ECOHYDROLOGY
Ecohydrol. **3**, 0–0 (2010)
Published online in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/eco.168

AQ1

Benthic and •hyporheic invertebrate community responses to seasonal flow recession in a groundwater-dominated stream

Rachel Stubbington,[1]* Paul J. Wood,[1] Ian Reid[1] and John Gunn[2]

[1] *Department of Geography, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK*
[2] *Limestone Research Group, School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK*

ABSTRACT

Natural hydrological variability in lotic ecosystems can include prolonged periods of flow recession. A reduction in discharge is accompanied by abiotic changes in benthic and hyporheic habitats, often including reductions in s habitat availability. Whilst the benthic invertebrate community response to low flows is well documented, little research has considered how the composition of the community within the hyporheic zone is affected. We examined benthic and hyporheic invertebrate community composition during flow recession in a temperate karst stream, at sites with contrasting historic flow permanence regimes. Changes in the benthic invertebrate community composition primarily reflected changes in habitat availability associated with discharge variability; in particular, the population density of the dominant amphipod, *Gammarus pulex*, increased as the area of submerged benthic sediments declined. Concurrent significant increase in the hyporheic abundance of *G. pulex*, and moderate increase in the proportion of the total *G. pulex* population inhabiting the hyporheic zone were recorded. It is postulated that *G. pulex* migrated into the hyporheic zone to reduce exposure to intensifying biological interactions in the benthic sediments. Increase in the hyporheic abundance of *G. pulex* was particularly pronounced at sites with historic intermittent flow, which could be attributed to downwelling stream water dominating vertical hydrologic exchange. The increase in *G. pulex* abundance reduced community diversity in the benthic sediments, but had no apparent detrimental effects on the hyporheic invertebrate assemblages. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS low flows; benthos; hyporheos; hyporheic refuge hypothesis; flow permanence

Received 12 October 2009; Accepted 22 August 2010

INTRODUCTION

Hydrological variability is a key determinant of both habitat structure and invertebrate community composition in lotic ecosystems (Monk *et al.*, 2008). At one extreme of the hydrological continuum streambed drying can occur, and the distinction between the sites with intermittent and perennial flow (flow permanence) has particularly pronounced effects on both benthic and hyporheic invertebrate assemblages (Datry *et al.*, 2007; Stubbington *et al.*, 2009a). In both intermittent and perennial streams, flow recession and low flow form a natural part of the flow regime, and the abiotic changes accompanying a prolonged period of declining discharge can significantly alter the community composition (Dewson *et al.*, 2007).

In the surface channel, a decline in discharge typically leads to reductions in water depth and wetted width, and the resultant exposure of marginal habitats and/or mid-channel topographic high points is dependent on channel morphology (Dewson *et al.*, 2003). The extent of the saturated hyporheic zone remains largely constant until after surface water has been lost (Boulton, 2003).

As discharge declines external influences increase in importance, with consequences for many abiotic variables (Dewson *et al.*, 2007). In temperate regions, low flows often occur when air temperatures are close to the annual maximum (Langan *et al.*, 2001) and the elevation of surface water temperatures may be intensified by the increasing influence of solar radiation (Webb *et al.*, 2003). In contrast, if the proportion of channel water supplied by groundwater increases, water temperature may be reduced (James *et al.*, 2008). The thermal regime in the hyporheic zone may be relatively constant (Hannah *et al.*, 2009), although this is dependent on the direction of hydrologic exchange (Franken *et al.*, 2001). Any change in the water temperature affects dissolved oxygen (DO) levels, due to the inverse relationship between temperature and DO saturation concentrations (Murdoch *et al.*, 2000). Changes in the relative contributions of runoff and groundwater to streamflow can also modify water chemistry as discharge declines (Malcolm *et al.*, 2004), e.g. conductivity may increase due to the reduced dilution and increased residence time of groundwater inputs (Caruso, 2002).

For benthic invertebrates, flow recession represents a period of decreasing habitat availability and heterogeneity, and as a result, taxonomic richness generally declines (McIntosh *et al.*, 2002; Wood and Armitage, 2004). Changes in benthic invertebrate densities are more variable: decline in abundance have been linked to reduced habitat diversity and habitat degradation (Wood

* Correspondence to: Rachel Stubbington, School of Science and Technology, Nottingham Trent University, Clifton Lane, Nottingham, Nottinghamshire, NG11 8NS, UK. E-mail: rachel.stubbington@ntu.ac.uk

and Armitage, 1999; Datry *et al.*, 2008), whilst increasing densities have been attributed to the concentration of individuals into a smaller submerged area (James *et al.*, 2008). Such habitat contraction can intensify biological interactions including predation and competition (Covich *et al.*, 2003). Whilst these effects of low flows on benthic invertebrates are relatively well documented, little research has compared community response to flow recession at adjacent sites with contrasting historic flow permanence, although it has been suggested that the communities of intermittent sites should be more resistant to adverse environmental changes (Boulton, 2003; Lake, 2003).

