

1 The hyporheic zone as an invertebrate refuge: a review of variability in space, time,  
2 taxa and behaviour

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7

8 *Abstract*

9 The hyporheic zone is a potential refuge that can promote persistence of benthic  
10 invertebrates during adverse conditions in surface streams. For decades, changes in  
11 invertebrate depth distribution have been investigated in relation to flood, low flow  
12 and drying events, but evidence for use of the hyporheic refuge remains equivocal.  
13 This review examines the evidence for the hyporheic zone's refugial role during  
14 hydrological disturbances. Refuge potential is influenced by determinants in four  
15 categories. First, refuge use varies spatially in relation to physical habitat parameters,  
16 including sediment porosity and hydrologic exchange. Second, refuge use is  
17 temporally variable, and reflects disturbance characteristics including rate of onset.  
18 Third, refuge use is taxon-specific, depending on a range of morphological,  
19 behavioural and physiological traits. Fourth, the behaviours governing refuge use  
20 vary, with both active migrations and passive habitat use playing important roles in  
21 community persistence. These four determinants interact to influence refuge use; for  
22 example, the physical habitat providing an adequate refuge will vary between taxa.  
23 Despite this variability, the hyporheic zone is an important component in the suite of  
24 refuges that facilitate community resilience to disturbance events. As such, its  
25 ecological integrity should be safeguarded through sensitive management and  
26 effective rehabilitation schemes.

27

28 *Additional keywords*

29 Refugium, refugia, macro-invertebrate, hyporheic refuge hypothesis, epigean

30

31 *Running head*

32 Variability in the hyporheic zone refuge

33

## 34 **Introduction**

35 In recent decades, the contribution of the hyporheic zone (HZ) to the ecological  
36 functioning of lotic ecosystems has become increasingly clear (Stanford and Ward  
37 1993; Boulton *et al.* 1998; Krause *et al.* 2011). As an ecotone connecting the surface  
38 stream and groundwater, hydrologic exchange through the HZ allows water, nutrients,  
39 organic matter and organisms to move between ecosystem components (Brunke and  
40 Gonsler 1997; Malard *et al.* 2002; Williams *et al.* 2010). Ecosystem services provided  
41 by the HZ include pollutant attenuation (Gandy *et al.* 2007; Domagalski *et al.* 2008),  
42 secondary production (Smock *et al.* 1992; Wright-Stow *et al.* 2006), and habitat  
43 provision for both spawning salmonids (Malcolm *et al.* 2004) and an invertebrate  
44 community comprising permanent hyporheic residents and transient migrants from the  
45 benthic zone.

46

47 A key ecological role proposed for the HZ is as a refuge that promotes persistence of  
48 benthos during disturbances in the surface stream (Orghidan 1959, 2010; Wood *et al.*  
49 2010; Dole-Olivier in press), in particular during the hydrological extremes of floods  
50 (Williams and Hynes 1974; Marchant 1988; Dole-Olivier *et al.* 1997) and drying  
51 (Clifford 1966; Delucchi 1989; Clinton *et al.* 1996). At both extremes, some studies  
52 have recorded increases in the hyporheic abundance of invertebrates during a  
53 disturbance, providing evidence of refuge use, whilst other research has reported no  
54 significant changes in depth distributions (summarised in Tables 1 and 2). In addition,  
55 increased hyporheic abundance of benthos has been noted during low flows, due to  
56 submerged habitat contraction and a concurrent increase in biotic interactions (e.g.  
57 predation, competition) in the benthic zone (Covich *et al.* 2003; Stubbington *et al.*  
58 2010, 2011a, 2011b). In contrast, other studies have observed no change in the depth  
59 distribution of benthic taxa as flow declines (James *et al.* 2008; James and Suren  
60 2009; Table 3).

61

62 Whilst these inconsistent reports of refuge use can be explained in part by differences  
63 between sampling strategies (Dole-Olivier 2011), the equivocal evidence also  
64 indicates that vertical migrations depend on certain criteria being met. Refuge use is  
65 therefore likely to vary spatially at multiple scales. In addition, whilst the HZ is a  
66 more stable habitat than the benthic zone, its sediments vary temporally, and refuge  
67 use may therefore differ between disturbance events. Finally, the HZ poses challenges

68 to interstitial inhabitation and resource availability, and refuge use may therefore be  
69 taxon-specific.

70

71 This review uses evidence presented for and against the hyporheic refuge hypothesis  
72 (HRH) to examine variability in the HZ as a benthic invertebrate refuge during  
73 adverse hydrological conditions. Published data is used to develop a conceptual model  
74 from which behavioural responses to adverse conditions can be inferred from changes  
75 in depth distribution. Conclusions drawn highlight the importance of ensuring the  
76 ecological integrity of the HZ through sensitive management and rehabilitation  
77 activities.

78

### 79 **Hydrological conditions as invertebrate stressors**

80 Hydrological variability is a key influence on instream habitat heterogeneity (Poff and  
81 Ward 1990; Monk *et al.* 2008) and has profound effects on invertebrate communities  
82 (Statzner and Higler 1986; Konrad *et al.* 2008). In particular, hydrological extremes  
83 (floods and streambed drying) can modify habitats and severely reduce both  
84 invertebrate abundance and taxon richness, regardless of whether conditions are  
85 unpredictable disturbance events (Resh *et al.* 1988; Death 2008; Sponseller *et al.*  
86 2010) or occur within the typical flow regime (Poff 1992). In addition, low flows  
87 represent relatively moderate hydraulic conditions but have marked effects on  
88 instream communities due to reduced habitat availability (Wood and Petts 1999;  
89 Suren *et al.* 2003a, b; Dewson *et al.* 2007a), increased population densities and biotic  
90 interactions (Extence 1981; Malmqvist and Sackmann 1996), and changes in food  
91 resources (Englund and Malmqvist 1996) and water quality (Wood *et al.* 2010).

92

93 Invertebrates survive adverse conditions through resistance (an ability to persist)  
94 and/or resilience (an ability to recover afterwards; Webster *et al.* 1975; Lake and  
95 Barmuta 1986). Whilst biota may have evolved adaptations that confer resistance  
96 and/or resilience to predictable seasonal flow variation (Reice *et al.* 1990; Lytle and  
97 Poff 2004), community resistance to both floods and drying is typically low (Miller  
98 and Golladay 1996; Fritz and Dodds 2004). Despite this, invertebrates persist in  
99 frequently disturbed systems, with communities typically proving highly resilient  
100 (Miller and Golladay 1996; Kroon and Ludwig 2010). This resilience is facilitated by  
101 adaptations, which may be morphological, physiological, life history related, or

102 behavioural (Townsend and Hildrew 1994; Lytle and Poff 2004; Watanabe 2006), the  
103 latter involving use of physical habitat refuges (Lake 2000, 2011).

104

105 Instream habitat heterogeneity causes invertebrate distribution and persistence to vary  
106 spatially (Robertson *et al.* 1995). Some habitats are refuges, where survival is  
107 enhanced due to reduced adverse impacts (Sedell *et al.* 1990; Lancaster and Belyea  
108 1997). A habitat's ability to act as a refuge depends on the disturbance. During high  
109 flows, refuges are areas of low hydraulic stress, such as dead zones (Lancaster and  
110 Hildrew 1993; Lancaster 1999), inundated floodplains (Townsend *et al.* 1997;  
111 Matthaei and Townsend 2000), stable clasts (Cobb *et al.* 1992; Matthaei *et al.* 2000),  
112 woody debris (Palmer *et al.* 1996) and marginal vegetation (Robinson *et al.* 2004; Fig.  
113 1a). In contrast, drying refuges retain free water or high humidity (Humphries and  
114 Baldwin 2003), for example crayfish burrows, woody debris, leaf packs, pools and  
115 spaces beneath large clasts (Boulton 1989; Boulton and Lake 2008; Stubbington *et al.*  
116 2009a; Fig. 1b). There is therefore little overlap between high- and no-flow refuges,  
117 and many occur sporadically. The HZ is a potential exception to this; it may retain  
118 water after surface drying and may remain stable during floods (Boulton *et al.* 1998).

119

#### 120 **The hyporheic zone as a permanent habitat**

121 The HZ is also a non-refugial habitat, with its location at the interface between surface  
122 and groundwater being reflected by the hyporheos, a fauna that comprises both  
123 permanent and occasional contingents (Williams and Hynes 1974). Species of  
124 permanent hyporheos complete their lifecycle in the HZ, and include a diverse  
125 assemblage of meiofauna (Dole-Olivier *et al.* 2000; Stead *et al.* 2004) and  
126 groundwater specialists (Dole-Olivier and Marmonier 1992a; Robertson *et al.* 2009).  
127 Occasional hyporheos move between benthic and hyporheic zones, this community  
128 being dominated by early-instar insect larvae (Williams 1984; Malard *et al.* 2001).

129

130 The physical habitat of the HZ is recognised as highly heterogeneous (Orghidan 1959,  
131 2010), with several spatiotemporally variable parameters identified as influencing  
132 hyporheic community composition. These influences relate primarily to hydrology,  
133 sediment characteristics and the biotic suitability of the hydrological medium (i.e.  
134 water quality). The biotic effects of single habitat characteristics are often difficult to  
135 disentangle, due to both relationship complexity and the failure of many sampling

136 techniques to characterise the fine scale at which biota experience their environment  
137 (Strayer *et al.* 1997; Storey and Williams 2004). Nonetheless, some relationships can  
138 be stated with confidence, as described below.

