Ecological effects of a supra-seasonal drought on macroinvertebrate communities differ between near-perennial and ephemeral river reaches

1 **Ecological effects of a supra-seasonal drought on macroinvertebrate communities differ**

2 **between near-perennial and ephemeral river reaches**

3 **Running title:** Aquatic macroinvertebrate biodiversity following supra-seasonal drought

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24 **Abstract**

25 The duration, intensity and frequency of hydrological droughts are predicted to increase significantly

26 over the 21st century globally, threatening the long-term stability of lotic communities. In this paper

27 we examine the recovery and recolonization of macroinvertebrate taxa in ephemeral and near-

28 perennial reaches of the River Lathkill (UK) after a supra-seasonal drought event. Following flow

29 resumption, species accumulation (recolonization) occurred rapidly over a four-month period, with a

30 steady increase observed thereafter. Taxonomic richness was significantly higher in the near perennial

31 section than the naturally ephemeral reach. Serial correlation was observed in the near perennial

32 section but not in the upstream ephemeral reach. Serial correlation in the near perennial section may

33 due to (1) the ongoing process of ecological recovery or (2) the macroinvertebrate community

34 following a new ecological trajectory. Our results suggest that supra-seasonal droughts may cause

35 initial reductions in lotic diversity during stream desiccation events but may effectively re-set

36 ecological succession and / or temporarily provide new ecological niches, thereby supporting

37 increased taxonomic diversity when the full range of hydrological conditions are considered.

38 Quantifying the recovery of ecological communities to supra-seasonal drought can provide detailed

39 information to develop ecologically effective conservation and management strategies.

40 **Key words:** aquatic conservation, biodiversity, community composition, disturbance, ephemeral

41 streams, lotic habitat.

Introduction

Global climate models predict that the duration, intensity and frequency of drought events are likely to increase significantly over the 21st century (Prudhomme et al. 2014). Climatic variability combined with increasing abstraction pressures and the construction of artificial impoundments to supply increasing human populations, globally, is likely to increase the number of waterbodies that experience channel drying (Larned et al. 2010), extend the duration of drying events in waterbodies that already experience dewatering (Benejam et al. 2010; Rahiz and New 2013; Skoulikidis et al. 2017) and lead to significant changes to biological communities, such as the loss of taxa poorly adapted to drying events (Datry et al. 2014).

Supraseasonal drought is defined here as an extended duration of reduced rainfall and surface water availability over multiple seasons or years (Lake 2011). This differs to seasonal drought which is characterised by seasonal reductions in rainfall and water availability, such as those regularly experienced in semi-arid or Mediterranean ecosystems (Gasith and Resh 1999). Extreme, high magnitude but low frequency supra-seasonal events may significantly increase the spatial and temporal extent of stream drying (Boulton 2003; Wood and Armitage 2004) and in some instances affect historically perennial sites (Stubbington et al. 2015).

Surface water drying is a primary determinant of aquatic floral and faunal diversity and community structure in intermittent lotic ecosystems (Lake 2003; Stubbington et al. 2011; Aspin et al. 2018) with streambed drying events commonly being associated with reductions in aquatic diversity (Soria et al. 2017). Following streambed drying, harsh environmental conditions selectively remove taxa which are dependent on surface flow and good water quality (Wood and Petts 1999; Datry et al. 2013) and may cause an increase in faunal densities and competition as habitat availability is reduced (James et al. 2008). However, recovery of flow and the recolonization of aquatic flora and fauna flowing channel drying in intermittent streams can be rapid, reflecting the range of traits / adaptations which

68 promote resilience and resistance in temporary waterbodies (Fritz and Dodds 2004; Stubbington and

69 Datry 2013; Vander Vorste et al. 2015; Sarremejane et al. 2017). Resistance can be enhanced due to

70 strong dispersal capacity with taxa being able to migrate from the stream as it dries and rapidly

71 recolonize when flow resumes (Leigh et al. 2016). Resilience can be facilitated by physiological and

72 morphological traits that enable drought survival *in situ* (e.g., short life cycles, desiccation resistant

73 eggs or adult life stages able to persist in moist sediments; Williams 2006; Vander Vorste et al. 2015).

74 Resilience strategies may also be strongly influenced by the presence of refuges, such as nearby

75 perennial pools, the hyporheic zone, perennial downstream reaches or patches of moist leaf litter,

76 proximal to intermittent streams (Chester and Robson 2011; Hill and Milner 2018).

77

78 In streams that experience regular or predictable drying, the effect of seasonal drought on aquatic

79 communities may be limited compared to those of perennially flowing systems (Côté and Darling

80 2010; Vander Vorste et al. 2015; Chessman 2015). Typically, perennial streams have high ecosystem

81 stability and may be dominated by a limited number of highly abundant flora and fauna (Fisher 1983;

82 Milner et al. 2008). However, supra-seasonal droughts and the subsequent recolonization and

83 recovery period may encourage the development of distinct faunal assemblages (Boulton 2003; Chadd

84 et al. 2017), and may help maintain, and in some instances enhance, habitat and faunal diversity at the

85 landscape scale. Supra-seasonal droughts potentially open new ecological niches for some organisms

86 following the removal or rapid reduction in abundance of numerically dominant and highly

87 competitive taxa or through the disturbance and re-setting of ecological trajectories. For example, the

88 gradual drying and ponding of surface water in a river channel as it dries may provide suitable

89 conditions for colonization by a wide range of taxa associated with lentic conditions (Sheldon et al.

90 2010; Hill and Milner 2018).

91

92 While the process of recolonization and recovery following stream drying and drought events within

93 seasonally intermittent waterbodies has been widely studied (Boulton 2003), there is a paucity of

94 research examining the aquatic biodiversity following supra-seasonal drought events (Lake 2003).

4

95   This is particularly apparent in temperate regions due to the difficulties associated with collecting

96   long-term data and predicting the onset and termination of supra-seasonal drought events. In arid

97   landscapes, Bogan et al. (2015) found that robust recovery after a supra-seasonal drought occurred in

98   streams with historically predictable intermittency, with these communities demonstrating both

99   resistance and resilience mechanisms. In the same study, the response of perennial macroinvertebrate

100 communities to supra-seasonal drought differed due to a lack of resistance traits in the predrought

101 community; long lived (>1 year) weak dispersing macroinvertebrates were replaced by short lived (<1

102 year) strong dispersers that were able rapidly recolonize.

103

104 A supra-seasonal drought in the UK between December 2010 and April 2012 (Parry et al. 2013),

105 which subjected both perennial and ephemeral reaches of the River Lathkill to drying, provided a

106 unique opportunity to examine the response of macroinvertebrate communities to flow recovery. As a

107 result, this is one of the first studies to examine ecological responses to supra-seasonal drought from

108 communities in ephemeral and historically perennial flow sites in temperate regions. This study aimed

109 to characterise the recolonization of aquatic macroinvertebrate communities of naturally ephemeral

110 and near-perennial sites (flowing except under extreme drought conditions) in the River Lathkill (UK)

111 following a high magnitude supra-season drought.

