The concept of environmental flows has been developed to manage human alteration of river flow regimes, as effective management requires an understanding of the ecological consequences of flow alteration. This study explores the concept of macroinvertebrate sensitivity to river flow alteration to establish robust quantitative relationships between biological indicators and hydrological pressures. Existing environmental flow classifications used by the environmental regulator for English rivers were tested using multilevel regression modelling. Results showed a weak relationship between the current abstraction sensitivity classification and macroinvertebrate response. An alternative approach, based on physically derived river types, was a better predictor of macroinvertebrate response. Intermediate sized lowland streams displayed the best model fit, while upland rivers exhibited poor model performance. A better understanding of the ecological response to flow variation in different river types could help water resource managers develop improved ecologically appropriate flow regimes, which support the integrity of river ecosystems.

**KEYWORDS**
abstraction sensitivity, ecohydrology, flow–ecology relationships, hydroecology, LIFE index, mixed effects modelling
to changes in river flow (Dunbar et al., 2010a; Poff et al., 1997), hence they should also differ in their ecological response to water abstraction. This sensitivity may be influenced by river size, geology and landscape characteristics (Booker et al., 2015). These differing responses may be useful in determining locations where more or less water may be removed, allowing a more nuanced approach to resource allocation which is able to maximize water availability while ensuring environmental protection at locations more susceptible to altered flow regimes.

The Water Framework Directive (WFD) is the main legislative tool which governs the protection and management of inland surface, transitional, coastal and ground waters within Europe. Central to the Directive is the creation of typologies of water bodies (rivers or stretches of rivers) based on instream characteristics and biological communities that represent conditions unaffected by anthropogenic pressures (Logan & Furse, 2002). These typologies are often referred to as “reference conditions” to which current or observed conditions or biological communities can be compared to, to determine whether a site’s ecological status may have deviated from the reference or ideal conditions (Hughes et al., 1998). Using ecological metrics such as macroinvertebrate (LIFE (Extence et al., 1999), WHPT (Paisley et al., 2014), PSI (Extence et al., 2013)), fish (IBI: Karr, 1981) and diatom indices (TDI; Kelly, 1998), an ecological quality ratio (EQR) synthesising the comparison between observed and expected biological quality, and hence a likelihood of impact of anthropogenic pressure can be determined (Jones et al., 2010). The use of an EQR rather than comparison of species composition, abundance or density data allows the comparison of sites covering a large geographical area and intercalibration between a range of sites and countries (Arle et al., 2016).

Given the use of typologies and classifications in tandem with EQR assessments in environmental legislation and the perceived sensitivity of waterbodies to changes in flow because of water withdraws and discharges, typologies are increasingly being used in determining water resource availability (e.g., Milano et al., 2013; Munia et al., 2018; Viviroli et al., 2007). The use of classifications as general “rules of thumb” for assessing which waterbodies may be more or less sensitive to altered flow regimes are particularly useful for regulatory authorities in determining allowable abstraction limits (Acreman et al., 2006, 2008; UKTAG, 2013). Within the criteria, a river’s sensitivity to flow alteration as a result of water abstractions is taken into account in the form of Abstraction Sensitivity Bands (ASBs; Environment Agency, 2013a). ASBs are intended to reflect the perceived sensitivity of instream biota to anthropogenic changes in flow with ASB group 1 rivers deemed to have the lowest sensitivity to changes in water flow (hence, more water may be taken) and ASB group 3 being the most sensitive and where less water should be taken (Supplementary material Table S1). This approach is used to determine where water may be available for new abstraction and to highlight where abstraction pressure may be having an undesirable ecological effect. However, it is limited currently by the confidence of its ecological justification and making best use of new evidence. Alternative empirically derived classification methods based on physical river characteristics have been found to provide adequate flow alteration–ecological response relationships (e.g., Poff et al., 2010; Snelder & Biggs, 2002) and may provide a more robust method of determining macroinvertebrate community sensitivity to flow alteration.

