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Regional flow–ecology relationships in small, temperate rivers

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Abstract

Flow–ecology relationships within river systems are an important area of ongoing investigation, because of potential applications such as understanding the ecological impact of flow alteration at modified sites. This study analyses relationships between flow characteristics and benthic macroinvertebrates from 18 streams of similar size and typology within Northern England, to develop quantitative flow–ecology relationships applicable at regional scale. High and low flow event frequencies displayed statistically significant relationships with the ecological metrics of LIFE Score, Shannon's Diversity and a velocity flow affinity trait score. Results suggest that flow event frequencies have a significant role in influencing ecology within the river network system. Hence, this indicates that future flow regime design in the region may be enhanced if this variable is considered.

KEYWORDS
catchment management, ecohydrology, modelling, remediation, river

1 | INTRODUCTION

A global increase in water demand and energy requirements has led to the widespread proliferation of flow impoundments. The resulting flow modification, even by small impoundments and hydropower schemes, can adversely impact riverine ecology (Anderson et al., 2017; Poff et al., 1997), and despite recent efforts, there remains a lack of consensus as to how ecological impacts arising from flow regime change should be mitigated (Gillespie, Desmet, et al., 2015). A better understanding of the relationship between ecology and flow regime is therefore a critical area of investigation. Such understanding is imperative for the design of mitigation measures such as environmental flows (e.g., Gillespie, Brown, et al., 2015; Hough et al., 2019), defined by the Brisbane Declaration, 2007 as '… the quantity, timing, and quality of water flows required to sustain freshwater and estuarine ecosystems and the human livelihoods and well-being that depend on these ecosystems.' (Overton et al., 2014, p. 861).

Several theoretical frameworks describe the relationship between riverine ecology and the flow regime (e.g., Junk et al., 1989; Poff et al., 1997; Vannote et al., 1980), and there is substantive and growing evidence to show how components of the flow regime, such as the timing, magnitude, frequency, duration and variability of flow peaks, can influence a range of ecological metrics (e.g., Praskievicz & Luo, 2020).

Magnitude is seen as a significant influence in the river system because of its effects upon river morphology, river habitat, sediment and nutrient transport, and physical forcing upon biota (Power et al., 1995). Timing is also because of morphological and behavioural adaptations of biota (Lytle & Poff, 2004). Frequency, duration and variability are likewise influential, because of their impact on nutrient cycling (Junk et al., 1989) or role as biological filters (Rolls et al., 2012).

Previous studies have discussed the challenges presented by rivers as open systems and the degree of uncertainty often associated with studies investigating specific variables (Konrad et al., 2011), when attempting to better understand flow–ecology relationships and possible mitigation of ecological impacts (e.g., arising from flow modification as a result of impoundments). The challenge is further enhanced because of the conflicting interests of multiple stakeholders present in most systems (Summers et al., 2015), such as water utility companies, industry and the general public. Developing mitigation measures that satisfy multiple stakeholders, while also making sufficient provision for environmental requirements such as ideal flow times and volumes for the system's biota, is a difficult task.

The building block approach (King & Louw, 1998) has been widely used to determine environmental flows as a means of mitigating the impact of modified flows, for example, for the design of flows downstream of impoundments. However, this site-specific, intensive approach relies upon expert judgement, which is impractical for mitigating the impacts of the majority of smaller-scale systems (i.e., flows >5 m^3/s), which are widespread and frequently failing to meet legislated ecological targets (Voulvoulis et al., 2017). Thus, there is a need for general and transferable information about flow–ecology relationships to support flow design in such systems.

This study focuses upon the relationship between flow and ecology at a regional level, with the aim of informing future mitigation recommendations. Specifically, we consider flow–ecology implications within smaller-scale river systems as an area in need of further research (Voulvoulis et al., 2017). Studies continue to affirm the use of regional-scale efforts (O'Brien et al., 2018) rather than site-specific evaluation, as such work can offer significant scientific value and act as a first step towards designing mitigation measures within impacted systems without detailed and expensive site investigation (Hough, 2020; Poff et al., 2010). Flow–ecology trends identified at a regional level, based on considering combined datasets from different sites, may allow for the establishment of transferable environmental flow principles between sites of similar character (Arthington et al., 2006), which may increase the number of sites meeting legislated targets.

This study thus aims to make first steps towards addressing the needs of smaller-scale riverine systems by developing a flow–ecology model applicable at a regional scale. We utilize and agglomerate historic long-term flow and ecological datasets across sites in the north of England to identify ecologically-influential flow characteristics at a regional level. Such data are freely available and thus allow for analyses that are not too resource- or time-intensive, maximizing transferability. Analyses were performed on river systems of similar characteristics in order to reduce the likelihood of noise from uncontrolled sources of variation obscuring observable relationships (Konrad et al., 2011) and allow clearer examination of a range of hydrological drivers; magnitude of flow in particular may overwhelm other hydrological drivers when assessed across too broad a scale, because of its dominant influence upon hydraulics and morphology (Monk et al., 2006). This investigation therefore focuses on rivers of a similar magnitude of mean daily flow and physical character, located across the region of Northern England.

The study also focuses on functional, as well as taxonomic, measures of ecological community structure. Focusing upon taxonomic composition alone may not detect some influences that flow exerts upon ecosystems, such as in cases where composition is altered but overall richness is not (Chinnayakanahalli et al., 2011). A broader suite of metrics is therefore required to fully assess ecological impact (Arthington et al., 2018). In this study, we combine diversity and trait characteristics with ecologically important flow metrics to identify the strongest flow–ecology relationships within the region studied.

2 | METHODS

This study utilized Indicators of Hydrologic Alteration (Richter et al., 1996) derived from historical flow data, in order to identify hydrological characteristics at each site. Sites were characterized ecologically based on macroinvertebrate diversity and flow preference. Relationships between flow and ecology metrics across all the selected sites were analysed using multiple linear regression.

2.1 | Site selection and data

Sites were selected from a range of sites across Northern England (Figure 1) and were chosen using the Environment Agency's (EA) online Catchment Data Explorer (Environment Agency, 2018). Selected study sites ranged from 0.31 to 2.83 m^3/s annual mean daily flow, with a minimum of 5 years continuous flow and ecological sampling data, with samples in both seasons each year. When identifying appropriate sites, some were also excluded because of external factors that could influence invertebrate composition, such as poor water quality. The sites selected for study were of ‘good’ chemical quality according to the most recent EA assessment. Eighteen sites were selected for analysis. They were all low gradient, straight or low sinuous, alluvial reaches on a sandstone and/or mudstone bedrock. Most were unmodified reaches in agricultural areas, although some reaches were in urban or suburban settings with some channel modification (see Appendix 1). Site characteristics were obtained from EDINA Digimaps Ordnance Survey Service (2020) and Google Earth Pro.

Publicly available time series datasets were obtained from the EA and the Centre of Ecology and Hydrology National River Flow Archive (CEH, 2021). Flow data were in the form of mean daily flows. The time series of flow data varied from 12 to 56 years of continuous data between sites; with 10 sites having over 30 years of data. Appendix 3 addresses potential concerns relating to the use of time series of varying lengths. Ecological data, collected as part of EA routine monitoring, included taxon abundance at a species or family level and Lotic-invertebrate Index for Flow Evaluation (LIFE) scores (Extence et al., 1999), typically with samples taken in spring and autumn each year and spanning 5–10 years. The coordinates of the data were checked to ensure that the sites for the flow and ecology data had no significant intervening flow inputs such as tributaries between them.