112

113 **Materials and Methods**

114 *Study sites*

115 The River Lathkill (Derbyshire, UK) is a groundwater-fed river in the White Peak area of the Peak

116 District National Park. Land-use in the catchment is predominantly low intensity grazing on

117 unimproved grassland (Stubbington et al. 2016). The perennial source originates at Bubble Springs (SK

118 2049 6612, 159m AOD; Figure 1) and the entire catchment of the river above the springs is underlain

119 by Carboniferous limestone.

120

121 A total of 11 sites within two zones upstream of the perennial source (Bubble Springs), based on their

122 historic flow permanence (after Wood et al. 2005), were studied. Zone 1 comprised ephemeral

123 headwater sites (Sites 1-6; Figure 1) which typically experience surface water drying for at least six-

124 months per-annum, although flows can occur in response to high rainfall events (two to four times per

125 year; Stubbington et al. 2016). Exposed limestone bedrock with boulder to gravel size clasts

126 dominated headwater sites. Finer organic rich sediments with patches of semi-aquatic and terrestrial

127 flora were also present. The second downstream zone (zone 2) comprises of five near-perennial sites;

128 3 sites dry sporadically (typically every 5 years) and 2 sites that have dried only once in the last 30

129 years (Sites 7-11; Figure 1). The substratum in zone 2 consisted predominately of mixed alluvial

130 deposits (sand to cobble sized angular clasts) with instream vegetation dominated by mosses and

131 liverworts (Stubbington et al. 2011). All study sites were upstream of the confluence between the R.

132 Lathkill and the River Bradford (Figure 1).

133

134 *Hydroclimatic conditions*

135 The 2010-2012 supra-seasonal drought affected large parts of England, particularly southern and

136 midland areas (Parry et al. 2013). By the end of March 2012, 14 of the previous 24 months had

137 recorded <70% of average rainfall across lowland England (10 of those recorded <55% of average

138 rainfall: Marsh et al. 2013). As a result, the channel was dry upstream of the perennial source (Bubble

139 Springs) and both study reaches (zone 1 and zone 2) remained dry for the longest duration since the

140 start of historical monitoring in 1998. After a nine-month dry period, flow resumed in the ephemeral

141 headwaters but dried again in mid-March 2012 for ca. 28 days (Stubbington et al. 2016). The supra-

142 seasonal drought ended abruptly in April 2012 which experienced double the monthly average rainfall

143 (Parry et al. 2013). As a result, surface flow resumed throughout zone 2 in April 2012 and the channel

144 remained wet throughout the remainder of the study. Overall, 2012 was the wettest year in England

145 since 1910 (Parry et al. 2013). Flow remained ephemeral in zone 1 and streambed drying occurred on

146 three additional occasions; (1) ca. 28 days from mid-March 2012, (2) ca. 39 days from mid-May

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147 2012; and (3) ca. 46 days from early August 2012 (Stubbington et al. 2016). Regional monthly mean

148 temperatures for 2012 were within 0.5 °C of the long-term average (1961-1990; Met Office 2015).

149

150 *Macroinvertebrate sampling*

151 Aquatic macroinvertebrate samples were collected from 11 sites along the R. Lathkill at monthly

152 intervals where possible (some samples could not be taken during high flow events or dry periods)

153 between December 2011 and September 2012. A total of 138 samples were collected; 72 from zone 1

154 and 66 from zone 2 (Figure 1b). Two additional macroinvertebrate sampling events were undertaken

155 in November 2012 and February 2013. Samples comprised a three-minute kick samples (using a pond

156 net fitted with l mm mesh) divided equally between mesohabitats present. Aquatic macroinvertebrate

157 samples were preserved in the field with 4% formaldehyde solution prior to processing and

158 identification in the laboratory. The majority of macroinvertebrate taxa were identified to species

159 level but Diptera, Leuctridae, Baetidae, Sphaeriidae and Planariidae were resolved to family level and

160 Oligochaeta, Tricladida (non-Planariidae) and Collembola were recorded as such.

161

162 *Statistical analysis*

163 To examine temporal changes in diversity and the relative abundance of individual taxa over time

164 mixed-effects models were fitted to selected taxon and community metrics. Prior to statistical

165 analysis, data were examined to ensure they met the assumptions of statistical tests (e.g., normal

166 distribution). The following taxa; *Asellus aquaticus, Gammarus pulex, Isoperla grammatica,*

167 *Serratella ignita,* Baetidae and *Perlodes mortoni* were selected for further investigation as they

168 typically occurred in greater abundances and in multiple samples throughout the study period. The

169 month of sample collection and sample sites were fitted as random effects to account for potential

170 spatial and temporal dependence, and month and zone were fitted as fixed interacting factors.

171 Taxonomic richness was tested via a Generalised Linear Mixed Effects Model (GLMM) fitted using a

172 Poisson distribution and log link structure via the '*glmer*' function in the lme4 package (Bates et al.

7

173   2018). Community abundance and abundances of individual taxa were tested via a Linear Mixed

174   Effects Model (LMM) using the '*lmer*' function in the lme4 package with the restricted maximum

175   likelihood (REML) estimation function. Abundances were log10(x+1) transformed to normalise

176   residuals prior to model fitting. Conditional R^2 (proportion of variance explained by the fixed and

177   random factors; r^2 c) values were extracted using '*rsquared.glmm*' function in the MuMIn package

178   (Bartoń 2018). To account for the non-linear association of *I. grammatica* with time, a third order

179   polynomial model was fitted. This technique has been shown to reliably model nonlinear associations

180   without model overfitting (Kennen et al. 2014). Species accumulation plots were constructed to

181   examine the rate of recolonization over time for zone 1 and zone 2 and a linear model fitted to assess

182   if the rate of invertebrate colonisation differed over time between the zones. All univariate analyses

183   were conducted using R version 3.2.3 (R Development Core Team 2015).

184

185   Heterogeneity of macroinvertebrate communities between zones was assessed using Analysis of

186   Similarity (ANOSIM) and visualised using Non-metric Multidimensional Scaling (NMDS) ordination

187   plots (using Bray Curtis dissimilarity). To identify changes in community composition among months

188   in each zone, spearman rank correlations (RELATE) and centroid NMDS ordination plots were

189   examined. A monthly similarity matrix (Bray-Curtis) for each site was compared to a linear sequence

190   (the sampling months in this study) to examine if similarity among macroinvertebrate assemblages

191   was higher in adjacent sampling months than in more distant sampling months (*Serial* RELATE;

192   Clarke and Gorley 2006). Distances among centroid matrices were constructed by calculating the

193   averages (e.g., the centroid - the centre-point of all replicates for each month in multi-dimensional

194   space) in the 'Bray-Curtis space' of macroinvertebrate compositions from the replicate samples for

195   each month (Anderson et al. 2008). Centroid NMDS ordinations were generated using the distance

196   among centroid matrices. Similarity Percentage analysis (SIMPER) was used to determine which

197   species were driving the differences in community composition between zones. Faunal abundance

198   data was log transformed prior to ANOSIM, NMDS, centroid NMDS, SIMPER and RELATE

199   analysis, which was undertaken in PRIMER V7 (PRIMER-E Ltd, Plymouth, UK).

