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RECENT PERSPECTIVES ON TEMPORARY RIVER ECOLOGY

Spatial variability in the hyporheic zone refugium of temporary streams

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Abstract A key ecological role hypothesized for the hyporheic zone is as a refugium that promotes survival of benthic invertebrates during adverse conditions in the surface stream. Many studies have investigated use of the hyporheic refugium during hydrological extremes (spates and streambed drying), and recent research has linked an increase in the abundance of benthic invertebrates within hyporheic sediments to increasing biotic interactions during flow recession in a temporary stream. This study examined spatial variability in the refugial capacity of the hyporheic zone in two groundwater-dominated streams in which flow permanence varied over small areas. Two non-insect taxa, *Gammarus pulex* and *Polycelis* spp. were common to both streams and were investigated in detail. Hydrological conditions in both streams comprised a four-month period of flow recession and low flows, accompanied by reductions in water depth and wetted width. Consequent declines in submerged benthic habitat availability were associated with increases in population densities of mobile benthic taxa, in particular *G. pulex*. The reduction in the spatial extent of the hyporheic zone was minimal, and this habitat was therefore a potential refugium from increasing biotic interactions in the benthic sediments. Concurrent increases in the hyporheic abundance and hyporheic proportion of a taxon's total (benthic + hyporheic) population were considered as evidence of active refugium use. Such evidence was species-specific and site-specific, with refugium use being observed only for *G. pulex* and at sites dominated by downwelling water. A conceptual model of spatial variability in the refugial capacity of the hyporheic zone during habitat contraction is presented, which highlights the potential importance of the direction of hydrologic exchange.

Keywords Hyporheic refuge hypothesis · Low flows · Habitat contraction · Hyporheos · Benthos · Gammarus

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Introduction

Refugia are places where organisms have an increased probability of surviving a disturbance event, due to relatively low disturbance impacts (Lancaster and Belyea 1997). In lotic ecosystems, the hyporheic zone (HZ) has been demonstrated to act as a refugium that promotes persistence of invertebrates during adverse conditions in the surface (benthic) sediments (Orghidan 1959, 2010; Williams and Hynes 1974; Robertson and Wood 2010). Research examining the HZ as a refugium has focussed on the extremes of the hydrological continuum, namely spates and streambed drying (Boulton and Stanley 1995; Dole-Olivier et al. 1997), and this refuge is therefore of particular relevance for the persistence of temporary stream communities. Several studies have inferred active invertebrate migrations into the HZ as the water table falls below the sediment surface (Cooling and Boulton 1993; Clinton et al. 1996) whilst others have noted passive refugium use following streambed drying (Del Rosario and Resh 2000;

Fenoglio et al. 2006). However, evidence for the hyporheic refuge hypothesis (Williams and Hynes 1974) during drying is equivocal, with many studies finding that few benthic taxa actively exploit the HZ (Boulton 1989; Boulton and Stanley 1995; Belaidi et al. 2004).

These contrasting reports suggest that the HZ must fulfil certain criteria in order to function as a refuge, with some studies attributing a lack of refugium use to a single factor such as anoxia (Smock et al. 1994) or the loss of interstitial free water (Boulton and Stanley 1995) following surface drying. The importance of hydrologic exchange has also been highlighted, with downwelling water facilitating migrations into deeper sediments (Dole-Olivier et al. 1997). Sediment composition is also an influential determinant of hyporheic community composition, with a high proportion of fine sediment (variously defined as <150 μm (Richards and Bacon 1994), <1 mm (Olsen and Townsend 2005) and <2 mm (Weigelhofer and Waringer 2003)) reducing inhabitable space (Belaidi et al. 2004; Olsen and Townsend 2005). Considering the heterogeneity of instream habitats (Winemiller et al. 2010), refugium use is likely to vary over small areas depending on the character of the hyporheic sediments (Lancaster and Belyea 1997).

Little research has considered the HZ refugium during flow recession and low flows, despite their inevitable occurrence prior to the dry phase in temporary streams. As discharge decreases, submerged habitats contract and topographic high points become exposed (Cowx et al. 1984; Dewson et al. 2003). Reduced submerged habitat availability typically concentrates mobile invertebrates into smaller areas, with many studies noting increasing benthic population densities as flow declines (Fritz and Dodds 2004; James et al. 2008). Many biotic interactions are density dependent and increasing population densities may intensify competition, predation and cannibalism (Savage 1996; Covich et al. 2003; Holomuzki et al. 2010).

The HZ may act as a refugium from biotic interactions, due to lower population densities when compared with the benthic sediments (Williams and Hynes 1974; Davy-Bowker et al. 2006). The HZ is recognised as a nursery which reduces predation on vulnerable invertebrates such as early instar insect larvae (Puig et al. 1990). Experimental work has also demonstrated that *Gammarus pulex* (Amphipoda: Crustacea) may migrate into smaller interstices in response to an increase in intraspecific predation (McGrath et al. 2007). In addition, one field study has linked submerged habitat contraction and an increase in benthic population densities to migrations into the HZ (Stubbington et al. 2011). In contrast, other studies have recorded no increase in the hyporheic abundance of benthic taxa in response to flow reduction (James et al. 2008; Stubbington et al. 2009a; Wood et al. 2010). Such inconsistent reports emphasize the potential importance of spatially variable habitat parameters in determining benthic invertebrate use of the HZ. In the current study, spatial variation in the use of the HZ refuge during flow recession and low flows was examined in two temporary streams in relation to three hyporheic habitat parameters: the direction of hydrologic exchange, oxygen availability and sediment composition.

Methods

Study location

Two temperate-zone groundwater-dominated streams were investigated (Fig. 1). The River Lathkill (Derbyshire, UK; 53°11.2′N, 1°43.1′W) is a 2nd order stream which flows for 8.5 km through an incised valley, the sides of which are vegetated by deciduous woodland. The River East Glen (Lincolnshire, UK; 52°45.9′N, −0°25.8′E) is a 3rd order stream flowing for 37 km through a predominantly agricultural catchment. The Lathkill receives mean monthly rainfall of between 58 mm in August and 136 mm in December (1991–2000 mean; British Atmospheric Data Centre (BADC) 2009), has a mean annual temperature of 8°C, with temperatures peaking in July (Wood et al. 2005). The Glen catchment is drier and seasonal differences in