Central to developing improved relationships between the magnitude of anthropogenic river flow alteration and ecological response is the availability of adequately paired hydrological and biological data from which pressure–response relationships can be derived (Monk et al., 2007). An idealized relationship between a macroinvertebrate indicator and flow alteration is shown in Figure 1. A flow regime below natural (i.e., below 100% of natural flow) should manifest as impacted biota (reflected in the decrease of the macroinvertebrate indicator). Previous research (White et al., 2021) has shown that flow above natural flow (i.e., at discharge-rich sites) negatively affects instream biota; however, the sparsity of further empirical evidence necessitates a split response curve as shown at flows >100.

The research aim of this study is to assess how well the current (ASB) method and an alternative physically based river classification approach are able to predict the biological response (indices of observed macroinvertebrate community composition and their deviation from an expected condition, expressed as observed/expected macroinvertebrate scores) to changes in flow (expressed as percentage deviation from “natural” flow). A paired multi-site and multi-year (including seasonal) historical hydrological and biological dataset is used, allowing the use of multilevel (mixed effects) additive regression modelling, a modern statistical tool being increasingly used by ecologists (Bolker et al., 2009; Pedersen et al., 2019). This analytical approach has already shown its potential in modelling the biological response to flow changes (Dunbar et al., 2006, 2010a, 2010b; Klaar et al., 2014). Given the increasing evidence of the combined impact of poor water quality, habitat modification and flow alteration acting in tandem to increase the individual stressor impact on ecological integrity (e.g., Birk et al., 2020) resulting in failures declines in waterbody status as determined by the WFD (Lemm et al., 2021), we included these interactions within our models. Testing of these relationships and
classification approaches will provide a better understanding of the links between hydromorphological pressures, chemical status and river ecology to determine their role in maintaining good ecological integrity.

2 | METHODS

Biological, chemical and physical data collected and administered by the Environment Agency (EA) is used throughout this study. This study has focussed on a time period covering 2008–2014 to limit the confounding effects of changes in sampling methods and improvements in water quality over time (Friberg et al., 2011; Vaughan & Gotelli, 2019). This time period also ensured the data covered two drought periods (2005/2006 and 2010/2011).

Throughout this paper, the term abstraction is used as a shorthand to include groundwater and surface water abstraction (withdrawal), and flow regulation by reservoirs. Augmentation is used to refer to situations where individual waterbodies have flows elevated above natural, whether by reservoir release, effluent discharge or water transfer. The term flow alteration is used to refer to either situation.

2.1 | Datasets

Macroinvertebrate biotic scores, modelled flow alteration, habitat alteration and environmental data were obtained from the Environment Agency’s (EA) national databases, and matched at the site level using the EA’s unique water body identification number. Spatial analysis of the proximity of data points from the differing datasets were assessed to ensure that they were within each waterbody polygon, with no tributaries entering the waterbody between data points which might influence waterbody characteristics.

2.1.1 | Hydrological alteration

River flow alteration data were obtained from an existing EA dataset, based on recent actual abstraction licence returns and consented discharges, accompanied by modelled data on naturalized flows (Environment Agency, 2013b; Klaar et al., 2014). Abstraction and discharge data comprised an aggregate for the period 2008–2014 as a result of the variable nature of licensed flow alterations. A measure of flow alteration was derived by comparing the difference in flow between modelled “natural” flow and modelled recent actual flow, using recorded data on abstractions and discharges (Klaar et al., 2014), and expressed as percentage of the residual flow, i.e.:

\[
\left( \frac{\text{recent actual flow}}{\text{natural flow}} \right) \times 100 = \%\text{ residual of natural flow.}
\]

Using this flow alteration value, values closer to 100% indicate that there is little alteration from the expected “natural” flow regime, values less than 100% indicate recent actual flows below natural, and values above 100% indicate augmented locations, mainly rivers supported by reservoir release flows or by treated effluent discharges. Values higher than 150% were removed to exclude atypical biology responses to flow (Poff et al., 2007), which were unlikely to fit a generic model. Flow alteration (% residual flow) was calculated at two flow percentiles; Q30 (flows exceeded 30% of the time, representative of medium-high flows), and Q95 (flow exceeded 95% of the time, indicative of low flow periods), by
taking the ratio of recent actual flow to natural flow at the same percentile. This is an inherent simplification as these flows may not occur at the same time in practice, but it was chosen for simplicity and consistency.