200

Results

Spatial macroinvertebrate diversity and variability in community composition in ephemeral and near-perennial reaches

Following the supra-seasonal drought (2011-2013), a total of 101 taxa were recorded from zone 1 (total: 65 taxa, mean: 7.1, range: 3-13) and zone 2 (total: 85 taxa, mean: 14.6, range: 5-25) during the 12 surveys from the 11 sample sites. Of the 101 taxa recorded between 2011-2013, the most widely distributed taxa were: Chironomidae, Tipulidae, Simuliidae, Oligochaeta, *A. aquaticus*, *G. pulex* (recorded at all 11 sites) and, Baetidae, *G. truncatula* and *Nemurella picteti* (recorded at 10 sites). The most diverse orders were Trichoptera (23 taxa), Coleoptera (21 taxa), Plecoptera (14 taxa) and Diptera (14 taxa).

Taxonomic richness (df=9, t=3.905, p=0.004) and total relative abundance (df=9, t=3.615, p=0.006) were significantly higher in zone 2 than zone 1 (Figure 2). No significant differences in the abundance of *A. aquaticus, I. grammatica, S. ignita,* Baetidae and P. mortoni between zones 1 and 2 were recorded; however, *G. pulex* had significantly greater abundances in zone 2 than zone 1 (df=9, t=2.425 p=0.038). Significant differences were observed in macroinvertebrate community composition between zone 1 and zone 2 (ANOSIM *r*=0.457 p=0.01; Figure 3a). The top four macroinvertebrate taxa driving the differences in macroinvertebrate community composition between zones were *A. aquaticus* (contributing 6% to the dissimilarity) which were recorded in greater abundances in zone 1 sites and Baetidae (8.4% dissimilarity), Chironomidae (7.3% dissimilarity) and *I. grammatica* (6% dissimilarity) which were recorded in greater abundances from zone 2 sites. A total of 16 taxa were unique to zone 1 and 35 taxa to zone 2 (see Supplementary Material Part 2).

Temporal diversity and variability in community composition in ephemeral and near-perennial reaches

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226   At a regional scale, a steep increase in taxonomic richness was recorded in both zones over the first

227   three months after flow resumed (December 2011 to March 2012), with a more gradual increase in

228   taxa richness in zones 1 and 2 from month 4 (April 2012) to the end of the study (Figure 4). Species

229   accumulation was determined to be significantly greater in zone 2 ($t_{3,23}$=2.604, p=0.017), although the

230   rate of colonisation over time did not differ between zones ($t_{3,23}$=0.390, p=0.7; Figure 4). At an alpha

231   scale, both taxonomic richness (GLMM) and total abundance (LMM) were significantly greater

232   (p<0.001) in zone 2 and demonstrated little variation over time (Figure 2, Table 1). When examining

233   individual zones, mean taxonomic richness in zone 1 was similar (between 5-10 taxa) among all

234   sampling months, whilst in zone 2 taxonomic richness was highest 2-3 months after flow resumed

235   (February 2012 and March 2012), but was similar (between 10-15 taxa) for the other sampling periods

236   (Figure 2a). Mean macroinvertebrate abundance increased rapidly up to 3-months after flow resumed

237   in zone 2 (March 2012) and subsequently declined gradually thereafter to the end of the survey period

238   (Figure 2b). Similarly, mean abundance increased rapidly up to 3 months after flow resumed in zone

239   1, but was more variable in the proceeding months, decreasing at month 4 (April 2012 - reflecting

240   spate conditions) and month 6-9 (June-September 2012- reflecting the periods of desiccation in zone 1

241   headwaters: Figure 3b).

242

243   Abundances of *A. aquaticus* increased monthly in both zones (p<0.001 in both instances; Table 1),

244   reaching their greatest abundance in the final survey month (Feb 2013; Figure 5a) but demonstrated

245   no differences by zone (p>0.05; Table 1). *G. pulex* abundances were consistently and significantly

246   greater in zone 2 than zone 1 (Table 1). *G. pulex* abundance was broadly similar over the 12-months

247   after flow resumed in zone 1 before rising to a peak in the final sampling month. In zone 2, *G. pulex*

248   abundance was stable for 5-months after flow resumed (Dec 2011- April 2012) but was markedly

249   reduced during month 6-7 (May and June 2012) as flow declined (Figure 5b). *I. grammatica* was

250   more abundant in zone 2 than zone 1 (Table 1) and was initially recorded 4 months after flow

251   resumed in zone 1, and 3 months after flow resumed in zone 2 (Figure 5c). Abundances of *I.*

252   *grammatica* peaked 3 months after flow resumed (March 2012) in zone 1 and 5 months after flow

resumed (May 2012) in zone 2. However, its abundance declined throughout the summer months and only increased again 11 months after flow resumed (Nov 2012; Figure 5c). *S. ignita* was not recorded from zone 1 during the 2011-2013 study and was first sampled in zone 2 three months after flow resumed (Feb 2012), reaching its greatest abundance 5 months after flow resumed (May 2012) and declining thereafter (Figure 5d). In both zones Baetidae demonstrated highly variable abundances throughout the survey period. Baetidae was first recorded 2 months after flow resumed (Feb 2012) in zone 2 and three months after flow resumed (March 2012) in zone 1, reaching its highest abundance 7-8 months after flow resumed in both zones (Figure 5e). Temporal changes in Baetidae populations were determined to be significantly different between zones (Table 1) with zone 2 abundances increasing at a faster rate compared to zone 1. *P. mortoni* was initially recorded 4 months after flow resumed (April 2012) in zone 1 and remained consistent throughout the remainder of the study (Figure 5f). In zone 2, *P. mortoni* was first recorded 6 months after flow resumed (June 2012) with abundances increasing rapidly and peaking 8 months after flow resumption (August 2012; Figure 5f). Abundances of *P. mortoni* were significantly greater in zone 2 and varied between zones over time (Table 1). Across zone 1, *A. aquaticus, G. pulex, I. grammatica* and Baetidae all demonstrated a reduction in abundance from the 3rd to 4th month after flow resumed (March 2012 to April 2012), although abundance of *P. mortoni* increased between this period. In addition, *A. aquaticus,* Beatidae, *P. mortoni* and *I. grammatica* demonstrated reduced abundances from the 8th to 9th month after flow resumed (August 2012 to September 2012) in zone 1 (Figure 5a, b, c, e, f).