139

140 *i) Sediment composition*

141 A critical influence on the hyporheic community is sediment composition, which  
142 influences substrate porosity, permeability and interstitial architecture (Maridet *et al.*  
143 1992; Schmid and Schmid-Araya 2010), and therefore determines the volume of  
144 inhabitable space and the network of movement pathways between clasts. Coarse  
145 substrata can support high-density diverse communities (Strayer *et al.* 1997), whilst  
146 meiofauna dominate sandy sediments (Malard *et al.* 2002), and a depauperate fauna  
147 resides within a colmated HZ (Richards and Bacon 1994; Wood and Armitage 1997).  
148 Several studies have demonstrated negative correlations between community metrics  
149 and the proportion of 'fine' sediment, variously defined as <150  $\mu\text{m}$  (Richards and  
150 Bacon 1994), 63  $\mu\text{m}$  to 1 mm (Olsen and Townsend 2003) and <2 mm (Weigelhofer  
151 and Waringer 2003). Sediment mobility is also important, with stable sediments  
152 supporting richer faunas than those prone to erosion (Marmonier *et al.* 2010).

153

154 *ii) Hydrology*

155 The direction and strength of hydrologic exchange is a crucial variable, with  
156 contrasting communities characterising upwelling and downwelling zones (Stanley  
157 and Boulton 1993; Franken *et al.* 2001; Olsen and Townsend 2003). Hypogean taxa,  
158 including microcrustaceans, Amphipoda and Isopoda, typically dominate upwelling  
159 groundwater zones (Dole-Olivier and Marmonier 1992b; Claret *et al.* 1999;  
160 Marmonier *et al.* 2010), which can elevate population densities and richness (Malard  
161 *et al.* 2003a; Datry *et al.* 2007). In contrast, downwelling surface water favours  
162 epigeal occasional hyporheos, such as Ephemeroptera, Trichoptera and Coleoptera  
163 (Boulton and Foster 1998; Franken *et al.* 2001), which can also boost abundance and  
164 richness (Davy-Bowker *et al.* 2006). The influence of water movement along  
165 hyporheic flowpaths on the distribution of hyporheos is reviewed in detail by Dole-  
166 Olivier (2011).

167

168 Other hydrological influences on the hyporheos include flow velocities and flow  
169 permanence. Hyporheic velocities may be negatively correlated with meiofauna

170 abundance, a faunal group that typically lack adaptations to resist displacement  
171 (Richardson 1992; Robertson *et al.* 1995). However, relationships between interstitial  
172 flow and macroinvertebrate distribution are complex and poorly quantified (Wagner  
173 and Bretschko 2002). Flow permanence also affects metrics including abundance,  
174 richness and stability, with intermittent sites typified by a depauperate community of  
175 desiccation resistant taxa (Datry *et al.* 2007). However, such relationships may be less  
176 apparent where drying occurs over small (sub-reach) areas or for short (days to  
177 weeks) durations (Stubbington *et al.* 2011a).

178

### 179 *iii) Water quality*

180 Dissolved oxygen has been identified as an influential water quality variable.  
181 Hyporheic concentrations are generally low compared with the surface stream and  
182 decrease with depth (Williams and Hynes 1974; Findlay 1995; Marmonier *et al.*  
183 2010), reflecting penetration by oxygenated inputs (Fowler and Death 2001).  
184 Concentrations are typically highest in zones supplied by oxygen-rich stream water  
185 (Grimm and Fisher 1984; Jones *et al.* 1995), whilst groundwater inputs, slow  
186 exchange rates and long residence times reduce availability (Findlay 1995; Olsen and  
187 Townsend 2003; Marmonier *et al.* 2010; Fig. 2). Positive correlations between oxygen  
188 concentrations and invertebrate abundance (Williams and Hynes 1974; Franken *et al.*  
189 2001), taxon densities (Boulton and Stanley 1995), taxon richness (Boulton *et al.*  
190 1997; Franken *et al.* 2001) and biomass (Strommer and Smock 1989) have been  
191 documented. However, relationships may be weak (Strayer *et al.* 1997; Malard and  
192 Hervant 1999), particularly in well-oxygenated sediments, indicating that oxygen is  
193 only an important community determinant at low concentrations (Franken *et al.* 2001;  
194 Olsen and Townsend 2003).

195

196 Other potential influences on the invertebrate community include temperature, pH and  
197 nutrient concentrations (Boulton and Stanley 1995; Plenet *et al.* 1995; Davy-Bowker  
198 *et al.* 2006). However, relationships are typically complex and/or specific to certain  
199 systems (Malard *et al.* 2003b) and will not be considered further.

200

### 201 *iv) Relationships between sediment composition, hydrology and water quality*

202 These habitat variables are interdependent and interact to determine HZ habitat  
203 characteristics (Vervier *et al.* 1992; Fig. 2). Firstly, hydrologic exchange influences

204 benthic and hyporheic sediment characteristics. During base flow, upwelling  
205 groundwater and high flow velocities may reduce siltation, whilst downwelling  
206 surface water introduces sediment into interstices, particularly where velocities are  
207 slow (Brunke and Gonser 1997; Fig. 2). Equally, sediment composition and porosity  
208 influence hydrologic exchange, with fine sediments reducing the strength of exchange  
209 whilst coarse substrata allow free water movement (Brunke 1999; Hancock 2002).  
210 Clogged sediments consequently receive a reduced oxygen supply whilst coarse  
211 sediments are well-oxygenated if flow velocities are sufficient (Findlay 1995; Wu  
212 2000). The direction of exchange also influences oxygen content, with downwelling  
213 surface water typically being better oxygenated than upwelling groundwater (Grimm  
214 and Fisher 1984; Valett 1993; Franken *et al.* 2001; Fig. 2).

215

216 The suitability of the HZ as a habitat for benthic invertebrates is therefore a trade-off,  
217 with no single set of conditions being ideal. Downwelling zones have hydrological  
218 and water quality benefits but interstitial space may be limited whereas the unclogged  
219 interstices of upwelling zones may be resource-poor (Fig. 2).

220

### 221 **The hyporheic zone as a refuge**

222 The potential for the HZ to provide a refuge for benthic invertebrates was recognised  
223 by Orghidan (1959, 2010) following freezing in a surface stream. Other early  
224 evidence of this refugial role was provided by Clifford (1966) and Williams and  
225 Hynes (1974) who observed benthos in the HZ after surface drying and during a spate,  
226 respectively; other seminal research is described by Dole-Olivier (2011). The  
227 Hyporheic Refuge Hypothesis (HRH) was later formally stated by Palmer *et al.*  
228 (1992). By moving into the HZ, it is proposed that benthic invertebrates increase their  
229 probability of surviving an adverse condition in the surface stream. When conditions  
230 improve, refugees potentially recolonise benthic habitats from the HZ, thus  
231 facilitating community recovery.

232

233 The adverse conditions from which benthic refugees may seek shelter include both  
234 biotic and abiotic stresses. The HZ may be a protective nursery for early instar insect  
235 larvae (Giberson and Hall 1988; Puig *et al.* 1990; Jacobi and Cary 1996) and also a  
236 predation refuge for other vulnerable groups (e.g. moulting individuals; McGrath *et*  
237 *al.* 2007). In addition, the HZ is a potential shelter from environmental conditions

238 including surface freezing (Orghidan 1959, 2010), low temperatures (Malard *et al.*  
239 2001), high temperatures (Evans and Petts 1997; Wood *et al.* 2010) and pollution  
240 (Jeffrey *et al.* 1986; Belaidi *et al.* 2004). Most research considering the HRH,  
241 however, has focussed on the extremes of the hydrological continuum, namely floods  
242 and streambed drying. During high flows, the HZ reduces displacement, since flow  
243 velocities remain relatively slow and sediments relatively stable (Boulton *et al.* 2004).  
244 During drying, the HZ may retain free water, a necessity for most aquatic biota.  
245 However, despite receiving more attention than other potential refuges, evidence for  
246 the HRH remains equivocal during floods, drying, and low flows (Tables 1-3; Dole  
247 Olivier 2011).

248

#### 249 *Types of evidence for the hyporheic refuge hypothesis*

250 The HRH remains contentious, in part due to differing interpretations of what  
251 constitutes refuge use. Therefore, before presenting the evidence itself, a conceptual  
252 model (Fig. 3) will be used to assess these contrasting interpretations, and a definition  
253 of acceptable evidence will be outlined.

254

#### 255 *Evidence type 1: Presence of benthic invertebrates in the hyporheic zone*

256 Some studies have simply observed benthic invertebrates in the HZ during adverse  
257 surface conditions, without knowledge of temporal change in depth distribution  
258 (Imhof and Harrison 1981; Fenoglio *et al.* 2006). Others have noted that, despite  
259 declining hyporheic abundance, a few benthic individuals persist in the HZ during  
260 both drying (Griffith and Perry 1993; del Rosario and Resh 2000) and spates (Boulton  
261 *et al.* 2004; Bruno *et al.* 2009). Such data provide no evidence of active shelter-  
262 seeking behaviour, but demonstrate passive refuge inhabitation (Box 2, Fig. 3), which  
263 is also an important mechanism promoting invertebrate survival.