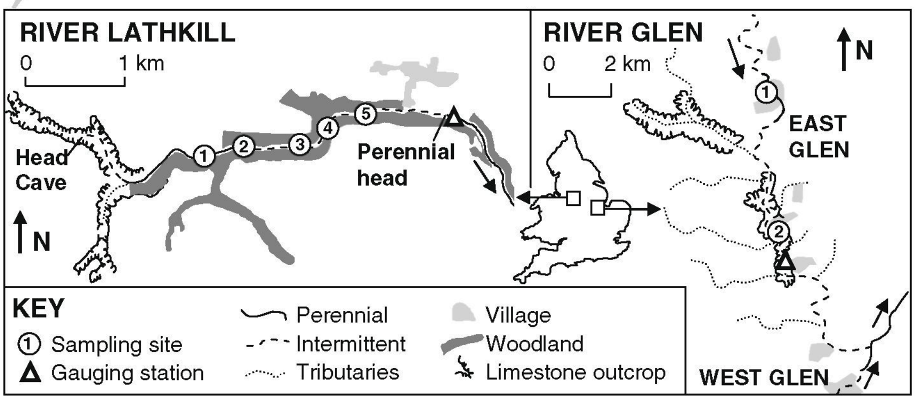

Fig. 1 Location maps and flow regimes of the River Lathkill and River Glen

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rainfall are less pronounced, with mean values ranging from 36 mm in February to 61 mm in October (1980–2008 mean; British Atmospheric Data Centre (BADC) 2009). The region has a mean annual temperature of 10.5°C, with the highest temperatures occurring in July and August (Met Office 2009). Reaches of both rivers typically dry during summer, partly due to natural features of the underlying karst aquifers (Maddock et al. 1995; Stubbington et al. 2009b). In the Lathkill, this loss of flow is exacerbated in some reaches by underlying disused mine drainage soughs, whilst losses on the Glen are increased by abstractions for public water supply. Upwelling groundwater sustains perennial flow in other reaches of both rivers.

Seven sites (designated Lathkill 1–5 and Glen 1–2) were selected on the two rivers to characterise spatial variability in the flow regime (Fig. 1). On the Lathkill, two sites have perennial flow (Lathkill 1–2) and three sites typically dry during the summer (Lathkill 3–5). On the Glen, one perennial site (Glen 1) and one intermittent site (Glen 1) were investigated. In both rivers, the substrate consists predominantly of cobble and pebble gravels, although clast sizes range from silt to boulder. During the study, phytobenthos was dominated by bryophytes in the Lathkill, whilst filamentous algae were abundant in the Glen; emergent reeds were also present in marginal areas of both rivers.

Hydrological conditions

During the study period (May–September 2008), flow recession in the Lathkill proceeded uninterrupted from May until August (Fig. 2a), although above-average precipitation resulted in surface flow remaining connected throughout the study area. Discharge then increased considerably in late August following heavy rainfall. On the Glen, a series of rain-fed low-magnitude flow increases occurred between May and June sampling. Discharge then declined, culminating in streambed drying at Glen 2 in late July and early September, with surface flow returning briefly between drying events (Fig. 2b).

Field sampling

The seven sites were sampled at monthly intervals over a 5 month period from May to September 2008, with the exception of Lathkill 5, which was inaccessible in the first month of the study. However, only flow recession and low flows are of relevance to the current investigation, and, therefore, data collected from the Lathkill between May and August and from the Glen between June and September are presented. These months are referred to as months 1–4 in combined analyses of both rivers.

Four sampling points were selected at each site to reflect the prevailing instream conditions. At each sampling point, three open-ended polyvinylchloride (PVC) pipes (19 mm internal diameter) were driven into the substrate using a stainless steel T-bar (Boulton and Stanley 1995; Wood et al. 2010). These pipes functioned as permanent hyporheic invertebrate sampling wells for the duration of the study. Pipes were inserted to depths of 10, 20 and 30 cm, respectively, and were positioned ≥0.5 m apart to minimise any influence of sampling in one well on the sediments sampled by adjacent wells. Each well was sealed between sampling occasions to prevent sediment deposition and colonisation by benthic invertebrates. Each month, 6 L of water were extracted from the base of each sampling well using a hand-operated bilge pump and passed through a 125 μm sieve to retain macroinvertebrates (e.g. Boulton and Stanley 1995).

Due to the inaccessibility of hyporheic habitat, all invertebrate sampling techniques have significant limitations (Palmer 1993). Manual pump sampling, for example, favours the collection of smaller, less tenacious invertebrates (Fraser and Williams 1997) and sampling efficiency varies with sediment hydraulic conductivity (Scarsbrook and Halliday 2002). However, pump sampling causes minimal disturbance to the sediments and therefore allows repeated collection of quantitative samples from the same location during a temporal sequence, which was essential in the current study (see Stubbington et al. 2009a). Other quantitative methods (e.g. coring, colonisation pots) do not

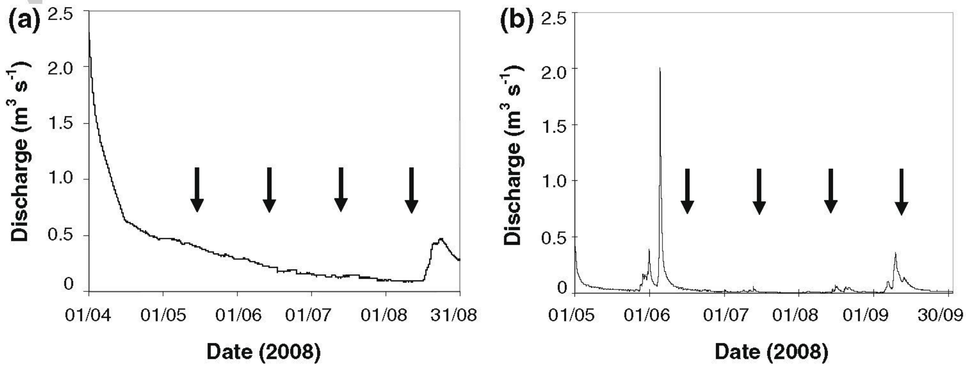

Fig. 2 Hydrographs of: **a** mean hourly discharge on the River Lathkill, April–August 2008; **b** mean 15-min discharge on the River Glen, May–September 2008. *Arrows* indicate sampling dates. Location of gauging stations shown in Fig. 1

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fulfil this criterion and were therefore unsuitable. In addition, several previous studies have demonstrated the ability of pump sampling to characterise changes in hyporheic community composition in response to hydrological variability and flow permanence (e.g. Boulton and Stanley 1995; Hancock 2006; Datry et al. 2007).

