

1 **An index to track the ecological effects of drought development and recovery**
2 **on riverine invertebrate communities.**

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19 **Abstract**

20 In rivers, the ecological effects of drought typically result in gradual adjustments of invertebrate
21 community structure and functioning, punctuated by sudden changes as key habitats, such as wetted
22 channel margins, become dewatered and dry. This paper outlines the development and application of
23 a new index (Drought Effect of Habitat Loss on Invertebrates - DEHLI) to quantify the effects of
24 drought on instream macroinvertebrate communities by assigning weights to taxa on the basis of their
25 likely association with key stages of channel drying. Two case studies are presented, in which the
26 DEHLI index illustrates the ecological development of drought conditions and subsequent recovery.
27 These examples demonstrate persistent drought effects months or several years after river flows
28 recovered. Results derived using DEHLI are compared with an established macroinvertebrate flow
29 velocity-reactive index (Lotic-invertebrate Index for Flow Evaluation - LIFE score) and demonstrates
30 its greater sensitivity to drought conditions. Data from a number of rivers in south east England were
31 used to calibrate a statistical model, which was then used to examine the response of DEHLI and
32 LIFE to a hypothetical multi-year drought. This demonstrated a difference in response between
33 sampling seasons, with the spring model indicating a lagged response due to delayed recolonisation
34 and the autumn model differentiating habitat loss and flow velocity-driven responses. The application
35 of DEHLI and the principles which underlie it allow the effects of drought on instream habitats and
36 invertebrates associated with short or long term weather patterns to be monitored, whilst also allowing
37 the identification of specific locations where intervention via river restoration, or revision of existing
38 abstraction licensing, may be required to increase resilience to the effect of anthropogenic activities
39 exacerbated by climate change.

40 **Key words**

41 River; habitat; invertebrates; drought; index; disturbance

42 **1. Introduction**

43 Droughts have an important role in shaping lotic ecosystems (Extence 1981, Lake, 2011, Lu et al.,
44 2016; Piniewski et al., In Press). A potential increase in extreme events associated with our changing
45 climate suggests the frequency of droughts is likely to increase in many areas of the globe (Dai, 2011;
46 Prudhomme et al., 2014). Some recent studies indicate that the magnitude and frequency of short

47 duration drought events (<18 months) will increase in the future in tandem with rises in flood
48 frequency (Ledger and Milner 2015; Watts and Anderson, 2013). While climate change is expected to
49 intensify drought in many regions, its short and long-term ecological effects are poorly understood
50 (Bogan *et al.* 2014; Van Loon *et al.*, 2016).

51 Drought is a natural disturbance in rivers that influences community structure and functioning (Lu *et*
52 *al.*, 2016), altering species composition, abundance and richness (Atkinson *et al.*, 2014) and favouring
53 specialist species (Mainstone 1999). The impact of drought on ecological communities depends both
54 on its duration and intensity, as well as antecedent conditions (Bogan *et al.*, 2015; Chessman 2015;
55 Stubbington *et al.* 2015). Lake (2003) distinguishes between regular seasonal and predictable
56 droughts, as in Mediterranean regions, from supra-seasonal droughts which are usually unpredictable
57 in nature and are associated with longer periods of drying across multiple seasons. Supra-seasonal
58 droughts normally include one or more seasons typically associated with higher river flows. The
59 distinction between different types of drought is important since the biota within rivers which
60 experience regular seasonal channel drying typically display adaptations to such conditions (Boulton
61 2003; Bogan *et al.*, 2015), whereas unpredictable supra-seasonal droughts have the potential to
62 result in greater ecological effects due to their protracted nature (e.g. Wood and Armitage 2004). In
63 addition, the antecedent conditions and timing of supra-seasonal droughts are important controls on
64 the community effects (Dewson *et al.*, 2007; Lake, 2011). The effects of a drought on river
65 macroinvertebrate communities will vary according to the river type, in particular whether it is a
66 groundwater or surface water-dominated river, the pattern of drying and degree of physical
67 modification (see Lake, 2011 for review). More physically diverse river reaches, including those with
68 marginal habitats or with variable water depth and flow-velocity, provide habitat heterogeneity to
69 support a wider range of taxa. This physical heterogeneity is widely considered to result in
70 populations and communities which are more resilient to extreme hydrological events by the provision
71 of refugia which facilitate rapid recovery following disturbances (Townsend and Hildrew, 1994; Dunbar
72 *et al.* 2010a; Dunbar *et al.* 2010b; Chester and Robson, 2011).

73 Drought disturbances typically exhibit a ramp pattern with the magnitude of effects growing with
74 increasing duration of the event. Conditions during a drought may fluctuate, however, with brief
75 rainfall events providing occasional inputs of water, but the magnitude of the drought steadily
76 increases over time (ramps up) and often affects progressively greater spatial scales (Lake 2000;
77 Parry *et al.*, 2017). The response of the aquatic stages of lotic communities to drought is punctuated
78 by significant step changes, as thresholds between critical water levels are crossed (Boulton, 2003;
79 Boulton and Lake, 2008). The step-like nature of these changes, as thresholds are exceeded, result
80 from the abrupt loss or fragmentation of habitats (e.g. riffle areas), alteration in physico-chemical
81 conditions and the loss of lateral, longitudinal and/or vertical connectivity (Boulton, 2003; Boulton and
82 Lake, 2008). The ability of biota to withstand a disturbance (resistance) and their subsequent capacity
83 to re-colonise (resilience) reflect the availability of refugia in the channel and wider catchment (Lake
84 2000). Species and communities which possess strategies to survive low-flows, lentic conditions and
85 drying, or are highly mobile, may be able to recolonize and recover rapidly after the cessation of
86 drought conditions. The time taken to re-colonise, however, is typically taxon-specific and reflects the
87 timing, intensity, and duration of individual drought events (Boulton, 2003; Boulton and Lake 2008).

88 There is a need to understand the ecological effects of high magnitude supra-seasonal drought
89 events in order to anticipate the effects of climate change and help to balance the need for
90 anthropogenic water supply, whilst maintaining the ecological integrity of river habitats (Wilby *et al.*,
91 2010). There is also a growing recognition for the need for more robust and defensible data to
92 address multiple issues related to water resources and environmental legislation, such as
93 management of protected species and habitats and maintenance of ecological standards for healthy
94 ecosystems enshrined in the European Community Habitats Directive and Water Framework Directive
95 (WFD) (Acreman and Ferguson, 2010). To make use of these data we need tools and techniques to
96 ascertain the influence of different environmental pressures. The need to assess the ecological

97 effects of variations in river flow led to the development of the macroinvertebrate index: Lotic-
98 invertebrate Index for Flow Evaluation (LIFE; Extence *et al.*, 1999). LIFE uses recognized flow
99 associations to weight invertebrate groups according to their preference for flow velocity. Existing
100 biological indices, such as LIFE in the UK, and others developed in Canada (Armanini *et al.*, 2012),
101 Australia (Rose *et al.*, 2008) and New Zealand (Caruso 2002), have been correlated with historic
102 hydrological conditions and hydraulic parameters (Extence *et al.* 1999; Monk *et al.* 2008; Dunbar *et al.*
103 2010a, 2010b) with some degree of success. The relationship between the LIFE index and flow
104 volume (discharge) breaks down, however, under extreme low flow conditions (Monk *et al.* 2006)
105 possibly reflecting the ramp disturbance and threshold-crossing nature of drought pressures.

106 To address this deficiency, this study aimed to develop a new macroinvertebrate community-based
107 metric, the Drought Effect of Habitat Loss on Invertebrates (DEHLI) index. This paper aims to outline
108 the process of DEHLI calculation and to test its utility by using data from two case studies (involving
109 monthly and annual sampling, respectively) and by undertaking a modelling exercise to test the
110 drought response of both the DEHLI and LIFE indices to a hypothetical multi-year drought, calibrated
111 to actual data from 114 samples. The index is based upon the concept outlined in Boulton and Lake
112 (2008) linking the steps of the ramp disturbance with the sequential loss of aquatic invertebrates to
113 changing abiotic and biotic conditions. It has initially been designed to be derived using data from the
114 Environment Agencies of the United Kingdom, but could be readily adapted for use in any country or
115 global region.

116 **2. Methods**

117 **2.1 Index structure**

118 The primary theoretical element of the ramp disturbance model of drought (*sensu* Lake 2000) is the
119 sequence of changes in hydrological connectivity and wetted habitat (Boulton 2003, Boulton and Lake
120 2008) as the drought progresses (see Figure 1). The gradual intensifying of drought conditions will
121 initially lead to a reduction in river flow (volume, depth and in some instances, velocity) severing
122 lateral connectivity to marginal riparian habitat (2) and subsequently longitudinal connectivity (3), as
123 topographic high points on the river bed are exposed. Ultimately, only isolated pools of water may
124 remain (4) and as the drought progresses these will continue to shrink until surface water is lost and
125 only moist sediments and subsurface water remains (5). Each stage of the ramp disturbance will
126 potentially be characterised by a loss of indicator taxa relating to a reduction in available habitat and
127 associated changes to abiotic parameters (*e.g.*, water chemistry and flow velocity).