Several studies have noted the hyporheic zone as a refugium that promotes the survival of benthic invertebrates following streambed drying at sites with intermittent flow (Griffiths and Perry, 1993; Clinton *et al.*, 1996). In contrast, few studies have considered how use of the hyporheic zone by benthic invertebrates changes during a gradual decline in discharge (James and Suren, 2009; Stubbington *et al.*, 2009b; Wood *et al.*, in press). Of these, no study has linked changes in the benthic component of the hyporheic zone fauna to flow recession, despite predictions that benthic invertebrates should become more abundant in the hyporheic zone as flow declines (James *et al.*, 2008; Wood *et al.*, in press). Marmonier and Creuzé des Châtelliers (1991) compared the hyporheic community composition during spates and periods of constant low flow, and found occurrence of benthic invertebrates in the hyporheic sediments to be greatest during low flow in areas of downwelling water. It is not known, however, how such increases in benthic invertebrate abundance within the hyporheic zone affect the permanent hyporheic community.

Questions therefore remain regarding how benthic and hyporheic invertebrate communities respond to prolonged periods of declining discharge, how use of the hyporheic zone by benthic invertebrates is affected, and how historic flow permanence influences the community response. An uninterrupted 4-month flow recession on the River Lathkill (Derbyshire, UK) provided an opportunity to address these questions at adjacent sites with contrasting historic flow permanence regimes. We predicted that: (i) benthic invertebrate abundance in the hyporheic zone would increase if habitat availability declined in the benthic sediments, (ii) the permanent hyporheic community would be detrimentally affected by any increase in benthic invertebrates and (iii) community responses would be related to the historic flow permanence.

METHODS

Study area

The River Lathkill (Derbyshire, England; 53°11·2′N, 1°43·1′W) flows through Lathkill Dale, a wooded valley in the Derbyshire Dales National Nature Reserve. Land use in the surrounding catchment is predominantly pastured. The region has a temperate climate, with a mean annual rainfall of ~1200 mm and a mean annual air temperature of 8·0 °C, ranging from 1·7 °C in January to 14·5 °C in July (Wood *et al.*, 2005).

Lathkill Dale is underlain by Carboniferous limestone, and the river discharges autogenic water, which has only been in contact with carbonate rocks (Banks *et al.*, 2009). Whilst the limestone aquifer provides the river with significant baseflow, water is lost through the streambed to natural features of the karst bedrock, and transmission losses are exacerbated by underlying drainage levels and remnants of historic lead mining activity (James, 1997). Consequently, some reaches within the study area typically lose all surface water during the summer months.

Five sites in the upper reaches were selected to represent the spatial variability in the river's flow regime. In terms of historic flow permanence, two sites (1 and 2) were perennial (Figure 1) and three sites (3–5) were intermittent (Figure 1). The substrate consisted of mixed alluvial deposits dominated by sand- to cobble-sized clasts. Instream vegetation was dominated by mosses and liverworts, with scattered patches of reeds in the marginal areas.

Hydrological and meteorological conditions

The River Lathkill is almost entirely groundwater-fed, and the response to low-moderate rainfall events is therefore subdued and flow recession is slow when compared with surface water fed streams. Flow recession on the river usually begins in April/May and continues until September/October. Reaches with intermittent flow typically begin to lose surface water in May and dry completely by late July. Downstream of the study area, groundwater is forced to the surface by a basalt barrier, and discharge is measured at a gauging station downstream of these perennial springs (Figure 1).

In 2008, the seasonal flow recession followed the usual pattern, with discharge decreasing sharply in April then continuing to decline slowly (Figure 2). When sampling commenced in mid-May, discharge had reached ~0·43 m^3 s^{-1}. Flow recession continued uninterrupted throughout the study period, with the lowest hourly discharges, of 0·090–0·096 m^3 s^{-1}, occurring during mid-August, in the days preceding the final sampling date. However, due to above-average rainfall inputs, particularly in July [190% of the 1971–2000 long-term average (LTA)] and August (150% LTA; Met Office, 2009), the extent to which decline in flow was reduced compared to a typical year and all sites retained some surface water throughout the study.

Air temperature data from an automated weather station located 8 km from the River Lathkill indicated that the mean air temperature in the 28 days preceding sampling increased by approximately 2 °C each month, from 8·6 °C in May to 14·6 °C in August. Maximum hourly air temperature in the 28 days preceding sampling also increased during the study, from 21·3 °C in May to 24·4 °C in August.