Invertebrates were collected from the benthic sediments above each set of hyporheic sampling wells using a standard Surber sampler (0.1 m^2, 1 mm mesh net), by manually disturbing the substrate within the frame to a depth of ~5 cm for 30 s. The current study analysed only macroinvertebrate fauna (body size >1 mm), and therefore the different mesh sizes used to sample benthic and hyporheic sediments is not of relevance.

To assess the effects of discharge variability on habitat availability, water depth was measured at each sampling point. Wetted width was then determined by applying depth measurements to cross-sectional profiles generated using standard tacheometric survey data. To assess the suitability of the HZ as an invertebrate refugium, hyporheic dissolved oxygen concentrations (DO, mg L^{-1}), the direction of hydrologic exchange and sediment composition were examined. DO was measured in situ using standard instrumentation (Hanna Instruments, Leighton Buzzard, UK). The direction of hydrologic exchange was estimated using mini-piezometers, consisting of a pair of open-ended PVC pipes (19 mm internal diameter), one perforated with 2 mm holes and the other intact. These pipes were positioned ~20 cm apart and were inserted to a depth of 30 cm, as described for hyporheic sampling wells. The tops of the mini-piezometers were left protruding several cm above the expected highest water level. This equipment was clearly visible, resulting in unacceptable impacts on visual amenity at Lathkill 1; this site was therefore not instrumented. Each month, an electronic dipstick was inserted into each pair of mini-piezometers and the two water levels compared to provide an indication of the direction of hydrologic exchange. At some sampling points, water did not refill the intact mini-piezometer; this suggested strongly downwelling water, but was also potentially due to sediment clogging (Boulton 2007). Measurements were therefore supplemented by other information, including on-site observations, water temperature and water chemistry data, and the typical flow permanence regime. After completion of the sampling programme, sediments were collected using a McNeil sampler to characterise bulk sediment composition to a depth of 25 cm (following Bunte and Abt 2001).

Laboratory procedures

Invertebrates were identified to the lowest taxonomic resolution possible, in many cases species level, but groups including the Oligochaeta were left at a higher taxonomic level. Sediment samples were oven dried at 105°C until a constant weight was recorded, gently disaggregated, then dry-sieved through a sieve nest (8, 4, 2, and 1 mm, 500, 250, 125 and 63 µm) and each fraction weighed to determine the grain size distribution. To reduce the influence of large particles on the calculated percentage of fine sediment, clasts with an *a*-axis >75 mm were excluded (following Rice 1995).

Data analysis

Changes in environmental variables (surface water depth, wetted width, DO) were analysed using repeated measures (RM) ANOVA. Two-way RM ANOVA with site as a between-subjects factor was used to determine the significance of spatial differences and the interaction with site. One-way RM ANOVA was used to examine temporal variability at all sites combined and, where a significant interaction with site had been identified, at individual sites. For all RM ANOVA tests, where the assumption of sphericity was violated, Greenhouse-Geisser tests were used to determine significance. Benthic and hyporheic data were analysed separately, whilst preliminary RM ANOVA tests indicated comparable patterns of temporal change at the three hyporheic depths, and all were therefore pooled.

Water depth data were applied to cross-sectional channel profiles to determine the area of submerged habitat available each month. At most sites, a single cross-section was considered representative of conditions at all sampling points, whilst depth data were applied to two Lathkill 4 cross-sections ((1) and (2) in Table 1) due to longitudinal variation in bed morphology.

The abundance of common benthic taxa (>1% of all invertebrates present in Surber samples) was determined separately for benthic and hyporheic habitats. Preliminary analysis showed comparable patterns of variability in community composition at the three hyporheic depths, and

Table 1 Temporal change in extent of submerged benthic sediments as a percentage of the maximum recorded

Month[a]	Submerged % of benthic sediments							
	River Lathkill sites						River Glen sites	
	1	2	3	4(1)[b]	4(2)[b]	5	1	2
1	100	100	100	100	100	100	100	90
2	40	42	35	48	97	100	81	23
3	58	42	29	100	100	94	81	100
4	34	23	17	31	84	20	53	90

[a] Month 1–4 = May–August 2008 on the Lathkill and June–September 2008 on the Glen

[b] Bracketed numbers refer to sampling areas

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all were therefore pooled. Insect taxa were excluded from analyses due to the confounding influence of seasonal adult emergence. Taxa identified to group level and likely to include multiple representatives (e.g. the Oligochaeta) were also excluded, to avoid inaccurate inference of ecological patterns (Datry et al. 2010). To investigate use of the HZ by selected individual benthic taxa, the number of individuals present in the HZ was divided by the total (benthic + hyporheic) number of individuals recorded, to determine the *hyporheic proportion* of the taxon's population. Proportional data facilitates comparison of populations sampled using different methods. Abundance data were square-root transformed and proportions arcsine square-root transformed prior to subsequent analysis. Transformed metrics were used as dependent variables in RM ANOVA tests to examine spatial and temporal variability in invertebrate distribution, as outlined for environmental data.

Temporal change in the submerged benthic habitat area was calculated between months 1–2, 2–3 and 3–4, with area in the latter month being described as a % of that recorded in the former. Scatter plots were then used to investigate relationships between monthly variation in habitat availability and concurrent % changes in invertebrate abundance. Benthic and hyporheic abundances were considered both separately and simultaneously. Pearson's correlation coefficients were then calculated to examine the strength and significance of relationships.

Results

Availability of submerged benthic habitat

Considering all sites, reductions in both water depth ($F_{3,63} = 59.014$, $p < 0.001$) and wetted width ($F_{1.339,6.694} = 45.416$, $p < 0.001$) were significant between months 1 and 4. The interaction with site was also significant for both depth ($F_{18,63} = 9.021, p < 0.001$) and width ($F_{8.032,6.694} = 12.671$, $p = 0.002$), and the extent and timing of reductions in submerged habitat availability were site-specific (Table 1). Habitat availability was highest in month 1 and lowest in month 4 at all sites except Glen 2, where the submerged area was particularly low in month 2 (Table 1).

Invertebrate abundance in the benthic sediments

The Lathkill community was dominated by *Gammarus pulex* (40.8% of total invertebrate abundance (TIA)); *Polycelis felina* (Turbellaria: Planariidae; 6.8% TIA) and the Oligochaeta (4.9% TIA) were also common. In the Glen, oligochaetes were the dominant non-insect taxon (17.3% TIA); other common taxa (>1% TIA) included Hydracarina, *G. pulex*, *Asellus aquaticus* and *Polycelis tenuis*. Suitable taxa which were sufficiently abundant in both rivers to justify detailed analysis therefore comprised *G. pulex* and *Polycelis* spp.