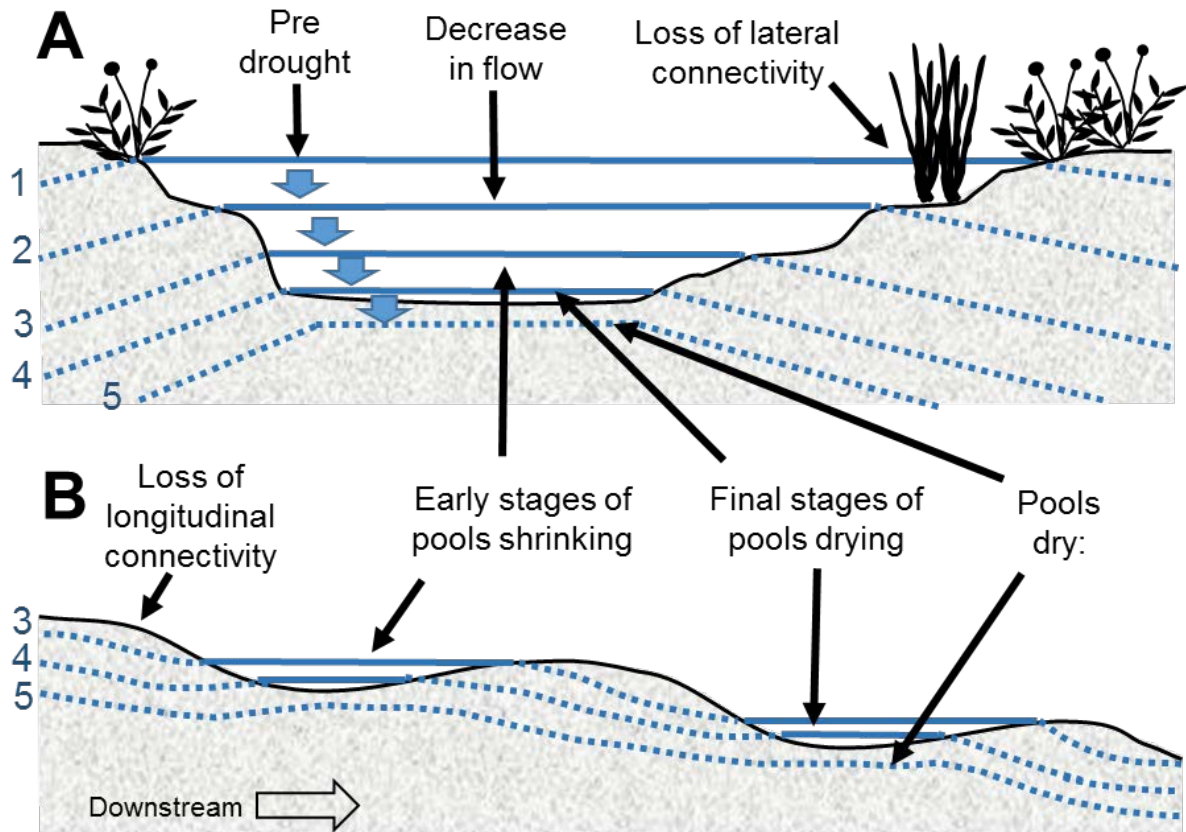
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129 **Figure 1. Sequential changes in hydrological connectivity and wetted habitat**
130 **as a drought progresses – adapted from Boulton, 2003.**

131 A - river cross-section, B - longitudinal profile.

132 1 = Decrease in flow; 2 = Loss of lateral connectivity; 3 = Loss of longitudinal connectivity; 4

133 = Stages of pools shrinking; 5 = Pools dry



134

135

136 The Drought Effect of Habitat Loss on Invertebrates (DEHLI) index places the aquatic stages of
137 invertebrate taxa into groups based on these sequential stages of habitat availability, according to the
138 invertebrates' relative tolerance to the loss of suitable habitat at each stage.

139 As outlined in Boulton and Lake (2008), stage 1 is characterised by the presence of taxa which
140 require very fast flowing water or cool, well-oxygenated flowing water for effective metabolism, in
141 order to carry out feeding and processing of nutrients. Such conditions become less common when
142 river discharge declines during the early stages of drought, with associated reductions in flow velocity
143 beside reduction of turbulence. The relevant taxa lost at this stage are all families and genera of
144 aquatic insects in the orders Ephemeroptera, Plecoptera and Trichoptera.

145 Taxa lost at stage 2 use stream-side vegetation for emergence, food, shelter and case-building
146 material and/or are intimately associated with floodplains. The disconnection of marginal habitats
147 effectively removes the necessary elements required for survival. Such taxa include, for example,
148 Odonata or Lepidoptera.

149 As the river moves to stage 3, taxa which not only require lotic water to respire effectively, but also
150 some which need a current for provision of food (e.g. Hydropsychidae and Simuliidae), may be

151 progressively lost as the river enters a fully lentic phase, resulting in a sharp decline in lotic taxon
152 richness. This loss is typically balanced by colonisation by lentic taxa, such as certain Hemiptera,
153 Coleoptera and Diptera which are physiologically and anatomically adapted to lentic-water
154 environments.

155 In stage 4, remaining pools of surface water contract with a resulting deterioration in water quality
156 (specifically, reducing dissolved oxygen and concentration of nutrients such as phosphate, and an
157 increase in water temperature). This results in a decline in lentic taxa which require relatively high
158 levels of oxygen, such as certain Odonata and Ephemeroptera, and favours those taxa which can
159 persist in relatively deoxygenated conditions, such as certain Coleoptera. Predation tends to intensify
160 in such environments as total habitat availability declines.

161 At stage 5, free surface water is lost completely, leaving only moist sediments and taxa which are
162 adapted to such conditions, e.g., by producing desiccation-resistant stages or being physiologically
163 adapted to obtain sufficient oxygen in moist sediments. Few aquatic invertebrates are capable of this,
164 with the exception of certain Gastropoda, Coleoptera and Diptera. Finally, the streambed becomes
165 completely desiccated and almost all aquatic invertebrates are lost, though some resting stages (such
166 as eggs) may remain.

167 Each taxon has, therefore, been assigned a Drought Intolerance Score (DIS) based on its association
168 with instream habitats which are lost as a drought intensifies, incorporating relative physiological
169 tolerance to drying and behavioural or life-history adaptation which avoids (or fails to avoid) loss of the
170 aquatic stage of the taxon from the river reach. Lower individual scores indicate a greater tolerance to
171 the prevailing conditions as the drought event becomes progressively more severe, while higher
172 scores indicate a greater sensitivity to changes in flow volume, flow velocity and associated habitat
173 characteristics (in practical terms, there is a lower tolerance to reduced water quality, flow velocity or
174 both). Scores were allocated using a combination of expert judgement, published sources of data on
175 taxon/habitat relationships (references are appended as supplementary material) and trait-based
176 databases such as www.freshwaterecology.info (Schmidt-Kloiber and Hering, 2015). The presentation
177 of taxa is arranged in each ecological group according to phylogenetic convention to illustrate differing
178 responses among related orders and to facilitate calculation of the index (see Table 1).

179

180 **Table 1: Individual Drought Intolerance Score (DIS), by taxon. (*Taxa which can**
 181 **tolerate more than one stage of drying. The taxa must not be double-counted).**

HABITAT OR HABITAT CHANGE: ECOLOGICAL GROUP	FAMILY (GENUS)	DIS
Decrease in flow/volume: specialist torrenticoles or need fast-flowing, well oxygenated water	Heptageniidae (E)	10
	Ameletidae (E)	10
	Perlidae (P)	10
	Chloroperlidae (P)	10
	Taeniopterigidae (<i>Brachyptera</i> & <i>Rhabdiopteryx</i>) (P)	9
	Philopotamidae (<i>Philopotamus</i> & <i>Wormaldia</i>) (T)	10
	Rhyacophilidae (T)	10
	Odontoceridae (T)	9
Loss of lateral connectivity: uses stream edge habitats or vegetation	Hydrobiidae (G)	7
	Bithyniidae (G)	7
	Valvatidae (G)	7
	Platycnemididae (O)	7
	Lestidae (O)	7
	Calopterygidae (O)	7
	Aeshnidae (O)	7
	Nepidae (H)	7
	Hydraenidae (C)	7
	Phryganeidae (T)	7
	Beraeidae (T)	7
	Pyralidae (L)	7
	Thaumaleidae (D)	8
	Dixidae (Primarily <i>Dixella</i> spp.) (D)	8
Loss of longitudinal connectivity (flow ceases): Rheophiles	Gammaridae (M)	6
	Baetidae (<i>Baetis</i> ONLY) (E)	7
	Leptophlebiidae (<i>Paraleptophlebia</i> ONLY) (E)	6
	Perlodidae (P)	7
	Nemouridae (<i>Protonemura</i> , <i>Amphinemura</i> & <i>Nemurella</i>) (P)	7
	Taeniopterygidae (<i>Taeniopteryx</i> ONLY) (P)	6
	Leuctridae (P)	7
	Aphelocheiridae (H)	7
	Scirtidae (<i>Elodes</i> ONLY) (C)	6
	Brachycentridae (T)	6
	Lepidostomatidae (T)	7
	Glossosomatidae (T)	7
	Philopotamidae (<i>Chimarra</i> ONLY) (T)	6
	Hydropsychidae (T)	5
	Leptoceridae (T)	5
	Polycentropodidae (T)	6
	Goeridae (T)	8
	Sericostomatidae (T)	7
	Simuliidae (D)	6
	Pediciidae (D)	7
	Empididae (D)	6
Stratiomyidae (D)	7	
Muscidae (D)	5	
Early stages of pools shrinking: Moderately tolerant lentic taxa (or extremely versatile lotic taxa)	Unionidae (B)	6
	Coenagrionidae (O)	5