2.1.2 | Biological data

The LIFE (Lotic Invertebrate index for Flow Evaluation) biotic index (Exente et al., 1999) was used as a measure of invertebrate response as it had been linked with historical flow in previous studies (e.g., Dunbar et al., 2010a, 2010b; Monk et al., 2006, 2007). LIFE scores were standardized as observed/expected (O/E). Use of standardized rather than “actual” observed scores in this manner allows comparison of scores between rivers of varying characteristics or “ecotypes” (e.g., geology, altitude, size and alkalinity) and hence differing ecological composition, diversity and abundance, as would be expected at a national scale (Pollard & Huxham, 1998). Expected scores were derived using the River Invertebrate Classification Tool (RICT; available at FBA, 2021), which implements the River Invertebrate Prediction and Classification System (RIVPACS) IV model (Davy-Bowker et al., 2008). LIFE O/E at family level, covering two 6-year WFD reporting periods, from 2002 to 2014, were used to assess the biotic response to flow within the models. Data were separated by season (spring: March-May and autumn: September-November) as LIFE score response to historical flow has been shown to vary by season (Dunbar et al., 2010b).

2.1.3 | Other pressures

The 2015 physico-chemical WFD waterbody classification assessment data, based on dissolved oxygen and ammonia standards, were used to screen out any sites failing in either of these variables to limit any confounding water quality pressures in defining flow-ecology relationships. This screening resulted in a total of 11,745 records for the spring and 11,224 for the autumn dataset, covering 2,484 sites.

2.1.4 | Catchment and river morphology characteristics

Wider catchment characteristics (land-cover, morphological alterations and presence of flood defence works) were included to evaluate any potential interactions with these factors. Land-cover data were provided via a study on diffuse agricultural pollution (Naden et al., 2015). Six higher level aggregations of land cover were derived from the land-cover 2007 (LCM2007) map (Morton et al., 2011): percentage of arable/horticultural land, improved grassland, broad-leaved woodland, urban/suburban land, coniferous woodland, and broadly defined “agricultural” land cover. LCM2007 is a parcel-based classification, derived from satellite images and digital cartography and provides land-cover data. Land cover data were derived for a 50 m riparian buffer zone around the river, from the site upstream to each tributary source as marked on the 1:50,000 river network.

River morphological alteration metrics were derived from Environment Agency River Habitat Survey data (RHS; Raven et al., 1998) data covering ~16,700 sites surveyed between 1994 and 2004 (Naden et al., 2015). Habitat modification scores (HMS), HMS sub-scores (re-sectioned bed and banks and bank poaching (trampling) by livestock) and Habitat Quality Assessment (HQA) scores were used to assess the degree of the channel modification. Where multiple RHS surveys occurred on a waterbody, a median score was calculated. The percentage of historical flood defence works present at a surveyed site was obtained from an EA digitized dataset, covering a period from 1930 to 1980 (Brookes et al., 1983). This included the percentage of the length of river (km) with flood defence works, together with river channelization features of channel morphology modification: bank reinforcement, re-sectioning, re-alignment, re-grading and embankments.

2.2 | Alternative classifications

The applicability of the current ASB river sensitivity classification was tested for ecological relevance using biological response to flow alteration. Sites were categorized by their current ASB classification and modelled independently. The dataset comprised a total of 136 Band 1, 917 Band 2 and 941 Band 3 water bodies (Supplementary material Figure S1).

