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Lathouri, M, England, J, Dunbar, MJ et al. (2 more authors) (2021) A river classification scheme to assess macroinvertebrate sensitivity to water abstraction pressures. *Water and Environment Journal*, 35 (4). pp. 1226-1238. ISSN 1747-6585

<https://doi.org/10.1111/wej.12712>

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1 **A river classification scheme to assess macroinvertebrate sensitivity to water abstraction**
2 **pressures**

3

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ABSTRACT

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 to flow pressure. 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: hydroecology, ecohydrology, flow-ecology relationships, LIFE index, abstraction sensitivity, mixed effects modelling

35 Decreased availability of freshwater resources twinned with increasing demand is a global
36 problem. Water managers must balance anthropogenic resource needs with the ecological
37 consequences of delivering that resource (Horne et al., 2019). The concept of environmental
38 flows, which seeks to balance the quantity, timing and quality of water flows to sustain
39 freshwater and estuarine ecosystems and the human livelihoods which depend on them is
40 now a central tenet in water resource management (Acreman, 2016). Environmental policies
41 in many countries employ elements of environmental flow principles aiming to manage the
42 impact of water withdrawals (abstractions) or releases on river biota and habitats (Hughes &
43 Mallory, 2008).

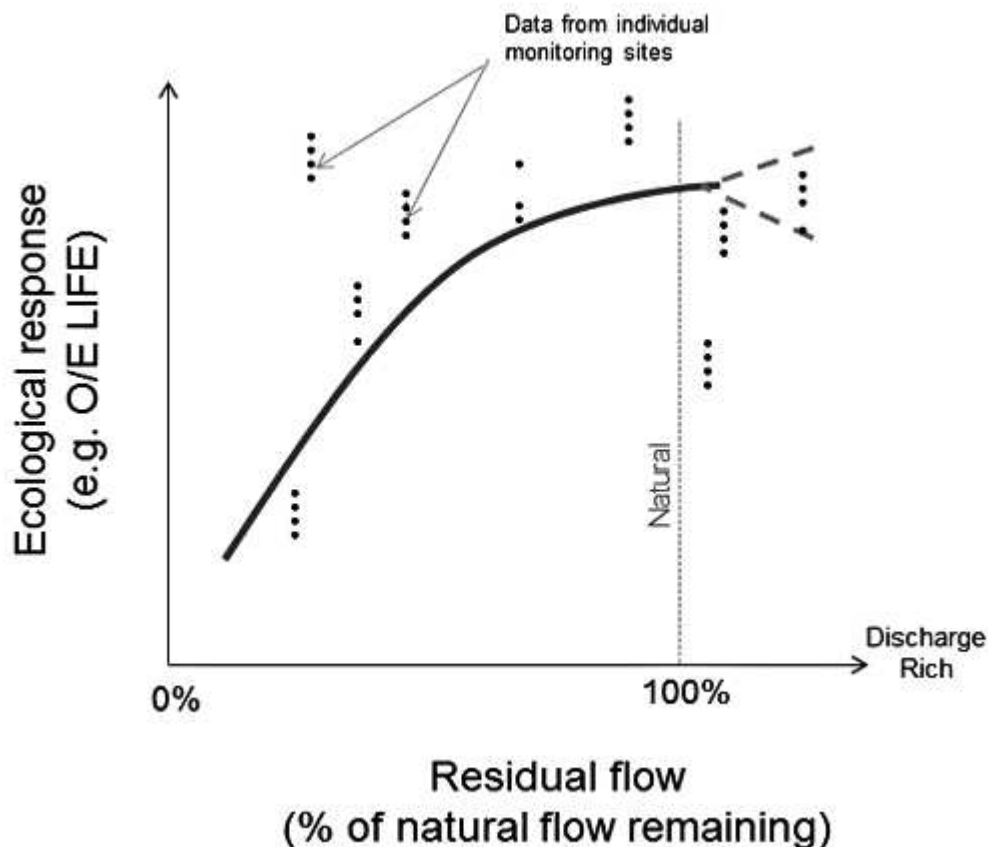
44 The practicalities underlying the laws and policies regulating how much water can be taken
45 from the environment have been a recurring research theme for applied ecologists and water
46 managers (Acreman et al., 2014). While river-specific observations (e.g. Bickerton et al., 1993;
47 Wood and Petts, 1994) and local studies (e.g. Bradley et al., 2017; Visser et al., 2017; White
48 et al. 2018) have made progress in elucidating the linkages between hydrological alteration
49 and ecological response, these site-specific relationships have been difficult for water
50 managers to apply at a regional or national-scale. Rivers differ in their ecological sensitivity
51 to changes in river flow (Poff et al., 1997; Dunbar et al., 2010a), hence they should also differ
52 in their ecological response to water abstraction. This sensitivity may be influenced by river
53 size, geology and landscape characteristics (Booker et al., 2015). These differing responses
54 may be useful in determining locations where more or less water may be removed, allowing
55 a more nuanced approach to resource allocation which is able to maximise water availability
56 while ensuring environmental protection at locations more susceptible to altered flow
57 regimes.