	Corduliidae (O)	4
	Libellulidae (O)	4
	Gomphidae (O)	5
	Siphonuridae (E)	5
	Ephemeridae (E)	5
	Baetidae (<i>Cloeon</i> ONLY) (E)	4
	Caenidae (E)	5
	Leptophlebiidae (<i>Habrophlebia</i> & <i>Leptophlebia</i> ONLY) (E)	5
	Nemouridae (<i>Nemoura</i> ONLY) (P)	6
	Sialidae (Me)	5
	Sisyridae (N)	6
	Elmidae (C)	5
	Hydrochidae (C)	5
	Helophoridae (C)	3
	Ecnomidae (T)	4
	Molannidae (T)	5
	Tanypodinae (D)	5
	Orthoclaadiinae (D)	5
	Limoniidae (D)	5
	Tipulidae (D)	4
	Ptychopteridae (D)	5
	Dolichopodidae (D)	5
	Psychodidae (D)	4
	Tabanidae (D)	4
	Rhagionidae (D)	5
	Athericidae (D)	5
	Planariidae (Tr)	3
	Dugesidae (Tr)	3
	Lymnaeidae (G)	2
	Physidae (G)	3
	Sphaeriidae (B)	2
	Asellidae (M)	2
	Corixidae (H)	2
	Gerridae (H)	2
	Hydrometridae (H)	2
	Notonectidae (H)	1
	Naucoridae (H)	3
	Veliidae (H)	2
	Mesoveliidae (H)	2
	Gyrinidae (ADULTS ONLY) (C)	2
	Hydrophilidae (C)	3
	Scirtidae (EXCLUDING <i>Elodes</i>) (C)	3
	Dytiscidae (C)	1*
	Ephydriidae (D)	2
	Chironomini (D)	1
	Culicidae (D)	1
	Syrphidae (D)	1
	Ceratopogonidae (D)	1*
	Pools dry: Taxa with desiccation-resistant stages or able to survive in moist streambed	
	Planorbidae (G)	1
	Dytiscidae (C)	1*
	Ceratopogonidae (D)	1*
	Taxon group abbreviations are as follows: E, Ephemeroptera; P, Plecoptera; T, Trichoptera; G, Gastropoda; O, Odonata; H, Hemiptera; C, Coleoptera; L, Lepidoptera, D, Diptera; M, Malacostraca; B, Bivalvia; Me, Megaloptera; N, Neuroptera; Tr, Tricladida	

183 DEHLI is based on the calculation of an average of the component Drought Intolerance Scores in
184 Table 1, using the following equation:

$$185 \quad \text{DEHLI} = \sum \text{DIS} / n$$

186 Where n = the number of scoring taxa in the invertebrate sample.

187 DEHLI index values towards 10 imply little or no evidence of an ecological drought effect and values
188 towards 1 imply significant effects associated with the advanced stages of a drought.

189 Some taxa are capable of existing at either end of the continuum, such as the stonefly family
190 Nemouridae, some species of which thrive in lotic conditions but some taxa can, at least in the short
191 term, survive in wet interstices where the surface water is virtually absent; or the caddis family
192 Phryganeidae, which is closely associated with lotic marginal habitats but can also survive in lentic
193 environments with negligible marginal habitat. The utility of these examples is in demonstrating the
194 step-change associated with drought at an early stage, such as the loss of rheophilic (flowing)
195 conditions (Nemouridae) or marginal habitat (Phryganeidae). At a later stage of drought development,
196 the taxa may become concentrated in the remaining habitat patches which persist, though occurring
197 under sub-optimal conditions. Therefore, these taxa have been given a DIS to reflect the changes
198 occurring during the earliest stage of the drought / ramp disturbance. It is possible that DEHLI values
199 could be inflated during drought extremes, but the current weightings will help highlight any loss of
200 taxa during the early stages of drought (as thresholds of lateral and longitudinal connectivity are
201 severed) and their recolonisation during the recovery phase.

202 To ensure reproducibility of the final metric, the index should ideally be derived from samples
203 obtained using the standard protocols employed by the UK regulatory bodies (Environment Agency,
204 Natural Resources Wales, Scottish Environment Protection Agency and Northern Ireland Environment
205 Agency) as outlined in Murray-Bligh *et al.* (1997). This involves timed three-minute pro-rata multi-
206 habitat sampling with a Freshwater Biological Association pattern pond-net (square aperture of 0.5
207 m², 1-mm net mesh) with an additional 1-minute hand search. This has been demonstrated to
208 produce a good consistency and comparability of data and representation of the fauna present (Furse
209 *et al.*, 1981; Birk and Hering, 2006).

210 Although DEHLI has been designed to operate at family level, some adjustments would be required at
211 the genus level in calculation of the index, as some families include genera with starkly differing
212 habitat requirements (see, for example, Leptophlebiidae and Taeniopterygidae in Table 1). Therefore,
213 it is recommended that data used to derive the metric should be resolved to species level wherever
214 practical, both to ensure accurate calculation of the metric and to facilitate the derivation of
215 complementary metrics used as part of routine monitoring or for specific pressures, such as the Lotic-
216 invertebrate Index for Flow Evaluation (LIFE - Extence *et al.*, 1999), Proportion of Sediment-sensitive
217 Invertebrates index (PSI – Extence *et al.*, 2011), mixed level empirically-weighted PSI (E-PSI, Turley
218 *et al.* (2016) and Community Conservation Index (CCI – Chadd and Extence, 2004). Furthermore,
219 there is evidence which suggests that the highest possible level of taxonomic resolution produces
220 metric outputs of maximum efficacy (*e.g.* Monk *et al.*, 2012, Pickwell, 2012, Vilmi *et al.* 2015).

221 **2.2 Study sites**

222 DEHLI has been designed for wide application across a range of temporal scales and river types.
223 Below we illustrate its application using two case studies from England at different temporal
224 resolutions and a modelling exercise demonstrating the response of DEHLI to a hypothetical multi-
225 year drought, across a wider spatial scale. All of the case study sites and examples presented are
226 located on calcareous geologies for reasons of data availability, but the index is applicable to other
227 geological settings, in the UK and more widely.

228 Apart from changes in water quantity, none of the sample sites used in provision of data were subject
229 to any other significant stressors, such as anthropogenic water quality issues or substantial
230 morphological modifications. This was to ensure that confounding factors did not adjust the target
231 metric output, specifically, the impact of habitat loss mediated by reducing water availability. As
232 outlined above, this does result in 'natural' changes in water quality in the final stages, but this
233 concept has been integrated into derivation of the index.

234 **Figure 2: Location of the three study**
235 **sites.**



236

237 **2.2.1 River Tham (Glen Brook), Lincolnshire**

238 The River Tham (also known as Glen Brook) is a small calcareous stream draining a catchment of
239 24.3km² in Lincolnshire, UK. It rises 1.1km southeast of North Witham at 115m aOD, and flows for
240 11km in a south-easterly direction before joining the West Glen at Little Bytham (Figure 2). The river
241 rises from a limestone aquifer, the nature of the rock making the bed prone to fracture. As a result, as
242 flows naturally decline in summer, the presence of natural sinkholes leads to near-total cessation of
243 surface flow (see Figure 2). This provided a useful opportunity to study the ecological effect of drying
244 across four seasons. Invertebrate data were collected monthly over 14 months (November 2007 –
245 December 2008) from a site upstream of Park House Farm, 3.4km downstream of its source (SK
246 96547 20463). Samples were taken following the standard three-minute protocol, sampling habitats in
247 proportion to their occurrence, with 1 minute additional hand searching (Murray-Bligh *et al.*, 1997;
248 ISO, 2012).