Spearman's rank correlations comparing the similarity matrices of monthly macroinvertebrate communities were statistically significant for all sites from zone 2 (Table 1) demonstrating a strong serial correlation (Figure 3c). In zone 1, 5 of the 6 sites displayed low and non-significant ρ values demonstrating a weak serial correlation (Table 2) and do not follow in series in the centroid NMDS biplot (Figure 3b – particularly 3-5 months after flow resumed, March-April 2012); only site 3 recorded a significant Spearman's rank correlation (Table 2).

11

280 **Discussion**

281 *Macroinvertebrate recolonization of ephemeral and near-perennial reaches following a supra-*

282 *seasonal drought*

283 Following the resumption of surface flow after the supra-seasonal drought, we found rapid

284 macroinvertebrate recolonization (species accumulation) on the R. Lathkill with the cumulative

285 number of taxa plateauing after approximately 6 months. Similar findings have been recorded from

286 streams in Georgia, USA and Berkshire, UK (Wright et al. 2004; Churchel and Batzer 2006) where

287 rapid recolonization of streams was observed immediately following the onset of flow after drought,

288 with species accumulation also beginning to plateaux after 5 to 6 months.

289

290 Different recolonization processes, however, probably operated in the two zones (reaches) of the R.

291 Lathkill examined. Zone 1 (ephemeral) is in the headwaters and is hydrologically more isolated from

292 perennial water sources. The lack of lateral or longitudinal connectivity and frequent channel drying

293 in zone 1 suggests that resilience strategies may have been an important mechanism for the rapid

294 recolonization in this zone. Many taxa have developed adaptations to survive *in-situ* in dry river beds

295 such as producing diapause eggs (e.g., the macroinvertebrate seedbank; Stubbington and Datry, 2013),

296 having short development times (Lytle and Poff 2004; Bogan and Lytle 2011) or persisting in damp

297 leaf patches and sub-surface water in the hyporheic zone (Stubbington et al. 2009a, 2011, although

298 this is not the case for all rivers; Datry 2012). In this study, *A. aquaticus* recolonized quickly after

299 flow resumed in zone 1, potentially surviving the period of flow desiccation as small individuals in

300 damp sediments and organic matter in the hyporheic zone (Leberfinger and Herrmann 2010; Vadher

301 et al. 2017).

302

303 Zone 2 (near perennial) was located between the ephemeral headwaters (zone 1) and the fully

304 perennial reach further downstream. The return of lateral and longitudinal aquatic connectivity

305 between the perennial reaches and zone 2 is likely to have been an important factor influencing the

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306   recolonization of zone 2. Previous studies have demonstrated that perennial reaches may act as a

307   refuge for taxa capable of dispersal (Chester and Robson 2011; Bogan et al. 2015), with rapid

308   recolonization after the drought event being possible in this study from the proximal perennial zone

309   via resistant mechanisms (life stages) such as aerial dispersal, or through upstream migration

310   (Williams and Hynes 1976; Verberk et al. 2008; Chester et al. 2015). The coleopteran, *Agabus*

311   *guttatus* was recorded as early as two months after flow resumed in zone 2 and previous studies have

312   indicated them to be one of the first predators to aerially colonise intermittent reaches (Davy-Bowker

313   et al. 2002; Stubbington et al. 2016). Further, the significantly greater abundances of *G. pulex* in zone

314   2 may reflect this species rapid ability to recolonize from perennial reaches downstream (White et al.

315   2018) and through vertical connectivity with the hyporheic zone (Stubbington et al. 2009) and

316   subterranean caves (Wood et al. 2005). Based on the results of this study, the effective recolonization

317   of biological communities to drought in ephemeral and near-perennial reaches is likely to be the result

318   of a combination of resistance and resilience strategies (Bogan et al. 2015).

319

320   The mean number of taxa remained consistent throughout the sampling months in zone 1 but a peak in

321   richness was recorded in zone 2 during February 2012. A significant rainfall event prior to sampling

322   in February 2012 increased the discharge in the R. Lathkill and may have provided connectivity to

323   facilitate upstream migration of taxa from the perennial reaches downstream. The loss of surface flow

324   in zone 1 on three separate occasions during the sampling period may explain the reductions in

325   abundance of *A. aquaticus, G. pulex, P. mortoni, I. grammatica* and Baetidae at months 3 and 4, and

326   months 8 and 9, as it is likely many of the taxa were unable to complete their life-cycle and those that

327   did may have had to disperse as flow receded (Dobrin and Giberson 2003).

328

329   Macroinvertebrate communities within zone 1 did not display a serial correlation, with adjacent

330   sampling months being heterogeneous. This may be the result of the loss of surface flow on a number

331   of occasions during the study period (March, May and August 2012) continually re-setting succession

332   and re-starting the community recolonisation process (Sponsellor et al. 2010). This suggests that

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ephemeral stream reaches are in a constant state of resetting of community succession, with recovery

and recolonization only partially occurring until they are re-set by the next drying event. In contrast,

flow was continually present throughout zone 2 following the supra-seasonal drought and as such

macroinvertebrate assemblages in zone 2 demonstrated serial correlation, with adjacent sampling

months being most similar, and the first and last sample recording the greatest heterogeneity in

community composition. In perennial rivers, macroinvertebrate assemblages typically follow a

seasonal cycle (e.g., successive winter communities record similar community assemblages: Giller

and Twomey 1993; Leunda et al. 2009) and therefore, the significant serial correlation recorded in

zone 2 indicates that two possible ecological processes may be occurring in the R. Lathkill: *(i)*

recolonization and ecological recovery are ongoing. Despite the rapid recolonization by many taxa,

the full recovery of macroinvertebrate communities had not occurred during the study period, as

communities from January 2012 and February 2013 were most heterogeneous. This suggests that the

ecological effect of the supra-seasonal drought on macroinvertebrate communities was evident for

multiple seasons following the event (Churchel and Batzer 2006; Bogan and Lytle 2011), with

ecological recovery being a long-term process (Wood and Petts 1999; Churchel and Batzer 2006) that

typically takes significantly longer than hydrological recovery; and *(ii)* the supra-seasonal drought

may have reset the ecological trajectory of the macroinvertebrate community which is possibly now

heading towards a new ecological equilibrium (Bogan and Lytle 2011), reflecting the high

heterogeneity between samples. Supra-seasonal drought may cause macroinvertebrate assemblages to

permanently differ from pre-drought assemblages. For example, research by Bogan and Lytle (2011)

on intermittent streams in Arizona has shown that supra-seasonal drought can cause regime shifts in

invertebrate community composition from long-lived sedentary taxa to smaller short-lived and highly

vagile taxa.