DOI: 10.1002/eco

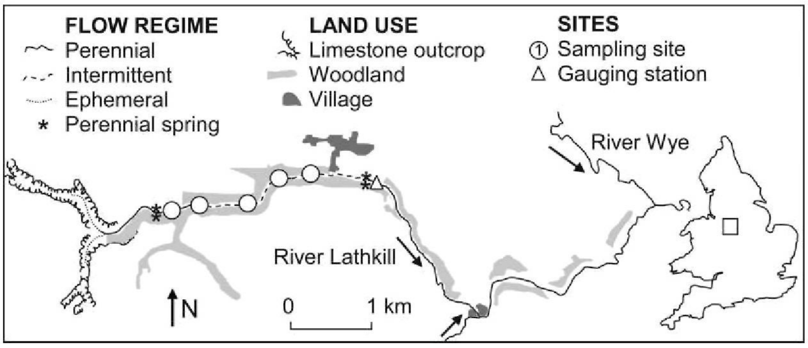

Figure 1. Location map of the River Lathkill, indicating sampling points.

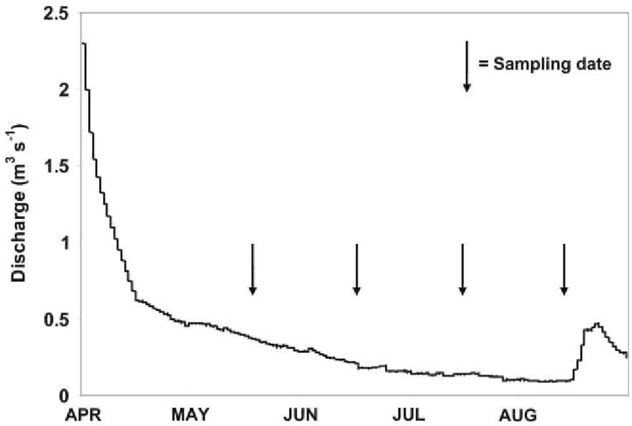

Figure 2. Hydrograph of mean hourly discharge on the River Lathkill, April-September 2008. Location of gauging station shown in Figure 1.

Field sampling

Sampling was undertaken at each site at monthly intervals between May and August 2008, with the exception of site 5 (Figure 1), which was not accessible in May. Four sampling points were selected at each site in riffle or run habitat. Prior to commencing the sampling programme, three polyvinylchloride pipes (19-mm internal diameter), were installed at each sampling point to depths of 10, 20 and 30 cm respectively, using a stainless steel T-bar. These pipes functioned as hyporheic invertebrate sampling wells for the duration of the study. Wells were placed ≥50 cm apart to minimize the effects of sampling on the area of sediments sampled by adjacent wells. Each well was sealed between sampling occasions to prevent sediment deposition and invertebrate colonization.

Each month, benthic invertebrates were collected at each sampling point using a Surber sampler (0·1 m^2, 250-μm mesh net) by disturbing the substrate within the Surber frame manually to a depth of ~50 mm for 30 s. Large clasts present within the Surber frame were inspected individually and any attached invertebrates included in the sample. Hyporheic invertebrates were pumped from the base of each sampling well using a hand-operated bilge pump according to the procedure outlined by Boulton *et al.* (1992). This technique causes minimal disturbance of the sediments and allows the collection of samples from the same location on multiple occasions during a temporal sequence (Stubbington *et al.*, 2009b). Each sample consisted of 6 l of hyporheic water, sediment and invertebrates, which was passed through a 125-μm sieve to retain invertebrates. Invertebrate samples were preserved in the field using a 4% formaldehyde solution.

At each sampling point, three hydrological variables were measured: water depth, mean flow velocity (at 0·6× depth) and wetted width. Depth and velocity were measured using an ADS SENSA-RC2 flow meter (ADS Environmental Services, Huntsville, USA). Wetted width was measured at the mid-point of each sampling location. Temperature, pH, conductivity and DO (mg l^{-1} and % saturation) were measured *in situ* in both surface water and hyporheic water pumped from each sampling depth, using standard instrumentation (Hanna Instruments, Leighton Buzzard, UK).

Laboratory analysis

Invertebrate samples were stored at 4 °C in darkness prior to processing. Invertebrates were identified to the lowest taxonomic resolution possible, in many cases to species level, although *Baetis* (Ephemeroptera), some *Leuctra* (Plectoptera) and adult and larval *Oulimnius* and *Hydraena* (Coleoptera) were identified to genus; Sphaeriidae (Bivalvia), larval Dytiscidae and Scritidae (Coleoptera) and some Diptera (Ceratopogonidae, Chironomidae, Empididae, Muscidae, Stratiomyidae, Simuliidae, Tipulidae) were identified to family level; and Cladocera, Cyclopoida (Copepoda), Harpacticoida (Copepoda), Nematoda, Oligochaeta and Hydracarina were left at the group level.