249 **2.2.2 Little Stour, Kent**

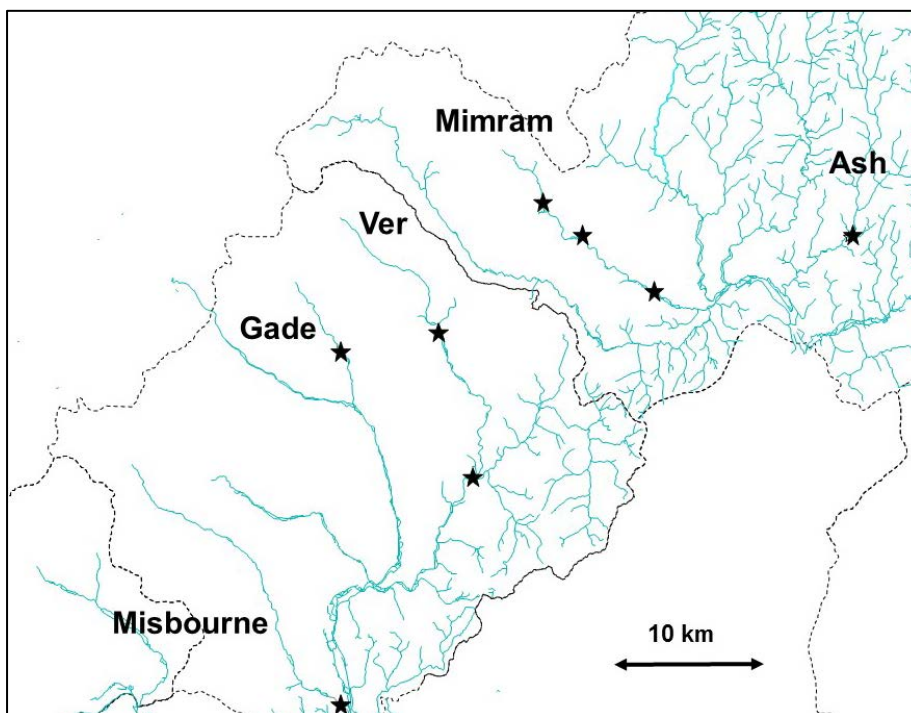
250 The Little Stour River is 11.5 km long, with a catchment area of approximately 213.3 km² rising about
251 4 km east of Canterbury (Figure 1). Together with the Nailbourne River, an intermittent winterbourne

252 stream, and the Wingham River, it forms a tributary of the Great Stour. Although the river rises from
253 chalk, gravels and alluvium are found in the lower valley (Wood and Petts, 1999). Regular annual
254 monitoring was undertaken between 1992 and 2001 to assess macroinvertebrate responses to low
255 flow variability (see Wood and Petts, 1999; Wood et al., 2000 and Wood and Armitage, 2004 for more
256 detail). Invertebrate samples were collected in early September using a non-standard methodology
257 (two-minute kick sample with a 250- μ m mesh pond net). The primary site of interest was located
258 adjacent to the village of Wickhambreaux and was dry in the 1992 and 1997 drought periods.

259 2.2.3 Modelling the effect on Chiltern and Hertfordshire chalk streams

260 Eight sites draining an area of Cretaceous Chalk which forms the Chiltern Hills and extends into
261 Hertfordshire were used in the modelling exercise (Figure 3). The rivers form the upper tributaries of
262 the Rivers Lee and Colne within the Thames Basin and include the Rivers Ash, Mimram (River Lee
263 catchment) and Ver, Gade, and Misbourne (River Colne catchment). The sites were chosen to have
264 relatively complete data records over the period 1988 to 2013, a total of 114 macroinvertebrate
265 samples being available for analysis. Macroinvertebrate samples were collected according to the
266 protocols as described for the River Tham above, with data from the northern hemisphere spring
267 (March-May) and autumn (September-November) seasonal sampling periods being used in the
268 analysis.

269 **Figure 3: Location of the study sites within the modelling analysis.**



270

271 Each site was paired with an Environment Agency flow gauging station on the same river reach. In
272 each case the flow regime at the gauge was assessed to ensure its representativeness of the flow
273 history of the paired macroinvertebrate sampling site, with no major intervening flow discontinuities
274 caused by either tributary inflows, abstractions or discharges. Daily mean flow time series from 1986
275 and 2014 were extracted from Environment Agency archives and divided into six monthly flow-
276 seasons for the summer (186 days) and winter (185 or 186 days for leap-years) periods. Hereafter,
277 the six-month summer and winter periods (summer, winter) are referred to as flow-seasons to avoid
278 confusion with the three-month macro-invertebrate sampling seasons (spring and autumn). For each
279 flow record and each individual flow-season, a flow duration curve was derived and summarised into
280 three easily calculated and widely utilised flow statistics: flow magnitude exceeded for 95%, 50% and

281 10% of the time (hereafter Q95, Q50, Q10), indexing the high, medium and low aspects of the flow
 282 series and resulting in a time series for each gauge and statistic on a six monthly time-step. Finally, to
 283 place the flows on a common scale, each series (7x gauges, 2x flow-seasons, 3x statistics) was
 284 standardised by deriving z-scores for each site (Kreysig, 1979).

285 The procedure for matching the seasonal antecedent flow data to the seasonal macroinvertebrate
 286 sample indices broadly followed the methodology outlined in Dunbar *et al.* (2010a, 2010b). The
 287 seasonal (summer = April to September, winter = October to March) six monthly aggregate
 288 antecedent flow statistics describing both high and low flow events during those periods were derived,
 289 and then matched to the biotic scores on a sample by sample basis (sample-season autumn matched
 290 to flow-season summer, sample season spring match to flow-season winter). Furthermore, in order to
 291 investigate the response to antecedent drought, each sample was then also matched to lagged low
 292 flow (Q95) statistics for summer flow-seasons one (suffixed LS1 – lagged summer 1) and two
 293 (suffixed LS2 – lagged summer 2) calendar years prior to sampling.

294 In order to compare the properties of DEHLI and LIFE calculated from the macroinvertebrate data
 295 sampled in the spring and autumn sampling periods, four separate models were calibrated (DELHI-
 296 spring, DELHI-autumn, LIFE-spring, LIFE-autumn). The modelling approach broadly followed that
 297 described in Dunbar *et al.* (2010a, 2010b): essentially multilevel/mixed effects multiple linear
 298 regression of the selected macroinvertebrate index, using seasonal standardised flow statistics as
 299 explanatory variables. Two broad modifications were:

- 300 1. The models were simplified so that only a site random intercept term was fitted. No attempt
 301 was made to evaluate random slope terms for any explanatory variable, due to the relatively
 302 small number of sites, and the aim of the exercise being to describe the general pattern.
- 303 2. The models were extended to predict the selected macroinvertebrate index using the wider
 304 series of lagged flow terms described above – not only flows from the immediately antecedent
 305 flow-season but also from the summer flow-season one and two years prior to sampling.
 306 Furthermore, selected interaction terms were fitted: between terms representing both high
 307 and low flows in the immediate antecedent period, and between summer low flow terms in
 308 different years (Table 2).

309 Following Dunbar *et al.* (2010b), a linear year trend term was fitted to account for a general increase
 310 in scores over time not related to inter-annual changes in flow.

311 Multi-model inference (Burnham and Anderson, 2002, Anderson 2008; Grueber *et al.* 2011) was used
 312 to tabulate a model set with a realistic degree of complexity while avoiding over-fitting arising from the
 313 relatively large number of potential predictors (themselves inter-correlated) but relatively small
 314 number of sites and samples. The use of model ranking and multi-model inference ensured the
 315 models were robust to effects of correlations between explanatory variables which would otherwise
 316 act to inflate the standard errors of parameters when applying a simple stepwise approach to model
 317 simplification.

318 Models were ranked using corrected Akaike Information Criterion (AICc) values (Burnham and
 319 Anderson, 2002). All models with an AICc Δ_i of 4 of the top model were tabulated.

320 **Table 2: Summary of explanatory variables.**

Main effects
Q95, Q50, Q10 flows in flow-season immediately prior to sample being taken (winter flows-spring samples, summer flows-autumn samples) (Q95z, Q50z, Q10z)
Q95 flows in summer before year of sample (Q95zLS1)
Q95 flows in summers before year of sample (Q95zLS2)
Calendar year of sample (1998 taken as base year)