2.2 | Data analysis

A number of ecologically relevant flow variables were obtained from the flow data, based on principles outlined by Richter et al. (1996) and using indicators advocated for within the hydrological community (Dunbar et al., 2010; Monk et al., 2006): Q10, Q25, Q50, Q95,

FIGURE 1 Locations (solid circles) of all study sites across the North of England

standard deviation, range, annual maxima and minima, mean daily flows, and frequency and duration of high and low flow events. Statistical analysis of IHA variables was conducted to check that the length of time series data at each site was sufficient to generate stable and reliable flow statistics. Ecological data from each site were processed to provide velocity affinity and Shannon's diversity metrics for spring and autumn seasons; LIFE score was already available in EA data. LIFE is a widely used metric for the ecological monitoring of freshwater benthic macroinvertebrates based upon the flow affinities of macroinvertebrate species and families (Dunbar et al., 2010). Taxonomic diversity was used as a measure of ecological response between sites using the Shannon diversity index (H′) for macroinvertebrate family data in spring and autumn:

$$H' = \sum_{i=1}^{s} p_i \ln p_i$$

where s is the number of families present in the sample and p_i is the proportional abundance of each family.

Because of variation in the taxonomic resolution of the invertebrate data (data varied between species and family level depending upon site and time of measurement), all data were converted to family level, and the mean annual family abundances were calculated for each site separately in spring and autumn samples.

2.2.1 | Velocity affinity

Velocity affinity has been utilized in a number of ecological analyses (Schneider et al., 2016, Conallin et al., 2010). It was used in this study because of its strong relationship with the flow rate, and it represents the expected response of biota to various flow conditions. Species preferences were taken from Bis and Usseglio-Polatera (2004). Preferences were assigned to families by taking the mean trait affinity value of all species present within that family, an approach justified by the general similarity of traits within families, as seen in other studies such as White et al. (2017). Each family was also sorted into particular categories of flow preference,

TABLE 1 Trait score categories and associated weightings

Flow velocity preference	Trait score	Weighting
No flow (0 cm/s)	1	10
Low flow (0–10 cm/s)	2	7
Low-medium flow (10–20 cm/s)	3	7
Low-medium flow (generalists)	4	4
Medium flow (20–30 cm/s)	5	1
Medium-fast flow (generalists)	6	4
Medium-fast flow (30–40 cm/s)	7	7
Fast flow (>40 cm/s)	8	10

described in Table 1. These categories were based upon defined flow ranges by Bis and Usseglio-Polatera (2004), with additional categories created for more generalist families that displayed affinities for a broad range of flows. Populations within each category were summed up at each site based on the mean annual abundances of each family within a given category within spring and autumn. The distribution of abundances between categories provides an insight into functional composition of a site. Once population distributions across trait categories were calculated at each site, more extreme categories (e.g., very fast flow) were given higher weightings (see Table 1) because of the fact that taxa possessing extreme traits tend to be less common in typical conditions, yet the presence of even small numbers of such taxa is suggestive of a system's character (Petchey & Gaston, 2006). Generally across sites, species preferring medium flows were prolific, and thus, weightings were used to better demonstrate fluctuations in functional distributions. Flow velocity categories were each given a score between 1 and 8. The abundances of families present in each category, relative to the total population, were multiplied by the weighted score. The sum of these values constituted the overall trait score, that is, a trait score of ‘1’ indicates a site dominated by lentic flow affinity species, whereas ‘8’ indicates that fast flow affinity species dominate.

Many families, while having some affinities for either high or low flows, also exhibited moderate affinities for a range of flows and therefore may be considered rather generalist with regard to flow preference. These were put into two categories; generalists with low-medium preferences, and generalists with medium-fast preferences, demonstrated in Table 1. At low-medium flows, most families in the sampled regions appear to be generalists, with those of specific low-medium affinity being very rare. As such, the weighting for the low-medium affinity was weighted the same as the low-flow affinity, which was also rare at most sites. Trait scores varied between spring and autumn seasons because of differing family populations between the two periods, and thus, ecological metrics were assigned to both seasons separately.

This form of trait-based analysis allows for ecological characteristics to be compared across sites directly alongside flow characteristics, for example, Alexandridis et al. (2017), Petchey and Gaston (2006).

2.2.2 | Flow variables and relationships

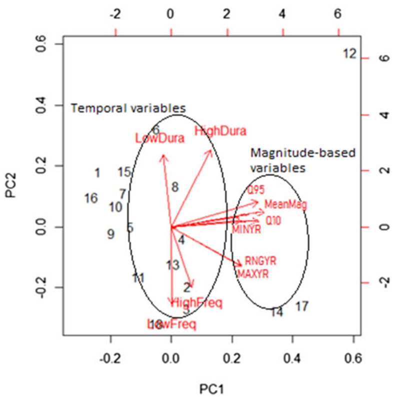
Using the data across all selected sites, a principal components analysis (PCA) was undertaken to reduce redundancy among the hydrological variables. PCA is a method commonly used in redundancy analysis and the approach followed Monk et al., 2006, Gillespie, Brown, et al., 2015, and Chinnayakanahalli et al., 2011.

PCA was based on a Pearson product moment correlation using the metrics listed in Table 2 and performed using *R* version 3.2.4 (R Core Team, 2016). Variables were sorted into distinct groups based upon the strength and direction of vectors within in the PCA biplot. The biplot distinguished two groups within the variables which were labelled ‘magnitude’ and ‘temporal’ (Figure 2 in Section 3). The groups were used to identify redundant variables, as variables within the same group were correlated and were considered to have a high degree of mutual explanatory power in relation to the dependent variable. Thus, multiple variables from the same group were not used in subsequent regression modelling.

TABLE 2 Summary of flow and ecological metrics, along with their shorthand used in subsequent sections

Metric	Characteristic described
Mean daily flow	Describes general magnitude of flow based on daily mean
Q10	Discharge exceeded 10% of the time (i.e., very high flow)
Q25	Discharge exceeded 25% of the time (i.e., moderately high flow)
Q95	Discharge exceeded 95% of the time (i.e., very low flow)
Mean annual minima (MINYR)	Describes extreme lows
Mean annual maxima (MAXYR)	Describes extreme highs
Mean annual range (RNGYR)	Describes general yearly range
Mean annual low flow frequency (LowFreq)	How frequently low flow events occur annually (median flow −25%), as a mean
Mean annual low flow duration (LowDura)	How long low flow events tend to last annually (median flow −25%), as a mean
Mean annual high flow frequency (HighFreq)	How frequently high flow events occur annually, (median flow +25%) as a mean
Mean annual high flow duration (HighDura)	How long high flow events tend to last annually, (median flow +25%) as a mean
Velocity affinity (velocity t)	Family affinity for flow conditions, scored 1 to 8. 1 is very low flow affinity, 8 is fast flow affinity
Diversity	Shannon's diversity, used as a measure of taxonomic diversity
Family LIFE	LIFE score (at family level) as another metric for flow affinity

Abbreviation: LIFE, Lotic-invertebrate Index for Flow Evaluation.



Site key

1 - Blackfoss Beck	10 - Went
2 - Colne	11 - Calder
3 - Crimple Blackstones	12 - Church Beck
4 - Dearne	13 - Douglas (Wigan)
5 - Eastburn Beck	14 - Eden
6 - Foulness	15 - Eea
7 - Ryburn	16 - Heltondale
8 - Skell	17 - Pendle Water
9 - Spen Beck	

FIGURE 2 Principal components analysis (PCA) bi-plot demonstrating redundancy between flow variables, with the two variable categories circled

Six data matrices were then constructed, containing one of the three ecological indices (diversity, LIFE or velocity preference) for either spring or autumn seasons. Each matrix contained all independent flow variables identified from the PCA analysis. Ecological indices vary seasonally because of shifts in the ecological community between seasons, whereas the flow variables do not vary as these flow characteristics are based upon yearly flow statistics.