Statistical analysis: environmental variables

Repeated measured analysis of variance (RM ANOVA) tests with month as a within-subjects variable were used to examine variability in hydrological and water chemistry parameters. Two-way RM ANOVA tests with flow permanence (perennial, intermittent) as a between-subjects factor were conducted to identify differences between historically intermittent and perennial sites. Separate tests with surface water/hyporheic depth (surface, 10, 20 and 30 cm) as a between-subjects factor were used to examine differences in water chemistry variables in surface and hyporheic water. Where no significant differences were found between the three hyporheic depths,

DOI: 10.1002/eco

all were combined in subsequent analyses. One-way RM ANOVA was then used to assess temporal change in hydrological and water quality parameters.

To investigate the influence of antecedent hydrological conditions on invertebrate community structure, mean discharge at the downstream gauging station was calculated for the periods 24 h, 7 and 28 days prior to each sampling date.

Statistical analysis: invertebrate community data

Non-metric multidimensional scaling (NMDS) was used to examine spatial and temporal variability in invertebrate community composition, using the program PC-ORD (McCune and Mefford, 2006). NMDS is a robust ordination technique in which similarities between biotic assemblages are visualized by positioning the most similar samples closest together in an n-dimensional ordination space. Benthic and hyporheic invertebrate communities at each depth were initially analysed separately. This preliminary analysis indicated that similar patterns were observed at each hyporheic depth, and all were therefore pooled. Prior to each analysis, data were square root transformed to reduce skewness and reduce the influence of dominant taxa. NMDS was performed in two to six dimensions on a Bray-Curtis distance matrix using a random starting configuration and autopilot mode. Stress functions were calculated for each dimension as a measure of goodness of fit, with a final stress of $<0{\cdot}2$ considered ecologically interpretable (Clarke, 1993).

Three indices were calculated to describe the benthic and hyporheic invertebrate communities: total invertebrate abundance (TIA), taxon richness (number of taxa), and the Berger-Parker dominance index (a measure of the proportion of the community accounted for by the most common taxon). In addition, abundance of the most common taxa (calculated separately for benthic and hyporheic samples and defined as taxa accounting for $>1\%$ of individuals present in all the samples) was determined for each sampling occasion. To examine use of the hyporheic zone by benthic invertebrates, the proportion of the total (benthic + hyporheic) population found within the hyporheic zone (the hyporheic proportion) was calculated for TIA and for selected common benthic taxa. Using proportional data allows comparison of populations sampled using different techniques.

All community metrics (NMDS axis scores, indices, abundances and hyporheic proportions) were used as dependent variables in subsequent analyses. Prior to analysis, abundance data were square root transformed and proportional data were arcsine square root transformed to reduce skewness and reduce the influence of dominant taxa. To assess spatial and temporal variability in these community metrics, two-way and one-way RM ANOVA tests were conducted as described for environmental variables.

Pearson's product-moment correlation coefficients were calculated to examine relationships between all the community metrics and hydrological and water chemistry variables. Prior to analysis, abundances and indices were standardized by calculating z-scores for each sampling site. This method of standardization re-scales data from individual sites to allow comparison of the responses of multiple sites to the same external factor.

RESULTS

Environmental conditions

Significant reductions in water depth, flow velocity and wetted width occurred between May and August, although these general declines were interrupted by minor increases in depth and wetted width between June and July, and a small increase in velocity between July and August (Table I). Surface and hyporheic water at historically perennial sites had significantly higher conductivity and lower pH, temperature and DO (% saturation) compared with intermittent sites ($p < 0{\cdot}05$). Surface and hyporheic water underwent similar changes during flow recession, with significant linear changes being observed in DO (mg l^{-1}), pH and conductivity (Table I).

Invertebrate communities

A total of 30 812 individuals from 79 taxa were recorded from 75-benthic Surber samples. The freshwater shrimp, *G. pulex* (L.) (Amphipoda: Crustacea), dominated the benthic community accounting for 40·8% TIA. The Chironomidae (Diptera) were also abundant, and comprised 17·8%TIA. Eight other taxa made up 1-10% TIA: the flatworm *Polycelis felina*, the Oligochaeta, two mayflies (*Serratella ignita, Baetis* spp.), a stonefly (*Leuctra* spp.), a caddisfly (*Agapetus fuscipes*) and two riffle beetle larvae (*Elmis aenea, Riolus subviolaceus*).

A total of 8840 invertebrates were recorded from 226-hyporheic samples collected from depths of 10, 20 and 30 cm. The Ostracoda, Chironomidae and *G. pulex* dominated at all depths. The Ostracoda accounted for 19-29% TIA at each depth and decreased in abundance with increasing depth. The Chironomidae accounted for 18·9% TIA at 10 cm increasing to 30·3% at 30 cm, and occurred at similar densities at each depth. *G. pulex* decreased slightly in both abundance and dominance with increasing depth, from 17·1% TIA at 10 cm, to 14·2% TIA at 20 and 30 cm. Other taxa comprising 1-10% TIA were similar at all depths and included the Oligochaeta, Cyclopoida, Nematoda, *P. felina* and three insect taxa (*Nemoura* spp., *Leuctra* spp., and *S. ignita*).