58 The Water Framework Directive (WFD) is the main legislative tool which governs the
59 protection and management of inland surface, transitional, coastal and ground waters within
60 Europe. Central to the Directive is the creation of typologies of water bodies (rivers or
61 stretches of rivers) based on instream characteristics and biological communities that
62 represent conditions unaffected by anthropogenic pressures (Logan & Furse, 2002). These
63 typologies are often referred to as 'reference conditions' to which current or observed

64 conditions or biological communities can be compared to, to determine whether a site's
65 ecological status may have deviated from the reference or ideal conditions (Hughes et al.,
66 1998). Using ecological metrics such as macroinvertebrate (LIFE (Extence et al., 1999), WHPT
67 (Paisley et al., 2014), PSI (Extence et al., 2013)), fish (IBI; Karr, 1981) and diatom indices (TDI;
68 Kelly 1998), an ecological quality ratio (EQR) synthesising the comparison between observed
69 and expected biological quality, and hence a likelihood of impact of anthropogenic pressure
70 can be determined (Jones et al., 2010). The use of an EQR rather than comparison of species
71 composition, abundance or density data allows the comparison of sites covering a large
72 geographical area and intercalibration between a range of sites and countries (Arle et al.,
73 2016).

74 Given the use of typologies and classifications in tandem with EQR assessments in
75 environmental legislation and the perceived sensitivity of waterbodies to changes in flow due
76 to water withdrawals and discharges, typologies are increasingly being used in determining
77 water resource availability (e.g. Viviroli et al., 2007; Milano et al., 2013; Munia et al., 2018).
78 The use of classifications as general 'rules of thumb' for assessing which waterbodies may be
79 more or less sensitive to altered flow regimes are particularly useful for regulatory authorities
80 in determining allowable abstraction limits (Acreman & Ferguson, 2010).

81 Within England, the Environment Agency (EA) has overall responsibility for the management
82 of water resources. Their approach to water resource management (as outlined in Klaar et
83 al., 2014) incorporates best practice into a nationally consistent framework underpinned by
84 standards defined at the UK-level (UKTAG, 2013) and developed in line with the WFD
85 (European Commission, 2003). Central to this process is the identification of where current
86 water management activities may be adversely affecting the environment, and where there
87 may be additional water resources available for new licenses.



88

89 **Figure 1** Idealised flow alteration/biology relationship for use in water resource management
 90 planning. 0% (of natural flow) represents no flow, 100% corresponds to zero net impact
 91 (observed flow= modelled natural flow) and levels above 100% correspond to sites where
 92 flow is greater than modelled natural flow (discharge-rich).

93 England-wide environmental flow criteria for naturally perennial rivers (Klaar et al. 2014) are
 94 expressed as deviations from natural flow, which vary by river type and are based primarily
 95 on expert opinion (Acreman et al., 2006; 2008; UKTAG, 2013). Within the criteria, a river's
 96 sensitivity to flow alteration due to water abstractions is taken into account in the form of
 97 Abstraction Sensitivity Bands (ASBs; Environment Agency, 2013a). ASBs are intended to
 98 reflect the perceived sensitivity of instream biota to anthropogenic changes in flow with ASB
 99 group 1 rivers deemed to have the lowest sensitivity to changes in water flow (hence, more
 100 water may be taken) and ASB group 3 being the most sensitive and where less water should
 101 be taken (Supplementary Material Table 1). This approach is used to determine where water
 102 may be available for new abstraction and to highlight where abstraction pressure may be
 103 having an undesirable ecological effect. However, it is limited currently by the confidence of

104 its ecological justification and making best use of new evidence. Alternative empirically-
105 derived classification methods, based on physical river characteristics have been found to
106 provide adequate flow alteration- ecological response relationships (e.g. Snelder & Biggs,
107 2002; Poff et al., 2010) and may provide a more robust method of determining
108 macroinvertebrate community sensitivity to flow alteration.

109

110 Central to developing improved relationships between the magnitude of anthropogenic river
111 flow alteration and ecological response is the availability of adequately paired hydrological
112 and biological data from which pressure- response relationships can be derived (Monk et al.,
113 2007). An idealised relationship between a macroinvertebrate indicator and flow alteration
114 is shown in Figure 1. A flow regime below natural (i.e. below 100% of natural flow) should
115 manifest as impacted biota (reflected in the decrease of the macroinvertebrate indicator).
116 Previous research (White et al., 2021) has shown that flow above natural flow (i.e. at
117 discharge-rich sites) negatively affects instream biota, however the sparsity of further
118 empirical evidence necessitates a split response curve as shown at flows >100.

119

120 The research aim of this study is to assess how well the current (ASB) method and an
121 alternative physically-based river classification approach are able to predict the biological
122 response (indices of observed macroinvertebrate community composition and their deviation
123 from an expected condition, expressed as observed/expected macroinvertebrate scores) to
124 changes in flow (expressed as percentage deviation from “natural” flow). A paired multi- site
125 and multi-year (including seasonal) historical hydrological and biological dataset is used,
126 allowing the use of multilevel (mixed effects) additive regression modelling, a modern
127 statistical tool being increasingly used by ecologists (Bolker et al. 2009, Pedersen et al. 2019).
128 This analytical approach has already shown its potent in modelling the biological response to
129 flow changes (Dunbar et al., 2006; 2010a,b; Klaar et al., 2014). Given the increasing evidence
130 of the combined impact of poor water quality, habitat modification and flow alteration acting
131 in tandem to increase the individual stressor impact on ecological integrity (e.g. Birk et al.,
132 2020) resulting in failures declines in waterbody status as determined by the WFD (Lemm et
133 al., 2021), we included these interactions within our models. Testing of these relationships
134 and classification approaches will provide a better understanding of the links between

135 hydromorphological pressures, chemical status and river ecology to determine their role in
136 maintaining good ecological integrity.