Considering all sites, mean *G. pulex* abundance increased significantly from month 1 (54 ± 9 individuals 0.1 m^{-2}) to month 4 (166 ± 36 individuals 0.1 m^{-2}; Fig. 3a; Table 2). Abundance also varied spatially, being highest at Lathkill 1 and lowest at Glen 1 (Fig. 3a; Table 2). The interaction with site was also significant (Table 2) and site-specific patterns of temporal change were significant at Lathkill 1, Lathkill 4 and Glen 2 (Fig. 3a). Mean *Polycelis* spp. abundance was low in month 1 (4.7 ± 1.3 individuals 0.1 m^{-2}) and significantly higher in later months (≥19.7 ± 8.3 individuals 0.1 m^{-2}; Fig. 4a; Table 2). Spatially, the taxon was particularly abundant at Lathkill 1 and virtually absent from Lathkill 3–5 and Glen 1 (Table 2). The interaction with site was significant (Table 2) and abundance was sufficiently high at Lathkill 1 and 2 and Glen 2 to justify further analysis. The overall pattern of temporal change was observed at Lathkill 1 and 2, whilst at Glen 2, abundance peaked in month 2 and was very low in later months (Fig. 4a).

Spatial variability in hyporheic habitat

Whilst the reduction in submerged habitat availability was widespread in the benthic sediments, on-site observations indicated that the extent of the submerged HZ was largely unaltered, free water being present at a depth of 10 cm in all cases. However, DO concentrations, the direction of hydrologic exchange, and sediment composition may have affected the HZ's ability to function as a refugium.

RM ANOVA of hyporheic DO concentrations includes data collected between months 2 and 4 at Lathkill 1–5 and Glen 1, due to missing values in the month 1 and Glen 2 datasets. However, the available data indicate that DO concentrations were highest in month 1; a subsequent gradual reduction between months 2 and 4 was significant (Table 3). Considering all months, concentrations varied between sites ($F_{5,66} = 8.666$, $p < 0.001$), being highest at Lathkill 2 and low at Lathkill 1 and Glen 1; individual readings indicated lower mean values at Glen 2 (Table 3). The interaction between DO and site was significant ($F_{9.953,131.381} = 22.655$, $p < 0.001$) and patterns of temporal change were site-specific (Table 3).

The direction of hydrologic exchange at Lathkill 1 was strongly upwelling: rheocrene springs are present at the site margins, upwelling water was directly observed in sampling wells, and both surface and hyporheic water had distinctive qualities indicative of groundwater (high conductivity and low temperature). Upwelling water was also consistently recorded in mini-piezometers at Glen 1. In

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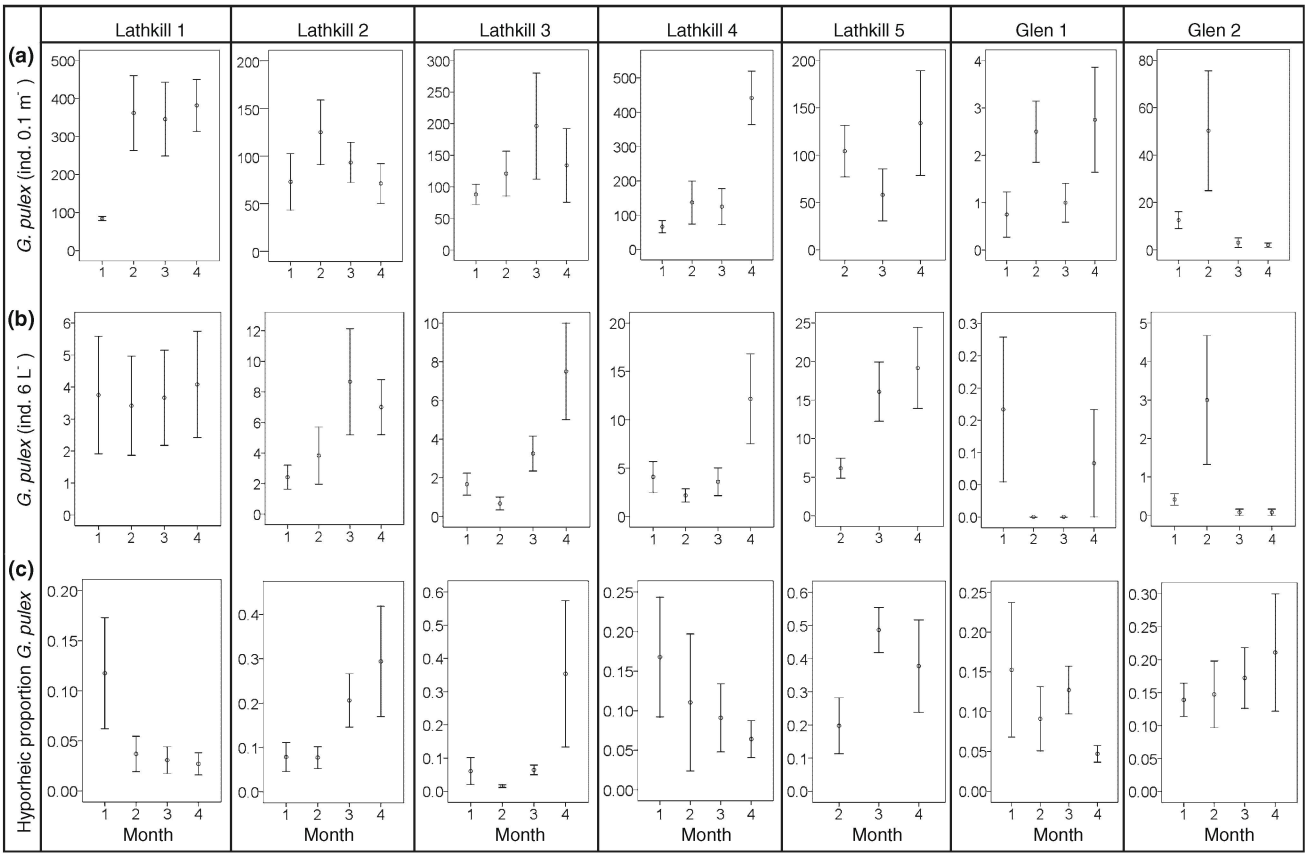

Fig. 3 Mean ± 1 SE *Gammarus pulex* at sites 1–5 on the River Lathkill and sites 1–2 on the River Glen: **a** benthic abundance (individuals 0.1 m^{-2}); **b** hyporheic abundance (individuals 6 L^{-1}); and **c** hyporheic proportion of the total (benthic + hyporheic) population. Months 1–4 are May–August 2008 on the Lathkill and June–September 2008 on the Glen