Interaction effects
Q95z : Q10z
Q95z : Q95zLS1
Q95zLS1 : Q95zLS2
Q95z : Q95zLS2

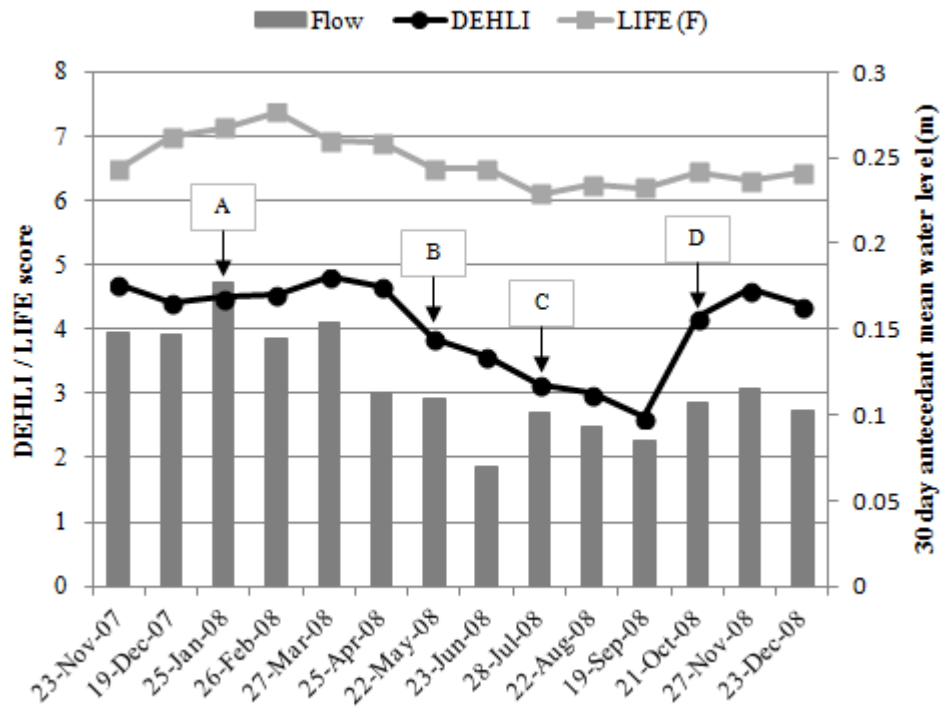
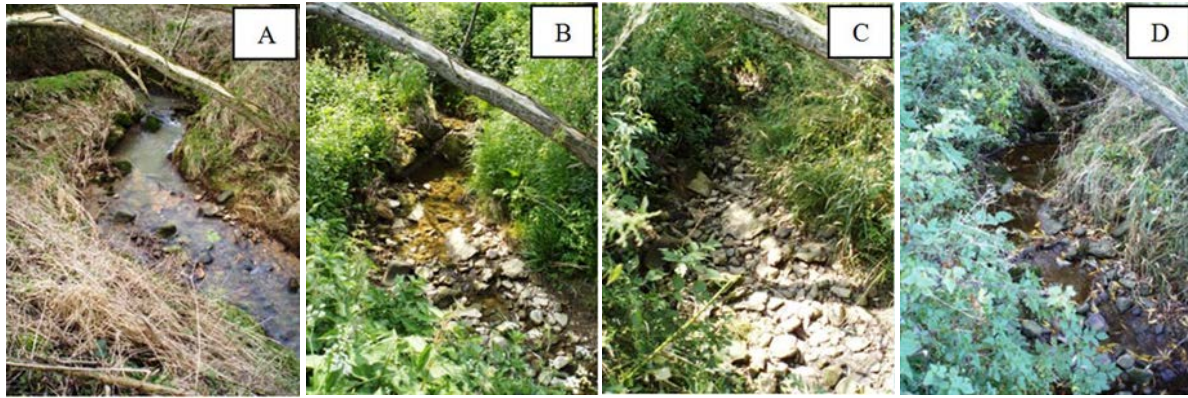
321

322 Having produced four multi-model sets, the resulting weighted multi-models were used to predict LIFE
323 and DEHLI response in the spring and autumn season to a developing synthetic multi-year drought,
324 with flows at average levels in the first year, progressively declining over the next four years, and then
325 a relatively rapid recovery in flows beginning in the next following winter, and proceeding for a further
326 two years. Although the year trend was highly significant and positive, for this exercise it was not used
327 in the predictions.

328 **3. Results**

329 ***3.1 River Tham (Glen Brook), Park House Farm, Lincolnshire***

330 **Figure 4: DEHLI and LIFE response, plus mean surface water flows at**
331 **downstream gauge-point (Castle Bytham 3.9 km downstream of sample point),**
332 **with monthly sampling (November 2007 to December 2008), matched with**
333 **fixed-point photographic record (River Tham/Glen Brook).**



334

335 **Table 3: Drought Intolerance Score (DIS) taxon list for time points A to D (R.**
 336 **Tham) – see Figure 4.**

DIS taxa presence			
25-Jan-2008 (Photo A)	22-May-2008 (Photo B)	28-July-2008 (Photo C)	21-Oct-2008 (Photo D)
<i>Baetis</i>	<i>Baetis</i>	Dixidae	Pediciidae
Pediciidae	Pediciidae	Gammaridae	Gammaridae
Gammaridae	Gammaridae	Asellidae	Caenidae
Caenidae	Caenidae	Veliidae	Elmidae
<i>Elodes</i>	<i>Elodes</i>	Dytiscidae	Orthocladiinae
Hydropsychidae	Hydropsychiidae	Gyrinidae	<i>Elodes</i>
Limoniidae	Orthocladiinae		Tipulidae
Simuliidae	Helophoridae		Psychodidae
Orthocladiinae	Hydrophilidae		Lymnaeidae
Helophoridae	Tipulidae		Dytiscidae
Tipulidae	Asellidae		Ceratopogonidae
Veliidae	Veliidae		
Chironomini	Dytiscidae		
Culicidae	Culicidae		
	Chironomini		

337

338 **Key to DIS scores: white = 7 or 8, light grey = 5 or 6, dark grey = 3 or 4 and black = 1 or 2**

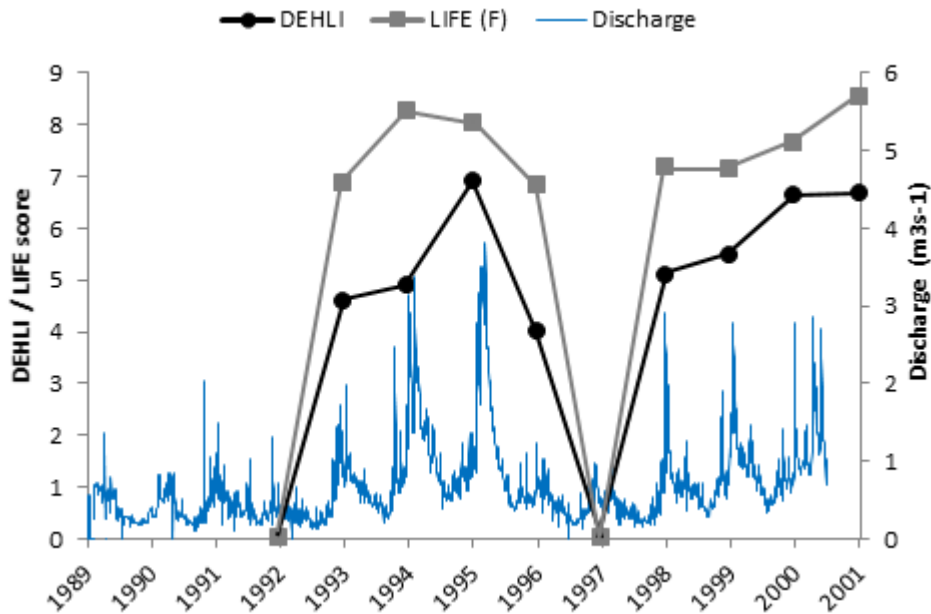
339 The results indicate that DEHLI scores responded to drought and its development in a more sensitive
340 manner than the LIFE index (Figure 4 and Table 3). From May 2008 and July 2008 there was a
341 marked reduction in surface water flow to the point where much of the river bed was dry and exposed
342 (Figure. 4B and 4C). LIFE scores, however, did not appear to respond to this, with scores remaining
343 relatively stable until October 2008. In contrast, DEHLI tracked the severity of low flow conditions, with
344 scores declining between May and July, through to September 2008, before some recovery in
345 October, when significant surface water flows began to return (Figure 4D). During the early phases of
346 drought development, from February 2008 (Figure 4A) to May 2008 (Figure 4B), the LIFE index
347 responded more readily than DEHLI to the gradual reduction in flow velocities. LIFE scores over this
348 period displayed a steady decline from 7.38 to 6.5 whereas DEHLI showed a limited response until
349 May when there was a marked drop in score from 4.67 to 3.87, likely to be the response to the
350 crossing of a connectivity threshold, early year spate flows transforming into a slow flowing and
351 shallow trickle during the initial stages of loss of longitudinal connectivity

352 The observed reduction in surface water availability and the associated progressive loss of habitat
353 from January to July was reflected in the gradual loss of many mid-high scoring DIS taxa (Table 3).
354 From January to May, when water levels began to decline and flow velocities were reduced,
355 rheophilic taxa (e.g. Simuliidae and Limoniidae) disappeared and there was a concomitant
356 appearance of lentic taxa (e.g. Asellidae and Dytiscidae). The further loss of rheophilic taxa continued
357 through to July when there was a complete cessation of surface water flows and only small
358 disconnected pools remained. At this point the invertebrate community became dominated by highly
359 tolerant lentic taxa. When surface flows returned in October the rheophilic taxa returned quickly (e.g.
360 Pediciidae and *Elodes*).