137

138 **METHODS**

139

140 Biological, chemical and physical data collected and administered by the Environment Agency
141 (EA) is used throughout this study. This study has focused on a time period covering 2008-
142 2014 to limit the confounding effects of changes in sampling methods and improvements in
143 water quality over time (Friberg et al., 2011; Vaughan & Gotelli, 2019). This time period also
144 ensured the data covered two drought periods (2005/2006 and 2010/2011).

145

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

151

152 **DATASETS**

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

159

160 *Hydrological alteration*

161 River flow alteration data were obtained from an existing EA dataset, based on recent actual
162 abstraction licence returns and consented discharges, accompanied by modelled data on
163 naturalised flows (Environment Agency, 2013b; Klaar et al., 2014). Abstraction and discharge
164 data comprised an aggregate for the period 2008-2014 due to the variable nature of licensed
165 flow alterations. A measure of flow alteration was derived by comparing the difference in flow
166 between modelled 'natural' flow and modelled recent actual flow (using recorded data on

167 abstractions and discharges (Klaar et al. 2014), and expressed as percentage of the residual
168 flow, i.e.;

169

$$170 \quad (\text{recent actual flow/ natural flow}) * 100 = \% \text{ residual of natural flow}$$

171

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

182

183 *Biological data*

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

198

199 *Other pressures*

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

205

206 *Catchment and river morphology characteristics*

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

217

218 River morphological alteration metrics were derived from Environment Agency River Habitat
219 Survey data (RHS; Raven et al., 1998) data covering ~16,700 sites surveyed between 1994 and
220 2004 (Naden et al., 2015). Habitat modification scores (HMS), HMS sub-scores (re-sectioned
221 bed and banks and bank poaching (trampling) by livestock) and Habitat Quality Assessment
222 (HQA) scores were used to assess the degree of the channel modification. Where multiple
223 RHS surveys occurred on a waterbody, a median score was calculated. The percentage of
224 historical flood defence works present at a surveyed site was obtained from an EA digitised
225 dataset, covering a period from 1930 to 1980 (Brookes et al., 1983). This included the
226 percentage of the length of river (km) with flood defence works, together with river
227 channelization features channel morphology modification: bank reinforcement, re-
228 sectioning, re-alignment, re-grading and embankments.

229

230 ALTERNATIVE CLASSIFICATIONS

231 The applicability of the current ASB river sensitivity classification was tested for ecological
232 relevance using biological response to flow alteration. Sites were categorised by their current
233 ASB classification and modelled independently. The dataset comprised a total of 136 Band 1,
234 917 Band 2 and 941 Band 3 water bodies (Supplementary Material Figure 1).

235

236 A second classification based on the most probable RIVPACS Super End Group (SEG), was also
237 tested. SEGs are a step within the process of predicting expected macroinvertebrate index
238 scores for a site; they reflect the ecological community similarities in the underlying clustering
239 of RIVPACS 'reference' sites using TWINSpan (Davy-Bowker et al., 2008; Friberg et al., 2011).
240 SEGs represent a potentially more ecologically-based classification as they are based on the
241 known associations between reference macroinvertebrate communities and physical site
242 characteristics. SEGs (Supplementary Material Table 2; Supplementary Material Figure 2)
243 were predicted for each site using the physical environmental characteristics required to run
244 the RIVPACS model (slope, altitude, stream width and depth, substratum composition,
245 average annual discharge category, alkalinity, average temperature conditions and distance
246 from source; Davy-Bowker et al., 2008). Super end group A was not included in this study as
247 this group is exclusively outside of England.

248

249 STATISTICAL ANALYSIS

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

256

257 A multilevel generalised additive mixed- effect modelling (GAMM) approach (using the
258 `gamm4` package, Wood, 2009) was applied to describe changes in LIFE O/E scores to flow
259 alterations separately for macroinvertebrate data collected in spring and autumn seasons.
260 The variation among the water bodies and sites were treated as nested because they are
261 hierarchically structured with multiple sites per water body. Multilevel modelling enabled the
262 explanatory variables to be used within the model by letting residual variance at different

263 levels (as random effects) to be modelled, allowing different responses among groups (at site/
 264 waterbody scale) to be taken into account (Table 1).

265
 266 Starting with a global model (all sites), alternative formulations of model predictors were
 267 fitted and ranked using the ‘dredge’ function from the R MuMIn package (Barton, 2016). The
 268 top four candidate models (determined using Akaike’s Information Criterion; AIC) were used
 269 to identify the most important predictors of LIFE O/E scores for Q30 and Q95, representing
 270 ‘high’ and ‘low’ flow statistics and the different seasons.