If taken in isolation, supra-seasonal droughts appear to have a negative effect on ecosystems, causing

an initial decline in taxonomic diversity during the period of stream desiccation (Lake 2003; Boulton

and Lake 2008; Aspin et al. 2019). However, when recolonization is examined over longer timescales,

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360 supra-seasonal droughts may actually facilitate the development of environmental conditions to

361 support a higher diversity through; (1) a reduction in competition and predation pressure (supra-

362 seasonal drought removed key predators and dominant taxa such as *G. pulex*); (2) an increase in the

363 availability and number of habitats (environmental niches: Ricklef & Schluter, 1993), as succession is

364 re-set and dominant environmental / ecological pressure are reduced and; (3) enabling new taxa (that

365 may be outcompeted in later succession lotic habitats) to utilise the increased spatio-temporal

366 environmental and biotic niches. However, it is unclear whether the macroinvertebrate communities

367 in the R. Lathkill will maintain this high diversity, whether successional processes are ongoing, or if

368 the community will be reset to follow another new ecological trajectory following the next flow

369 cessation event.

370

371 *Spatial variability of macroinvertebrate communities between zone 1 and zone 2*

372 Taxonomic richness was consistently greater within near perennial sites (zone 2) than the headwater

373 ephemeral sites (zone 1) and significant differences in macroinvertebrate assemblages were observed

374 between the zones following the 2011 supra-seasonal drought. Zone 1 was subject to multiple drying

375 events during 2012 and increasing flow intermittence has been shown to significantly reduce

376 taxonomic diversity across most biogeographic regions (Datry et al. 2013). Further, flow desiccation

377 in zone 1 (which continually re-sets communities) may remove taxa sensitive to drying, while zone 2

378 remained wet throughout the year and recolonization could progress providing variable

379 physicochemical and biological conditions for a wide range of taxa to exploit. Taxonomic richness

380 and community assemblage differences may also be the result of spatial organisation of colonist

381 sources (connectivity). The hydrological isolation of zone 1 from the perennial reaches reduces the

382 potential for colonisation (Bogan et al. 2015) while hydrological connectivity to the downstream

383 perennial zone provides zone 2 with a readily available and diverse source of colonists to enhance

384 taxonomic richness and develop a heterogeneous community composition.

385

386 Climate change and the increase in water abstraction from growing human populations is likely to

387 increase the number of rivers that experience drying (Larned et al. 2010), the severity / duration of

388 drying events (Rahiz and New 2013) and could lead to irrevocable changes to biological communities

389 and a loss of taxa that are ill adapted to drying (Datry et al. 2014). Currently, consideration of supra-

390 seasonal drought and management in lotic freshwaters is impeded by the lack of knowledge and

391 information available (Arscott et al. 2010). Future research should be directed towards the long-term

392 monitoring of macroinvertebrate communities before, during and after supra-seasonal droughts to

393 provide the information needed to fully quantify the ecological impacts of these disturbances,

394 understand the mechanisms and strategies macroinvertebrates use to persist / recolonise rivers

395 following an extreme drying event, identify possible regime shifts in intermittent freshwater

396 communities and identify strategies to manage drought impacts. For example, ensuring newly

397 intermittent streams are connected with drought refuge sites may facilitate a rapid recovery post-

398 disturbance (Robson et al. 2011).

399

400 **Conclusion**

401 This study has demonstrated that aquatic macroinvertebrate taxa can rapidly recolonise lotic habitats

402 after supra-seasonal drought episodes. The impact of supra-seasonal drought on macroinvertebrate

403 communities may persist for multiple seasons after the event, as the communities may not have

404 reached the end-point of recovery during the study period. The results of this study also suggest that

405 supra-seasonal droughts may cause some communities to head towards a new ecological equilibrium

406 rather than recover to their pre-disturbance composition; making the assessment of the end point of

407 recovery more difficult. Supra-seasonal droughts may therefore effectively re-set ecological

408 succession and during the initial recovery / recolonisation phase provide ecological and environmental

409 space for new taxa to colonise. Quantifying the recolonisation and recovery of biological communities

410 to extreme disturbances such as supra-seasonal drought is vital to provide the required information to

411 ensure the persistence of biodiversity through the implementation of ecologically effective

412 conservation and management strategies.

16

413

Reference

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to Software and

Statistical Methods. Plymouth: PRIMER-E.

Arscott DB, Larned S, Scarsbrook MR, Lambert P (2010) Aquatic invertebrate community structure

along an intermittence gradient: Selwyn River, New Zealand. J. N. Am. Benthol. Soc. 29: 530-

545.

Aspin TW, Hart K, Khamis K, Milner AM, O'Callaghan MJ, Trimmer M, Wang Z, Williams GM,

Woodward, G. and Ledger, M.E., 2019. Drought intensification alters the composition, body

size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment.

Freshwater Biol.

Aspin TW, Matthews TJ, Khamis K, Milner AM, Wang Z, O'callaghan MJ and Ledger ME, 2018.

Drought intensification drives turnover of structure and function in stream invertebrate

communities. Ecography 41: 1992-2004.

Barton K 2018. Multi modal inference. R package version 1.42.1. Accessible at; https://cran.r-

project.org/web/packages/MuMIn/MuMIn.pdf.

436   Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Scheipl F,

437   Grothendieck G, Green P (2018) Linear Mixed-Effects Models using 'Eigen' and S4. R package

438   version 1.1-18-1. Accessible at: https://cran.r-project.org/web/packages/lme4/lme4.pdf.

439   Benejam L, Angermeier PL, Munne A, Garcia Berthou E (2010) Assessing effects of water

440   abstraction on fish assemblages in Mediterranean streams. Freshwater Biol. 55: 628-642.

441   Bogan MT, Lytle DA (2011) Severe drought drives novel community trajectories in desert stream

442   pools. Freshwater Biol. 56: 2070-2081.

443   Bogan MT, Boersma KS, Lytle DA (2015). Resistance and resilience of invertebrate communities to

444   seasonal and supraseasonal drought in arid-land headwater streams. Freshwater Biol. 60: 2547-

445   2558.

446   Boulton AJ (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate

447   assemblages. Freshwater Biol. 48: 1173-1185.

448   Boulton AJ Lake PS (2008) Effects of drought on stream insects and its ecological consequences.

449   Aquatic insects: Challenges to populations, pp.81-102.

450   Chadd RP, England JA, Constable D, Dunbar MJ, Extence CA, Leeming DJ, Murray-Bligh JA, Wood

451   PJ (2017) An index to track the ecological effects of drought development and recovery on

452   riverine invertebrate communities. Ecol. Indic. 82: 344-356.

453   Chessman BC (2015) Relationships between lotic macroinvertebrate traits and responses to extreme

454   drought. Freshwater Biol. 60: 50–63.