Flow data were not normalized, as the main purpose of this study was to directly compare (and model) site flow against ecological response. This was appropriate for the study, as the river systems had a similar average mean daily flow range (within 1.2 m^3/s), with the exception of Eden and Pendle Water. Although distinctly higher in magnitude than other selected sites, these were retained by necessity as they presented good sources of data and met all of the criteria described for site selection in Section 2.1.

All metrics utilized are described in Table 2 below:

For each data matrix, multiple linear regression was used to fit a regionally applicable model for each ecological trait within each season. Regression models were created for all combinations of non-redundant variables (i.e., all combinations of variables that would contain one ‘magnitude’ and one ‘temporal’ variable), along with each variable individually (as univariate models).

Model fitting was performed for each ecological dependent variable with combinations of flow variables as the independent variables. The best fitting models for each dependent variable, in spring and autumn, respectively, were determined. These were judged from *p* values, R^2 values, and as the primary deciding factor, the Akaike information criterion (AIC); a measure of the relative quality of a statistical model, taking into account both the variation explained and the model complexity (Aho et al., 2014). Variables above a *p* value threshold of 0.2 were not analysed further to find their R^2 and AIC values, because of their obvious lack of statistical significance.

3 | RESULTS

Calculation of all ecological metrics was possible for all sites except one, where missing data meant that metrics could not be derived. Hydrological and ecological metrics for each site are listed in Table 3. Average annual mean daily flow across all 18 sites was 1.16 m^3/s. Of the sites, Skell (mean daily flow magnitude 1.51 m^3/s) was found to have the highest velocity trait score in both spring and autumn, whereas Calder (1.01 m^3/s) had the lowest score in spring and second lowest in autumn. Skell also had the highest LIFE score in both spring and autumn; an expected outcome as both LIFE and trait score are derived from similar data. Eastburn Beck (0.88 m^3/s) had the highest biodiversity in spring, and Heltondale (0.31 m^3/s) the highest in autumn. Blackfoss Beck (0.45 m^3/s) had the lowest biodiversity in spring, whereas Church Beck (0.85 m^3/s) had the lowest in autumn.

Results of the PCA analysis are shown in Figure 2. Variables were categorized into the two groups of ‘magnitude’ and ‘temporal’ after observing that variables likely driven by magnitude of flow correlated, whereas variables based on temporal occurrence (duration and frequency) displayed correlation between variables of the same category. PC1 separates sites Eden (14) and Pendle Water (17) from the other sites on account on differences in flow magnitude. Although these sites did have the highest mean daily flows, the sites differed most notably on account of the highest flows, namely, the MAXYR and RANGYR values. The two principal components accounted for 93% of the total variation. To avoid the redundancy among the variables in subsequent analyses, variables within the same category (i.e., ‘temporal’ or ‘magnitude-based’ as seen in Figure 2) were not used within the same model.

Once variable clustering was determined, fitting of linear models was performed for all possible combinations of non-redundant variables using data from all selected sites. The best-fitting model was chosen for each dependent ecological variable, both in spring and autumn, based upon the best (lowest) AIC value.

Mean annual high flow event frequency, in a univariate model, was found to have the strongest relationship with velocity trait score and family LIFE score, while mean annual low flow event frequency, again in a univariate model, was found to have the strongest relationship with biodiversity. Model values for the best results can be seen in Table 4. The full list of models and associated statistics can be found in Appendix 2.

A number of statistically significant relationships were identified at regional scale, with all the best fitting models containing only one flow variable. These relationships are plotted in Figure 3. Mean annual

TABLE 3 All study sites with their associated hydrological and ecological variables

Site name	Mean daily (m^3/s)	Q10 (m^3/s)	Q25 (m^3/s)	Q95 (m^3/s)	MINYR (m^3/s)	MAXYR (m^3/s)	RNGYR (m^3/s)	LowFreq (events/ year)	LowDura (days)	HighFreq (events/ year)	HighDura (days)	Velocity trait (spring)	Velocity trait (autumn)	Diversity (spring)	Diversity (autumn)	Family LIFE (spring)	Family LIFE (autumn)
Heltondale	0.31	0.71	0.35	0.04	0.04	3.51	3.48	8.6	6.58	13.25	3.93	5.16	3.14	1.9	2.71	6.45	6.61
Blackfoss Beck	0.45	0.86	0.4	0.04	0.04	8.43	8.39	6.63	13.26	7.12	2.4	4.8	4.52	1.22	2.03	6.89	6.66
Went	0.57	1	0.57	0.16	0.17	7.22	7.06	10.43	8.3	7.76	2.87	4.65	5	2.23	2.53	7.4	7.41
Ryburn	0.61	1.25	0.56	0.2	0.19	7.83	7.64	9.31	9.21	9.22	3.17	5.02	2.83	1.39	2.03	6.29	6.56
Spen Beck	0.74	1.22	0.65	0.1	0.18	6.73	6.55	12.26	7.65	7.34	1.85	4.7	5.27	2.13	2.08	7.91	7.48
Church Beck	0.85	3.68	1.3	0.09	0.08	8.71	8.62	11.07	4.25	25.71	2.21	4.57	2.27	2.03	1.16	6.3	5.81
Eea	0.87	2.28	1.19	0.05	0.04	7.04	7	6.67	8.79	12.5	4.04	4.2	4.62	2.19	2.47	7.92	7.49
Eastburn Beck	0.88	2.18	0.96	0.07	0.07	12.71	12.64	9.38	11.38	16.1	2.02	4.14	3.97	2.57	2.53	8.14	7.55
Calder	1.01	2.57	0.98	0.05	0.06	12.1	12.05	10.6	4.32	22.65	2.08	4.09	2.57	1.46	1.81	6.26	6.41
Crimple Blackstone	1.06	1.95	0.91	0.15	0.13	36.59	36.46	13.47	6.81	6.77	1.46	5.59	3.03	2.01	2.35	6.18	6.03
Swindale Beck	1.20	3.15	1.32	0.08	0.07	15.19	15.12	13.61	4.08	30.72	1.89	No data	5.68	No data	2.5	No data	7.63
Douglas Wigan	1.22	2.37	1.33	0.37	0.41	9.26	8.85	13.56	3.4	17.59	2.58	6.74	6.3	1.7	1.29	7.75	7.6
Foulness	1.28	3.12	0.77	0.05	0.05	18.18	18.14	5	19.81	6.82	3.68	6.27	5.99	1.87	1.83	6.69	6.89
Dearne	1.36	2.86	1.41	0.27	0.26	18.94	18.68	11.51	8	10.54	2.52	6.11	6.75	2.31	2.64	7.9	7.73
Colne	1.44	3.18	1.54	0.33	0.29	17.31	17.02	17.03	5.7	13.34	2.39	6.43	7.1	2.4	1.85	7.43	7.07
Skell	1.51	3.7	1.8	0.15	0.13	18.01	17.88	6.68	13.06	12.77	2.68	6.89	7.01	1.84	2.18	8.3	8.29
Eden	2.66	6.74	2.7	0.17	0.15	43.84	43.69	9.42	6.16	24.62	2.19	5.55	4.06	1.57	2.42	7.22	7.34
Pendle Water	2.83	6.83	2.91	0.46	0.44	38.12	37.68	12.64	4.55	22.14	2.46	6.26	6.26	2.09	2.59	7.79	7.53

Note: Mean daily represents mean daily flows, MINYR, MAXYR and RNGYR represent mean minima, maxima and flow ranges per year respectively, and Freq and Dura variables represent flow durations and frequencies.