271

272 **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 resectioning) % 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

273

274 LIFE O/E response to flow pressure at waterbodies grouped by ASB was undertaken to test
 275 the validity of the current ASB classification. Waterbodies grouped using the SEGs then tested
 276 the potential use of this classification in determining flow-ecology relationships. As habitat
 277 modification has previously been shown to influence LIFE O/E (Dunbar et al., 2010a,b)
 278 additional analysis of the SEGs models was undertaken using an interaction factor, which

279 estimates the smoothed trend separately, allowing for a different trend for each re-sectioned
 280 category and for each super end group.

281

282 **RESULTS**

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

288

289 **MULTILEVEL MODELLING**

290 Cross-correlation analysis (Supplementary Material Figure 3), shows that the most highly
 291 correlated values were % agricultural land cover (hereafter termed % agriculture) and %
 292 arable (Spearman rank = 0.77), followed by % agriculture and % broadleaved, HQA scores and
 293 % arable, % re-sectioning and % horticulture, % agriculture and % coniferous and % agriculture
 294 and % improved grassland and (-0.47, -0.40, 0.40, -0.38 and -0.32, respectively). To avoid the
 295 high degree of correlation between land management practices, % arable, % grassland, %
 296 coniferous woodland and % agriculture were excluded from the global model, leaving only %
 297 broadleaf cover and % urbanisation within the model to represent natural vs modified land
 298 cover classifications respectively.

299

300 **Table 2** Summary of the MuMIN data dredge results produced from the global model for
 301 spring macroinvertebrate data. HMS= Habitat Modification Score; HQA = Habitat Quality
 302 Score; CapWks = Capital Works.

SPRING	% HMS Poaching	% Hms Resectioned	% 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	-38789	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	-0.00004	-0.0008	0.003	-38781	18.62	0.000
	0.000016	-0.000120		0.0005		-0.0008	0.003	-38781	18.64	0.000

303

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

313

314 **Table 3** Summary of the MuMIN data dredge results produced from the global model for
 315 autumn macroinvertebrate data. HMS= Habitat Modification Score; HQA = Habitat Quality
 316 Score; CapWks = Capital Works

AUTUMN	% HMS Poaching	% HMS Resectioned	% HQA	% broadleaf	% CapWks	% urban	Year	AIC	delta	weight
LIFE O/E		-0.000010		0.0008		-0.0006	0.002	-35011	0.00	0.893
Q30		-0.000012		0.0008			0.002	-35006	4.40	0.099
		-0.000011		0.0008		-0.0006	0.002	-35002	9.87	0.006
		-0.000011		0.0008	0.00021	-0.0007	0.002	-34997	14.09	0.001
LIFE O/E		-0.000010		0.0008		-0.0006	0.002	-35011	0.00	0.897
Q95		-0.000012		0.0008			0.002	-35006	4.40	0.100
		-0.000011		0.0007		-0.0006	0.002	-34999	12.60	0.002
		-0.000011		0.0008	0.000021	-0.0007	0.002	-34997	14.09	0.001

317

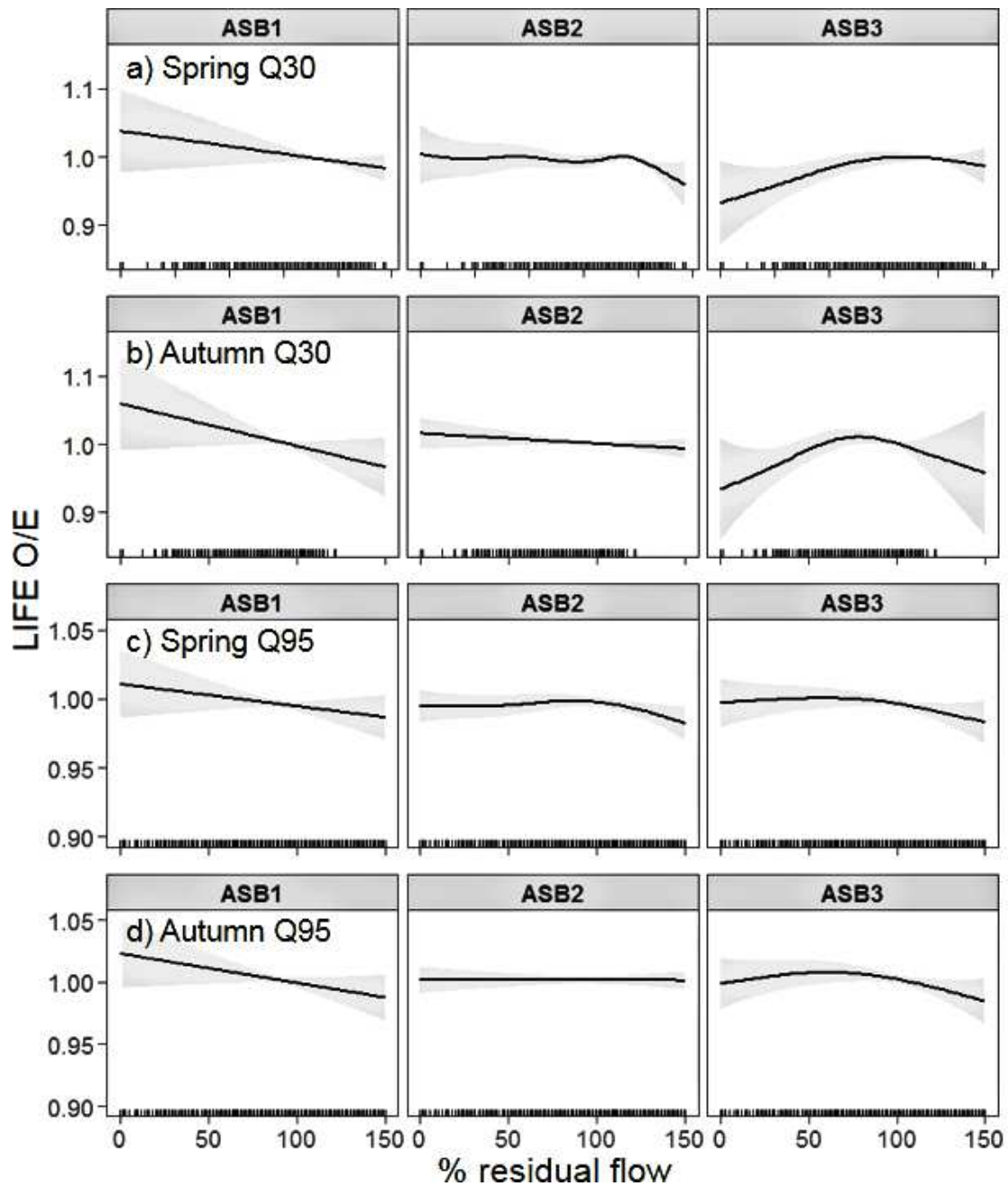
318 Autumn sampling models (Tables 2 and 3) consistently used year and re-sectioning as
 319 predictors in the top models, in addition to % broadleaf woodland. Percentage urban land
 320 use was an important (negative) influence in 3 out of 4 models in both high and low flow
 321 percentiles, while the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