264

#### 265 *Evidence type 2: An increase in abundance in the hyporheic zone*

266 Other studies have reported an increase in a benthic taxon's abundance in the HZ as  
267 evidence of refuge use (Dole-Olivier and Marmonier 1992a; Marchant 1995; Dole-  
268 Olivier *et al.* 1997). However, if densities concurrently increase in the benthic zone,  
269 then the proportion of a population in the HZ may be unchanged or may decline,  
270 indicating range extension but not shelter-seeking behaviour (Box 1, Fig. 3). Both  
271 floods and drying are, in fact, likely to decimate benthic populations (Hynes 1958;



272 Wood and Armitage 2004; Death 2008) and even if benthic densities are unknown, an  
273 increase in the hyporheic proportion can often be assumed to accompany an increase  
274 in hyporheic abundance (Dole-Olivier and Marmonier 1992a; Clinton *et al.* 1996;  
275 Dole-Olivier *et al.* 1997). In contrast, low flows may cause benthic population  
276 densities to increase as habitats contract (Extence 1981; Dewson *et al.* 2007b). In such  
277 cases, an increase in hyporheic abundance may be outweighed by rising benthic  
278 densities, causing the hyporheic proportion of a population to fall (Stubbington *et al.*  
279 2011b). As such, only vertical range extension of the benthic population can be  
280 inferred (Box 1, Fig. 3).

281

### 282 *Evidence type 3: An increase in a population's hyporheic proportion*

283 Other research has posited an increase in the hyporheic proportion of a taxon's total  
284 (benthic + hyporheic) population as evidence for the HRH. However, an increase in  
285 proportion may accompany a reduction in hyporheic abundance, so long as the decline  
286 is of a lesser magnitude than occurs in the benthic zone (Giberson and Hall 1988;  
287 Palmer *et al.* 1992; Olsen and Townsend 2005). Whilst survival may be enhanced for  
288 those animals in deeper sediments when a disturbance commences, such studies  
289 indicate passive refuge use (Box 2, Fig. 3), not active migrations.

290

### 291 *Evidence type 4: Concurrent increases in hyporheic abundance and proportion*

292 Evidence types 1-3 demonstrate that, regardless of how benthic abundance changes,  
293 simultaneous increases in the hyporheic abundance and proportion of a population  
294 provide the most convincing evidence of active migrations (Fig. 3). Such evidence is  
295 required for refuge use to be considered 'active' in Tables 1-3.

296

### 297 *The active-passive refuge distinction*

298 The distinction between active and passive refuge use has long been recognised with  
299 reference to the HZ (Robertson *et al.* 1995; Robertson and Wood 2010) and other  
300 refuges (Ward 1989; Lake 2000). Robertson *et al.* (1995) described models of refuge  
301 use including a 'catastrophe avoided' model of active migration, and 'incomplete  
302 catastrophe' and 'refuge as habitat' models, in which refuge inhabitants are passively  
303 protected. Lancaster and Belyea (1997) refined these models, their 'directed flux  
304 between microhabitats' scheme equating to active refuge use whilst in their 'no flux'  
305 and 'undirected flux' models, passive refuge use reduces disturbance impacts.

306 Robertson and Wood (2010, p. 284) suggest that “as long as survivorship in the HZ is  
307 [proportionally] higher than that in benthic habitats, then it will act as a refugium”.  
308 However, passive refuge use can have an even simpler condition attached: as long as  
309 survival *occurs* in the HZ, it may promote invertebrate persistence.

310

311 Both active and passive movements may therefore promote invertebrate survival, for  
312 example in downwelling zones during low-magnitude spates (Dole-Olivier *et al.*  
313 1997). However, active refuge use increases the potential of the HZ to protect a  
314 greater range of taxa during a greater range of disturbance types. Active migrations  
315 are necessary, for example, during slow-onset drying events in which flow velocities  
316 are insufficient to move macroinvertebrates, and during high-flow events in which the  
317 direction of hydrologic exchange opposes migratory movements.

318

319 Despite the earlier models (Robertson *et al.* 1995; Lancaster and Belyea 1997;  
320 Robertson and Wood 2010), inferring the behaviours behind refuge use from field or  
321 experimental data remains problematic. To address this, the model presented in Fig. 3  
322 provides a framework to guide interpretation of data collected during HRH research,  
323 as outlined above. However, although Fig. 3 can be used to *infer* behaviour, the model  
324 cannot distinguish between active migrants and refugees passively carried into the HZ  
325 (Dole-Olivier *et al.* 1997; Lancaster and Belyea 1997). Indeed, whilst laboratory  
326 experiments (Holomuzki and Biggs 2000) and field sampling campaigns (Palmer *et*  
327 *al.* 1992) may provide compelling evidence of active migrations, conclusive proof of  
328 whether individual movements are intentional or involuntary remains elusive. It is  
329 theoretically possible that an increase in the hyporheic abundance and proportion of a  
330 population may result entirely from passive displacement by downwelling water;  
331 equally, a decrease in hyporheic abundance may mask active migrations of a few  
332 individuals. As such, it is recognised that the changes in distribution taken as evidence  
333 of refuge use may result from a combination of active and passive movements  
334 (Robertson *et al.* 1995; Dole-Olivier *et al.* 1997; Lancaster 2000). Inferred behaviours  
335 should therefore be considered as the dominant, but not the only, behaviours  
336 influencing a population’s distribution (Fig. 3).

337

### 338 **Evidence for active use of the HZ refuge**

339 *i) Refuge use during floods*

340 It was the early observations of changes in invertebrate depth distributions after flood  
341 events that sparked interest in the HZ as a refuge (Clifford 1966; Williams and Hynes  
342 1974), and this has since been formalised in the Flood Refuge Hypothesis (Boulton *et*  
343 *al.* 2004). This hypothesis posits vertical migration as a behavioural response to an  
344 increase in flow velocity or other hydraulic stress (Boulton *et al.* 2004).

345

346 Evidence of active migrations has been reported by at least eight studies (Table 1,  
347 Section A), encompassing natural spates (Williams and Hynes 1974; Dole-Olivier and  
348 Marmonier 1992a; Dole-Olivier *et al.* 1997), prolonged high flows (Marchant 1988,  
349 1995), and their experimental equivalents (Holomuzki and Biggs 2000). Williams and  
350 Hynes (1974), for example, noted increased invertebrate abundance at and below 30  
351 cm after a flood, accompanied by equivalent reductions in shallower sediments, whilst  
352 total abundance remained stable. Supporting evidence from laboratory simulations is  
353 provided by Holomuzki and Biggs (2000) who observed shifts in the depth  
354 distribution of one mayfly, one snail and two caddisfly genera in response to short-  
355 term, high-magnitude increases in discharge.

356

357 Other studies have found no evidence of active migrations during floods (Table 1,  
358 Section B). In many cases, this has been attributed to inadequate habitat (e.g.  
359 sediment-clogged interstices), substrate instability and/or upwelling water (Palmer *et*  
360 *al.* 1992; Dole-Olivier *et al.* 1997; Olsen and Townsend 2005). In other cases,  
361 disturbance-related factors appear responsible, including rapid spate onset (Gayraud *et*  
362 *al.* 2000; Imbert and Perry 1999), and spate magnitude being too low to elicit a  
363 response (Boulton *et al.* 2004) or high enough to mobilise HZ sediments and fauna  
364 (Dole-Olivier *et al.* 1997; Stubbington *et al.* 2010). The importance of disturbance  
365 characteristics is also demonstrated by events that reduce the abundance of permanent  
366 hyporheos (Dole-Olivier and Marmonier 1992a; Olsen and Townsend 2005; Hancock  
367 2006). However, even when impacts are severe, benthic invertebrates are routinely  
368 present in HZ after a disturbance, albeit at low abundance (Table 1). This highlights  
369 the importance of passive refuge use in promoting community resilience, with the few  
370 survivors acting as potential recolonists of benthic sediments (Table 1, Section B).  
371 Such recolonisation is particularly important if the HZ has come to support a higher  
372 proportion of the total community (Giberson and Hall 1988; Stubbington *et al.* 2010).

373

374 *ii) Refuge use following streambed drying*

375 The HZ's potential as a refuge after streambed drying hinges on the availability of  
376 free water, or at least high humidity. The principal impetus for invertebrate migration  
377 is therefore to remain submerged, although stresses such as increasing surface water  
378 temperatures may also be involved (Wood *et al.* 2010).

379

380 Where free water is retained, changes in depth distribution have indicated that  
381 invertebrates can actively follow the receding water table into deeper sediments  
382 (Delucchi 1989; Clinton *et al.* 1996; Table 2, Section A). Many other studies have  
383 found passive inhabitation to facilitate population persistence (Table 2, Section B),  
384 with the diverse assemblage surviving in moist interstices including Isopoda,  
385 Amphipoda (Clifford 1966), Trichoptera (Imhof and Harrison 1981), and adult  
386 Coleoptera (Fenoglio *et al.* 2006). However, where the criterion of water availability  
387 is not fulfilled, the HZ fails as a refuge (Boulton and Stanley 1995). Therefore, whilst  
388 research into the HZ flood refuge has always found a small proportion of benthos to  
389 persist (Table 1), drying can eliminate virtually all benthic invertebrates, including  
390 both active and passive refugees (Table 2, Section C). However, as these studies have  
391 not considered dormant life stages present in dry sediments, community persistence  
392 may have been underestimated (Stubbington *et al.* 2009a; T. Datry unpublished data).

393

394 Refugial capacity may be reduced during drying if fine sediments are deposited in  
395 interstices as flow declines; sediment compaction and baking may then cause  
396 interstitial hypoxia (Gagneur and Chaoui-Boudghane 1991; Smock *et al.* 1994;  
397 Belaidi *et al.* 2004). Such habitat characteristics are invariably held responsible for the  
398 failure of the hyporheic refuge during drying events (Table 2), which, as gradual onset  
399 disturbances (Lake 2000, 2003), favour a behavioural response. The quality of the HZ  
400 refuge is, however, relative to other microhabitats, and vertical migrations may be  
401 reduced if alternative refuges exist. Boulton (1989), for example, found more refugee  
402 taxa and individuals in receding pools and nearby perennial waters than in the HZ of  
403 intermittent streams.