Community ordination

NMDS of the benthic community data yielded a three-dimensional (3D) solution (final stress = 0·15, final instability = 0, Monte Carlo test $p = 0{\cdot}004$; Figure 3). Separation of samples along axis 2 indicated clear differences in community composition at sites with historic intermittent and perennial flow ($p < 0{\cdot}001$; Figure 3(A)). Separation along axis 1 was more variable; however, axis

DOI: 10.1002/eco

Table I. Temporal change in hydrological and water chemistry variables in surface and hyporheic water during a 4-month flow recession.

	Surface water or hyporheic depth	May	June	July	August	Temporal change
Site-specific hydrological variables						
Water depth (cm)	—	16.6 ± 1.59	8.4 ± 1.24	10.1 ± 1.35	5.9 ± 1.09	**
Mean flow velocity (m s^{-1})	—	0.29 ± 0.04	0.18 ± 0.03	0.1 ± 0.02	0.14 ± 0.04	*
Wetted width (m)	—	8.1 ± 1.32	7.24 ± 1.03	7.51 ± 1.00	6.52 ± 0.092	**
Water chemistry variables						
DO (mg l^{-1})	surface	12.5 ± 0.35	9.9 ± 0.22	10.2 ± 0.67	8.7 ± 0.38	**
	10 cm	7.88 ± 0.74	7.44 ± 0.34	7.42 ± 0.69	5.72 ± 0.50	**
	20 cm	7.82 ± 0.34	6.44 ± 0.29	6.61 ± 0.63	4.91 ± 0.40	**
	30 cm	7.56 ± 0.98	6.48 ± 0.41	6.86 ± 0.60	4.68 ± 0.41	**
DO (% saturation)	surface	100 ± 0	95.5 ± 1.6	93.4 ± 1.82	91.4 ± 2.38	**
	10 cm	82.9 ± 6.38	79.8 ± 2.93	77.1 ± 3.84	72.4 ± 4.33	n/s
	20 cm	85.2 ± 3.79	72.6 ± 2.21	7.34 ± 4.55	65.2 ± 3.60	n/s
	30 cm	82.8 ± 6.19	70.4 ± 2.79	75.8 ± 4.12	62.7 ± 3.62	n/s
Water temperature (°C)	surface	11.1 ± 0.35	10.4 ± 0.21	11.4 ± 0.30	10.9 ± 0.34	n/s
	all hyporheic depths	10.96 ± 0.21	10.23 ± 0.14	11.80 ± 0.13	11.19 ± 0.18	**
pH	surface	8.09 ± 066	8.2 ± 0.04	8.36 ± 0.09	8.43 ± 0.73	**
	10 cm	7.99 ± 0.05	8.18 ± 0.07	8.32 ± 0.1	8.29 ± 0.1	*
	20 cm	7.97 ± 0.07	8.22 ± 0.09	8.28 ± 0.09	8.34 ± 0.08	**
	30 cm	7.93 ± 0.05	8.10 ± 0.07	8.18 ± 0.08	8.22 ± 0.07	**
Conductivity (µS cm^{-1})	surface	579 ± 1.93	597 ± 2.48	608 ± 5.80	605 ± 7.72	**
	all hyporheic depths	589.5 ± 1.1	607.5 ± 1.5	617.9 ± 2.4	618.2 ± 4	**

Values are presented as the mean ± 1 SE of all samples. For surface water and each hyporheic depth, $n = 16$ in May and $n = 20$ in June, July and August for all variables expect water depth, where $n = 16$ each month. Hyporheic depths (10, 20 and 30 cm) are combined where RM ANOVA indicated no significant difference between depths. Temporal change was analysed using RM ANOVA, with * and ** indicating significance levels of $p < 0.05$ and $p < 0.01$, respectively. SE, standard error.

scores were positively correlated with all discharge variables (Table II) and underwent linear temporal change, decreasing each month as the flow recession progressed ($p < 0.001$; inset, Figure 3(B)).

NMDS ordination of the hyporheic community data yielded a 3-D solution (final stress = 0.19, final instability = 0.0228, Monte Carlo test $p = 0.004$; Figure 4). Community composition could be distinguished according to historic flow permanence on both axis 1 ($p = 0.033$) and axis 2 ($p < 0.001$; Figure 4(A)). Despite considerable variability and overlap between months, temporal change was also significant on both axes, with axis 1 scores rising to a peak in July then declining moderately in August ($p < 0.001$; inset, Figure 4(B)) and the opposite pattern being observed for axis 2 scores ($p < 0.001$; Figure 4(B)); both axes had weak but significant correlations with all discharge variables as well as wetted width (Table II).