Abbreviation: LIFE, Lotic-invertebrate Index for Flow Evaluation.

TABLE 4 Best performing models for each ecological metric, based on Akaike information criterion (AIC)

Variables in model		p	R^2	AI
LIFE scores—SPRING				
HighFreq	—	0.056	0.161	40.256
HighFreq	MINYR	0.1366	0.131	41.72
HighFreq	Q25	0.138	0.13	41.743
HighFreq	MeanMag	0.1628	0.11	42.141
LIFE scores—AUTUMN				
HighFreq	—	0.0157	0.2561	34.872
LowDura	—	0.0543	0.1539	37.317
HighFreq	MINYR	0.0545	0.2181	36.666
HighFreq	Q25	0.0552	0.2167	36.699
Velocity trait score—SPRING				
HighFreq	—	0.0376	0.1959	49.79
HighFreq	Q25	0.055	0.2302	49.847
LowDura	Q25	0.0666	0.2103	50.307
LowDura	—	0.0793	0.1287	51.237
Velocity trait score—AUTUMN				
HighFreq	—	0.01335	0.269	69.421
HighFreq	Q25	0.03	0.2742	70.135
LowDura	—	0.0352	0.1906	71.357
HighFreq	RNGYR	0.0467	0.2329	71.186
Biodiversity—SPRING				
LowFreq	—	0.0132	0.301	12.518
LowFreq	RNGYR	0.0278	0.3148	13.005
LowFreq	MAXYR	0.0281	0.3139	13.028
LowFreq	MINYR	0.0394	0.28	13.849

Note: No statistically significant relationships were found for biodiversity in autumn.

high flow frequency provides the best fitting models for velocity trait scores and LIFE scores in both seasons. The best fitting models for biodiversity, on the other hand, relate to mean annual low flow frequency, and only during spring. R^2 values are generally low, indicating relatively high levels of unexplained variation.

4 | DISCUSSION

In this study, we have examined the degree to which there are general relationships between hydrological characteristics and ecological metrics, across a set of similar rivers in Northern England..

4.1 | Velocity preference trait and LIFE scores

The results suggest that in this region, high flow event frequency has a significant influence upon the functional composition of a system in terms of velocity preference of families, explaining 20%–27% of the variation in preference when considering trait score, and 16%–26% of variation when considering LIFE score (based on R^2 values). This suggests that it may be possible to identify particular aspects of the flow regime which could be important to focus on when developing potential mitigation solutions for flow alteration. IHA variables including the duration and frequency of high and low flow events were found to strongly influence stream macroinvertebrates in a similar study based on the ELOHA method in the United States using biological metrics primarily based on functional group composition such as measuring the percentage of individuals adapted for filter feeding (Buchanan et al., 2013). The mechanisms underpinning the positive relationships between high flow and flow preference and LIFE scores seem likely to be straightforward; the more frequently high flows occur, the more resilient the community at a site becomes in terms of functional composition.

The influences of high flow event frequency as an ecological driver may have significant implications when considering environmental flow regime design in the region and also suggest significant limitations in current 'fixed' hands-off flow-based regulations (Arthington et al., 2006). A lack of high flow events within a modified system may lead to a lack of an important biological filter, resulting in systems being dominated by species that are highly competitive within a steady, moderate-to-low flow environment, as discussed by a number of studies examining river deviation from natural flows (Lytle & Poff, 2004; Summers et al., 2015). Incorporating a moderate frequency of high flows events into environmental flow regimes to mitigate the impacts of modification through impoundments may serve to balance a system's functional composition and be one facet in ensuring a stable and diverse ecosystem.

The only detected effect on family diversity was that low flow event frequency is negatively related to diversity, but in spring samples only. This may be because of differing conditions between the two seasons; functional composition is likely to differ significantly between the two seasons, either because of life history or external drivers. As such, response to the flow modification may vary because of these differences in composition between seasons. A negative correlation between low flow and diversity is consistent with other studies (e.g., Pardo & Garcia, 2016), and Rolls et al. (2012) identify frequency of low flows as a 'key biological filter' and explain how low flows impact riverine ecology by controlling the extent, diversity and connectivity between physical habitats; mediating change in physical and chemical conditions and altering the sources and exchange of materials and energy within the systems.

If the influence of low flow event frequency is general, this could have significant implications for water managers wishing to increase biodiversity within managed systems. Low flows play a key role within natural river systems (Poff et al., 1997; Richter et al., 1996), and it would therefore be expected that such events would aid in regulating the ecosystem, preventing the dominance of certain species.