404

405 *iii) Refuge use during low flows*

406 Few studies have considered use of the HZ refuge during low flows (Table 3), with  
407 relatively benign hydrological conditions being a less obvious migration trigger.

408 However, James *et al.* (2008) hypothesized that vertical migrations would occur as  
409 flow receded if habitat contraction forced invertebrates into a smaller area, thus  
410 increasing biotic interactions. Such predictions are supported by observations that  
411 mobile taxa such as the amphipod *Gammarus pulex* migrate into smaller interstices in  
412 response to an increased risk of cannibalism (McGrath *et al.* 2007). However, only  
413 Stubbington *et al.* (2011a, 2011b) have inferred refuge use during flow recession, with  
414 *G. pulex* migrating into the HZ following habitat contraction and a concurrent  
415 increase in benthic densities (Table 3). In addition, Wood *et al.* (2010) noted active  
416 migrations of *G. pulex* during low flows, these migrations being linked to thermal, but  
417 not hydrological drivers. In other studies, surface sediments appear a preferable  
418 habitat, even if benthic population densities do increase (James *et al.* 2008; James and  
419 Suren 2009).

420

#### 421 **Variability in the hyporheic refuge**

422 The preceding discussion has identified use of the HZ refuge as very variable. Spatial  
423 variability depends on habitat characteristics whilst temporal variability reflects  
424 disturbance type. Additional variation is biotic; refuge use is restricted to certain taxa,  
425 and although poorly understood, biotic interactions may also affect active migrations.

426

#### 427 *Spatial variability in the hyporheic refuge*

428 Use of the hyporheic refuge is spatially variable, depending on the fulfilment of  
429 certain environmental criteria (Townsend 1989; Lancaster and Belyea 1997;  
430 Robertson and Wood 2010). Whilst refuges can promote population persistence at  
431 multiple spatial scales (Townsend and Hildrew 1994; Robertson *et al.* 1995; Robson  
432 *et al.* 2011), individual invertebrates always act at the smallest scales (Lancaster  
433 2008), and patch-scale variation is therefore particularly relevant to refuge use. The  
434 dependence of refuge use on the fulfilment of habitat-related criteria has been termed  
435 “refugial effectiveness” (Robertson and Wood 2010) and “refugial potential”  
436 (Stubbington *et al.* 2011b), the latter term recognising that sediments with suitable  
437 characteristics may nonetheless not be used as a refuge (Fig. 4). The habitat  
438 characteristics that influence the permanent hyporheos are also principal determinants  
439 of refuge potential: hydrologic exchange and sediment characteristics, which are  
440 interdependent and also influence water quality.

441

442 *i) Hydrologic exchange*

443 Despite recognition that downwelling zones promote refuge use during both high and  
444 low flows, the vital features of infiltrating water have not been isolated, and several  
445 factors may be relevant (Davy-Bowker *et al.* 2006). Movement of downwelling water  
446 is assumed to facilitate active and passive transport of benthos into the HZ, and this  
447 assumption may be valid at high flow velocities (Dole-Olivier *et al.* 1997). However,  
448 during flow recession, surface velocities may decline (Wright and Berrie 1987;  
449 Dewson *et al.* 2007a) and whilst rarely measured, velocities are probably even slower  
450 in the HZ (Angradi and Hood 1998). Therefore, it is unlikely that upwelling water  
451 prevents downwards migrations of mobile taxa during low flows.

452

453 However, water chemistry also varies depending on the direction of hydrologic  
454 exchange. Downwelling water typically resembles surface water in terms of oxygen,  
455 temperature, chemistry and organic matter content, whilst groundwater inputs have a  
456 distinct chemistry and are often oxygen- and resource-poor (Brunke and Gonser 1997;  
457 Datry *et al.* 2005, 2007). Such variables may influence migrations during low-  
458 magnitude disturbances such as flow recession (Stubbington *et al.* 2011b), but are of  
459 secondary importance to habitat stability during spates and to free water after drying.  
460 Equally, whilst the presence of free water may suffice for tolerant taxa and during  
461 short drying events (Williams and Hynes 1974; Danielopol 1989), as dry phase  
462 duration increases, long residence times and the absence of surface inputs affect water  
463 quality, with consequences for the survival of an increasing proportion of the  
464 community. Upwelling zones providing high-quality groundwater inputs may  
465 therefore have the highest refugial potential during drying events (Dole-Olivier 2011).  
466 Dole-Olivier (2011) provides greater detail on hydrological variables influencing  
467 refuge use.

468

469 *ii) Sediment characteristics*

470 No refuge use is possible without connectivity between the HZ and the surface  
471 stream, hence the central role of sediment composition in determining refuge  
472 potential. The most fundamental requirement is that a HZ exists, which is not the case  
473 in channels with impermeable strata (White 1993; Dole-Olivier 2011). The size of the  
474 HZ is also important and hyporheic sediments may be limited in spatial extent, as in  
475 many headwater streams (Stubbington *et al.* 2009a; Chester and Robson 2011).

476 Regardless of spatial extent, shallower sediments are more likely to be encountered by  
477 migrants (Williams and Hynes 1974; Marmonier *et al.* 2010), but the availability of  
478 deeper layers potentially increases survival due to reduced scour at high flows, and  
479 increased water availability after surface drying.

480

481 Once the basic criterion of a sufficiently voluminous HZ is met, then the same  
482 characteristics that support a speciose hyporheos also encourage refuge use, with  
483 coarse-grained, porous sediments facilitating both active and passive movements. The  
484 detrimental effects of fine sediment may, however, be exacerbated by a disturbance.  
485 Firstly, during spates, finer sediments are more easily mobilised, thus displacing any  
486 resident refugees (Palmer *et al.* 1992; Olsen and Townsend 2005). Equally, during  
487 drying, fine sediments may form a surficial crust which separates the HZ from  
488 atmospheric oxygen inputs and restricts invertebrate movements (Gagneur and  
489 Chaoui-Boudghane 1991; Belaidi *et al.* 2004).

490

#### 491 *Temporal variability in the hyporheic refuge*

492 Whilst the refugial role of the HZ depends in part on its stability, it is nonetheless a  
493 temporally dynamic habitat (Stanford and Ward 1993). Many determinants of refuge  
494 potential may be altered by the conditions triggering refuge use, especially high flows.  
495 If the effects of bed-mobilising floods extend into the HZ, refugial potential may be  
496 severely compromised (Matthaei *et al.* 1999; Wondzell and Swanson 1999); equally,  
497 sediment deposition may bury refugees, providing additional protection during a  
498 disturbance but impeding later recolonisation of the surface (Olsen *et al.* 2010). In the  
499 longer term, sediments reworked by high flows may have higher or lower fine  
500 sediment content (McKenzie-Smith *et al.* 2006; Olsen *et al.* 2010), influencing their  
501 refugial potential during future events. The direction and strength of hydrologic  
502 exchange may also be altered by changes in surface flow and disturbance-related  
503 changes in sediment composition (Baker and Vervier 2004; Boulton *et al.* 2004).

504

505 Despite this temporal variability in refuge potential, few studies have considered  
506 changes in refuge use over extended periods. Notable exceptions include Dole-Olivier  
507 and Marmonier (1992a) and Dole-Olivier *et al.* (1997), who considered a period of  
508 base flow interrupted by multiple spates in a regulated channel. These studies  
509 highlighted temporal variability in refuge use, with migrations depending on both

510 spate amplitude and habitat features. Similarly, Wood *et al.* (2010) considered a 7-  
511 month period of stable then declining discharge, finding evidence of active migrations  
512 in response to increasing surface water temperatures, but not flow recession. In  
513 addition, Smock *et al.* (1994) and Stubbington *et al.* (2010) have considered refuge  
514 use during consecutive, contrasting disturbances. Smock *et al.* (1994) recorded no  
515 refuge use during a storm or drying, due to hyporheic anoxia. In contrast, Stubbington  
516 *et al.* (2010) observed migrations of *G. pulex* during a flow recession, the species'  
517 hyporheic abundance then plummeting during a spate, thus demonstrating inter-  
518 disturbance variability in refuge potential.

519

#### 520 *Spatiotemporal variability in biotic interactions*

521 As well as being reduced by deteriorations in environmental quality relating to  
522 disturbance onset, long-term survival in refuges may be limited by unfavourable  
523 biotic conditions that develop as a consequence of refuge use (Lancaster and Belyea  
524 1997). In particular, any increase in population densities causes biotic interactions to  
525 intensify, including competition for limited resources (such as space, food and  
526 oxygen) and predation (Lancaster 1996). Active refuge use involves movement into a  
527 habitat that is usually less desirable than the benthic sediments, and increased biotic  
528 interactions may further reduce the attractiveness of the HZ. Individual invertebrate  
529 migrations may therefore be density-dependent as well as reflecting environmental  
530 conditions. However, whilst increased predation has been observed in surface refuges  
531 (Lancaster 1996), little evidence relates specifically to the HZ, and routine use of the  
532 zone as a predation refuge by vulnerable life stages (Jacobi and Cary 1996; McGrath  
533 *et al.* 2007) indicates that biotic pressures do not intensify significantly due to refugee  
534 influxes. This may be due to interstitial space limiting hyporheic densities of larger  
535 predatory macroinvertebrates (Franken *et al.* 2006), reductions in predation efficiency  
536 in interstices (Schmid and Schmid-Araya 1997) and/or reduced predator activity in a  
537 resource-limited habitat (Stubbington *et al.* 2009a; Robson *et al.* 2011).