Table 2 Temporal and spatial change in invertebrate occurrence in the benthic and hyporheic zones of the River Lathkill and River Glen

Taxon	Temporal change[a]		Spatial change[a]		Interaction[a]	
	F ratio	*p*	*F* ratio	*p*	*F* ratio	*p*
Benthic abundance						
Gammarus pulex	3.6	0.025	50.9	<0.001	2.9	0.008
Polycelis felina	3.0	0.073	10.9	<0.001	7.5	<0.001
Hyporheic abundance						
G. pulex	3.9	0.012	11.4	<0.001	2.6	0.001
P. felina	4.2	0.019	15.3	<0.001	3.5	<0.001
Hyporheic proportion						
G. pulex	3.4	0.048	5.9	0.001	1.6	0.102
P. felina	1.5	0.212	1.2	0.355	5.1	0.004

[a] Significance determined using RM ANOVA; see text for further details

contrast, mini-piezometer data, physicochemical data and an intermittent flow regime indicated the prevalence of downwelling water at Lathkill 3–5 and Glen 2. At Lathkill 2, evidence of both upwelling water (perennial flow and obligate groundwater taxa in the HZ) and downwelling water (mini-piezometer readings and water physicochemistry) was recorded.

For the purposes of summarising refugial potential (Table 4), fine sediment was defined following Olsen and Townsend (2005) as <1 mm; preliminary analyses had also indicated that this measure was most strongly correlated with community metrics. The percentage of fine sediment was lowest (<16%) at Lathkill 1–3 and exceeded 25% at all other sites (Table 4). The highest

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Fig. 4 Mean ± 1 SE *Polycelis felina* at sites 1, 2, 4 and 5 on the River Lathkill: **a** benthic abundance (individuals 0.1 m^{-2}); **b** hyporheic abundance (individuals 6 L^{-1}); and **c** hyporheic proportion of the total (benthic + hyporheic) population. Months 1–4 are May–August 2008

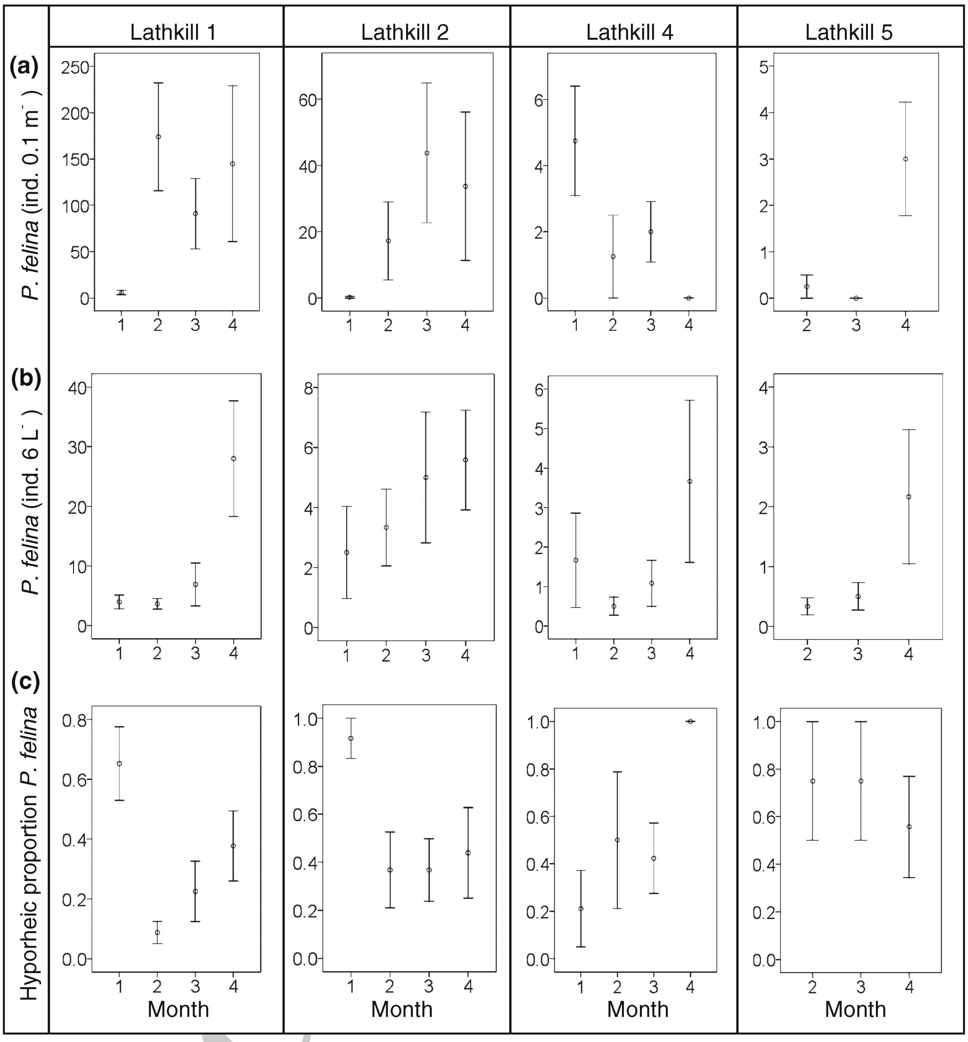

Table 3 Temporal change in hyporheic dissolved oxygen concentrations at sites on the River Lathkill and River Glen

		Mean ± 1 SE dissolved oxygen concentration (mg L^{-1})				Temporal change[a]	
		Month 1[b]	Month 2[b]	Month 3[b]	Month 4[b]	*F* ratio	*p*
Lathkill sites	1	7.3 ± 0.4	6.1 ± 0.1	4.8 ± 0.2	4.1 ± 0.2	18.1	<0.001
	2	N/A	5.5 ± 0.4	10.9 ± 0.5	5.1 ± 0.4	118.7	<0.001
	3	9.5 ± 0.4	7.7 ± 0.5	5.0 ± 0.3	5.5 ± 0.4	29.1	<0.001
	4	N/A	7.6 ± 0.4	6.7 ± 0.7	7.4 ± 0.5	2.6	0.099
	5	N/A	6.8 ± 0.3	6.8 ± 0.3	4.0 ± 0.7	12.0	0.002
Glen sites	1	6.6 ± 0.5	5.6 ± 0.6	2.6 ± 0.6	4.8 ± 0.8	17.3	<0.001
	2	N/A	2.9 ± 0.6	2.0 ± 0.6	N/A	2.6	0.132
All sites		7.3 ± 0.3	6.0 ± 0.2	5.6 ± 0.4	5.1 ± 0.2	9.9	<0.001

N/A data not available

[a] Significance determined using one-way RM ANOVA

[b] Month 1–4 = May–August 2008 on the Lathkill and June–September 2008 on the Glen; $n = 12$, except at Lathkill 3 in month 1 and at Lathkill 5 in month 2, where $n = 3$

percentage was recorded at Glen 1, where on-site observations also indicated the presence of clay layers in the substrate stratigraphy (Table 4). In addition, quantities of fines may have been underestimated at Glen 1 due to aggregation of silt and clay particles during oven drying.