361

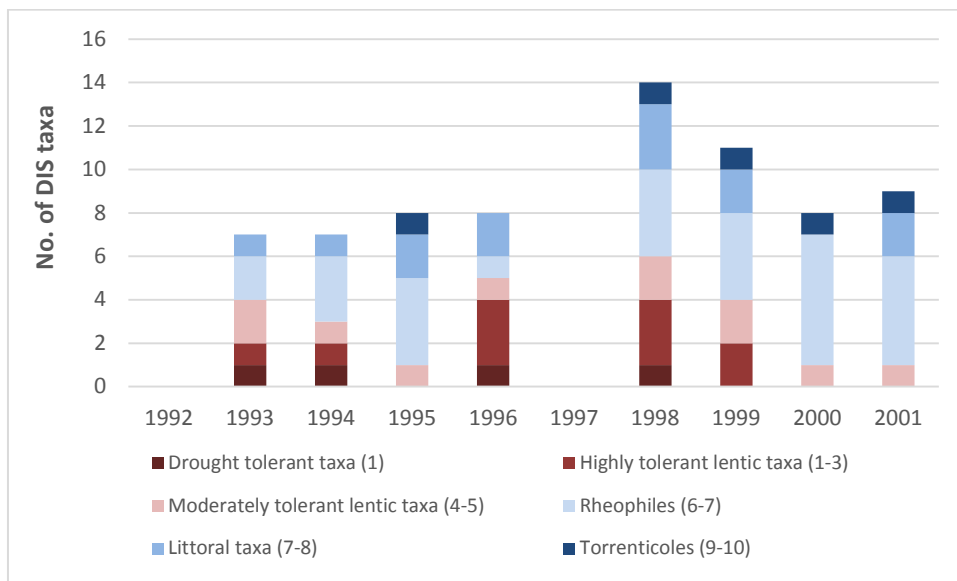
362 **3.2 Little Stour, Wickhambreaux, Kent**

363 **Figure 5: Annual DEHLI & LIFE response versus gauged discharge (Little**



364 **Stour).**

365 **Figure 6: Annual community composition (DIS taxa), Little Stour.**



366

367 Annual DEHLI and LIFE (family) scores for the Little Stour from 1992 to 2001, together with river
 368 discharge are shown in Figure 5. The river channel was dry during the 1992 and 1997 sampling
 369 periods. Between the summers of 1991 until the end of 1992, terrestrial vegetation colonised the
 370 channel bed, with most of it being subsequently removed with the resumption of flows in 1993. There
 371 was a progressive increase in flows between 1993 and 1995, LIFE scores quickly peaked in 1994 at
 372 8.25 before a gradual decline in scores with the 1996-97 drought (Figure 5). In contrast, from 1993
 373 DEHLI rose consecutively for the next two years mirroring the gradual recovery of flows from drought
 374 effects, peaking in 1995. In 1996 both LIFE and DEHLI indicate a reduction in response to a second
 375 supra-seasonal drought, with DEHLI displaying a more marked deterioration with a score that fell
 376 below that of the recovery phase in 1993, whereas LIFE declined to levels comparable to 1993. In

377 1998, following the 1997 drought period, both metrics show similar levels of recovery to that recorded
378 following the 1991-1992 drought with scores comparable to 1993 values.

379 The resumption of surface water flows in 1993 saw the return of an invertebrate community with a
380 notable proportion of lentic taxa and a relatively low number of rheophilic taxa (Figure 6). This
381 changed following the recovery of flow in 1994 and 1995, when faunal composition was dominated by
382 rheophilic taxa (e.g. Rhyacophilidae, Glossosomatidae and Simuliidae). With the onset of the 1996
383 drought, there was a return to the dominance of lentic taxa and a major reduction of rheophiles
384 associated with the loss of longitudinal connectivity on the river. With the return of surface water flows
385 in 1998, there was a rapid recovery and peak in taxon richness (DIS taxa = 14), which saw a strong
386 mixture of both lentic and lotic taxa. Following the recovery period, 1999-2001, the number of low
387 scoring DIS taxa declined, a result of the lentic taxa declining over the next three years from six to
388 one, with the rheophilic taxa once again dominating the community.

389 **3.3 Chilterns streams: modelled drought response**

390 In all four cases (spring and autumn DEHLI and spring LIFE, autumn LIFE), ranking of model sets
391 indicated the importance of more than one single model in describing the response of the indices to
392 antecedent flow. DEHLI produced more candidate models than LIFE, and spring produced more
393 candidate models than autumn (Table 4). Table 4 illustrates the numbers of models selected in a
394 candidate set within an AICc of 4 for the top model, along with the relative importance of each
395 explanatory variable. Relative importance illustrates the weighted proportion of candidate models with
396 the variable present, hence 1.00 indicates that the variable was present in every candidate model.
397 Residual vs fitted values plots were examined for each maximal model and indicated that model
398 assumptions were valid. Generally the flow terms closest in time to the sampling date were most
399 commonly selected, indicating the relatively greater strength and precision of response of the
400 macroinvertebrate community to antecedent flows immediately prior to the ecological sample
401 collection. The exception to this was for spring LIFE, where (flow-season winter) Q10z rarely
402 appeared in the model set. Summer lagged low flows one and two years prior to sampling also
403 appeared frequently. Overall this indicates the multi-faceted nature of the ecological response to flow,
404 and confirms that at a broad level, both DEHLI and LIFE respond to inter-annual drought, not simply
405 seasonal low flow. The most commonly occurring interaction effect was Q10z:Q95z, particularly for
406 both autumn DEHLI and LIFE. The presence and direction of this interaction indicated that when
407 antecedent summer high (Q10z) and low (Q95z) flows are lower than average, this is associated with
408 lower index scores. Conversely, when both Q10z and Q95z are high, index scores are slightly
409 lowered, although this may be a statistical artefact arising from the linear nature of the interaction
410 effect. Given the groundwater influence in the studied catchments, summer Q10z indicates the
411 influence of early summer high flows, whereas Q95z indicates the influence of late summer flows.

412

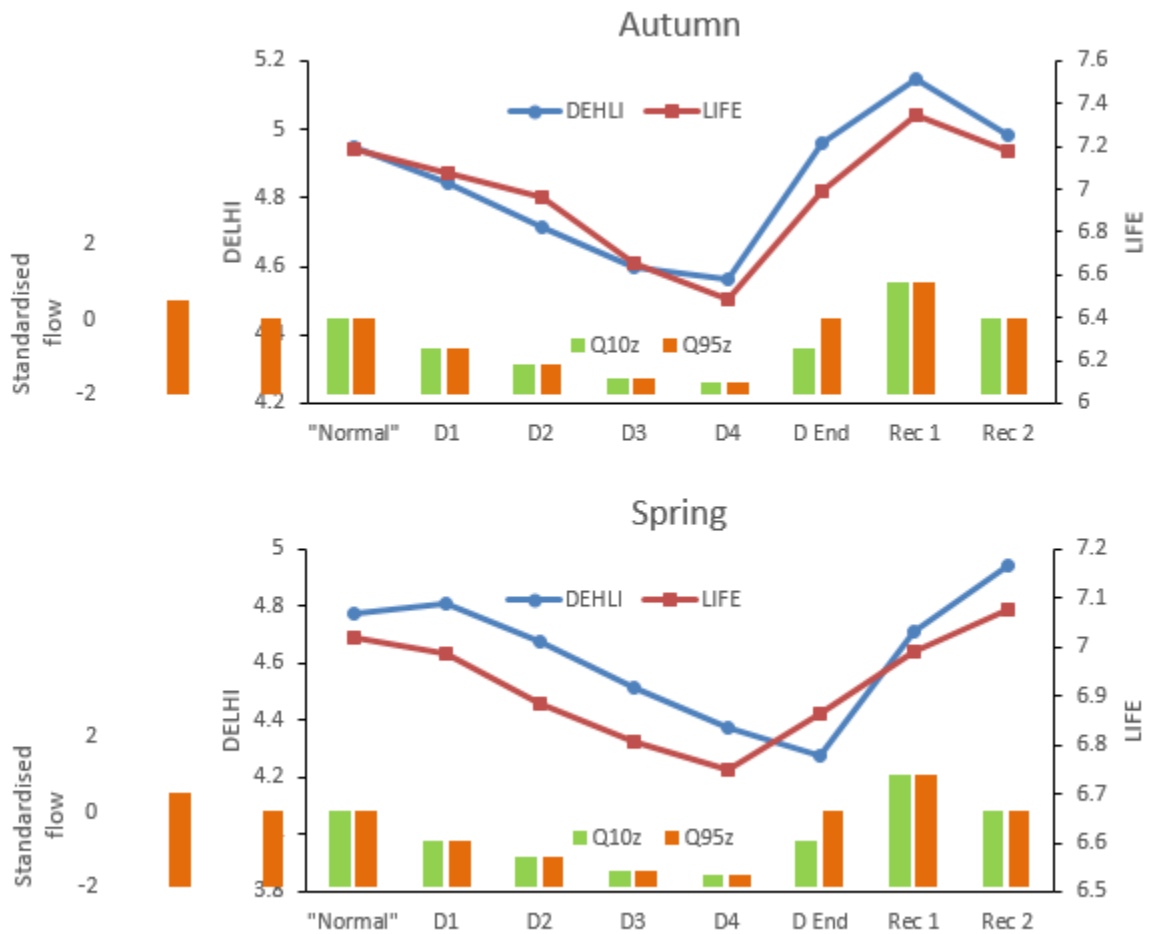
413 **Table 4. Relative importance for each explanatory variable in each of four**
 414 **separate multi-model sets (within Δ AICc = 4 of top model), and number of**
 415 **models in each candidate model set.**