Temporal change in benthic community composition

Mean taxon richness was comparable at historically intermittent sites (17.6 ± 0.56 taxa 0.1 m^{-2}) and perennial sites (19.0 ± 0.77 taxa 0.1 m^{-2}; $p = 0.412$) and varied little during the flow recession ($p = 0.070$; Figure 5(A)). The interaction with flow permanence was significant, due to taxon richness peaking in May at intermittent sites and in June at perennial sites ($p = 0.010$).

Mean TIA was similar at sites with historically intermittent and perennial flow ($p = 0.503$) and increased moderately between May (316.1 ± 41.2 individuals (ind.) 0.1 m^{-2}) and June (432.8 ± 56.2 ind. 0.1 m^{-2}), then stabilized ($p = 0.150$; Figure 5(B)). The interaction between TIA and historic flow permanence was not significant ($p = 0.391$). Mean abundance of the dominant benthic taxon, *G. pulex*, was similar at historically intermittent and perennial sites ($p = 0.936$). *G. pulex* abundance increased significantly between May (78 ± 8.9 ind. 0.1 m^{-2}) and August (244.9 ± 41.9 ind. 0.1 m^{-2}; $p < 0.001$; Figure 5(C)) and was negatively correlated with all discharge and hydrological variables (Table II). The interaction between *G. pulex* abundance and historic flow permanence was significant ($p = 0.01$), with abundance at perennial sites increasing between May and June then remaining stable ($p = 0.011$), whilst abundance at intermittent sites increased between May and June and again between July and August ($p = 0.002$; Figure 5(C)).

Berger-Parker dominance was comparable at sites with historically intermittent and perennial flow ($p = 0.498$). Dominance increased throughout the flow recession ($p < 0.001$; Figure 5(D)), and was negatively correlated with all discharge and hydrological variables (Table II). The increase in community dominance occurred as the proportion of *G. pulex* rose from 0.27 TIA in May to 0.49 TIA in August ($p < 0.001$; Figure 5(E)). The interaction with flow permanence was not significant for Berger-Parker dominance ($p = 0.07$), whilst a significant interaction with the proportion of *G. pulex* ($p = 0.016$) reflected a more pronounced increase at intermittent sites ($p = 0.001$) compared with perennial sites ($p = 0.073$; Figure 5(E)).

DOI: 10.1002/eco

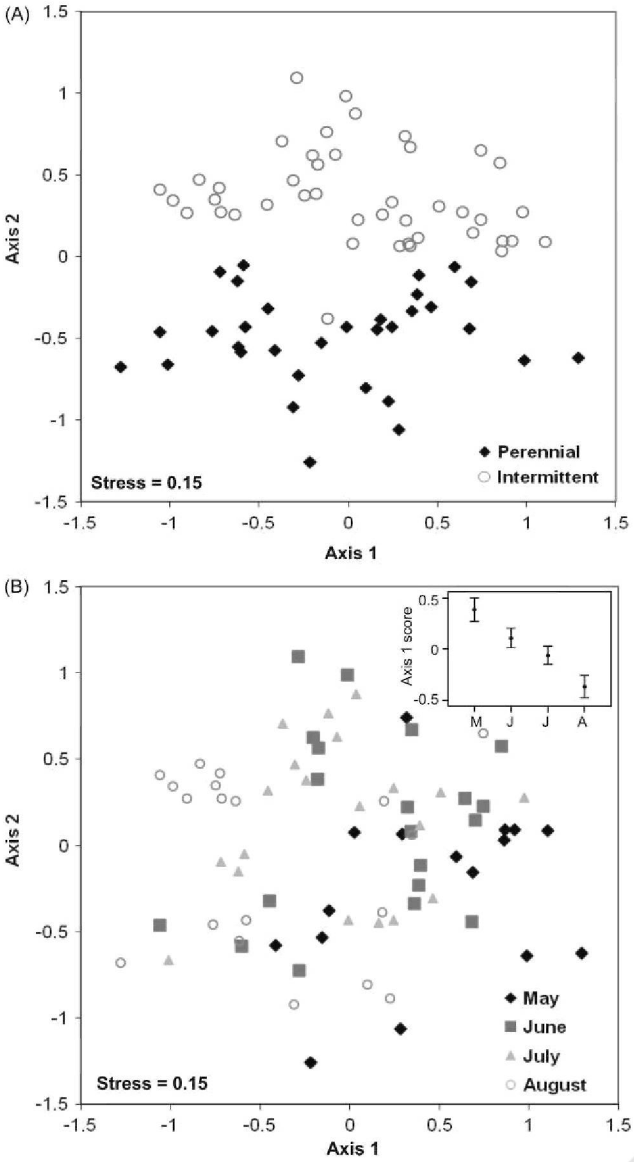

Figure 3. Two-dimensional (2D) NMDS ordination of benthic invertebrate community composition during a 4-month flow recession: (A) historic flow permanence and (B) temporal change (inset: mean ±1 SE temporal change in axis 1 score).