455   Chester ET, Robson BJ (2011) Drought refuges, spatial scale and recolonization by invertebrates in

456   non-perennial streams. Freshwater Biol. 56: 2094-2104.

457   Chester ET, Miller AD, Valenzuela I, Wickson SJ, Robson BJ (2015) Drought survival strategies,

458   dispersal potential and persistence of invertebrate species in an intermittent stream landscape.

459   Freshwater Biol. 60: 2066-2083.

460   Churchel MA, Batzer DP (2006) Recovery of aquatic macroinvertebrate communities from drought in

461   Georgia piedmont headwater streams. Am. Midl. Nat. 156: 259-272.

462   Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER E-Ltd: Plymouth, UK.

463   Côté IM, Darling ES (2010) Rethinking Ecosystem Resilience in the Face of Climate Change. PLoS

464   Biol. 8: DOI:10.1371/journal.pbio.1000438.

465   Datry T (2012) Benthic and Hyporheic invertebrate assemblages along a flow intermittence gradient:

466   effects of duration of dry events. Freshwater Biol. 57: 563-574.

467   Datry T, Fritz K, Leigh C (2016) Challenges, developments and perspectives in intermittent river

468   ecology. Freshwater Biol. 61: 1171-1180.

469   Datry T, Larned ST, Tockner K (2014) Intermittent rivers: a challenge for freshwater ecology.

470   Bioscience. DOI: 10.1093/biosci/bit027.

471   Datry T, Larned ST, Fritz KM, Bogan MT, Wood PJ, Meyer EI, Santos EN (2013) Broad-scale

472   patterns of invertebrate richness and community composition in temporary rivers: effects of

473   flow intermittence. Ecography 36: 001-011.

474   Davy-Bowker J (2002) A mark and recapture study of water beetles (Coleoptera: Dytiscidae) in a

475   group of semi-permanent and temporary ponds. Aquat. Ecol. 36: 435-446.

476   Dobrin M, Giberson DJ (2003) Life history and production of mayflies, stoneflies, and caddisflies

477   (Ephemeroptera, Plecoptera, and Trichoptera) in a spring-fed stream in Prince Edward Island,

478   Canada: evidence for population asynchrony in spring habitats? Can J Zool. 81: 1083-1095.

479   Fisher SG (1983) Succession in streams. In Stream Ecology (pp. 7-27). Springer, Boston, MA.

480   Fritz KM, Dodds WK (2004). Resistance and resilience of macroinvertebrate assemblages to drying

481   and flood in a tall grass prairie steam system. Hydrobiologia 527: 99-112.

482   Gasith A, Resh VH (1999). Streams in Mediterranean climate regions: abiotic influences and biotic

483   responses to predictable seasonal events. Annu Rev Ecol Syst. 30: 51-81.

484 Giller PS, Twomey H (1993) November. Benthic macroinvertebrate community organisation in two
485   contrasting rivers: between-site differences and seasonal patterns. In Biology and Environment:
486   Proceedings of the Royal Irish Academy (pp. 115-126). Royal Irish Academy.

487 Hill, MJ Milner, Vs (2018) Ponding in intermittent streams: a refuge for lotic taxa and a habitat for
488   newly colonising taxa? Sci. Total Environ. 628-629: 1308-1316.

489 James ABW, Dewson ZS, Death RG (2008) Do stream macroinvertebrates use instream refugia in
490   response to severe short-term flow reduction in New Zealand streams? Freshwater Biol. 53:
491   1316–1334.

492 Kennen JG, Riskin ML, Charles EG (2014) Effects of streamflow reductions on aquatic
493   macroinvertebrates: Linking groundwater withdrawals and assemblage response in southern
494   New Jersey streams, USA. Hydrolog. J. Sci. 59: 545–561.

495 Lake PS (2003) Ecological effects of perturbation by drought in flowing waters. Freshwater Biol. 48:
496   1161-1172.

497 Lake PS (2011). Drought and Aquatic Ecosystems: Effects and Responses. Wiley-Balckwell: Oxford,
498   UK.

499 Larned ST, Datry T, Arscott DB, Tockner K, (2010) Emerging concepts in temporary-river ecology.
500   Freshwater Biol. 5: 717–738.

501 Leberfinger K, Herrmann J, (2010) Secondary production of invertebrate shredders in open-canopy,
502   intermittent streams on the island of O¨ land SE Sweden. J. N. Am. Benthol. Soc. 29: 934-944.

503 Leigh C, Bonada N, Boulton AJ, Hugueny B, Larned ST, Vander Vorste R, Datry T, (2016)
504   Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in
505   intermittent rivers. Aquat. Sci. 78: 291–301.

506 Leunda PM, Oscoz J, Miranda R, and Ariño AH (2009) Longitudinal and seasonal variation of the
507   benthic macroinvertebrate community and biotic indices in an undisturbed Pyrenean river.
508   Ecol. Indic. 9: 52-63.

509   Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. Trends Ecol. Evo. 19: 94-100.

510   Marsh T.J, Parry S, Kendon MC, Hannaford J (2013) The 2010-12 drought and subsequent extensive

511   flooding. Centre for Ecology and Hydrology.

512   Met Office (2015) Accessible at:

513   http://www.metoffice.gov.uk/climate/uk/summaries/2012/annual/regional-values [Last

514   accessed 05/02/2016]

515   Milner AM, Robertson AL, Monaghan KA, Veal AJ, Flory EA (2008) Colonization and development

516   of an Alaskan stream community over 28 years. Front. Ecol. Environ. 6: 413-419.

517   Parry S, Marsh T, Kendon MC (2013) 2012: from drought to floods in England and Wales. Weather

518   68: 268-274.

519   Prudhomme C, Guintoli I, Robinson EL, Clark DB, Arnell NW, Dankers R, Fekete BM, Franssen W,

520   Gerten D, Gosling SN, Hagemann S, Hannah DM, Kim H, Masaki Y, Satoh Y, Stacke T, Wada

521   Y, Wisser D (2014) Hydrological droughts in the 21st Century, hotspots and uncertainties from

522   a global multimodel ensemble experiment. Proc. Natl. Acad. Sci. USA: 111, 3262-3267.

523   R Development Core Team. (2015) R: a language and environment for statistical computing. R

524   Foundation for Statistical Computing, Vienna.

525   Rahiz M, New M (2013) 21st century drought scenarios for the UK. Water Resour. Manag. 27: 1039-

526   1061.

527   Ricklefs RE, & Schluter D (1993) Species diversity in ecological communities. 414 pp University of

528   Chicago Press, Chicago IL.

529   Robson BJ, Chester ET, Austin CM (2011) Why life history information matters: drought refuges and

530   macroinvertebrate persistence in non-perennial streams subject to a drier climate. Marine and

531   Freshwater Research 62: 801-810.

532 Sarremejane R, Mykrä H, Bonada N, Aroviita J, Muotka T (2017) Habitat connectivity and dispersal

533   ability drive the assembly mechanisms of macroinvertebrate communities in river networks.