Variable	DEHLI spring	DEHLI autumn	LIFE (F) spring	LIFE (F) autumn
Year	1.00	1.00	1.00	1.00
Q95z	0.69	1.00	0.83	1.00
Q10z	0.57	1.00	0.17	1.00
Q10z:Q95z	0.17	1.00	0.05	1.00
Q95zLS2	0.73	0.83	0.30	0.78
Q95zLS1	1.00	0.35	0.94	0.46
Q95z:Q95zLS2	0.19	0.23	0.12	0.72
Q95z:Q95zLS1	0.21	0.12	0.77	0.31
Q95zLS1:Q95zLS2	0.56		0.05	0.06
Number of models in candidate set	22	7	9	6

416

417 Considering the predicted macroinvertebrate scores to the synthetic supra-seasonal drought (Figure
 418 7), for the autumn community, DEHLI displayed a linear decline from “normal” conditions (defined as
 419 a value of 0 for each standardised flow statistic) into increasingly severe drought. The reduction in
 420 DEHLI was less marked in years 3 to 4 of the drought. In contrast, LIFE showed a slower initial
 421 decline up to year 2, but it declined more rapidly in year 3, and while the decline became less steep in
 422 year 4, the rate was greater than for DEHLI. In terms of recovery, both indices recovered quickly
 423 during the first year after the drought, with DEHLI recovering slightly more quickly. In the second year
 424 of recovery, both DEHLI and LIFE recovered to levels above normal conditions.

425 **Figure 7. Predicted autumn and spring DEHLI and LIFE scores over a**
 426 **hypothetical multi-year drought.**



427

428 The Response of DEHLI and LIFE in spring differed from that of autumn. In autumn, the indices
 429 followed different trajectories during the developing drought conditions, whereas in spring, the indices
 430 showed a similar, relatively linear decline. Compared with the autumn community, however, the
 431 DEHLI scores for the spring community showed a notable lag in response as the synthetic drought
 432 developed, and continued to decline after the end of the drought. Once DEHLI began to recover,
 433 however, this occurred relatively rapidly, and again both indices recovered to levels above those at
 434 the beginning of the period

435 **4. Discussion**

436 The principle which underpins DEHLI is that the effect of drought on aquatic invertebrates follows a
 437 ramp disturbance and that this gradual change, punctuated by abrupt losses of habitat and
 438 concomitant loss of taxa, is a valuable model to help guide the management of freshwater
 439 ecosystems and the resources they support (Boulton, 2003; Boulton and Lake, 2008). It is widely
 440 documented that aquatic communities recover, even after the loss of surface water due to drought.
 441 Furthermore, it should be possible to re-establish ecological resilience through rehabilitation of
 442 degraded habitats (Boulton *et al.*, 2010; Leigh *et al.*, 2015). Studies over recent years have greatly
 443 improved our understanding of how rivers recover from drying events and the response of individual
 444 taxa (Stubbington *et al.*, 2016; Datry *et al.*, 2014, Leigh *et al.*, 2016). Use of refugia and the degree of
 445 connectivity are important for survival in extreme drought (Reich and Lake 2014). Connectivity with

446 the hyporheic zone is therefore of great importance (Boulton *et al.*, 2010), as is the ability for life
447 stages of many taxa to persist within the “seedbank” (Stubbington and Datry 2013).

448 **4.1 An empirical approach to drought effects on ecology**

449 This raises questions regarding the need for an empirical metric. A drying river can be clearly
450 illustrated using a photograph. However, this is not necessarily the point at which a drought is exerting
451 an ecological effect. The response observed using DEHLI in the River Tham case study demonstrates
452 rapid changes as the site began to contract into pools. The first important phase to be indicated as the
453 drought effect deepened was when the reduction in flow resulted in an ecological step-change,
454 indicated by the reduction in DEHLI scores from May through to September. These scores provide an
455 ‘impacted state’ against which to measure subsequent recovery. The second important re-wetting and
456 recovery phase during the drought was clearly shown in the results by the rise in DEHLI scores from
457 September to November (Time-point D in Figure 4). DEHLI provides evidence of both the ramp effect
458 of reduced flow and the recovery to pre-drought conditions with the resumption of flow (Point A in
459 Figure 4); in marked contrast to the relative stability recorded by LIFE scores over the same period.
460 This provides firm evidence that instream habitats were sufficiently complex and the concomitant
461 adaptation of the invertebrate community resistant to the effects of drying that they were able to
462 recover / re-colonise following the severe low flows. The empirical measures from January through to
463 April (prior to the drought onset) effectively provide the baseline condition for the site to achieve once
464 flows return. It is, of course, possible that the baseline condition at the Tham site is already
465 permanently degraded and the river has developed over a number of years to support a relatively
466 impoverished fauna. Thus, the ecological condition recovered from a state degraded by drought to a
467 lower baseline, so that the process was more rapid, but intervention to restore the habitat to a better,
468 more natural ‘baseline state’ is still necessary. This can easily be tested using predictive modelling
469 and empirical measures such as DEHLI are ideal for such a purpose. This strategy has proved
470 successful elsewhere in approaches to managing flows (e.g. Dunbar *et al.* 2010a, 2010b) and the
471 incorporation of DEHLI scores to help understand, quantify and ameliorate the effects of drought
472 could be a useful additional tool to draw upon. In essence, the ability DEHLI provides to give empirical
473 measures to nebulous processes such as drought recovery is of great utility in environmental
474 management. For example, DEHLI can be used to compare a variety of locations along a river during
475 drought, potentially revealing ‘sentinel’ locations where managers might most usefully site their
476 sampling stations to detect the early stages of water shortages (due to natural or anthropogenic
477 drought).

478 **4.2 Informing river management processes and decision-making**

479 In river reaches where resilience is low or where they are subject to high magnitude supra-seasonal
480 droughts (as illustrated by the Little Stour River case study), the effect of a drought indicated by the
481 DEHLI index may be extended over more than one year. Thus, the method may provide evidence to
482 identify sites where there is a need to increase habitat complexity and ecological resilience. At an
483 operational level, this may be achieved by managing abstraction, by undertaking morphological
484 restoration measures, or both. Consequently, by applying DEHLI and the principles which underlie it,
485 we can both monitor the effects of drought associated with short-long term weather patterns and
486 prioritise where intervention may be required to increase resilience to the impacts of climate change
487 and anthropogenic activities. For the UK, there is, to date, little evidence of changes to drought or low
488 flow frequencies, although some studies indicate increases in the magnitude and frequency of short
489 droughts (<18 months) in the future (Watts and Anderson 2013; Watts *et al.*, 2015). Addressing
490 morphological degradation is a widely accepted approach in adapting to climate change to help
491 protect our rivers from extreme events including drought (Henriques *et al.* 2015 and Orr *et al.* 2015),
492 increase ecological resilience (Dunbar *et al.* 2010a, 2010b and Dokulil 2016) and protect ecosystem
493 services (Zalewski, 2014).

494 **4.3 Tracking long-term drought effects on ecology**

495 The Little Stour case study clearly illustrates both the immediate effect of drought and subsequent
496 recovery associated with two high magnitude supra-seasonal droughts. There was a marked upward
497 shift in taxon richness in the Little Stour following the return of surface water in 1998 (Figure 6), with a
498 mixture of lentic and lotic taxa occurring. This is likely to be the consequence of a transitional recovery
499 period, following the end of the drought which is often characterised by a high flow event (Parry *et al.*,
500 2016) so that both types of taxa were able to coexist until higher flows occurred during the
501 subsequent winter. Following the recovery period, a number of lentic taxa disappeared and rheophilic
502 taxa once again dominated the community. The greater taxon richness observed on the Little Stour in
503 1998 after drought compared with 1993 (Figure 6) may be due to the relative severity of the preceding
504 droughts. The drought prior to 1998 was shorter in length: two years (1996-97) compared with four
505 years (1989-1992) prior to 1993. It is probable that the increased severity of the 1989-1992 drought
506 exerted a greater effect (drying the riverbed at the study site for more than 12 months) and as a result
507 it took longer for the recovery of the invertebrate community to occur, with full recovery, as shown by
508 DEHLI, not occurring until 1995. This change in community taxonomic composition may be expected,
509 given that drought acts as an important natural disturbance, modifying macroinvertebrate
510 communities and their associated food webs (Atkinson *et al.*, 2014; Lu *et al.*, 2016). In contrast,
511 James and Suren (2009), working in lowland New Zealand, found that the effects of increased
512 duration and magnitude of flow reduction on invertebrate communities was restricted to changes in
513 the abundances of relatively few taxa. Previous workers have found that the magnitude of impact
514 varies with the duration of the drought and streambed drying events (e.g. Wood and Petts 1999,
515 Wood *et al.* 2000, Stubbington *et al.*, 2009 and Datry, 2012). Fundamental to the impact of drying is
516 the severity of the event and the effect of flow permanence, with clear differences between sites that
517 are usually perennial and naturally intermittent river reaches (Extence, 1981, Boulton, 2003, Lake,
518 2003, Smith *et al.*, 2003, Boulton and Lake 2008).