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Table 4 Spatial variability in environmental determinants of the hyporheic zone's refugial potential

River	Site	Hydrologic exchange	DO	Fine sediment[a]
Lathkill	1	Strongly upwelling	4.1 ± 0.2	11.9 ± 1.8
	2	Up- and downwelling	5.1 ± 0.4	15.7 ± 4.3
	3	Downwelling	5.5 ± 0.4	13.8 ± 4.0
	4	Downwelling	7.4 ± 0.5	25.1 ± 2.4
	5	Downwelling	4.0 ± 0.7	28.4 ± 2.2
Glen	1	Upwelling	4.8 ± 0.8	33.1 ± 8.5[b]
	2	Downwelling	2.8 ± 0.6	27.0 ± 2.0

DO hyporheic dissolved oxygen (mg L^{-1}; mean ± 1 SE in month of lowest habitat availability; $n = 12$)

[a] Fine sediment (mean ± 1 SE proportion of sediments <1 mm)

[b] Presence of clay layers; $n = 2$–4

Benthic invertebrates in the hyporheic zone

The two non-insect taxa investigated in the benthic sediments (*G. pulex* and *Polycelis* spp.) were also common in the HZ, and the hyporheic abundance and hyporheic proportion of the population was therefore calculated for both taxa. Spatially, *G. pulex* was most abundant in the HZ at Lathkill 5, whilst abundance was particularly low at both Glen sites (Fig. 3b; Table 2). The hyporheic proportion was also highest at Lathkill 5, and was lowest at Lathkill 1 (Fig. 3c; Table 2). Considering all sites, the hyporheic abundance of *G. pulex* more than trebled between months 1 and 4 (Fig. 3b; Table 2), this increase being accompanied by a rise in the hyporheic proportion of the population (Fig. 3c; Table 2). The interaction with site was significant for hyporheic abundance but not for the hyporheic proportion (Table 2), although spatially variable patterns were apparent in both metrics (Fig. 3b, c).

Polycelis spp. were particularly abundant in the HZ at Lathkill 1, whilst few individuals occurred at Lathkill 3 and Glen 1–2 (Fig. 4b; Table 2); the latter three sites were therefore excluded from further analysis. The hyporheic proportion of the population was comparable at the remaining four sites (Lathkill 1, 2, 4 and 5; Fig. 4c). The hyporheic abundance of *Polycelis* spp. at Lathkill 1, 2, 4 and 5 was lowest in months 1 and 2, increased slightly in month 3 then peaked in month 4 (Fig. 4b; Table 2). However, the hyporheic proportion of the *Polycelis* population remained stable in all months at these sites (Fig. 4c; Table 2). The interaction with site was significant for both abundance and proportion (Fig. 4b, c; Table 2).

Relationships between invertebrate abundance and habitat availability

Negative correlations were recorded between the % change in submerged benthic habitat and the % change in the abundance of both *G. pulex* (Pearson's correlation coefficient = −0.380, $p = 0.016$) and *Polycelis* spp. (Pearson's correlation coefficient = −0.343, $p = 0.074$; Fig. 5). Invertebrate abundance in both the benthic and hyporheic zones contributed to this overall pattern, but the relationship was most pronounced in the benthic sediments (Fig. 5).

Discussion

Flow recession and low flows in the River Lathkill and River Glen provided an opportunity to examine benthic invertebrate use of the hyporheic refugium during conditions preceding the dry phase in temporary streams. Considering multiple sites across two rivers facilitated

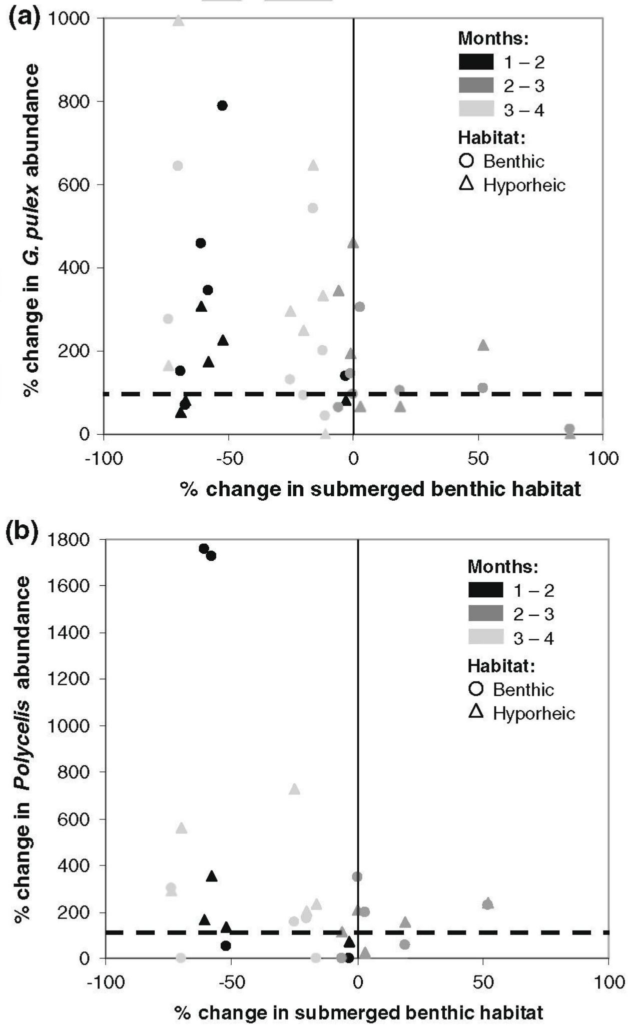

Fig. 5 Percentage change in invertebrate abundance in the benthic and hyporheic zones in relation to monthly changes in the availability of submerged benthic habitat: **a** *Gammarus pulex*; **b** *Polycelis* spp. *Dashed lines* indicate 100% of abundance recorded in the previous month i.e. no change

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examination of spatial variability in the general patterns of refugium use reported by Stubbington et al. (2011).