534   Freshwater Biol. 62: 1073–1082.

535 Sheldon F, Bunn SE, Hughes JM, Arthington AH, Balcombe SR, Fellows CS (2010) Ecological roles

536   and threats to aquatic refugia in arid landscapes: dryland river waterholes. Mar. Freshwater Res.

537   61: 885-895.

538 Skoulikidis NT, Sabater S, Datry T, Morais MM, Buffagni A, Dörflinger G, Zogaris S, del Mar

539   Sánchez-Montoya M, Bonada N, Kalogianni E, Rosado J (2017) Non-perennial Mediterranean

540   rivers in Europe: status, pressures, and challenges for research and management. Sci. Total

541   Environ. 577: 1-18.

542 Soria M, Leigh C, Datry T, Bini LM, Bonada N (2017) Biodiversity in perennial and intermittent

543   rivers: a meta analysis. Oikos 126: 1078-1089.

544 Sponseller RA, Grimm NB, Boulton AJ, Sabo JL (2010) Responses of macroinvertebrate

545   communities to long-term flow variability in a Sonoran Desert stream. Global Change Biol. 16:

546   2891-2900.

547 Stubbington R, Boulton AJ, Little S, Wood PJ (2015) Changes in invertebrate assemblage

548   composition in benthic and hyporheic zones during a severe supraseasonal drought. Freshw.

549   Sci. 34, 344-354.

550 Stubbington R, Datry T (2013) The macroinvertebrate seedbank promotes community persistence in

551   temporary rivers across climate zones. Freshwater Biol. 58: 1202-1220.

552 Stubbington R, Gunn J, Little S, Worrall TP, Wood PJ (2016) Macroinvertebrate seedbank

553   composition in relation to antecedent duration of drying and multiple wet-dry cycles in a

554   temporary stream. Freshwater Biol. 61: 1293-1307

555 Stubbington R, Wood PJ, Reid I, Gunn J (2011) Benthic and hyporheic invertebrate community

556   responses to seasonal flow recession in a ground water dominated stream. Ecohydrology 4:

557   500-511.

558 Stubbington R, Greenwood AM, Wood PJ, Armitage PD, Gunn J, Robertson AL (2009) The response

559   of perennial and headwater stream invertebrate communities to hydrological extremes.

560   Hydrobiologia 630: 229-312.

561 Stubbington R, Wood PJ, Boulton AJ (2009a) Low flow controls on benthic and hyporheic

562   macroinvertebrate assemblages during supra-seasonal drought. Hydrol. Process 23: 2252-2263.

563 Vadher AN, Leigh C, Millett J, Stubbington R, Wood PJ (2017) Vertical movements through

564   subsurface stream sediments by benthic macroinvertebrates during experimental drying are

565   influenced by sediment characteristics and species traits. Freshwater Biol. 62: 1730-1740.

566 Vander Vorste R, Corti R, Sagouis A, Datry T (2015) Invertebrate communities in gravel bed, braided

567   rivers are highly resilient to flow intermittence. Freshw. Sci. DOI: 10.1086/683274.

568 Verberk WCEP, Siepel H, Esselink H (2008). Life-history strategies in freshwater macroinvertebrates.

569   Freshwater Biol. 53: 1722-1738.

570 White JC, House A, Punchard N, Hannah DM, Wilding MA, Wood PJ (2018). Macroinvertebrate

571   community responses to hydrological controls and groundwater abstraction effects across

572   intermittent and perennial headwater streams. Sci. Total Environ. 610-611: 1514–1526.

573 Williams DD, Hynes HBN (1976). The recolonization mechanisms of stream benthos. Oikos 27: 265–

574   272.

575 Williams, DD (2006). The Biology of Temporary Waters. Oxford University Press, Oxford.

576 Wright JF, Clarke RT, Gunn RMJ, Kneebone NT, Davy-Bowker J (2004) Impact of major changes in

577   flow regime on the macroinvertebrate assemblages of four chalk stream sites, 1997-2001. River

578   Res. and Appl. 20: 775-794.

579   Wood PJ, Armitage PD, (2004) The response of the macroinvertebrate community to low flow

580   variability and supraseasonal drought within a groundwater dominated stream. Arch Hydrobiol.

581   161: 1-20.

582   Wood PJ, Gunn J, Smith H, Abas-Kutty A (2005) Flow permanence and macroinvertebrate

583   community diversity within groundwater dominated headwater streams and springs.

584   Hydrobiologia 545: 55-64.

585   Wood PJ, Petts GE (1999) The influence of drought on chalk stream macroinvertebrates. Hydrol.

586   Process 13: 387-399.

Tables

588   Table 1 - Univariate analysis for differences in taxonomic richness, total abundance and abundance of

589   individual taxon associated with zone (n=2), month (n =12) and the interaction of these factors.

590

Metric	Zone		Month		Month x Zone		R^2c
	Stat value	p value	Stat value	p value	Stat value	p value	
Taxonomic richness	4.34	**<0.001**	-0.77	0.443	0.15	0.880	62.56
Abundance	3.80	**<0.001**	0.75	0.450	-0.62	0.619	62.11
Baetidae	1.63	0.103	-1.24	0.214	3.56	**<0.001**	70.48
Asellus aquaticus	-1.61	0.106	3.40	**<0.001**	-0.41	0.682	67.02
Seretella ignita	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Gammarus pulex	2.50	**0.012**	1.59	0.110	-0.63	0.530	57.06
Isoperla grammatica	5.04	**<0.001**	6.70, -6.52, 6.39	<0.001	-0.564	0.574	42.76
Perlodes mortoni	2.57	**0.026**	-2.45	**0.025**	4.79	**<0.001**	46.01

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591   Table 2 - Spearman's rank correlation coefficients calculated among temporal macroinvertebrate

592   communities (serial RELATE analyses) at each site.

	Site	Spearman's correlation (ρ)
	1	0.013
	2	0.255
Zone 1	3	0.572***
	4	0.079
	5	0.178
	6	0.055
	7	0.626***
	8	0.593***
Zone 2	9	0.635***
	10	0.609***
	11	0.539***

*** $p < 0.01$

593

594   Table 3 - Top four macroinvertebrate taxa identified by SIMPER as most strongly influencing

595   between year dissimilarity. Number in parenthesis indicates the percentage contribution to

596   dissimilarity.

	1999-2000	2007	2011-2013
1999-2000			
2007	Oligochaeta (6.88), Chironomidae (6.65), Sphaeriidae (5.81), *Asellus aquaticus* (5.55)		
2011-2013	*Asellus aquaticus* (5.65), Oligochaeta (5.05), *Gammarus pulex* (4.84), Simuliidae (4.01)	*Gammarus pulex* (5.98), *Asellus aquaticus* (5.34), Chironomidae (5.33), Simuliidae (4.59)	

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Figure captions

Figure 1 – Location of study river (a) and sampling reach and sites (b): ephemeral zone 1 comprises

sites 1- 6 and near perennial zone 2 comprises sites 7-11.