323

324 *ASB classification and macroinvertebrate response*

325 In general, models representing the changes in LIFE O/E scores with residual flow grouped by
 326 ASB classifications were similar in both seasons and flow percentiles (Figure 2). ASB1 (low

327 perceived sensitivity to flow change) displayed a decline in LIFE O/E score with increasing
328 flow. The slope of this relationship is particularly steep in the autumn models. The large
329 confidence intervals, in combination with a marked negative relationship of
330 macroinvertebrate scores with increasing flow, suggest that the model performance is poor
331 for ASB1 waterbodies. ASB2 bands display a varied, yet relatively unresponsive relationship
332 between macroinvertebrate scores and residual flow; although the spring models (Fig. 2a and
333 c) highlight a sudden tailing off of LIFE score at discharge-rich (>100% residual flow). ASB3
334 (streams with a perceived high sensitivity to flow change) show a more responsive
335 relationship, more closely aligned to the 'idealised' flow- biology relationship proposed in Fig.
336 1. The Q30 models in particular (Fig. 2a and b) suggests that LIFE O/E scores increase with
337 increasing residual flow during high and low flow events, reaching a maximum at
338 approximately 80% of residual flow, before tailing off as flow increases.



339

340 **Figure 2** Modelled spring LIFE observed/ expected (O/E) response to changes in % residual
 341 flow at Q30 (a) and Q95 (c) and autumn LIFE O/E response at Q30 (b) and Q95 (d) using ASB
 342 groupings. The solid line is the predicted value of the dependent variable (LIFE O/E) as a
 343 function of the covariate (in the x-axis). The dashed lines show the 2x standard errors (SE) of
 344 the estimates, roughly 95% of the predicted values fall within the area, whereas the small
 345 lines along the x axis show the distribution of x values (residual flow). The y axis is in linear
 346 units so that the values are centred on 0 and extend to both positive and negative values.
 347 Note the differences in y axis scales between Q30 (a & b) and Q95 (c & d).