A second classification based on the most probable RIVPACS Super End Group (SEG) was also tested. SEGs are a step within the process of predicting expected macroinvertebrate index scores for a site; they reflect the ecological community similarities in the underlying clustering of RIVPACS “reference” sites using TWINSPAN (Davy-Bowker et al., 2008; Friberg et al., 2011). SEGs represent a potentially more ecologically based classification as they are based on the known associations between reference macroinvertebrate communities and physical site characteristics. SEGs (Supplementary material Table S2; Supplementary material Figure S2) were predicted for each site using the physical environmental characteristics required to run the RIVPACS model (slope, altitude, stream width and depth, substratum composition, average annual discharge category, alkalinity, average temperature conditions and distance from source; Davy-Bowker et al., 2008). Super end group A was not included in this study as this group is exclusively outside of England.

2.3 | Statistical analysis

Statistical analyses were undertaken using R (version 3.2.1; R Development Core Team, 2014). Given the large number of zero values in the HMS (re-sectioned) score, these data were rescaled using a log(1 + x) transformation. All other data remained unchanged. To test for redundancy, a cross-correlation (Spearman’s) test was applied to account for and identify any highly and significantly correlated
explanatory variables. Where variables were highly correlated, only one variable was chosen for inclusion in subsequent modelling.

A multilevel generalized additive mixed-effect modelling (GAMM) approach (using the gam4 package, Wood, 2009) was applied to describe changes in LIFE O/E scores to flow alterations separately for macroinvertebrate data collected in spring and autumn seasons. The variation among the water bodies and sites were treated as nested because they are hierarchically structured with multiple sites per water body. Multilevel modelling enabled the explanatory variables to be used within the model by letting residual variance at different levels (as random effects) to be modelled, allowing different responses among groups (at site/waterbody scale) to be taken into account (Table 1).

Starting with a global model (all sites), alternative formulations of model predictors were fitted and ranked using the “dredge” function from the R MuMIn package (Barton, 2016). The top four candidate models (determined using Akaike's Information Criterion; AIC) were used to identify the most important predictors of LIFE O/E scores for Q30 and Q95, representing “high” and “low” flow statistics and the different seasons.

### Table 1: Summary of the model variables used in GAMM models

| GAMM effects       | Variables                       |
|--------------------|---------------------------------|
| Smoothing function s() | % Residual Q30 % Residual Q95 |
| Fixed              | Year % land-cover (broadleaved woodland, urban) % Habitat Modification Scores (HMS; poaching and re-sectioning) % Habitat Quality Scores (HQA) % Flood defence works |
| Nested random      | Waterbody ID Site ID |
| Factors            | ASB Super end groups |
| Interactions       | % Residual Q30-HMS Re-sectioned scores % Residual Q95 = HMS Re-sectioned scores |

### Table 2: Summary of the MuMIn data dredge results produced from the global model for spring macroinvertebrate data

| SPRING | % HMS Poaching | % HMS Resected | % HQA | % broadleaf | % CapWks | % urban | Year | AIC | delta | weight |
|--------|----------------|----------------|-------|-------------|----------|---------|------|-----|-------|--------|
| LIFE O/E Q30 | -0.000012 | 0.0005 | -0.0008 | 0.003 | -38799 | 0.00 | 0.768 |
|          | -0.000014 |          | -0.0008 | 0.003 | -38796 | 2.45 | 0.226 |
|          | -0.000012 | 0.0005 | -0.0008 | 0.003 | -38799 | 10.49 | 0.004 |
|          | -0.000014 |          | -0.0008 | 0.003 | -38786 | 12.92 | 0.001 |
| LIFE O/E Q95 | -0.000012 | 0.0005 | -0.0008 | 0.003 | -38799 | 0.00 | 0.773 |
|          | -0.000014 |          | -0.0008 | 0.003 | -38796 | 2.45 | 0.227 |
|          | -0.000012 | 0.0005 | -0.000004 | 0.003 | -38781 | 18.62 | 0.000 |
| 0.000016 | -0.000120 | 0.0005 | -0.0008 | 0.003 | -38781 | 18.64 | 0.000 |

Abbreviations: CapWks, capital works; HMS, habitat modification score; HQA, habitat quality score.