538

#### 539 *Variability in benthic refugee taxa*

540 Whilst evidence for the HRH relates to a diverse assemblage, active migrations are  
541 often restricted to certain taxa (Table 4), indicating that morphological and/or  
542 behavioural taxon-specific characteristics influence refuge use. Robertson and Wood  
543 (2010) used the trait analysis of Poff *et al.* (2006) to identify features of active



544 migrants (Table 5). To assess the validity of this analysis, taxa identified as active  
545 migrators (Table 4) are compared to proposed traits (Table 5). All migrant taxa share  
546 one trait, *no attachments* (Table 5), suggesting this as a prerequisite for migration.  
547 However, evidence of active migration has been observed in Simuliidae larvae (pers.  
548 obs.), which attach to substrata using anal hooks. Simuliids can, however, move to the  
549 streambed using silk anchor threads and then use looping movements to enter the HZ  
550 (Wotton 1979). *No attachments* is therefore not a prerequisite for refuge use, so long  
551 as release can be achieved swiftly at the onset of a disturbance.

552

553 The trait *burrowing habit* indicates a predisposition towards interstitial inhabitation,  
554 which would seem vital for vertical migration. Evidence of refuge use in taxa lacking  
555 this trait is restricted to the caddisfly larvae of Leptoceridae (which Holomuzki and  
556 Biggs (2000) note as equally likely to remain on the surface as migrate) and  
557 Hydropsychidae and Polycentropodidae, regarding which Dole-Olivier and  
558 Marmonier (1992a) provide no details. The trait *high crawling rate* indicates a  
559 capacity to respond quickly at disturbance onset, which may be crucial during spates.  
560 Accordingly, two of three taxa lacking this trait (*Gammarus*, Leptophlebiidae) are  
561 instead strong swimmers, and some chironomids are also capable of vigorous  
562 movement to enter preferred habitats (Palmer *et al.* 1992; Armitage *et al.* 1995). This  
563 trait should therefore be broadened to *high movement rate*, because locomotory mode  
564 is less important than mobility (Claret *et al.* 1999); equally, this feature may be of  
565 little relevance during slow-onset events. Following migration, the trait *depositional*  
566 *rheophily* implies adaptation to sediment-depositing habitats, which the HZ may be  
567 during any hydrological disturbance. Eight of nine *burrowing* taxa also exhibited this  
568 trait, whilst chloroperlid stonefly nymphs did not; this taxon prefers erosional zones  
569 and its burrowing, and thus refuge use, may occur only in coarse gravels (Baumann *et*  
570 *al.* 1977).

571

572 Two morphological traits are suggested by Robertson and Wood (2010) as migrant  
573 attributes: *small size at maturity* (<9 mm) and *vermiform shape*. However, only four  
574 migrant taxa may be small when mature, with late instar Ephemeroptera, Plecoptera  
575 and Trichoptera (EPT) and *Gammarus* reaching sizes that could inhibit interstitial  
576 inhabitation (Robertson and Wood 2010). Indeed, HZ residents are typically small,  
577 irrespective of the ultimate size a taxon achieves (Cooling and Boulton 1993; Malard

578 *et al.* 2003b). *Size at maturity* is therefore less important than the occurrence of small  
579 instars within the life cycle, so long as the time taken to reach maturity exceeds  
580 disturbance duration. Maximum size will also relate to pore-size distribution, and will  
581 be influenced by morphology and behaviour, including the capacity to alter pore sizes  
582 through physical activity (Claret *et al.* 1999).

583

584 The trait *vermiform shape* is also only partly supported (Table 5), with flattened,  
585 blunt, robust, and/or streamlined forms also allowing HZ inhabitation. Williams and  
586 Hynes (1974) suggested two morphologies as suiting the HZ: long and flexible, to  
587 move between grains, and blunt and well-protected, to bludgeon past them.

588 *Vermiform* should thus be replaced by a rather general attribute: *morphologically*  
589 *suited*. Even then, morphological features of some migrants, such as mayflies with  
590 delicate gills, appear ill-suited to the HZ (Marchant 1988), emphasizing the influence  
591 of habitat characteristics on taxon-specific refuge use. Gilled EPT are also amongst  
592 refugees limiting support for the trait *tegument respiration*; mode of gas exchange  
593 does not appear to influence refuge use.

594

595 *Relationships between spatial, temporal and taxonomic variability*

596 For any individual inhabiting the benthic zone, migration into the HZ at disturbance  
597 onset is concurrently determined by factors in the four categories discussed: habitat  
598 characteristics, disturbance features, biotic interactions and migrant traits (Fig. 4).  
599 First, the HZ must provide an adequate habitat, with sufficient interstitial space,  
600 favourable water quality and adequate resources, as well as acceptably low biotic  
601 interactions (C1, Fig. 4). Second, disturbance characteristics must be conducive to  
602 refuge use, for example having a gradual onset, and not causing biotic risks to  
603 increase to intolerable levels in the HZ (C2, Fig. 4). Third, the invertebrate itself must  
604 be inclined to migrate in response to disturbance triggers (C3, Fig. 4); suitable habitat  
605 and disturbance characteristics do not automatically elicit a response.

606

607 All three criteria must be fulfilled for any individual to actively migrate (Fig. 4). For  
608 example, the HZ habitat may be suitable and disturbance characteristics may favour a  
609 response, but a taxon may employ an alternative survival strategy, such as entrance  
610 into the drift (Perry and Perry 1986) or use of other refuges (Boulton 1989; Cooling  
611 and Boulton 1993; Rempel *et al.* 1999). Alternatively, a taxon known to migrate may

612 be prevented from moving into suitable habitat by a disturbance characteristic, such as  
613 rapid onset (Imbert and Perry 1999; Gayraud *et al.* 2000; Stubbington *et al.* 2011b).  
614 This same potential refugee's vertical migration may be thwarted during a slow-onset  
615 disturbance by an inappropriate habitat feature (Olsen and Townsend 2005); features  
616 of importance and tolerance thresholds will differ between taxa.

617

618 Fig. 4 can be used to predict refuge use by a particular taxon if habitat and disturbance  
619 characteristics are known. However, whilst an initial migration can be predicted, HZ  
620 habitat quality may change as a disturbance progresses. In particular, water quality  
621 and resource availability may decline during drying events, with oxygen becoming  
622 limited as hyporheic water residence times increase. Therefore, an initial migration is  
623 only the first step in exploiting the HZ refuge (Dole-Olivier in press), and does not  
624 guarantee long-term survival.

625

#### 626 **Directions for future research**

627 Whilst recent research has continued to ask if the HZ is a refuge, the variable nature  
628 of refuge use means that the answer is never clear-cut. The HZ can be a refuge, but  
629 only for certain taxa, if the habitat fulfils their requirements, and if the disturbance has  
630 certain characteristics. This complexity of determinants leaves many questions  
631 concerning the occurrence of migrations remain unanswered, and further research is  
632 needed to elucidate the habitat characteristics that allow refuge use in particular taxa.  
633 In particular, Dole-Olivier (2011) argues that future research should seek to  
634 characterise hydrologic exchange patterns in greater detail to clarify the influence of  
635 upwelling and downwelling water on refuge use.

636

637 For the model presented in Fig. 3 to be employed as a framework for the inference of  
638 invertebrate behaviour, essential criteria for future research into the HRH include the  
639 collection of paired benthic-hyporheic samples (e.g. Belaidi *et al.* 2004; Wood *et al.*  
640 2010; Stubbington *et al.* 2011b) using non-destructive methods which allow repeated  
641 collection of quantitative samples from the same locations during a temporal sequence  
642 (Stubbington *et al.* 2009b). Variation in sampling efficiency between methods should  
643 be recognised (Fraser and Williams 1997; Scarsbrook and Halliday 2002; Kibichii *et*  
644 *al.* 2009), but the model remains valid where benthic and hyporheic sampling

645 techniques differ, so long as each is employed consistently. Such studies will provide  
646 valuable information to guide the rehabilitation of impacted systems.

647

648 Other pertinent questions relate to the long-term prospects of migrants. As the HZ  
649 remains connected to non-refugial areas when a disturbance ends, there is scope for  
650 benthic recolonisation. Accordingly, shifts from shallow to deeper layers and  
651 subsequent return to the original depth distribution have been observed in response to  
652 both spates (Williams and Hynes 1974; Dole-Olivier *et al.* 1997) and flow-related  
653 temperature changes (Wood *et al.* 2010). Such apparent shifts in migration direction  
654 highlight the importance of active migrations. However, experimental work is needed  
655 to confirm that individual vertical migrations are reversed, and that the HZ is a true,  
656 not a transient, refuge (Dole-Olivier 2011).

657

658 In particular, whilst downwelling water may facilitate initial refuge use, it is not  
659 known how this direction of exchange affects refugees attempting to exit the HZ  
660 (Dole-Olivier *et al.* 1997; Stubbington *et al.* 2011b). Hyporheic flowpaths are spatio-  
661 temporally variable and occur at multiple spatial scales (Jones and Holmes 1996;  
662 Montgomery and Buffington 1997; Dole-Olivier 2011), and both spatial and temporal  
663 changes in exchange direction may facilitate the return of migrants to the surface.  
664 Such pathways may be particularly important in redistributing passive refugees, for  
665 which the HZ is otherwise a trap (Marmonier and Creuzé des Châtelliers 1991). The  
666 active-passive distinction is thus highly relevant to long-term refugee survival.