Temporal change in hyporheic community composition

Mean taxon richness was comparable at historically intermittent sites ($7{\cdot}1 \pm 0{\cdot}3$ taxa 6 l^{-1}) and perennial sites ($5{\cdot}9 \pm 0{\cdot}3$ taxa 6 l^{-1}; $p = 0{\cdot}368$), and was lower in May ($5{\cdot}7 \pm 0{\cdot}4$ taxa 6 l^{-1}) and June ($5{\cdot}4 \pm 0{\cdot}3$ taxa 6 l^{-1}) than in July ($7{\cdot}3 \pm 0{\cdot}3$ taxa 6 l^{-1}) and August ($7{\cdot}7 \pm 0{\cdot}4$ taxa 6 l^{-1}; $p < 0{\cdot}001$; Figure 6(A)). The interaction between taxon richness and historic flow permanence was not significant ($p = 0{\cdot}559$), although the increase in richness was more pronounced at intermittent sites (Figure 6(A)). Increased richness reflected the occurrence of several insect taxa which were common in the benthos in all months but only occurred in the hyporheic zone in July and/or August [i.e. *Silo nigricornis, Chaetopteryx villosa* and *Drusus annulatus* (Trichoptera), *Elmis aenea* and *Riolus subviolaceus* (Coleoptera)].

Mean TIA was moderately higher at historically intermittent sites ($42{\cdot}1 \pm 3{\cdot}0$ ind. 6 l^{-1}) than at perennial sites ($27{\cdot}7 \pm 2{\cdot}3$ ind. 6 l^{-1}; $p = 0{\cdot}07$), increased between May ($19{\cdot}8 \pm 2{\cdot}7$ ind. 6 l^{-1}) and August ($54{\cdot}9 \pm 5{\cdot}7$ ind. 6 l^{-1}; $p < 0{\cdot}001$; Figure 6(B)), and had highly significant negative correlations with all discharge variables as well as velocity (Table II). The interaction between TIA and historic flow permanence was not significant ($p = 0{\cdot}319$), despite the increase in TIA being more pronounced at intermittent sites (Figure 6(B)). The Ostracoda and *G. pulex* were the principal taxa responsible for the increase in TIA. Ostracods were particularly abundant at historically intermittent sites ($p = 0{\cdot}010$), where mean abundance increased from $1{\cdot}9 \pm 0{\cdot}5$ ind. 6 l^{-1} in May to $14{\cdot}2 \pm 3{\cdot}0$ ind. 6 l^{-1} in July ($p < 0{\cdot}001$). Mean *G. pulex* abundance was similar at historically intermittent and perennial sites ($p = 0{\cdot}614$) and increased between May ($3{\cdot}0 \pm 0{\cdot}65$ ind. 6 l^{-1}) and August ($10{\cdot}0 \pm 1{\cdot}67$ ind. 6 l^{-1}; $p < 0{\cdot}001$; Figure 6(C)), as reflected by the negative correlations with all discharge and hydrological variables (Table II). Although, there was no significant interaction between month and historic flow permanence ($p = 0{\cdot}227$), the increase in *G. pulex* abundance was only significant at intermittent sites ($p = 0{\cdot}004$; Figure 6(C)).

Berger-Parker dominance was moderately higher at historically intermittent sites compared with perennial sites ($p = 0{\cdot}098$), and a significant interaction was also observed with the flow permanence ($p = 0{\cdot}012$). At sites with historically perennial flow, dominance increased between May and June and again between July and August ($p = 0{\cdot}03$; Figure 6(D)); this was associated with the Chironomidae between May and July, then with *P. felina* in August. At sites with intermittent flow, increasing dominance between May and July and a subsequent decrease in August ($p = 0{\cdot}003$) reflected seasonal changes in the Chironomidae (Figure 6(D)). A moderate increase in the proportion of TIA accounted for by *G. pulex* also occurred between June (0·12) and August (0·19; $p = 0{\cdot}108$; Figure 6(E)).

Interactions between benthic and hyporheic communities

The hyporheic proportion of total TIA was moderately higher at historically intermittent sites ($0{\cdot}30 \pm 0{\cdot}03$) than at perennial sites ($0{\cdot}20 \pm 0{\cdot}02$; $p = 0{\cdot}394$). Considering all sites, an increase in the hyporheic proportion of TIA between May ($0{\cdot}19 \pm 3{\cdot}2$) and August ($0{\cdot}30 \pm 4{\cdot}6$) was not significant ($p = 0{\cdot}280$; Figure 7(A)); neither was the interaction with historic flow permanence significant ($p = 0{\cdot}081$).