Invertebrate abundance in the benthic sediments

Differences in bed morphology resulted in site-specific extent and timing of habitat contraction (Table 1). Reductions in benthic habitat availability were associated with increases in the abundance (i.e. population densities) of benthic invertebrates (Fig. 5), as noted by previous studies (Fritz and Dodds 2004; James et al. 2008). In both rivers, taxa that increased in abundance included dominant, competitive species with the potential to increase biotic interactions. In particular, *G. pulex* is able to outcompete other taxa for resources (Hynes 1954; Graça et al. 1993) and is a generalist feeder with predatory and cannibalistic components in its diet (Dick 1995; Kelly et al. 2002). Peak *G. pulex* benthic densities were high (2,200–6,400 m^{-2} at all Lathkill sites; cf. Mortensen 1982; Crane 1994), representing conditions of considerable biotic risk for vulnerable individuals. *Polycelis* spp. are also predatory and consume taxa including *Gammarus* (Reynoldson 1981). *P. felina* reached particularly high abundance at Lathkill 1 (>3,100 m^{-2}), adding to the proposed increase in biotic interactions.

Distinguishing between active and passive refugium use

Previous studies have been inconsistent in their definition of 'refugium use'. Some studies have reported an increase in the numerical abundance of a benthic taxon as evidence of active migrations into deeper sediments (e.g. Williams and Hynes 1974; Clinton et al. 1996); however, this may reflect only passive dispersal of an expanding benthic population. Other research has considered an increase in the hyporheic proportion of a taxon's total (benthic + hyporheic) population as evidence of refugium use (e.g. Griffith and Perry 1993; Fenoglio et al. 2006). However, an increase in the hyporheic proportion may be concurrent with a reduction in hyporheic abundance, so long as the latter decline is of a lesser magnitude than occurs in the benthic sediments; again, such refugium use is only passive. Therefore, the most compelling evidence of *active* refugium use (i.e. shelter-seeking behaviour) is provided by concurrent increases in a taxon's hyporheic abundance and the hyporheic proportion of that taxon's total population (Wood et al. 2010).

Spatial variability in use of the hyporheic refugium

Habitat contraction did not affect the spatial extent of the HZ, which was therefore a potential refugium from increasing biotic interactions in the benthic sediments. Evidence of refugium use, as defined above, was recorded for *G. pulex* at Lathkill 2, 3 and 5. Refugial potential at these sites varied, being reduced by a high proportion of fine sediment at Lathkill 2 and 5, and further reduced by low DO concentrations at Lathkill 5 (Table 4). However, *G. pulex* can tolerate oxygen concentrations below the mean values recorded (Maltby 1995), and is able to burrow into fine sediments (Ward 1986). In addition, downwelling water dominated hydrologic exchange at these three sites, which may have promoted refugium use: firstly, the direction of water movement potentially facilitated both passive and active downwards migrations, and secondly, the influence of surface water on water chemistry increased suitability of the hydrological environment for benthic taxa (cf. Datry et al. 2007). Evidence of active refugium use was not, however, observed at two other sites dominated by downwelling water: Lathkill 4 and Glen 2. At Lathkill 4, this was due to an increase in the hyporheic abundance of *G. pulex* coinciding with a more pronounced increase in benthic abundance (Fig. 3); a concurrent increase in hyporheic proportion was restricted to a single sampling point. Similarly, a substantial reduction in habitat availability at Glen 2 between months 1 and 2 (Table 1) was accompanied by both a sevenfold increase in the hyporheic abundance of *G. pulex* and a fourfold increase in benthic abundance; the hyporheic proportion therefore increased only slightly (Fig. 3). At both sites, some active migration into the HZ may have occurred, but evidence is equivocal.

The hyporheic abundance of *G. pulex* remained very similar in all months at Lathkill 1, despite considerable habitat contraction and very high benthic population densities (Fig. 3; Table 1). Whilst *Gammarus* species are known to exhibit positive rheotaxis (e.g. Elser 2001), energetic costs of long-term position maintenance are likely to be relatively high in upwelling water. In addition, low DO concentrations (Table 4) may have discouraged hyporheic refugium use by *G. pulex*; whilst the taxon can tolerate such conditions, experimental work has shown that *Gammarus* species actively migrate into regions of higher oxygen availability (Henry and Danielopol 1999). In contrast to *G. pulex*, *P. felina* increased in abundance in the HZ of Lathkill 1 in months 3 and 4. This taxon is common in groundwater dominated streams (Rada and Puljas 2010), can tolerate very low oxygen concentrations (Russier-Delolme 1974) and is morphologically suited to inhabit interstices, and was therefore better equipped to exploit the HZ.

The observed spatial variability in refugium use may also reflect factors not characterised by the current study, for example hyporheic flow velocities (which should not be assumed to be proportional to surface flow velocities; Wagner and Bretschko 2002) and hyporheic sediment

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porosity (Maridet and Philippe 1995). Particulate and dissolved organic carbon, nitrate and phosphate concentrations were quantified in surface water and at all hyporheic depths but did not exhibit significant temporal change or have significant relationships with hyporheic invertebrate community parameters (data not presented; cf. Strayer et al. 1997; Davy-Bowker et al. 2006).

Seasonal changes in the abundance of *G. pulex* and *Polycelis* spp. can be discounted for two reasons. Firstly, the four-month sampling programme was repeated at Lathkill 5 in a second year, when no reduction in habitat availability occurred. During this period, neither the benthic abundance, hyporheic abundance, nor the hyporheic proportion of either taxon changed significantly between months. Secondly, whilst measuring the body size of hyporheic inhabitants was not justified due to the size bias of the pump sampling methodology, personal observations indicated that no discernable change in the proportion of small individuals accompanied increases in the abundance of either *G. pulex* or *Polycelis* spp. Both of these observations support the suggestion that temporal changes in abundance were linked to habitat availability rather than seasonal population dynamics.