667

### 668 **Implications for river management and restoration**

669 A refugial habitat is one of many contributions the HZ makes to stream ecosystem  
670 functioning. This role may become increasingly important, given predictions of  
671 climatic shifts involving increased drought and flood severity (IPCC 2007; Larned *et al.*  
672 *et al.* 2010; Aldous *et al.* 2011). However, anthropogenic deposition of fine sediment  
673 and channel modifications that reduce geomorphological complexity threaten the HZ  
674 refuge, by impeding hydrologic exchange and blocking the interstitial pathways upon  
675 which refuge use depends (Hancock 2002; Kondolf *et al.* 2006). The HZ therefore  
676 requires protection through environmental policy and legislative instruments such as  
677 the European Union Water Framework Directive (WFD; CEC 2000). The WFD  
678 requires a holistic approach to catchment management, including integrated

679 management of groundwater and surface waters (Environment Agency 2002, 2009),  
680 but does not explicitly consider the HZ. Indeed, in Europe and elsewhere the  
681 ecological integrity of the HZ is rarely addressed by either monitoring programmes or  
682 rehabilitation schemes (Boulton 2007; Kasahara *et al.* 2009; Tomlinson and Boulton  
683 2010; but see Kasahara and Hill 2006a, 2006b, 2007). There is therefore scope for  
684 regulators to ensure meaningful implementation of legislation to maximise ecological  
685 benefits for total river ecosystems.

686

687 Rehabilitation schemes are typically focussed on the surface stream (Bannister *et al.*  
688 2005; Boulton 2007), and whilst such efforts may benefit the subsurface (Boulton *et*  
689 *al.* 2010), hydrologic exchange must also be targeted if the HZ refuge is to be  
690 safeguarded (Jansson *et al.* 2007; Boulton 2007; Hester and Gooseff 2010). To date,  
691 HZ-specific rehabilitation has involved increasing geomorphological complexity, for  
692 example by introducing wood into streams (Kasahara and Hill 2006a, 2006b; Mika *et*  
693 *al.* 2008). Such schemes promote hydrologic exchange (Kasahara and Hill 2006b),  
694 and patterns of exchange (an upwelling zone shortly downstream of a downwelling  
695 zone) may favour HZ refuge use and subsequent benthic recolonisation (Boulton  
696 2007). Such schemes potentially have only localised effects, but since refuge use is  
697 patch-specific in heterogeneous habitats, localised refugial hot-spots may support  
698 enough individuals for subsequent recruitment and recolonisation of the surface  
699 (Robertson *et al.* 1995). Nonetheless, the HZ is a refuge only for certain taxa in  
700 certain circumstances, and rehabilitation schemes should therefore aim to create  
701 heterogeneous habitats incorporating a suite of potential refuges (Fig. 1).

702

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708

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- 1429 Young, B., Norris, R., and Sheldon, F. (in press). Is the hyporheic zone a refuge for  
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1431 Table 1: Evidence of active and passive use of the hyporheic refuge by benthic invertebrate taxa during high flows (modified from Robertson  
 1432 and Wood 2010).  
 1433 Evidence of active refuge use is provided by concurrent increases in the HZ abundance and proportion of a population; the proportion is inferred  
 1434 from observed or assumed changes in BZ abundance; evidence of passive refuge use is provided by the occurrence of benthic invertebrates in the  
 1435 HZ. HZ = hyporheic zone; BZ = benthic zone; EPT = Ephemeroptera, Plecoptera and Trichoptera.

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**Section A. Studies providing evidence of active refuge use**

Site description / location	Evidence	Explanation for lack of migrations	Reference
Riffle in headwaters of Speed River, Canada	Peak abundance of benthos at greater depth 1 day after spate; concurrent decrease in BZ abundance	-	Williams and Hynes 1974
Three forested sites, Thomson River, Victoria, Australia	Abundance of benthos lower at 0-10 cm and higher at 10-30 cm during high flows (at 1 of 3 sites)	-	Marchant 1988
Bypassed section of River Rhône River, France	More benthos (EPT, chironomids, flatworms) at 50 cm after spate, at upwelling sites	-	Marmonier and Creuzé des Châtelliers 1991
Bypassed section of River Rhône River, France	Benthos ( <i>Gammarus</i> , ostracods) abundance increased in deeper sediments 1 day after spate, then decreased	-	Dole-Olivier and Marmonier 1992
Sand-bottomed stream, Virginia, USA	Rotifer abundance increased in HZ and decreased in BZ after flood.	-	Palmer et al 1992
Upland sites, Acheron River, Victoria, Australia	Chironomid, elmud, mite and copepod (but not EPT) abundance higher in HZ (10-30 cm) in high flow months.	-	Marchant 1995
Bypassed section of Rhône River, France	<i>Gammarus</i> and chironomids at greater depths after small / medium spates in downwelling zones	-	Dole-Olivier <i>et al.</i> 1997
Experimental flow tank	Hydrobiidae, Leptophlebiidae and Leptoceridae occurred in deeper layers during experimental flow increases	-	Holomuzki and Biggs 2000

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**Section B. Studies providing evidence of passive refuge use**

Site description / location	Evidence	Explanation for lack of migrations	Reference
Uniform riffle, Brazos River, Texas, USA	Increased HZ proportion of benthos (hydropsychids, elmids larvae, leptophlebiids); HZ abundance not known	None stated; active migrations possible	Poole and Stewart 1976
Pool-riffle downstream lake outflow, Ontario, Canada	HZ simuliid abundance stable during spate whilst BZ abundance declined. Other taxa present at low density.	Other refuges used (stable substrates)	Giberson and Hall 1988
Bypassed section of River Rhône River, France	Increase in HZ proportion but reduced HZ abundance for chironomids, oligochaetes and copepods after spate	Sandy substrate; "wash out" effect	Marmonier and Creuzé des Châtelliers 1991
Upland sites, Acheron River, Victoria, Australia	Evidence of active migrations (Section A) not observed during 1 of 2 high flow events	Possibly sediment compaction	Marchant 1995
Bypassed section of Rhône River, France	Little or no increase in HZ abundance of benthos after small/medium spates in upwelling zones	Stable hydrology	Dole-Olivier <i>et al.</i> 1997
Bypassed section of Rhône River, France	Benthos drifted rather than entering the HZ during high magnitude floods in downwelling zones	Spate magnitude; mobile substrate	Dole-Olivier <i>et al.</i> 1997
Gravel-bed experimental streams, USA	Non-significant increase in HZ abundance following abrupt/stepped flow increases	Rapid onset/ low spate magnitude	Imbert and Perry 1999
Cobble-bed sub-Alpine stream, France	Densities of benthos were stable in HZ before and after an experimental flow increase	Rapid spate onset	Gayraud <i>et al.</i> 2000
Subtropical river, Australia	Benthic mite abundance stable in HZ before and after experimental spates	Low spate magnitude	Boulton <i>et al.</i> 2004
Kye Burn, New Zealand	HZ abundance of all benthos lower after spate, but reduction in BZ abundance greater	Fine sediments	Olsen and Townsend 2005
Alpine stream, Italy	Hyporheic abundance/diversity of benthos reduced at hydropeaking-impacted sites	Disturbance frequency	Bruno <i>et al.</i> 2009
Second order karst stream, England	HZ abundance of benthos lower after spate, but reduction in BZ abundance greater	Mobile sediments/ rapid spate onset	Stubbington <i>et al.</i> 2010

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- 1438 Table 2: Evidence of active, passive, minimal and no use of the hyporheic zone as a refuge by benthic invertebrates during streambed drying  
 1439 (modified from Wood *et al.* 2010).  
 1440 See Table 1 caption for additional details.

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**Section A. Studies providing evidence of active refuge use**

Site description and location	Evidence	Explanation for lack of migrations	Reference
Temporary stream, New York, USA	Directional cages traps indicate migration of chloroperlids and leptophlebiids into HZ of riffles	-	Delucchi 1989
Intermittent desert stream, Arizona, USA	Abundance of permanent hyporheos decreased at 30 and 50 cm and increased at 1 m as water table fell	-	Clinton <i>et al.</i> 1996

**Section B. Studies providing evidence of passive refuge use**

Site description and location	Evidence	Explanation for lack of migrations	Reference
Intermittent stream, Indiana, USA	Isopods, amphipods and coleopterans present in moist interstitial spaces	Migrations not studied	Clifford 1966
2 intermittent creeks, Ontario, Canada	Chironomids, oligochaetes, amphipods, coleopterans and others recolonised surface sediments from HZ	Not studied; may have occurred	Williams 1977
Intermittent headwater stream, Ontario, Canada	Hydropsychids, rhyacophilids and nemouriids observed in moist interstices after surface drying	None suggested	Imhof and Harrison 1981
Intermittent streams, Australia	A few taxa (1 isopod, oligochaete, flatworm, mite, and leptophlebiid) occurred in the HZ of a dry stream	High streambed temperature	Boulton 1989
Intermittent wadi headwaters, Algeria	A few benthic taxa survived the dry phase at low abundance in the HZ	Compaction/baking of fine sediments	Gagneur and Chaoui-Boudghane 1991
Intermittent streams, Arizona, USA and Australia	35-69 % of benthic taxa present in HZ during dry phase	Migrations not studied	Boulton <i>et al.</i> 1992
Arid-zone intermittent stream, Australia	Benthos including mites, EPT, chironomids and simuliids found in HZ below dry streambed	-	Cooling and Boulton 1993