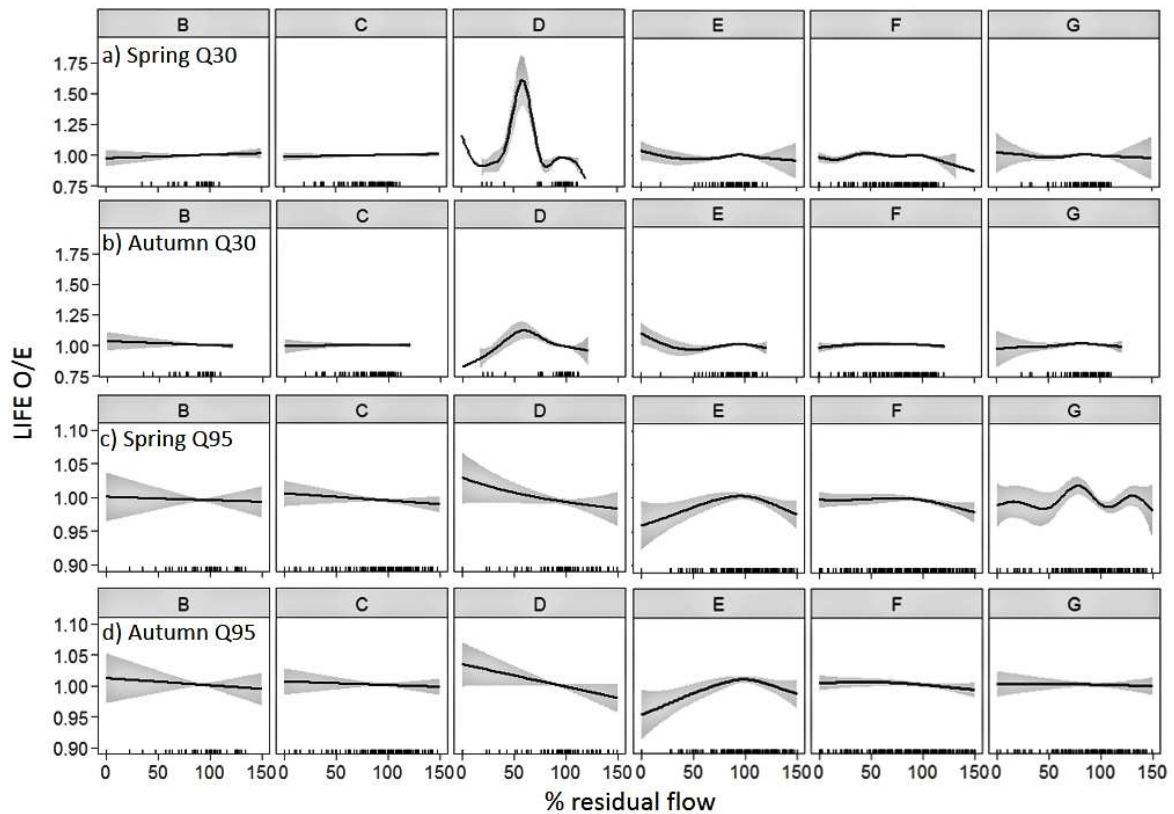
348

349 *Physically-based super end group modelling*

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

363

364 Autumn LIFE O/E metrics and residual flow changes for streams classified as groups B, C, F
365 and G show no response in LIFE O/E scores during high flows (Figure 3b), with a near flat line
366 predicted response. Group D shows a peak in LIFE O/E scores with an increase when flow is
367 60% of the modelled natural flow. The predicted macroinvertebrate response in autumn low
368 flows (Fig. 3d), shows a marked decrease in LIFE O/E for group D as residual flow increases,
369 but note the large error bars. A similar decrease in autumn LIFE O/E with increasing residual
370 flow at Q95 is also observed at the end groups B and C and to some (smaller) extent at the
371 end groups F and G, although the slope of response at these sites is much shallower. Super
372 end group E streams (intermediate sized lowland streams) shows the best response in
373 predicted autumn LIFE O/E.



374

375 **Figure 3** Modelled a) spring and b) autumn Q30 and c) spring and d) autumn LIFE observed/
 376 expected (O/E) response to changes in % residual flow, using super end groups, as indicated
 377 as indicated by the letter at the top of each plot. Note the differences in y axis scales between
 378 Q30 (a & b) and Q95 (c & d).

379 **Table 4** Summary of goodness-of-fit (adjusted R-squared) from the spring and autumn
 380 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