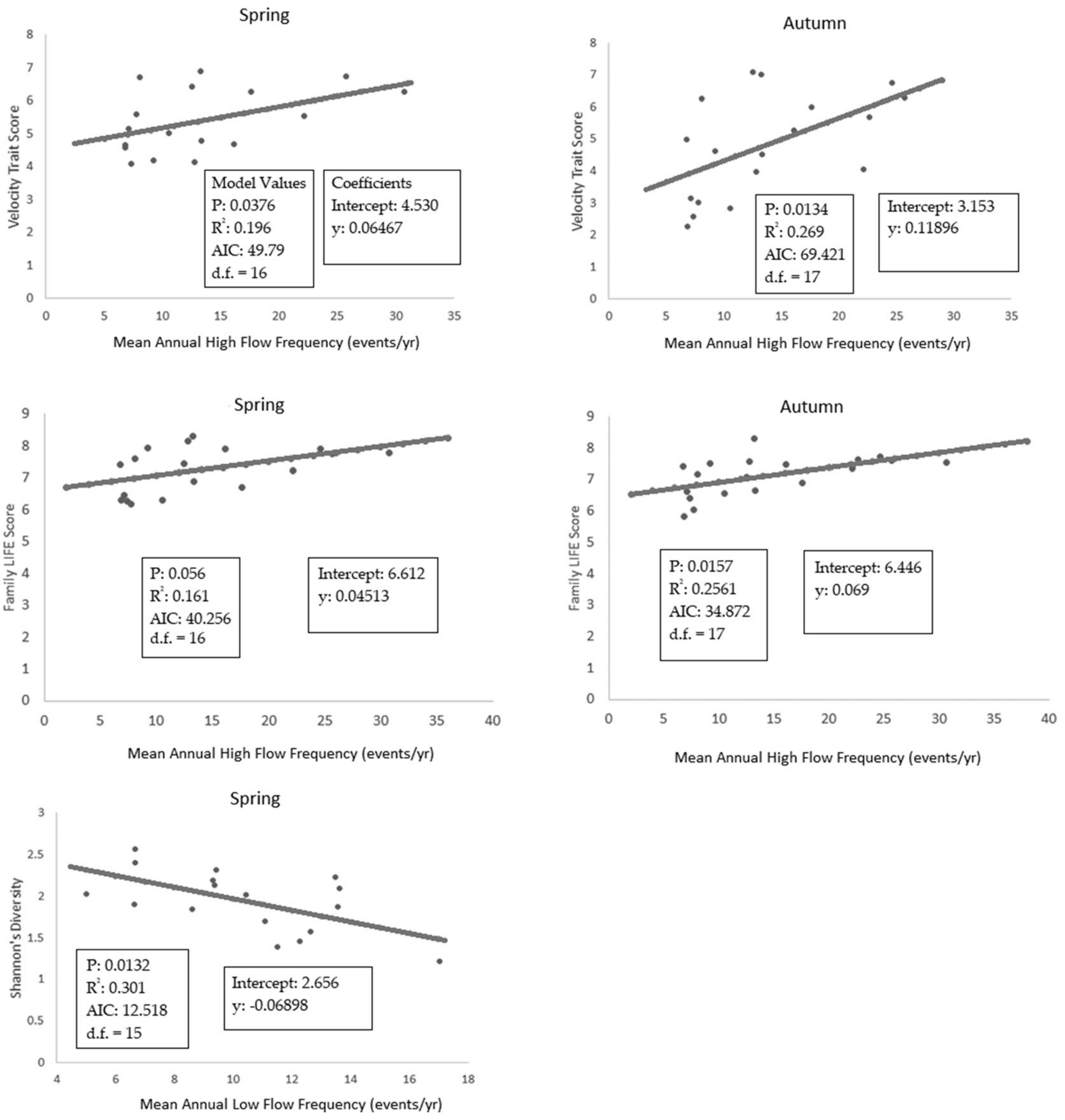


FIGURE 3 Univariate plots of the significant relationships between ecological indices and flow variables across the study sites, together with linear regionally applicable models, identified from the multiple regression analysis

5 | CONCLUSIONS

Results from this study have provided evidence that there are key flow characteristics that are strongly associated with ecological response and that significant predictive relationships can be found on a regional scale. Despite limitations such as the narrow scope of variables utilized, results do affirm the conceptual frameworks and empirical evidence on flow–ecology relationships that the magnitude, timing, duration and variability of flows influence macroinvertebrate diversity and composition. This suggests that highly modified flows, such as those observed within impounded systems, are likely to result in ecological communities different from those which might be expected under the natural flow regime. This conclusion is similar to findings from other studies investigating the impacts of flow modification (Gillespie, Brown, et al., 2015; Nichols et al., 2006). This study also affirms the suggestion of Chinnayakanahalli et al. (2011) that taxon richness and functional composition respond differently to flow alternation, and using only one of these metrics may fail to recognize significant changes within the ecosystem and that a broader suite of ecological metrics are required in order to fully evaluate changes within the ecosystem (Arthington et al., 2018; Poff et al., 2017). Results from this study are likely to have implications for water management decisions, such as the integration of flow variation into the environmental regime design. From the results, one might derive principles for similar river systems, for example, that having few high flow events (compared with non-modified flow conditions) is likely to cause a shift in functional composition within the ecosystem. River systems of similar flow magnitudes, geological characteristics and climate to those studied could be assessed in terms of hydrological characteristics through the process described here. Environmental flow regimes could be designed around influential flow characteristics such as flow event frequency, as in Hough et al. (2019), although further empirical testing is required in order to confirm that alteration of this metric via river modification follows the ecology–flow relationship observed in this study. We offer these observations as a promising area of further research in the context of mitigating anthropogenic impact on river systems, particularly through informing environmental flow design. Further research would help to develop specific design recommendations; further analysis of the seasonal timings of flow events, for example, may further understanding of the impact that events may have based upon when in the year they occur. The use of other metrics such as LIFE OE may also reveal further insights into how flow alteration is limiting the ecosystem.

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DATA AVAILABILITY STATEMENT

Publicly available time series datasets were obtained from the EA and the Centre of Ecology and Hydrology National River Flow Archive.

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APPENDIX 1

Site characteristics

Site	Gradient	Sinuousity	Topsoil	Confinement	Modification	Land use
Blackfoss Beck	0.020	1.044	Alluvial	Not confined	None visible	Agriculture
Colne	0.020	1.040	Alluvial/engineered	Not confined	Heavily modified	Urban
Crimple Blackstones	0.010	1.147	Alluvial	Not confined	None visible	Agriculture
Dearne	0.050	1.090	Alluvial	Not confined	Weirs	Suburban
Eastburn Beck	0.010	1.009	Alluvial	Not confined	Weirs	Agriculture
Foulness	0.007	1.039	Alluvial	Not confined	None visible	Agriculture
Ryburn	0.060	1.034	Alluvial	Not confined	None visible	Woodland/suburban
Skell	0.011	1.030	Alluvial/sand	Not confined	Weirs, Bridges	Suburban
Spen Beck	0.010	1.049	Alluvial	Not confined	None visible	Agriculture
Went	0.006	1.013	Alluvial	Not confined	Railway bridge	Agriculture
Calder	0.008	1.007	Alluvial	Not confined	None visible	Agriculture
Church Beck	0.017	1.007	Alluvial	Not confined	Weir	Agriculture
Douglas Wigan	0.020	1.083	Alluvial/engineered	Confined (Engineered)	Heavily modified	Urban
Eden	0.020	1.062	Alluvial	Not confined	None visible	Agriculture
Eea	0.015	1.103	Alluvial	Not confined	None visible	Agriculture/suburban
Heltondale	0.021	1.033	Alluvial	Not confined	None visible	Agriculture
Pendle Water	0.007	1.012	Alluvial	Not confined	None visible	Agriculture
Swindale Beck	0.020	1.016	Alluvial	Confined	Weirs	Agriculture

Gradient was calculated by taking elevations 50-m upstream and 50-m downstream of the flow gauging location; sinuosity was calculated along this same stretch by measuring the thalweg along the river, and the shortest direct path between upstream and downstream points, and dividing the thalweg length by the direct path between the two points. Topsoil, river confinement, river modification and land use were assessed visually through Google Earth Pro.

Site locations:

Site name	Flow gauging OS location	Ecology sample OS location	Distance between flow and ecology measurement sites
Blackfoss Beck	SE7249147392	SE7251947416	36 m
Colne	SE1364416110	SE0910914447	830 m
Crimple Blackstones	SE4013252956	SE3787951685	4000 m
Dearne	SE3497007279	SE3477007932	690 m
Eastburn Beck	SE0203545263	SE0148144826	702 m
Foulness	SE7797637277	SE7800738044	763 m
Ryburn	SE0354718938	SE0404819773	970 m
Skell	SE3157070949	SE3185270904	286 m
Spen Beck	SE2247621023	SE2261920934	242 m
Went	SE5506416309	SE5650116142	1440 m
Calder	SD4978643349	SD4988943319	108 m
Church Beck	SD3063997190	SD3020097600	605 m
Douglas Wigan	SD5861706027	SD5860906011	19 m
Eden	NY6045228312	NY6039128147	175 m
Eea	SD3643176385	SD3610076600	390 m
Heltondale	NY4943720421	NY4923520205	290 m
Pendle Water	SD8366535152	SD8365535455	296 m
Swindale Beck	NY5146113169	NY5360016300	3800 m

Site data and geology:

Site	Flow data	Superficial deposits	Bedrock
Blackfoss Beck	1974–2016	Silty gravelly sand, alluvium (silty clay)	Sandstone and mudstone
Colne	1978–2016	Alluvium, sand and gravel with sandstone	Mudstone
Crimple Blackstones	2000–2016	Alluvium (clay, silt, sand and gravel)	Sandstone and mudstone
Dearne	1960–2016	(Alluvium (clay and silt)	Sandstone
Eastburn Beck	1988–2016	Alluvium (clay, silt, sand and gravel), Alluvial fan deposits (clay, silt, sand and gravel)	Sandstone and mudstone
Foulness	2000–2016	Alluvium (silty clay), clayey sand, silty clay	Mudstone
Ryburn	1981–2016	Alluvium (clay, sand, and gravel)	Sandstone
Skell	1984–2016	Alluvium (clay, silt, sand and gravel)	Mudstone (calcerious)
Spen Beck	1982–2016	Alluvium (clay, sand and gravel)	Sandstone, mudstone, and siltstone