2 <sup>nd</sup> order Appalachian headwater streams, USA	Suggested that 2 stonefly genera more abundant in deeper HZ layers due to earlier drying	-	Griffith and Perry 1993
2 intermittent creeks, California, USA	Abundance of most temporary hyporheos decreased in the HZ during the dry phase	Water lost from HZ above 0.6 m	Del Rosario and Resh 2000
Sub-Alpine river, Italy	<i>Agabus paludosus</i> (Dytiscidae: Coleoptera) present in deep sediments during the dry phase	Migrations not studied	Fenoglio <i>et al.</i> 2006
Intermittent lowland stream, England	Abundance of benthos in BZ and HZ decreased after repeated short-term drying	Fine sediment, water loss/hypoxia	Stubbington <i>et al.</i> 2012
Normally perennial 5 <sup>th</sup> order river, SE Australia	Oligochaetes, dipterans, a hydroptilid, mites, elmids and dytiscids present in HZ after surface drying	Migrations not studied	Young <i>et al.</i> in press

### Section C. Studies providing minimal or no evidence of refuge use

Site description and location	Evidence (lack thereof)	Explanation for no refuge use	Reference
Headwater stream, coastal forest, South Carolina, USA	No active invertebrates present after flow ceased	Anoxia/dry, sandy substrate	Smock <i>et al.</i> 1994
Sycamore Creek, intermittent Sonoran desert stream, USA	Ceratopogonids abundant at 0-10 cm immediately after flow resumption	Hypoxia/small interstices	Stanley <i>et al.</i> 1994
Sycamore Creek, intermittent Sonoran desert stream, USA	Very few benthic taxa survive dry phase in HZ	HZ dried	Boulton and Stanley 1995
Regulated intermittent wadi, NW Algeria	Very few benthic invertebrates present in HZ during dry phase	Baking of fine sediments; anoxia	Belaidi <i>et al.</i> 2004
Normally perennial 5 <sup>th</sup> order river, SE Australia	Virtually no active invertebrates present in the HZ during dry phase	HZ dried to depth of 0.4 m	Young <i>et al.</i> in press

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1443 Table 3: Evidence of active and passive use of the hyporheic refuge by benthic invertebrates during reduced flows (modified from Wood *et al.*  
 1444 2010).  
 1445 See Table 1 caption for additional details.

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**Section A. Studies providing evidence of active refuge use**

Site description / location	Evidence	Explanation for lack of migrations	Reference
Lowland chalk stream, England	Decreased BZ abundance/increased HZ abundance of benthos linked to temperature, not discharge	-	Stubbington <i>et al.</i> , 2009; Wood <i>et al.</i> 2010
Two small limestone streams, England	Increase in HZ abundance and HZ proportion observed for <i>Gammarus</i> at downwelling sites	-	Stubbington <i>et al.</i> 2011; Stubbington <i>et al.</i> 2012

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**Section B. Studies providing evidence of passive refuge use**

Site description / location	Evidence	Explanation for lack of migration	Reference
Three small cobble-bottom streams, North Island, New Zealand	Benthos present in HZ; vertical distribution similar before and after 88-96 % flow reductions	BZ preferable	James <i>et al.</i> 2008
Experimental channels in a New Zealand lowland river	15 % of benthos present in HZ both before and after 25-98 % flow reductions	Stable submerged area; BZ preferable	James and Suren 2009
Two small limestone streams, England	HZ abundance stable whilst BZ abundance increased for <i>Gammarus</i> at upwelling site	Water movement/ water chemistry	Stubbington <i>et al.</i> 2011; Stubbington <i>et al.</i> 2012
Normally perennial 5 <sup>th</sup> order river, SE Australia	Many taxa present in HZ at sites with 80% bed exposure, but assemblage similar to that at sites with greater flow	BZ preferable	Young <i>et al.</i> in press

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1446 Table 4: Taxon-specific evidence of active migrations by benthic macroinvertebrate  
 1447 into the hyporheic zone. Studies noting active migrations identified using Tables 1-3;  
 1448 only taxa recorded as actively migrating by some studies are noted.

Class	Taxon	Active migrator?	References
Tricladida	Planariidae	Yes	Marmonier and Creuzé des Châtelliers 1991
Gastropoda	<i>Potamopyrgus</i>	Yes	Holomuzki and Biggs 2000
Amphipoda	<i>Gammarus</i>	Yes	Dole-Olivier and Marmonier 1992; Dole-Olivier <i>et al.</i> 1997; Wood <i>et al.</i> 2010; Stubbington <i>et al.</i> 2012
		No	Dole-Olivier <i>et al.</i> 1997 Gayraud <i>et al.</i> 2000
Ephemeroptera	Not specified	Yes	Marmonier and Creuzé des Châtelliers 1991
		No	Marchant 1995; Gayraud <i>et al.</i> 2000 (Heptageniidae)
	Leptophlebiidae	Yes	Delucchi 1989; Holomuzki and Biggs 2000
Plecoptera	Not specified	Yes	Marmonier and Creuzé des Châtelliers 1991
		No	Marchant 1995
	Chloroperlidae	Yes	Delucchi 1989; Dole-Olivier and Marmonier 1992
Trichoptera	Not specified	Yes	Marmonier and Creuzé des Châtelliers 1991
		No	Marchant 1995
	Hydropsychidae	Yes	Dole-Olivier and Marmonier 1992
	Leptoceridae	Yes	Holomuzki and Biggs 2000
	Polycentropodidae	Yes	Dole-Olivier and Marmonier 1992
	Sericostomatidae	Yes	Holomuzki and Biggs 2000
Coleoptera	Elmidae larvae	Yes	Marchant 1988; Dole-Olivier and Marmonier 1992; Marchant 1995
Diptera	Chironomidae	Yes	Marchant 1988, 1995; Dole-Olivier <i>et al.</i> 1997
		No	Gayraud <i>et al.</i> 2000

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1452 Table 5: Evidence for proposed traits of taxa identified as active migrants  
 1453 Traits proposed by Robertson and Wood (2010). Active migrants identified in Table  
 1454 4. Trait assignment requires some, not all, members of a taxon to have the trait.

		Proposed traits of active migrants							
		No attachments	Burrowing habit	Depositional rheophily	High crawling rate	Small (<9 mm) at maturity	Tegument respiration	Vermiform shape	Total traits (max. 7)
Taxa identified as active migrants	Chironomidae	✓	✓	✓	✗	✓	✓	✓	6
	Planariidae	✓	✓	✓	✓	✓	✓	✗	6
	<i>Potamopyrgus</i>	✓	✓	✓	✓	✓	✗	✗	5
	Elmidae (larvae)	✓	✓	✓	✓	✓	✗	✓	5
	<i>Gammarus</i>	✓	✓	✓	✗	✗	✗	✗	3
	Chloroperlidae	✓	✓	✗	✓	✗	✗	✗	3
	Leuctridae	✓	✓	✓	✓	✗	✗	✗	3
	Leptoceridae	✓	✗	✓	✓	✗	✗	✗	3
	Sericostomatidae	✓	✓	✓	✓	✗	✗	✗	3
	Hydropsychidae	✓	✗	✗	✓	✗	✗	✗	2
	Leptophlebiidae	✓	✓	✓	✗	✗	✗	✗	2
	Polycentropodidae	✓	✗	✗	✓	✗	✗	✗	2
Total taxa (max. 12)		12	9	9	8	4	2	2	

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1457 **Fig. 1.** Conceptualisation of the hyporheic zone as one of a suite of invertebrate  
1458 refuges available during (a) high flows, and (b) streambed drying. *Gammarus pulex*  
1459 (Crustacea: Amphipoda) is depicted (not to scale), as a representative benthic  
1460 invertebrate.

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1462 **Fig. 2.** Interactions between sediment characteristics, hydrologic exchange (HE), flow  
1463 velocity and dissolved oxygen concentrations in the hyporheic zone. Italics indicate  
1464 high refuge potential.

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1466 **Fig. 3.** Behaviour inferred from changes in absolute and relative abundance of benthic  
1467 and hyporheic invertebrates. HZ = hyporheic zone; BZ = benthic zone. Examples:  
1468 <sup>1</sup>Stubbington *et al.* 2011, 2012; <sup>2</sup>Pers. obs., River Glen (Lincolnshire, UK) during  
1469 habitat contraction; <sup>3</sup>Stubbington *et al.* 2012; <sup>4</sup>James *et al.* 2008; <sup>5</sup>Williams and Hynes  
1470 1974, Marchant 1988, Wood *et al.* 2010; <sup>6</sup>Giberson and Hall 1988, Palmer *et al.*  
1471 1992, James and Suren 2009; <sup>7, 8, 9</sup>No known examples.