LIFE O/E response to flow pressure at waterbodies grouped by ASB was undertaken to test the validity of the current ASB classification. Waterbodies grouped using the SEGs then tested the potential use of this classification in determining flow-ecology relationships. As habitat modification has previously been shown to influence LIFE O/E (Dunbar et al., 2010a, 2010b) additional analysis of the SEG models were undertaken using an interaction factor, which estimates the smoothed trend separately, allowing for a different trend for each re-sectioned category and for each super end group.

### Results

Biological community response (LIFE O/E) to flow alteration was found to vary by season and flow condition (Q30 vs Q95). Multilevel modelling of these responses in relation to the current method of classifying waterbody sensitivity to flow change (ASBs) and an alternative classification derived from physical characteristics (RIVPACS SEGs) and habitat modification further established the flow-ecology relationships.

#### 3.1 Multilevel modelling

Cross-correlation analysis (Supplementary material Figure S3) shows that the most highly correlated values were % agricultural land cover (hereafter termed % agriculture) and % arable (Spearman rank = 0.77), followed by % agriculture and % broadleaf, HQA scores and % arable, % re-sectioning and % horticulture, % agriculture and % coniferous and % agriculture and % improved grassland and (−0.47, −0.40, 0.40, −0.38 and −0.32, respectively). To avoid the high degree of correlation between land management practices, % arable, % grassland, % coniferous woodland and % agriculture were excluded from the global model, leaving only % broadleaf cover and % urbanization within the model to represent natural vs modified land cover classifications respectively.

The top four models sorted for each season and flow percentile (Tables 2 and 3) showed that for spring, % re-sectioning and % urban were the strongest predictors in the top candidate models, with year
having a slightly positive relationship, and re-sectioning and % urban land-cover negatively related to biotic scores. Percentage broadleaf woodland was an important factor in the top candidate models for both Q30 and Q95 and was also included in the third high flow (Q30) model and in the third and fourth low flow (Q95) models. Percentage flood defence works were used as a predictor in the third low flow model, indicating that it had a negative impact on LIFE O/E score, whereas livestock poaching was used in the fourth low flow model, suggesting a slightly positive influence on LIFE O/E.

Autumn sampling models (Tables 2 and 3) consistently used year and re-sectioning as predictors in the top models, in addition to % broadleaf woodland. Percentage urban land use was an important (negative) influence in 3 out of 4 models in both high and low flow percentiles, while the % flood defence works was used in the fourth candidate model of both flow percentiles, indicating that it may have a positive influence on LIFE O/E scores.

### 3.1.1 ASB classification and macroinvertebrate response

In general, models representing the changes in LIFE O/E scores with residual flow grouped by ASB classifications were similar in both seasons and flow percentiles (Figure 2). ASB1 (low perceived sensitivity to flow change) displayed a decline in LIFE O/E score with increasing flow. The slope of this relationship is particularly steep in the autumn models. The large confidence intervals in combination with a marked negative relationship of macroinvertebrate scores is evident in group G. Groups B, C and D predict a decrease in spring LIFE O/E scores with increasing residual flow at Q95, the response of which is most pronounced for end group D.

### 3.1.2 Physically based super end group modelling

Modelling of macroinvertebrate LIFE O/E response to residual flow change classified by SEGs reveals a more varied relationship between river classifications. In general, there is no relationship (shown as a flat line) between biotic response and residual flow pressure at Q30 (Figure 3a) for end groups B and C (upland streams in Northern England and intermediate sized rivers respectively; Table S2) in both seasons. End groups E, F and G show relatively unresponsive relationships with spring LIFE O/E scores and high (Q30) flow. Group D streams (small, steeper upland streams) displays a large increase in spring LIFE O/E score when residual flow at Q30 rises from 40 to 60% of residual flow, before declining up to 80% residual flow. At Q95 (Figure 3c), groups E and G (intermediate size and lowland, fine sediment dominated rivers) show a general peak at near natural (100% residual) flows, similar to the “idealized” relationship illustrated in Figure 1. A second peak in macroinvertebrate scores is evident in group G. Groups B, C and D predict a decrease in spring LIFE O/E scores with increasing residual flow at Q95, the response of which is most pronounced for end group D.