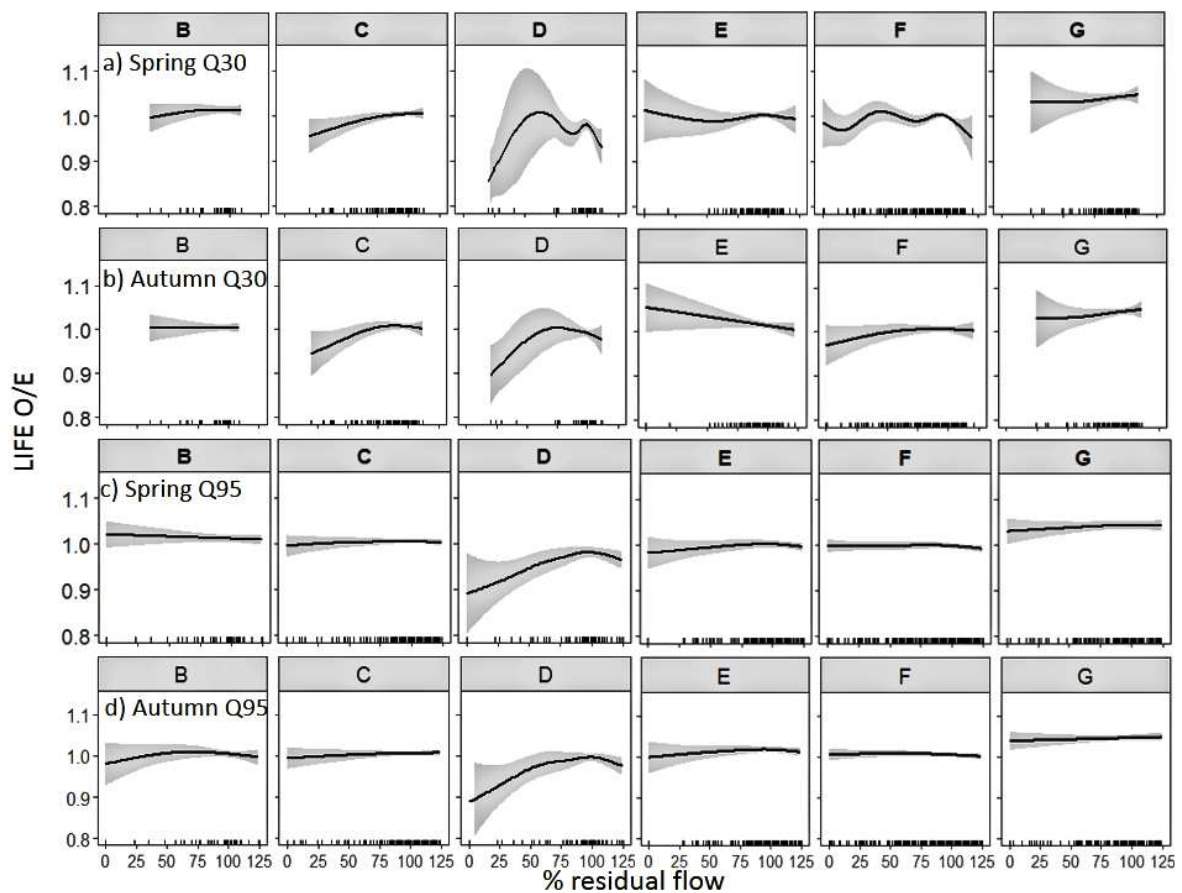
381

382 *Habitat modification and end group modelling*

383 Inclusion of habitat modification as an interaction term in the end group modelling (Figure 4)
 384 shows a high uncertainty in the models at low and high residual flows for both seasons, as
 385 represented by the large confidence intervals, reflecting the small number of values at the
 386 high and low ends of the dataset. Macroinvertebrate response to flow pressure at higher
 387 flows (Q30; Fig. 4a,b) shows a less instinctive relationship, with macroinvertebrate O/E scores
 388 displaying a double peak at moderate flow pressure (~50% residual flow) and at natural flow
 389 (100% residual flow) for most end group members. This response was particularly obvious in
 390 groups D and F; characterised as smaller waterbodies.

391
 392 The goodness-of-fit test (Table 4) reveals a fairly good relationship between the modelled
 393 spring LIFE O/E response to residual flow at Q95 and the habitat modification for most end
 394 groups. In Groups D and E, macroinvertebrate scores show a decline with decreasing flow
 395 pressure (increasing residual flow). These groups explain better (~50% of the variability) the
 396 fitted model at both high (Q30) and low (Q95) flows.

397



398

399 **Figure 4** Modelled spring a) Q30, b) Q95 and autumn c) Q30, d) Q95 LIFE observed/ expected
400 (O/E) responses to changes in % residual flow, using super end groups and the modelled
401 interaction using re-sectioned scores. Super end groups are indicated by the letter at the top
402 of each plot.

403

404

DISCUSSION

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

417

418 A limited number of studies have quantified flow alteration-ecological response relationships
419 across multiple sites (e.g. Bradley et al., 2017; White et al., 2018; Krajenbrink et al., 2019).
420 Most hydroecological assessments have examined biotic responses to historical inter-annual
421 flow variability (e.g. Dunbar et al. 2010a,b, Wood and Petts, 1994; Monk et al., 2006; Worrall
422 et al., 2014), which means that abstraction impacts have to be inferred indirectly. Regional
423 hydroecological models such as those of Bradley et al. (2017) and Visser et al. (2017) are
424 useful in developing local regulatory decisions, but little is known about macroinvertebrate
425 response to flow changes at an even broader (i.e. national) scale (although see Tonkin et al.
426 2018). Our modelling of the residual flow-biology relationships provides such a national-scale
427 assessment and illustrates the importance of habitat-based explanatory variables in the
428 development of empirical statistical models of macroinvertebrate metric response to changes
429 in flow.

430

431 PERFORMANCE OF RIVER CLASSIFICATIONS IN PREDICTING BIOTIC SENSITIVITY

432 The ASB classification (based on UKTAG: Acreman et al., 2006; 2008) was not a strong
433 discriminator of changes in macroinvertebrate response to low (Q95) flow pressure for either
434 spring or autumn macroinvertebrate data. Super end groups (SEG) displayed a better
435 relationship between flow alteration and macroinvertebrate LIFE O/E score. For the D, E, F
436 and G groups, there was a decline in macroinvertebrate scores at flows higher than natural
437 (discharge-rich scenarios). This may reflect that flow augmentation could be associated with
438 effluent discharges and thus impaired water quality (Metcalf-Smith, 1996; Friberg et. al.,
439 2010). Although sites were filtered for poor water quality based on dissolved oxygen and
440 ammonia, there may have been other ecological effects from effluent discharges.
441 Alternatively, flows elevated above natural may be associated with a more homogeneous
442 flow regime (Poff et al. 2007) with lower than natural variability in flow magnitudes over time.
443 Further research is needed to confirm the influence of flows above natural and explore the
444 mechanisms behind the response.