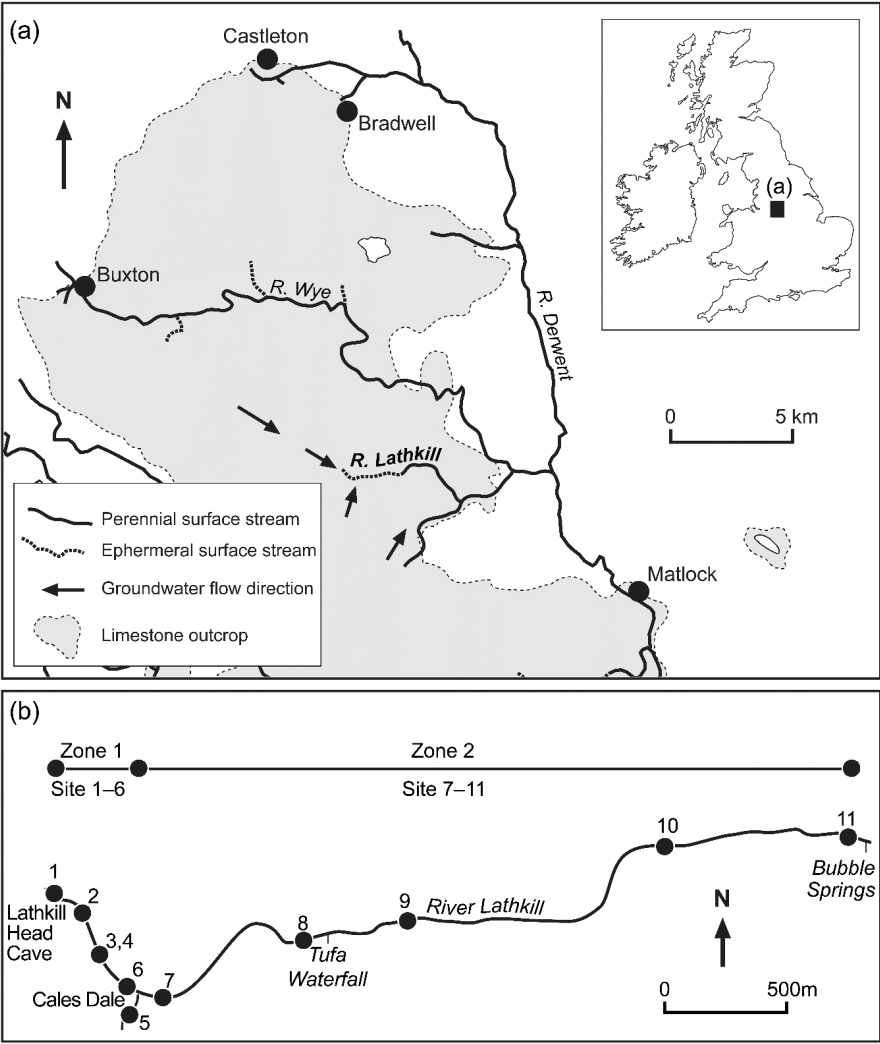Figure 2 - Number of taxa (a) and $\log_{10}$ macroinvertebrate abundance (b) across the sampling period

in near perennial (zone 1) and naturally ephemeral (zone 2) river reaches on R. Lathkill (UK).

Figure 3 – (a) NMDS ordination of macroinvertebrate assemblages from near perennial (zone 1) and

naturally ephemeral (zone 2) study sitesand; centroid NMDS plots of macroinvertebrate communities

from the 12 sampling periods in near perennial zone 1 (b) and naturally ephemeral zone 2 (c).

Figure 4 - Species accumulation plot for the months sampled from near perennial (zone 1) and

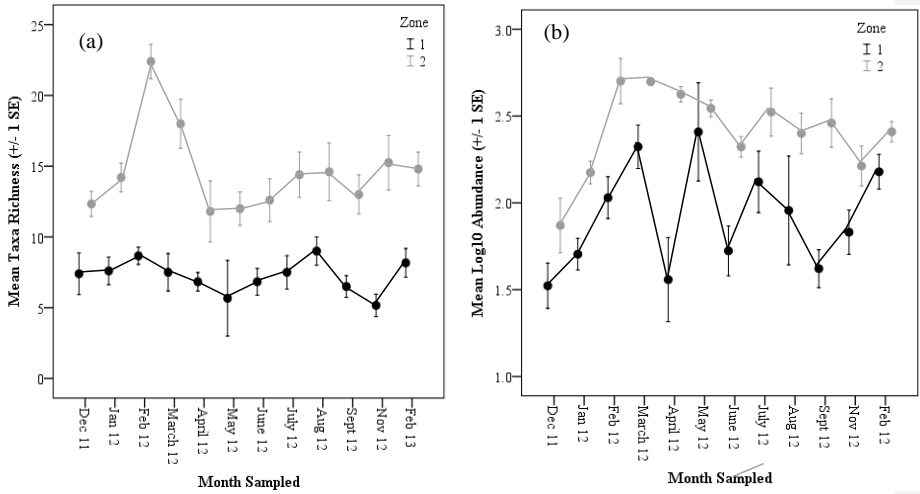naturally ephemeral (zone 2) river reaches on R. Lathkill (UK).

Figure 5 - Mean *Asellus aquaticus* (a) *Gammarus pulex* (b) *Isoperla grammatica* (c) *Serratella ignita*

(d) Baetidae (e) and *Perlodes mortoni* (f) abundance from each sampling month from near perennial

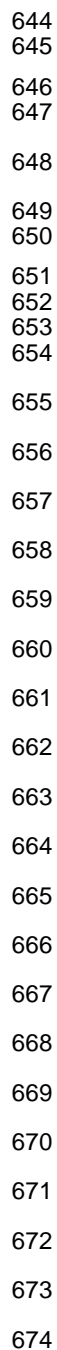(zone 1) and naturally ephemeral (zone 2) study sites on the R. Lathkill (UK).

611   Figure 1

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622 Figure 2
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Figure 3

(a)

2D Stress: 0.19

● Zone 1
○ Zone 2

(b)

2D Stress: 0.08

April 12
March 12
Dec 11
May 12
Feb 12
Jan 12
June 12
July 12
Sept 12
Aug 12
Nov 12
Feb 13

(c)

2D Stress: 0.04

Sept 12
Nov 12
Feb 13
Aug 12
July 12
June 12
Dec 11
Jan 12
April 12
May 12
March 12
Feb 12

675   Figure 4

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