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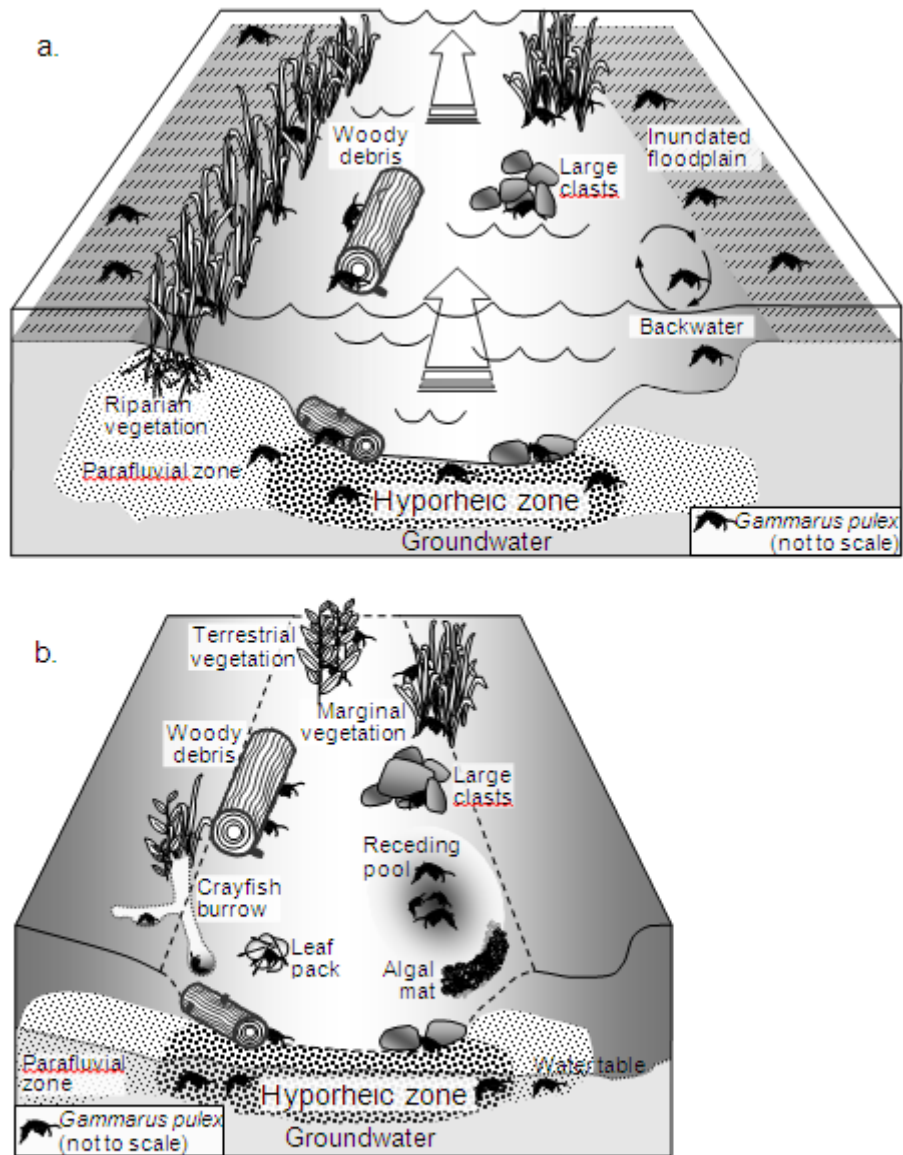
1473 **Fig. 4.** Flow chart for predicting use of the hyporheic zone (HZ) as a refuge. C1-3  
1474 indicate three criteria that must be met for active refuge use to occur.

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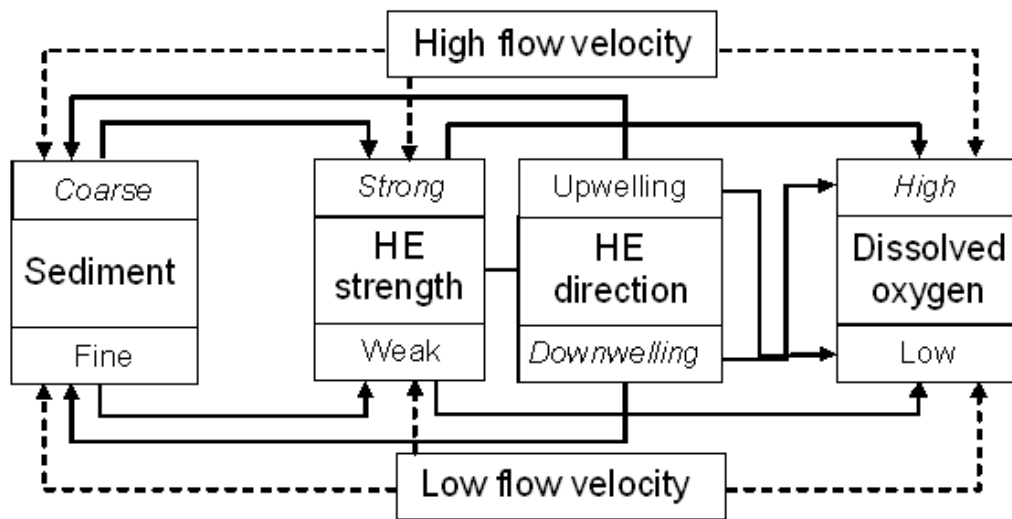
1478



**Fig. 1.** Conceptualisation of the hyporheic zone as one of a suite of invertebrate refuges available during (a) high flows, and (b) streambed drying. *Gammarus pulex* (Crustacea: Amphipoda) is depicted (not to scale), as a representative benthic invertebrate.

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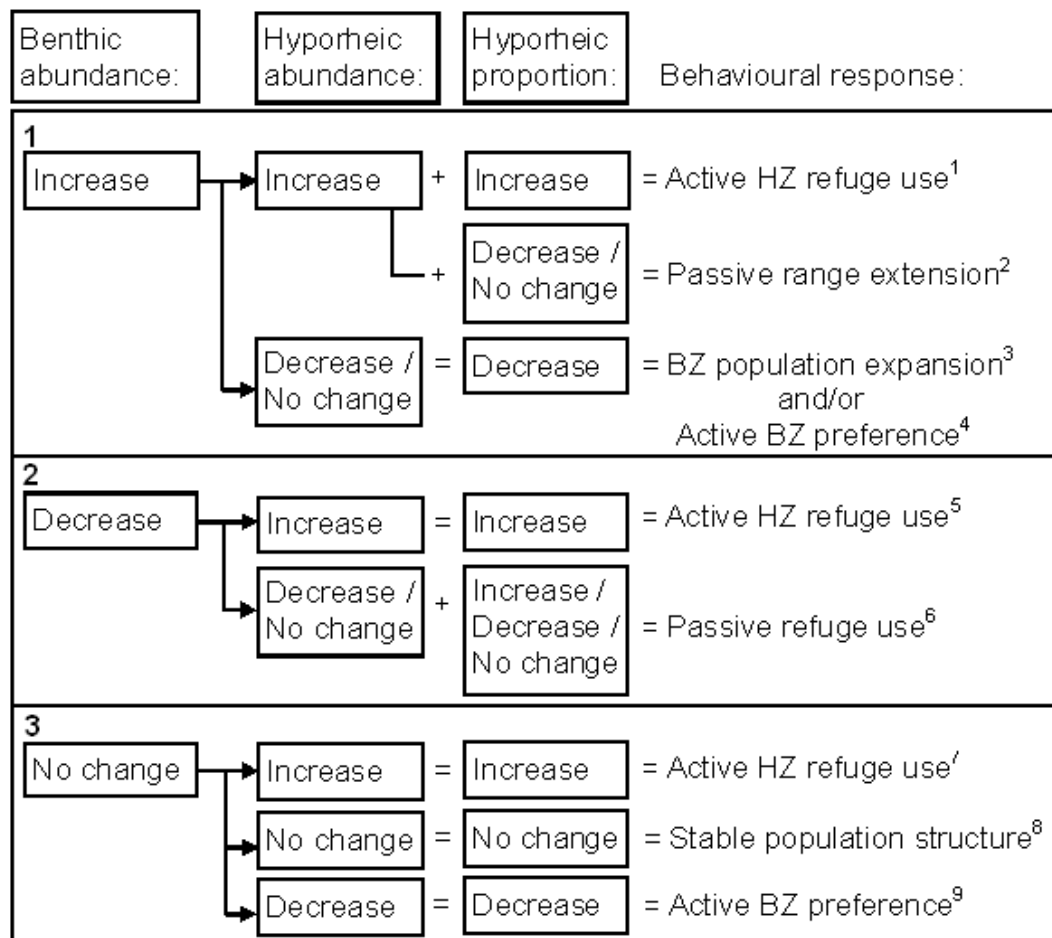
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**Fig. 2.** Interactions between sediment characteristics, hydrologic exchange (HE), flow velocity and dissolved oxygen concentrations in the hyporheic zone. Italics indicate high refuge potential.

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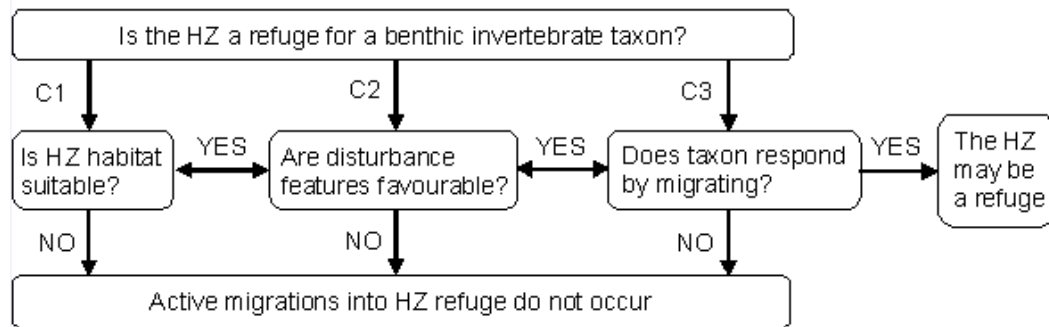
1482



**Fig. 3.** Behaviour inferred from changes in absolute and relative abundance of benthic and hyporheic invertebrates. HZ = hyporheic zone; BZ = benthic zone. Examples: <sup>1</sup>Stubbington *et al.* 2011, 2012; <sup>2</sup>Pers. obs., River Glen (Lincolnshire, UK) during habitat contraction; <sup>3</sup>Stubbington *et al.* 2012; <sup>4</sup>James *et al.* 2008; <sup>5</sup>Williams and Hynes 1974, Marchant 1988, Wood *et al.* 2010; <sup>6</sup>Giberson and Hall 1988, Palmer *et al.* 1992, James and Suren 2009; <sup>7, 8, 9</sup>No known examples.

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1484



**Fig. 4.** Flow chart for predicting use of the hyporheic zone (HZ) as a refuge. C1-3 indicate three criteria that must be met for active refuge use to occur.

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