### 3.1.3 Physically based super end group modelling

Autumn LIFE O/E metrics and residual flow changes for streams classified as groups B, C, F and G show no response in LIFE O/E scores during high flows (Figure 3b), with a near flat line predicted response. Group D shows a peak in LIFE O/E scores with an increase when flow is 60% of the modelled natural flow. The predicted macroinvertebrate response in autumn low flows (Figure 3d) shows a marked decrease in LIFE O/E for group D as residual flow increases, but note the large error bars. A similar decrease in autumn LIFE O/E with increasing residual flow at Q95 is also observed at the end groups B and C and to some (smaller) extent at the end groups F and G, although the slope of response at these sites is much shallower. Super end group E streams (intermediate sized lowland streams) shows the best response in predicted autumn LIFE O/E.
3.1.3 Habitat modification and end group modelling

Inclusion of habitat modification as an interaction term in the end group modelling (Figure 4) shows a high uncertainty in the models at low and high residual flows for both seasons, as represented by the large confidence intervals, reflecting the small number of values at the high and low ends of the dataset. Macroinvertebrate response to flow pressure at higher flows (Q30; Figure 4a,b) shows a less instinctive relationship, with macroinvertebrate O/E scores displaying a double peak at moderate flow pressure (~50% residual flow) and at natural flow (100% residual flow) for most end group members. This response was particularly obvious in groups D and F, characterized as smaller waterbodies.

The goodness-of-fit test (Table 4) reveals a fairly good relationship between the modelled spring LIFE O/E response to residual flow at Q95 and the habitat modification for most end groups. In Groups D and E, macroinvertebrate scores show a decline with decreasing

**FIGURE 2** Modelled spring LIFE observed/expected (O/E) response to changes in % residual flow at Q30 (a) and Q95 (c) and autumn LIFE O/E response at Q30 (b) and Q95 (d) using ASB groupings. The solid line is the predicted value of the dependent variable (LIFE O/E) as a function of the covariate (in the x-axis). The dashed lines show the 2x standard errors (SE) of the estimates, roughly 95% of the predicted values fall within the area, whereas the small lines along the x axis show the distribution of x values (residual flow). The y axis is in linear units so that the values are centred on 0 and extend to both positive and negative values. Note the differences in y axis scales between Q30 (a & b) and Q95 (c & d)
flow pressure (increasing residual flow). These groups explain better (~50% of the variability) the fitted model at both high (Q30) and low (Q95) flows.

4 | DISCUSSION

This study has shown that the inclusion of physical characteristics within river classifications of ecological sensitivity to flow alteration can provide a useful tool in setting water management policies at a national level. Our models show that the use of physically derived river types were a stronger predictor of macroinvertebrate response to flow alteration. Two river types (intermediate sized lowland rivers and small, steep rivers located within 13 km of the river’s source) appear to respond more strongly to these alterations, often displaying the “idealized” relationship between the macroinvertebrate indicator and flow alteration. By using empirically derived relationships of waterbody characteristics and ecological response to abstraction and discharge pressures, this work sets the basis of future evidence-based environmental policies and practice. The work also recognizes the potential interaction of environmental stressors in driving declines in ecological integrity and status as determined by the Water Framework Directive (Lemm et al., 2021).

A limited number of studies have quantified flow alteration-ecological response relationships across multiple sites (e.g., Bradley et al., 2017; Krajenbrink et al., 2019; White et al., 2018). Most hydro-ecological assessments have examined biotic responses to historical inter-annual flow variability (e.g., Dunbar et al., 2010a, 2010b; Monk et al., 2006; Wood & Petts, 1994; Worrall et al., 2014), which means that abstraction impacts have to be inferred indirectly. Regional hydroecological models such as those of Bradley et al. (2017) and Visser et al. (2017) are useful in developing local regulatory decisions, but little is known about macroinvertebrate response to flow changes at an even broader (i.e., national) scale (although see Tonkin et al., 2018). Our modelling of the residual flow-biology relationships provides such a national-scale assessment and illustrates the importance of habitat-based explanatory variables in the development of empirical statistical models of macroinvertebrate metric response to changes in flow.

