioned at greater distances from perennial sources (Armitage and Bass, 2013; Berrie and Wright, 1984; Wright et al., 1984).

5.4. Study implications

Although the ecological implications of groundwater abstraction practices have been examined on chalk river systems within the UK, such research has been confined to perennial systems (e.g. Bickerton et al., 1993; Castella et al., 1995). The influences of groundwater abstraction on instream communities has been rarely examined due to difficulties quantifying the influences that such water management practices have on surface waters. This study examined macroinvertebrate community responses to groundwater abstraction influences on the magnitude and duration of flow events. These two facets of river flow regimes (see Poff et al., 1997) have been proven to have widespread ecological effects across intermittent and perennial river systems (Chinnayakanahalli et al., 2011; Belmar et al., 2013; Solans and García de Jalón, 2016). This study utilized a regional groundwater model to compare historic and naturalised discharge time series from the same section of river (i.e. each individual model stream cell), rather than flow outputs between different reaches/stream cells. As such, this approach does not wholly consider the spatial implications of groundwater contributions to flow variability along intermittent rivers (see Konrad, 2006; Kath et al., 2016). However, this approach was adopted due to local hydrogeological influences on flow variability not always being reliably accounted for by the groundwater model; whereas differences between model runs from the same stream cell are driven exclusively by anthropogenic activities, which can be more readily incorporated into the groundwater model. As such, this approach was deemed to be the most reliable method of quantifying the effects of groundwater abstraction on instream communities. To date, few studies have examined any form of hydrological alteration within temporary waterways and greater research attention is required to address this knowledge gap. A notable exception to this is Chessman et al. (2010), who examined macroinvertebrate responses to water extraction influences (as well as other hydrological alterations) and reported similar ecological trends to those observed within this study, with biotic differences between intermittent and perennial systems being greater than those associated with flow modifications. Recent studies have highlighted that establishing flow-ecology relationships can be related to modelled groundwater abstraction influences in order to predict biotic responses along a gradient of hydrological disturbance (Bradley et al., 2014; Kennen et al., 2014). Given the vulnerability of intermittent rivers to increased water extraction globally (Datry et al., 2014b; Larned et al., 2010), further studies are needed to examine the ecological implications of groundwater abstraction influences within intermittent rivers.

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Supplementary material

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2017.06.081.

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