(Continues)

Site	Flow data	Superficial deposits	Bedrock
Went	1979–2016	Alluvium (clay, sand and gravel) with nearby silty clay deposits	Mudstone, sandstone, and dolomitic limestone local (lack of data resolution to see specific bedrock at sample site)
Calder	1997–2016	Alluvium (clay, sand and gravel)	Sandstone
Church Beck	2001–2017	Alluvium (silt and gravel)	Siltstone and mudstone local (lack of data resolution to see specific bedrock at sample site)
Douglas (Wigan)	1977–2014	Alluvium (clay, silt, sand and gravel)	Mudstone, siltstone, and sandstone
Eden	1964–2017	Till (diamicton)	Sandstone
Eea	2005–2017	Clay, silt, sand, and gravel	Mudstone, siltstone, and sandstone
Heltondale	1998–2016	Till (diamicton)	Sandstone
Pendle Water	1976–2016	No superficial deposit data available around site, closest visible deposits are Alluvium (clay, silt, sand and gravel) and Till (diamicton)	Mudstone and sandstone

Details on modification:

Site	Status
Eden	Not designated as artificial or heavily modified
Heltondale Beck	Not designated as artificial or heavily modified
Blackfoss Beck	Not designated as artificial or heavily modified
Colne	Heavily modified: flood protection, urbanization
Crimple Beck, Blackstones	Heavily modified: further data unavailable
Dearne	Heavily modified: flood protection, land drainage, urbanization
Eastburn Beck	Heavily modified: urbanization
Foulness	Not designated as artificial or heavily modified
Ryburn	Not designated as artificial or heavily modified
Skell	Heavily modified: flood protection, urbanization
Spen Beck	Heavily modified: flood protection, urbanization
Went	Heavily modified: flood protection
Calder	Heavily modified: flood protection, barriers (ecological discontinuity)
Church Beck	Not designated as artificial or heavily modified
Douglas Wigan	Heavily modified: water regulation, barriers (ecological discontinuity)
Eea	Not designated as artificial or heavily modified
Pendle Water	Not designated as artificial or heavily modified
Swindale Beck	Heavily modified: water regulation, drinking water supply

APPENDIX 2

Temporal and magnitude-based trait combinations used in modelling. Note that combinations with a P value of 0.2 or greater were not given further statistical consideration in terms of R^2 or AIC

TABLE B1 Spring LIFE score multivariate model fitting results

LIFE score—Spring				
Variable 1	**Variable 2**	***p***	***R*^{2}**	**AIC**
HighFreq	None	0.056	0.161	40.256
HighFreq	MINYR	0.1366	0.131	41.72
HighFreq	Q25	0.138	0.13	41.743
HighFreq	MeanMag	0.1628	0.11	42.141
HighFreq	RNGYR	0.1697	0.105	42.241
HighFreq	MAXYR	0.1699	0.1052	42.243
LowDura	None	0.45	n/a	n/a
LowDura	Q25	0.5231	n/a	n/a
LowDura	MINYR	0.5235	n/a	n/a
LowFreq	None	0.55	n/a	n/a
HighDura	MINYR	0.5605	n/a	n/a
HighDura	None	0.6	n/a	n/a
LowFreq	Q25	0.6244	n/a	n/a
LowDura	MeanMag	0.636	n/a	n/a
LowFreq	RNGYR	0.6727	n/a	n/a
LowFreq	MAXYR	0.6766	n/a	n/a
LowDura	RNGYR	0.6808	n/a	n/a
LowDura	MAXYR	0.6848	n/a	n/a
HighDura	Q25	0.69	n/a	n/a
HighDura	RNGYR	0.7153	n/a	n/a
HighDura	MAXYR	0.7218	n/a	n/a
LowFreq	MeanMag	0.735	n/a	n/a
LowFreq	MINYR	0.7382	n/a	n/a
HighDura	MeanMag	0.822	n/a	n/a

TABLE B2 Autumn LIFE score multivariate model fitting results

LIFE score—Autumn				
Variable 1	**Variable 2**	***p***	***R*^{2}**	**AIC**
HighFreq	None	0.0157	0.2561	34.872
LowDura	None	0.0543	0.1539	37.317
HighFreq	MINYR	0.0545	0.2181	36.666
HighFreq	Q25	0.0552	0.2167	36.699
HighFreq	RNGYR	0.0581	0.2117	36.82
HighFreq	MAXYR	0.0582	0.2116	36.823
HighFreq	MeanMag	0.0593	0.2097	36.869
LowDura	MINYR	0.1011	0.1552	38.135
LowDura	Q25	0.1298	0.1284	38.729
LowDura	RNGYR	0.1422	0.1184	38.946
LowDura	MAXYR	0.1434	0.1175	38.965
LowDura	MeanMag	0.1478	0.1141	39.038
HighDura	Q25	0.6611	n/a	n/a
LowFreq	RNGYR	0.8038	n/a	n/a

(Continues)

TABLE B2 (Continued)

LIFE score—Autumn				
Variable 1	**Variable 2**	***p***	**R^2**	**AIC**
HighDura	RNGYR	0.8039	n/a	n/a
HighDura	MAXYR	0.8087	n/a	n/a
LowFreq	MAXYR	0.8088	n/a	n/a
LowFreq	Q25	0.8132	n/a	n/a
LowFreq	MINYR	0.8468	n/a	n/a
HighDura	MINYR	0.8698	n/a	n/a
HighDura	MeanMag	0.8727	n/a	n/a
LowFreq	None	0.8966	n/a	n/a
HighDura	None	0.9093	n/a	n/a
LowFreq	MeanMag	0.9224	n/a	n/a

TABLE B3 Spring velocity trait score multivariate model fitting results

Velocity trait score—Spring				
Variable 1	**Variable 2**	***p***	**R^2**	**AIC**
HighFreq	None	0.0376	0.1959	49.79
HighFreq	Q25	0.055	0.2302	49.847
LowDura	Q25	0.0666	0.2103	50.307
LowDura	None	0.0793	0.1287	51.237
HighFreq	RNGYR	0.0802	0.1905	50.752
HighFreq	MAXYR	0.081	0.1893	50.778
HighFreq	MeanMag	0.0937	0.1735	51.126
HighDura	None	0.094	0.11	51.573
HighFreq	MINYR	0.1041	0.1618	51.378
LowDura	MeanMag	0.1187	0.147	51.693
LowDura	RNGYR	0.197	n/a	n/a
LowDura	MAXYR	0.197	n/a	n/a
LowDura	MINYR	0.225	n/a	n/a
HighDura	Q25	0.2314	n/a	n/a
HighDura	MINYR	0.252	n/a	n/a
HighDura	MeanMag	0.2573	n/a	n/a
HighDura	RNGYR	0.259	n/a	n/a
HighDura	MAXYR	0.259	n/a	n/a
LowFreq	Q25	0.3697	n/a	n/a
LowFreq	MeanMag	0.6084	n/a	n/a
LowFreq	None	0.77	n/a	n/a
LowFreq	MINYR	0.827	n/a	n/a
LowFreq	RNGYR	0.934	n/a	n/a
LowFreq	MAXYR	0.936	n/a	n/a