A conceptual model of hyporheic refugium use during low flows

Patterns observed in the Lathkill and Glen have facilitated development of a conceptual model describing environmental factors controlling HZ refugium use as flow declines (Fig. 6). Variable bed morphology results in spatial variability in the extent of benthic habitat contraction during flow recession. Any reduction in habitat availability is inversely related to an increase in benthic population densities as mobile taxa become concentrated into a smaller space. Density-dependent biotic interactions (e.g. competition, predation, cannibalism) increase biotic risks, particularly for vulnerable groups (e.g. juveniles and individuals at moult; Dick 1995; McGrath et al. 2007). The HZ is a potential refugium from these biotic pressures due to lower population densities (Williams and Hynes 1974; Davy-Bowker et al. 2006) and reduced predation efficiency. However, the results of this study suggest that the refugial potential of the HZ is spatially variable due to heterogeneity in environmental parameters. The direction of hydrologic exchange is of particular importance, with upwelling water lowering refugial potential, possibly due to higher energetic costs (long-term position maintenance against the direction of flow) in a resource-poor environment (low oxygen, reduced allochthonous inputs). In contrast, downwelling water facilitates refugium use, with the direction of flow providing physical forces that promote downward migrations as well as inputs of organic matter and oxygen (Dole-Olivier et al. 1997; Fig. 6). In both upwelling and downwelling zones, refugial potential may also be influenced by factors such as sediment composition, with fine sediments clogging interstices and preventing inhabitation (Belaidi et al. 2004; Olsen and Townsend 2005).

Temporal variability in the hyporheic refugium

Benthic invertebrates entering the HZ during habitat contraction appear ideally placed to persist during any subsequent dry phase in temporary streams. However, the long-term survival of low-flow refugees following surface

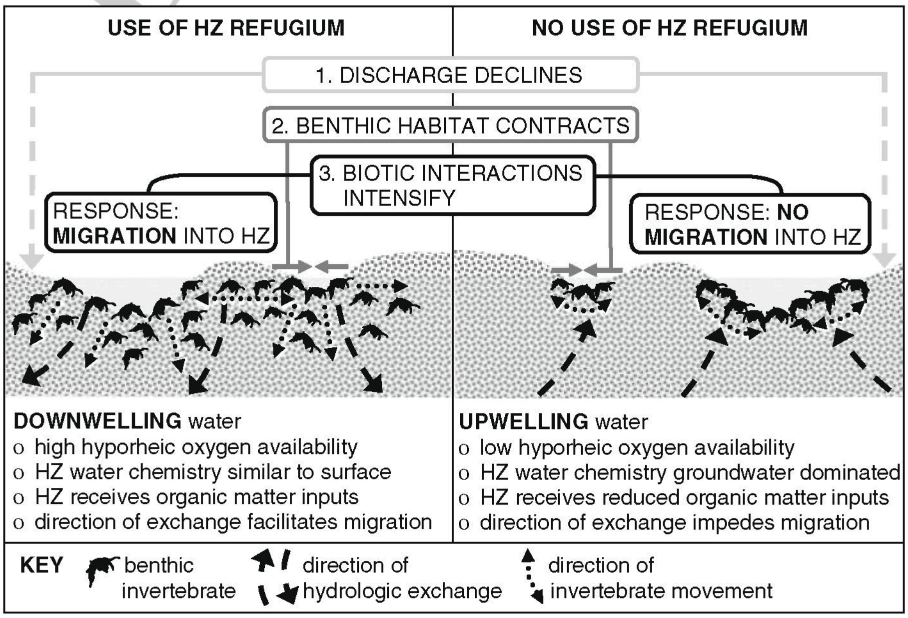

Fig. 6 Spatial variability in the refugial potential of the hyporheic zone (HZ) during flow recession and low flows, in relation to the direction of hydrologic exchange

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drying remains uncertain. At Glen 2, where short duration streambed drying occurred between months 2–3 and 3–4, hyporheic abundance of *G. pulex* and *Polycelis tenuis* was extremely low following drying events despite their previous inhabitation of the HZ during habitat contraction (Fig. 3). This highlights additional variability in the HZ's ability to function as a refugium: refugial potential may vary temporally in response to changing environmental conditions (Stubbington et al. 2009a). Hyporheic sediments were not characterised during the dry phase at Glen 2. However, the proportion of fine sediment was high at this site (Table 4) and may have peaked due to deposition as flow declined and ceased (Belaidi et al. 2004); hyporheic DO concentrations were low in month 3 (Table 3) and were probably further reduced during dry phases (Smock et al. 1994); and the responsiveness of this losing reach may have resulted in the loss of interstitial free water from the shallow hyporheic sediments (Boulton and Stanley 1995; Maddock et al. 1995). Any one of these temporally variable factors would be sufficient to explain low hyporheic abundance of *G. pulex* and *P. tenuis* between dry phases.

An assumption underlying all tests of the hyporheic refuge hypothesis is that refugees are able to recolonise the benthic sediments after a disturbance and complete their lifecycle (Lancaster and Belyea 1997). However, the low benthic and hyporheic abundance of both *G. pulex* and *P. tenuis* following short duration drying events at Glen 2 highlights a limitation of all investigations of the HZ refugium conducted to date: the return of hyporheic refugees to the benthic sediments has not been demonstrated (Dole-Olivier et al. 1997). Whilst the ability of invertebrates including *G. pulex* to migrate through the sediments in both vertical directions is known (Elser 2001; Bo et al. 2006), further studies are required to confirm the mid- to long-term survival prospects of hyporheic refugees. As technologies become available, future field and experimental research should attempt to track individual invertebrates, to ascertain how vertical positioning changes in response to hydrological variability (Whitfield-Gibbons and Andrews 2004). Multi-dimensional cage traps (see Elser 2001) may also prove fruitful in investigation of small-scale directional invertebrate movements. In the meantime, irrefutable evidence of the HZ as true refugium promoting long-term survival remains elusive.

Conclusion

The paired benthic-hyporheic sampling approach adopted in the current study was effective in identifying spatial variability, temporal variability and taxon specificity in hyporheic refugium use. Habitat contraction, benthic population changes and consequent refugium use were found to vary both within and between sites, an unsurprising observation given the widely recognised heterogeneity of instream habitats. This inherent patchiness makes the HZ a vital component of a range of instream refugia with the potential to promote long-term invertebrate persistence during habitat contraction and subsequent dry phases in temporary streams. Climate change scenarios predict an increasing drought frequency in many regions, with consequent shifts from perennial to intermittent flow likely in some systems; these climatic changes are likely to be accompanied by increasing pressures on limited water resources (Davies 2010; Larned et al. 2010). Therefore, the importance of the HZ as a refugial habitat is set to increase. However, the integrity of the HZ habitat is increasingly threatened by anthropogenic activities that deposit fine sediment in fluvial ecosystems, potentially clogging hyporheic interstices, compromising hydrologic exchange and reducing refugial potential (Hancock 2002), particularly in downwelling areas. By highlighting the particular importance of these downwelling zones as potential refugia, this study has drawn attention to the need for sensitive management strategies that recognise the importance of the HZ in invertebrate persistence and take rehabilitative action where appropriate.

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