4.1 | Performance of river classifications in predicting biotic sensitivity

The ASB classification (based on UKTAG: Acreman et al., 2006, 2008) was not a strong discriminator of changes in

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**FIGURE 3** Modeled (a) spring and (b) autumn Q30 and (c) spring and (d) autumn LIFE observed/expected (O/E) response to changes in % residual flow, using super end groups, as indicated by the letter at the top of each plot. Note the differences in y axis scales between Q30 (a & b) and Q95 (c & d).
macroinvertebrate response to low (Q95) flow pressure for either spring or autumn macroinvertebrate data. Super end groups (SEG) displayed a better relationship between flow alteration and macroinvertebrate LIFE O/E score. For the D, E, F and G groups, there was a decline in macroinvertebrate scores at flows higher than natural (discharge-rich scenarios). This may reflect that flow augmentation could be associated with effluent discharges and thus impaired water quality (Friberg et al., 2010; Metcalfe-Smith, 1996). Although sites were filtered for poor water quality based on dissolved oxygen and ammonia, there may have been other ecological effects from effluent discharges. Alternatively, flows elevated above natural may be associated with a more homogeneous flow regime (Poff et al., 2007) with lower than natural variability in flow magnitudes over time. Further research is needed to confirm the influence of flows above natural and explore the mechanisms behind the response.

There was a notable lack of response for SEG B, representing upland streams mainly located in northern England and C, intermediate-sized rivers, often in northern and south west England. This may reflect the diverse range of geologies within the groups influencing biotic response (Booker et al., 2015), or it may simply reflect a lack of data across the full range of flow alteration.

**TABLE 4** Summary of goodness-of-fit (adjusted R-squared percentage) from the spring and autumn models for the macroinvertebrate data

| Super end group | LIFE O/ \(E_{spring}^{*}\)Q95% | LIFE O/ \(E_{spring}^{*}\)Q30% | LIFE O/ \(E_{autumn}^{*}\)Q95% | LIFE O/ \(E_{autumn}^{*}\)Q30% |
|-----------------|---------------------------------|--------------------------|--------------------------|--------------------------|
| B               | 25.6                            | 24.7                     | 20.6                     | 16.3                     |
| C               | 45.0                            | 44.0                     | 39.9                     | 41.3                     |
| D               | 49.5                            | 54.0                     | 47.0                     | 45.6                     |
| E               | 50.5                            | 47.0                     | 43.2                     | 43.6                     |
| F               | 34.0                            | 36.0                     | 29.7                     | 31.5                     |
| G               | 26.8                            | 27.1                     | 24.0                     | 26.8                     |
SEG D consistently showed a responsive relationship between LIFE O/E and flow with a characteristic peak in macroinvertebrate scores at 60% of the modelled natural flow. A similar relationship has been observed by Bradley et al. (2014) which suggested minimal impacts of low flows on macroinvertebrates when the abstraction effect was between 60 and 80% of Q75. Group D rivers are characterized as being small and steep and located within 13 km of the river’s source. It is possible that this observed trend reflects the interaction of other factors influencing macroinvertebrate communities. Previous studies of the impact of flow alteration on macroinvertebrates indicated that abstraction was most pronounced in headwater sites that had substantial dewatering effect (Armitage & Petts, 1992; Bickerton et al., 1993). However, within small steep headwater sites, abstractions are less common or large in volume, because of their typical inaccessibility and limited agricultural use which restricts abstraction demand. As headwaters are vulnerable to other pressures because of their high connectivity with adjacent land and large contributing catchment relative to their size (Riley et al., 2018), further research and data are needed to disentangle the interaction of flow alteration and other pressures in headwater streams.