TABLE B4 Autumn velocity trait score multivariate model fitting results

Velocity trait score—Autumn				
Variable 1	**Variable 2**	***p***	***R*²**	**AIC**
HighFreq	None	0.01335	0.269	69.421
HighFreq	Q25	0.03	0.2742	70.135
LowDura	None	0.0352	0.1906	71.357
HighFreq	RNGYR	0.0467	0.2329	71.186
HighFreq	MAXYR	0.0468	0.2328	71.188
LowDura	Q25	0.046	0.2345	71.146
HighFreq	MeanMag	0.0458	0.2349	71.136
HighFreq	MINYR	0.0515	0.2235	71.417
LowDura	MeanMag	0.0752	0.1859	72.314
LowDura	MINYR	0.0981	0.1584	72.947
LowDura	MAXYR	0.1165	0.1401	73.354
LowDura	RNGYR	0.1165	0.1401	73.355
HighDura	None	0.3449	n/a	n/a
HighDura	Q25	0.4644	n/a	n/a
HighDura	MINYR	0.496	n/a	n/a
LowFreq	Q25	0.509	n/a	n/a
HighDura	RNGYR	0.527	n/a	n/a
HighDura	MAXYR	0.5277	n/a	n/a
HighDura	MeanMag	0.5445	n/a	n/a
LowFreq	MeanMag	0.75	n/a	n/a
LowFreq	None	0.8729	n/a	n/a
LowFreq	MAXYR	0.9712	n/a	n/a
LowFreq	RNGYR	0.9713	n/a	n/a
LowFreq	MINYR	0.984	n/a	n/a

TABLE B5 Spring Biodiversity multivariate model fitting results

Biodiversity—Spring				
Variable 1	**Variable 2**	***p***	***R*²**	**AIC**
LowFreq	None	0.0132	0.301	12.518
LowFreq	RNGYR	0.0278	0.3148	13.005
LowFreq	MAXYR	0.0281	0.3139	13.028
LowFreq	MINYR	0.0394	0.28	13.849
LowFreq	Q25	0.0426	0.2719	14.039
LowFreq	MeanMag	0.0472	0.2611	14.289
LowDura	MINYR	0.14	n/a	n/a
HighFreq	MINYR	0.14	n/a	n/a
HighDura	MINYR	0.14	n/a	n/a
LowDura	None	0.2016	n/a	n/a
LowDura	RNGYR	0.3757	n/a	n/a
LowDura	MAXYR	0.38	n/a	n/a

(Continues)

TABLE B5 (Continued)

Biodiversity—Spring				
Variable 1	**Variable 2**	***p***	***R*²**	**AIC**
LowDura	Q25	0.42	n/a	n/a
LowDura	MeanMag	0.4515	n/a	n/a
HighDura	None	0.4613	n/a	n/a
HighDura	RNGYR	0.55	n/a	n/a
HighDura	MAXYR	0.5636	n/a	n/a
HighDura	Q25	0.76	n/a	n/a
HighDura	MeanMag	0.77	n/a	n/a
HighFreq	MAXYR	0.92	n/a	n/a
HighFreq	RNGYR	0.92	n/a	n/a
HighFreq	None	0.9322	n/a	n/a
HighFreq	MeanMag	0.97	n/a	n/a
HighFreq	Q25	0.99	n/a	n/a

TABLE B6 Autumn biodiversity multivariate model fitting results

Biodiversity—Autumn				
Variable 1	**Variable 2**	***p***	***R*²**	**AIC**
HighDura	None	0.18	n/a	n/a
HighDura	RNGYR	0.29	n/a	n/a
HighDura	MAXYR	0.29	n/a	n/a
LowDura	RNGYR	0.31	n/a	n/a
LowDura	MAXYR	0.32	n/a	n/a
LowDura	None	0.36	n/a	n/a
HighDura	Q25	0.39	n/a	n/a
HighDura	MeanMag	0.4	n/a	n/a
HighDura	MINYR	0.42	n/a	n/a
HighFreq	RNGYR	0.42	n/a	n/a
LowFreq	RNGYR	0.43	n/a	n/a
LowFreq	MAXYR	0.43	n/a	n/a
LowDura	MeanMag	0.6	n/a	n/a
LowDura	Q25	0.62	n/a	n/a
LowDura	MINYR	0.64	n/a	n/a
HighFreq	None	0.65	n/a	n/a
LowFreq	None	0.7	n/a	n/a
LowFreq	Q25	0.78	n/a	n/a
LowFreq	MeanMag	0.79	n/a	n/a
HighFreq	MAXYR	0.8	n/a	n/a
HighFreq	MeanMag	0.8	n/a	n/a
HighFreq	Q25	0.8	n/a	n/a
HighFreq	MINYR	0.9	n/a	n/a
LowFreq	MINYR	0.92	n/a	n/a

APPENDIX 3

This appendix demonstrates that the use of datasets of differing length has a negligible impact on data, and their use is a justifiable approach. Four randomly selected sites from the dataset were chosen for this demonstration.

Before going into each individual site, a table is presented to show the range of values across all sites (maximum value minus minimum value) for each of the described metrics, so as to put any differences between full and shortened periods into perspective.

Metric	Range across sites (max–min)
Mean annual flow (m^2/s)	2.52
Low flow frequency	12.03
Low flow duration (days)	16.41
High flow frequency	23.95
High flow duration (days)	2.58

The above table will demonstrate, when the results below are observed, that the differences shown between the full and shortened datasets at any single site are very minor relative to the full range of the data across sites.

Blackfoss Beck (1974–2016) shows a higher occurrence of extreme events in recent years, but overall metrics for flow frequencies and durations see little change when comparing a full dataset with a 1998–2016 dataset. The mean daily flow between the two datasets does see some differences despite the majority of the dataset having regular flow patterns; as mentioned, this may be because of the decreased resilience to extreme events in the case of shorter datasets.

Church Beck (2003–2017) is mostly similar when comparing the full and the shortened datasets (2011–2017). The most significant difference between datasets is the mean duration of low flow events. Given that there is little change in mean annual flow or the frequency of low flows, it is possible that one or two extreme events are driving this discrepancy. Given that the shortened dataset in this case is only

Blackfoss Beck			
Full period		**1998–2006**	
Mean annual flow (m^2/s)	0.45	Mean annual flow (m^2/s)	0.56
Low flow frequency	7	Low flow frequency	7
Low flow duration (days)	6	Low flow duration (days)	7
High flow frequency	10	High flow frequency	12
High flow duration (days)	4	High flow duration (days)	4

Church Beck			
Full period		**2011–2017**	
Mean annual flow (m^2/s)	0.82	Mean annual flow (m^2/s)	0.87
Low flow frequency	12	Low flow frequency	13
Low flow duration (days)	4	Low flow duration (days)	6
High flow frequency	28	High flow frequency	30
High flow duration (days)	2	High flow duration (days)	2

Colne			
Full period		**1997–2016**	
Mean annual flow (m^2/s)	1.44	Mean annual flow (m^2/s)	1.48
Low flow frequency	17.5	Low flow frequency	13
Low flow duration (days)	2.25	Low flow duration (days)	4
High flow frequency	17	High flow frequency	18
High flow duration (days)	2.25	High flow duration (days)	2