445

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

451

452 SEG D, consistently showed a responsive relationship between LIFE O/E and flow with a
453 characteristic peak in macroinvertebrate scores at 60% of the modelled natural flow. A similar
454 relationship has been observed by Bradley et al. (2014) which suggested minimal impacts of
455 low flows on macroinvertebrates when the abstraction effect was between 60 and 80% of
456 Q75. Group D rivers are characterised as being small and steep, and located within 13 km of
457 the river's source. It is possible that this observed trend reflects the interaction of other
458 factors influencing macroinvertebrate communities. Previous studies of the impact of flow
459 alteration on macroinvertebrates indicated that abstraction was most pronounced in
460 headwater sites that had substantial dewatering effect (Armitage and Petts, 1992; Bickerton
461 et al., 1993). However, within small steep headwater abstractions are less common or large

462 in volume, due to their typical inaccessibility and limited agricultural use which restricts
463 abstraction demand. As headwaters are vulnerable to other pressures due to their high
464 connectivity with adjacent land and large contributing catchment relative to their size (Riley
465 et al., 2019), further research and data are needed to disentangle the interaction of flow
466 alteration and other pressures in headwater streams.

467

468 Modelling of SEG E showed the most 'idealised' relationship (Fig. 1) of macroinvertebrate
469 response to changes in flow. At both Q95 and Q30, macroinvertebrate O/E scores increased
470 as flow approached natural (flow pressure decreased), peaking at 100% and dropping slightly
471 at discharge-rich events (>100%). As these rivers represent intermediate sized lowland
472 streams (including chalk streams), these results support the well documented evidence of the
473 sensitivity of biological communities in these stable, groundwater-dominated rivers to flow
474 pressure due to abstraction (Armitage and Petts, 1992; Bickerton et al., 1993; Wood and
475 Petts, 1994; Boulton, 2003; Acreman et al., 2006, 2008; Dewson et al., 2007, Dunbar et al.,
476 2010a).

477

478 RIVER HABITAT MODIFICATION INFLUENCE ON IN FLOW ALTERATION-BIOLOGY 479 RELATIONSHIPS

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

493

494 The interaction between ecological response and flow alteration with re-sectioning and bank
495 poaching (trampling by livestock) confirms previous work, which highlighted the relationship
496 between habitat modification and the LIFE-flow relationship (Dunbar et al. 2010a, 2010b). In
497 turn this could be interpreted as habitat modification playing an important role in a river's
498 ecological sensitivity to flow variation. Our results suggest that ecosystems of physically
499 modified rivers could be more sensitive to flow alteration than more (semi-) natural rivers,
500 although the exact mechanism for this is unclear. The response may in part reflect the lack of
501 flow refuges in modified channels i.e. the loss of water velocity as flow reduces and marginal
502 slow flowing areas with increased flow (Boulton, 2003), as previous work has found that the
503 magnitude of flow was an influential component on the macroinvertebrate communities
504 (Lynch et al., 2018; Monk et al., 2006). This highlights the role of river morphology as a useful
505 index of the general sensitivity of macroinvertebrate communities to flow change, whether
506 caused by natural or anthropogenic factors. In turn this suggests that river morphology should
507 be considered when developing flow standards for the management of water abstraction and
508 river regulation.

509

510 Studies elsewhere have reported strong associations between habitat conditions and
511 macroinvertebrate assemblage level response (Chen et al., 2014; Moya et al., 2014). The
512 development of the empirical statistical models presented here provides a first attempt to
513 offer quantitative evidence of relationships between flow alteration and ecological response
514 in the presence of possible confounding factors for effective water resource management
515 practices. Further work is needed to develop and refine these models to help take into
516 account channel habitats and physical characteristics to characterise ecosystem sensitivity
517 and produce ecologically-driven environmental flow criteria.

518

519

520

CONCLUSIONS

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

- 525 2. The Environment Agency's existing abstraction classification bands were not a strong
526 predictor of changes in macroinvertebrate response to low (Q95) flow alteration.
- 527 3. The integration of the physically-based classification and habitat modification
528 improved model performance, allowing the assessment of the relative impacts of flow
529 pressure/ changes flow and physical habitat degradation on the macroinvertebrate
530 community.
- 531 4. The results highlight that spatial variables used in the physically-based modelling,
532 including channel slope, width, depth and distance from source as key factors in
533 classifying macroinvertebrate community response to flow alteration.
- 534 5. Further development of an abstraction-flow pressure classification, based on
535 hydrological, biological, morphological and physical characteristics is imperative to
536 characterise ecological sensitivity and set flow standards that are ecologically
537 meaningful.

538

539

ACKNOWLEDGMENTS

540 The views expressed in this paper reflect those of the authors and are not necessarily
541 indicative of the position held by the Environment Agency. The authors would like to thank
542 numerous colleagues in the Environment Agency who have contributed to the data collection,
543 collation and advice on the analysis and early drafts of the manuscript, especially Sarah Peet,
544 Judith Bennett, Mark Warren and Alison Futter. This project was jointly funded by a research
545 grant awarded to the University of Birmingham by the Environment Agency and the Irish
546 Environmental Protection Agency, Office of Evidence and Assessment.

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816 **Data availability statement**

817 Biological data is freely available on <https://environment.data.gov.uk/ecology-fish/>

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

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

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821 **Word count: 8301**

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