519 **4.4 Incorporation in multi-metric approaches**

520 In the current study, the combined use of LIFE and DEHLI was useful for observing the changes
521 associated with drought and in helping to interpret their probable causes, as the strength of both
522 indices lies in an inherent basis with an explicit mechanism. Following the return of surface water on
523 the Little Stour, the LIFE index rapidly returned to pre-drought conditions (within 1 year – following
524 both 1989-1992 and 1996-1997 events), reflecting the resilience of the rheophilic/torrenticole
525 community and their effect on the derivation of the LIFE score. In marked contrast, the DEHLI index
526 indicated ongoing effects up to 1999, two years after the return of flows, with drought-tolerant and
527 highly tolerant lentic taxa still forming a major component of the community. The ecological
528 mechanisms which underpin the indices, relating to habitat loss for DEHLI and flow velocity response
529 for LIFE, explain the differences recorded. Drying can result in the local extinction of fauna associated
530 with particular habitat types (e.g., when riffles become exposed as water level declines), so recovery
531 may require recolonisation, perhaps from sources beyond the local environment. Recolonisation may
532 be further constrained by seasonal patterns of invertebrate reproduction and/or differences in drying-
533 resistant life stages. The less responsive nature of LIFE during drought reflects its sensitivity to
534 reducing water velocities. Examination of LIFE scores from both case studies clearly indicates that
535 small populations of rheophilic and torrenticole taxa persisted, especially in environments with habitat
536 which is less degraded and more resilient to reducing flows. Thus, the capacity remained for rapid
537 recolonisation and recovery once velocities rose. These differences reflect the scores assigned to
538 taxa, for example, the dragonfly family Aeshnidae were allocated a high DIS of 7 (Table 1), reflecting
539 loss of lateral connectivity. In the LIFE index, the same family is assigned to Flow Group IV, indicating
540 a preference for still water environments or marginal dead waters in rivers. As a result we would
541 advocate the application of multiple metrics wherever possible. The use of multiple metrics is a well-
542 documented approach when attempting to disentangle the relative responses to multiple stressors
543 within aquatic environments (e.g. Extence *et al.* (in press)). For example, Clews and Ormerod (2008)

544 in their study of the Welsh River Wye, concluded that simple pressure-specific indices have bio-
545 diagnostic capability and advocated the further development and testing of the combined use of
546 pressure-specific metrics in other locations. It is widely acknowledged as best practice not to use
547 biotic indices in isolation, but to test all potential stressors against the same dataset. The UK
548 regulatory bodies routinely undertake this approach, plotting modelled index scores as a ratio against
549 observed scores, to simultaneously demonstrate organic pollution stress, fine sediment deposition
550 and flow stress. These outputs are further modified by consideration of physical modification and
551 measures of trophic state. It is suggested that, used in combination and informed by the use of other
552 pressure-sensitive indices, the LIFE and DEHLI indices will improve our understanding of how aquatic
553 invertebrate communities respond to drought.

554 The modelling of integrated data from the Chilterns streams was undertaken to compare the response
555 of DEHLI and LIFE to changes in flow associated with drought over a wider spatial and temporal scale
556 and to further understand the relative properties of the two complementary approaches. The results
557 showed differential response by season. The delay in response of DEHLI to returning flows in spring
558 is likely to be due to a season-driven lag in recolonisation and perhaps to the persistence of drought
559 tolerant fauna (also reflected in the empirical case studies). The loss of fauna as the marginal habitats
560 dried during drought would be followed by a subsequent reconnection in autumn through to the
561 following spring. Whilst the habitat was subsequently reconnected, recolonisation may have lagged
562 behind because of a delay relating to breeding season in late spring and early summer, as well as the
563 need for recovery of resources, such as food supplies, to sustain populations. In comparison, LIFE
564 response to rising flow velocities and establishment of mid-channel rheophiles in the early part of the
565 year would be more rapid, as recolonisation would be derived from the maintenance of populations in
566 refugia. Autumn response, by contrast, shows different trajectories between the two indices. DEHLI
567 shows a steady decline associated with the impacts of the ramp disturbance, whereas LIFE may
568 remain elevated as taxa move into high-velocity refugia, masking the early impacts of drought. The
569 results of both the modelling and field investigations illustrate how access to refugia, including flowing
570 water refugia, (Reich and Lake 2014) such as isolated riffles and the hyporheic zone (Stubbington
571 and Datry 2013, Stubbington *et al.* 2015 and Verdonschot *et al.* 2015) is critical to the drought
572 recovery process.

573 The results of the modelling exercise indicate interaction effects between antecedent high (Q10 - high
574 flow exceeded only 10% of the time) and low flows (Q95 - low flows exceeded 95% of the time),
575 demonstrating the potentially complex ways in which macro-invertebrate communities may be
576 influenced by antecedent flows. Whilst the choice of flow statistics in the modelling exercise was
577 guided by previous work, there are likely to be other ways of summarising flow data in an ecologically
578 useful way, perhaps guided by the various questions to which DEHLI might be applied. Groundwater
579 recharge during the winter is regarded as the dominant control on the flow regimes in the rivers
580 studied in the Chilterns. Hence, for the summer period (April to September), the highest flows occur in
581 the early part (April-May), and the low flows typically occur later (August-September). This illustrates
582 the importance of April-May flows in controlling the autumn macro-invertebrate community (Wood *et*
583 *al.* 2000; Wood and Armitage 2004) and is reflected in the response of the two indices. It is important
584 to recognise that DEHLI has been designed to reflect progressive step-changes to habitat as droughts
585 proceed, whereas LIFE responds to changes in flow velocities and as a result, DEHLI is more
586 sensitive to change as lotic ecosystems enter into and exit from severe drought. The modelling
587 exercise reinforces the potential utility of the multi-metric approach advocated by Clews and Ormerod
588 (2008).

589 **4.5 Conclusions and future work**

590 DEHLI presents a valuable tool to help gauge the effects of drought (historic and in real time), guide
591 management and regulate the impacts of drought and water abstraction. Its utility in providing an
592 empirical measure for decision-making in environmental management is of paramount importance, as

593 it facilitates the use of complex ecological data for strategic decisions, potentially made by non-
594 specialists. Its use in highlighting habitat loss through ramp disturbance adds to existing tools
595 available to guide riverine management decisions associated with habitat restoration programmes,
596 enhancement of ecosystem resilience and regulatory licencing strategies. In this study, we have
597 utilised the data widely available from the UK regulatory bodies following standard approaches, such
598 as those outlined by Murray-Bligh *et al.* (1997) and ISO (2012). While it is preferable to utilise a
599 sampling method that covers all habitats present within a site to understand the full impacts
600 associated with drought and associated habitat changes, it is possible to employ other methods of
601 sampling, (e.g. fully quantitative methods such as the Surber sampler, see Chadd, 2010), so long as
602 the methods are used consistently in comparison of metric outputs. Both semi- and full-quantitative
603 methods used in standard protocols derive abundance data for taxonomic categories. It is recognised
604 that DEHLI, unlike other metrics such as LIFE, does not have an abundance weighting in the manner
605 in which it is derived. Future work could look to incorporate these data into the final metric, so as to
606 provide a potentially more accurate measure of drought effects on instream ecology. Consideration
607 should also be given to sampling the full habitat composition at a site in a drying river, including bed
608 sediments. Alternative techniques being developed in the monitoring of temporary rivers and
609 ephemeral streams, such as the rewetting of river bed-sediment (see Stubbington *et al.* 2016) and
610 sampling of macroinvertebrates of exposed riverine sediments and riparian zones, will help in our
611 understanding of how rivers are affected by and respond to drought. Taking this approach might have
612 amplified the DEHLI response in the Tham and Little Stour case studies, by incorporating fauna fully
613 adapted to states close to full drying and moderating the influence of rheophilic taxa surviving in
614 pools. Further research into the use of broader suites of riparian taxa should examine the efficacy of
615 such approaches and determine the value of their adoption by regulatory bodies.

616
617 Furthermore, it is acknowledged that the river typologies used in this paper are all on calcareous
618 geologies in lowland areas of the south and east of England and consequently largely fed by
619 groundwater. Future work should look to test the index in surface-input impermeable geologies and/or
620 in upland areas of Britain as well as expanding its use into continental Europe in both upland and
621 lowland topologies. It is anticipated that ecological changes will be much more abrupt in surface-water
622 dominated, particularly upland, catchments, as habitat loss and re-wetting are likely to be over a
623 shorter time scale. Expanding the geographical and topological scope of the index (including potential
624 application in different continents, with some taxonomic adaptation) may further encourage its wider
625 use in regulation and research efforts worldwide.

626

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628

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639 **6. References**

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841 **Supplementary material: references used to assign DIS weights.**

- 842 Much of the weighting process was informed by personal communication with Andrew Boulton, using
843 work already carried out in Australia by him and Sam Lake. Adaptation of the weights for UK use was
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