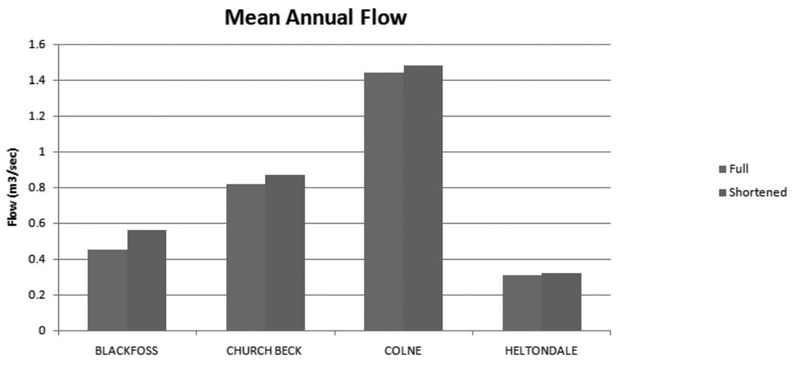
Heltondale Beck			
Full period		**2006–2016**	
Mean annual flow (m^2/s)	0.31	Mean annual flow (m^2/s)	0.32
Low flow frequency	8	Low flow frequency	8
Low flow duration (days)	6	Low flow duration (days)	5
High flow frequency	15	High flow frequency	18
High flow duration (days)	2	High flow duration (days)	2

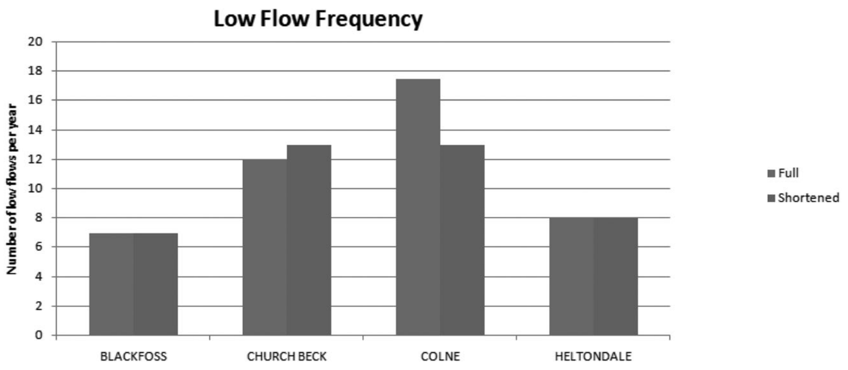
6 years, this seems a good possibility—given that a shorter dataset will become increasingly less resilient to the influence of such events.

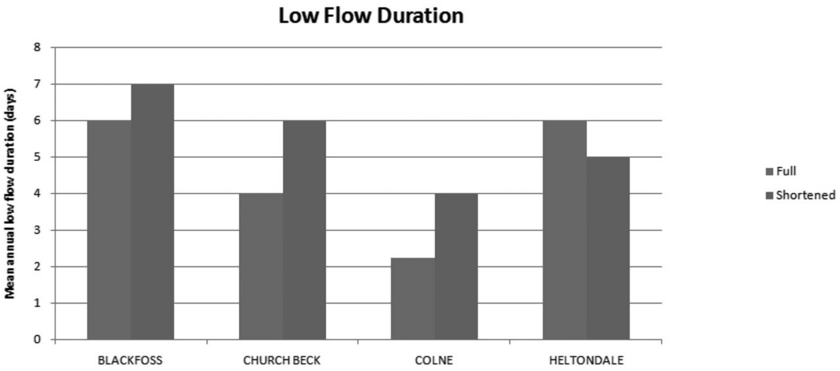
Colne (1978–2016) shows little characteristic change in terms of overall flow patterns across the dataset, and retains a very similar mean daily flow when comparing full and limited (1997–2016) datasets. High flow frequency and durations also remain similar between ranges of time. Low flows see some differences between full and shortened datasets; based on the similarities of all other metrics, this is likely because of the influence of extreme low flow events having a greater influence over the shorter dataset, and arguably the longer dataset better reflects mean and long-term conditions.

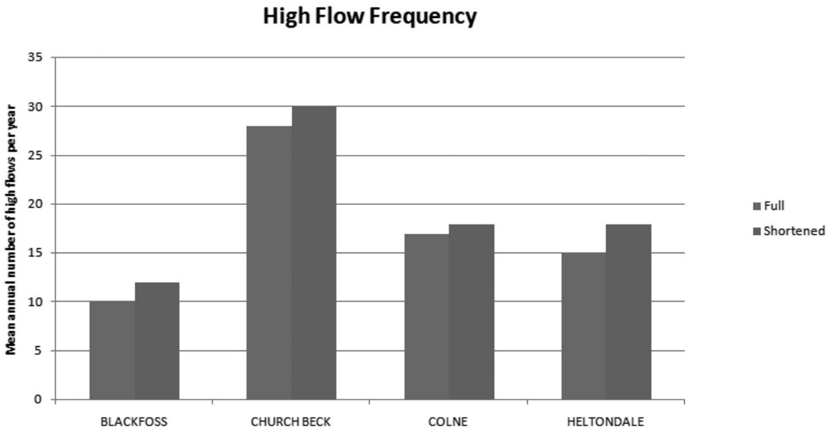
Heltondale Beck (1998–2016) has almost identical mean annual flows between full and shortened datasets (2006–2016). High and low flow duration and frequency are likewise almost identical between the two time periods. This flow time series appears to have few, if any, extreme events, which is likely why the shortened dataset remains so closely aligned to the metrics of the full dataset.

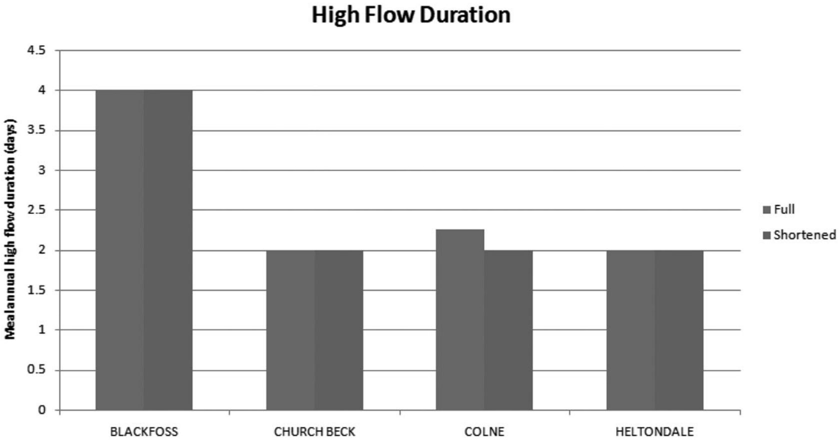
To conclude on the results of this testing, we believe that there is good evidence that the length of the time series carries only a minor impact on calculated IHA metrics, justifying the approach used. We would also mention that overly shortening time series data would theoretically decrease the resilience of our metrics to extreme events, meaning that longer time series would be expected to better characterize the general hydrological character of each site, and hence we have used as much data as was available for each site.Graphs providing a visual illustration of differences between datasets for each metric follow.






Low Flow Duration
Mean annual low flow duration (days)
0
1
2
3
4
5
6
7
8
BLACKFOSS
CHURCH BECK
COLNE
HELTONDALE
■ Full
■ Shortened


High Flow Frequency
Mean annual number of high flows per year
0
5
10
15
20
25
30
35
BLACKFOSS
CHURCH BECK
COLNE
HELTONDALE
■ Full
■ Shortened


High Flow Duration
Mealannual high flow duration (days)
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
BLACKFOSS
CHURCH BECK
COLNE
HELTONDALE
■ Full
■ Shortened