Modelling of SEG E showed the most “idealized” relationship (Figure 1) of macroinvertebrate response to changes in flow. At both Q95 and Q30, macroinvertebrate O/E scores increased as flow approached natural (flow pressure decreased), peaking at 100% and dropping slightly at discharge-rich events (>100%). As these rivers represent intermediate sized lowland streams (including chalk streams), these results support the well-documented evidence of the sensitivity of biological communities in these stable, groundwater-dominated rivers to flow pressure as a result of abstraction (Acreman et al., 2006, 2008; Armitage & Petts, 1992; Bickerton et al., 1993; Boulton, 2003; Dunbar et al., 2010a; Dewson et al., 2007; Wood & Petts, 1994).

4.2 River habitat modification influence on in flow alteration-biology relationships

River morphology and hydrology have been increasingly recognized as fundamental integrating components in characterising river system behaviour (Booker et al., 2015; Rinaldi et al., 2016). The varying performance of the relationships for individual SEGs may reflect these differing influences of environmental and physical features on hydroecological relationships. For example, SEGs D, E and F (small steep upland rivers/intermediate lowland, including chalk streams/ small lowland streams, including chalk streams respectively) appeared to have biological communities which were the most responsive to changes in flow when habitat modification was incorporated into the model. This highlights the importance of river morphology, which has been shown to influence macroinvertebrate response to historical flow (Dunbar et al., 2010a, 2010b; Jusik et al., 2015; Worrall et al., 2014). The introduction of the HMS re-sectioning interaction term to the SEG modelling improved the models’ predictive capabilities demonstrating that linking flow alteration and river morphology could provide more robust assessments of the water abstraction impact on aquatic ecology.

The interaction between ecological response and flow alteration with re-sectioning and bank poaching (trampling by livestock) confirms previous work, which highlighted the relationship between habitat modification and the LIFE-flow relationship (Dunbar et al., 2010a, 2010b). In turn this could be interpreted as habitat modification playing an important role in a river's ecological sensitivity to flow variation. Our results suggest that ecosystems of physically modified rivers could be more sensitive to flow alteration than more (semi-) natural rivers, although the exact mechanism for this is unclear. The response may in part reflect the lack of flow refuges in modified channels i.e., the loss of water velocity as flow reduces and marginal slow flowing areas with increased flow (Boulton, 2003), as previous work has found that the magnitude of flow was an influential component on the macroinvertebrate communities (Lynch et al., 2018; Monk et al., 2006). This highlights the role of river morphology as a useful index of the general sensitivity of macroinvertebrate communities to flow change, whether caused by natural or anthropogenic factors. In turn this suggests that river morphology should be considered when developing flow standards for the management of water abstraction and river regulation. Studies elsewhere have reported strong associations between habitat conditions and macroinvertebrate assemblage level response (Chen et al., 2014; Moya et al., 2011). The development of the empirical statistical models presented here provides a first attempt to offer quantitative evidence of relationships between flow alteration and ecological response in the presence of possible confounding factors for effective water resource management practices. Further work is needed to develop and refine these models to help take into account channel habitats and physical characteristics to characterize ecosystem sensitivity and produce ecologically driven environmental flow criteria.

5 CONCLUSIONS

1. An England-wide assessment of flow-ecology relationships demonstrated linkages between river macroinvertebrate response and anthropogenic flow alteration, with macroinvertebrate LIFE score decreasing with increased flow alteration including artificially high flows.

2. The Environment Agency's existing abstraction classification bands were not a strong predictor of changes in macroinvertebrate response to low (Q95) flow alteration.

3. The integration of the physically based classification and habitat modification improved model performance, allowing the assessment of the relative impacts of flow pressure/changes flow and physical habitat degradation on the macroinvertebrate community.

4. The results highlight that spatial variables used in the physically based modelling, including channel slope, width, depth and
distance from source as key factors in classifying macroinvertebrate community response to flow alteration.

5. Further development of an abstraction-flow pressure classification based on hydrological, biological, morphological and physical characteristics is imperative to characterize ecological sensitivity and set flow standards that are ecologically meaningful.

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DATA AVAILABILITY STATEMENT
Biological data is freely available on https://environment.data.gov.uk/ecology-fish/

Land use data is available on https://www.ceh.ac.uk/services/land-cover-map-2015

River flow data is available from the Environment Agency on request.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the Supporting Information section.

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