The hyporheic proportion of the *G. pulex* population was also moderately higher at historically intermittent sites ($0{\cdot}17 \pm 0{\cdot}03$) compared with perennial sites ($0{\cdot}11 \pm 0{\cdot}02$; $p = 0{\cdot}692$), and also increased during the flow recession, from 0·11 in May to 0·19 in August ($p = 0{\cdot}263$; Figure 7(B)). There was no interaction with flow permanence ($p = 0{\cdot}998$), although the increase was more pronounced at intermittent sites (Figure 7(B)).

DOI: 10.1002/eco

Table II. Pearson correlation coefficients between selected hydrological and water chemistry variables, and invertebrate community metrics.

	NMDS axis score					
	Axis 1	Axis 2	TIA[a]	Taxon richness[a]	Berger-Parker dominance[b]	*G. pulex* abundance[a]
A. Benthic invertebrates						
Discharge variables[c]						
Discharge during sampling	0·501**	−0·223	−0·222	0·178	−0·532**	−0·386**
24-h mean discharge	0·496**	−0·217	−0·226	0·180	−0·533**	−0·389**
7-days mean discharge	0·502**	−0·200	−0·227	0·181	−0·536**	−0·390**
28-days mean discharge	0·509**	−0·194	−0·223	0·182	−0·534**	−0·385**
Site-specific hydrological variables						
Water depth (cm)	−0·013	0·447**	−0·205	0·002	−0·232*	−0·236**
Mean flow velocity (m s^{-1})	0·422**	−0·362*	−0·111	0·097	−0·227*	−0·158
Wetted width (m)	0·137	−0·082	−0·300	−0·293	−0·285	−0·323*
Water chemistry variables						
DO (% saturation.)	0·286*	0·358**	−0·168	0·063	−0·119	−0·220
Water temperature (°C)	−0·006	−0·379**	−0·102	−0·097	−0·047	−0·078
pH	−0·029	0·218	0·071	−0·024	0·247*	0·159
Conductivity (µS cm^{-1})	−0·140	0·313**	0·131	−0·019	0·347**	0·249*
B. Hyporheic invertebrates						
Discharge variables[c]						
Discharge during sampling	−0·146*	0·224**	−0·378**	−0·233**	−0·168*	−0·218**
24-hr mean discharge	−0·146*	0·218**	−0·381**	−0·238**	−0·165*	−0·223**
7-days mean discharge	−0·133*	0·209**	−0·384**	−0·245**	−0·159*	−0·230**
28-days mean discharge	−0·134*	0·208**	−0·369**	−0·236**	−0·161*	−0·213**
Site-specific hydrological variables						
Water depth (cm)	−0·099	0·117	−0·169*	−0·104	−0·025	−0·129
Mean flow velocity (m s^{-1})	0·035	0·141*	−0·211**	−0·164*	−0·037	−0·173**
Wetted width (m)	−0·254**	0·152	−0·118	−0·131	0·008	−0·160
Water chemistry variables						
DO (% saturation)	0·120	0·059	−0·073	−0·006	−0·144	0·012
Water temperature (°C)	0·253**	0·132*	0·080	0·119	−0·090	0·125
pH	0·105	−0·316**	0·064	0·006	0·058	0·097
Conductivity (µS cm^{-1})	−0·102	−0·164*	0·212**	0·125	0·149*	0·097

[a] Square root transformed z-scores.
[b] Untransformed z scores.
[c] 24 h/7 days/28 days refer to the period immediately preceding sampling.
* $p < 0{\cdot}05$.
** $p < 0{\cdot}01$.

DISCUSSION

Environmental changes during flow recession

The flow recession on the River Lathkill represented an extended period of moderate instream conditions in a system that regularly experiences hydrological extremes. Prolonged periods of declining flow can act as 'ramp' disturbances that increase in strength over time (Lake, 2003) and can have significant effects on invertebrate communities due to reductions in water quality and habitat availability (Dewson *et al.*, 2007). In the River Lathkill, flow recession was accompanied by significant reductions in water depth and wetted width, resulting in streambed drying in marginal and mid-channel areas and therefore a reduction in submerged habitat availability, although the impact on submerged hyporheic sediments was negligible. Associated changes were also observed in many water chemistry parameters, including a reduction in DO concentrations, however, these changes were minor and unlikely to have had biotic effects (Datry *et al.*, 2008).

Benthic community response to flow recession

The NMDS ordination distinguished between benthic communities at sites with historic intermittent and perennial flow, and also identified a significant, linear, temporal change in community composition, which principally reflected an increase in the abundance and dominance of *G. pulex*. *G. pulex* abundance was negatively correlated with discharge and site-specific hydrological variables, suggesting that habitat contraction concentrated the benthic population of this competitive, mobile taxon into a smaller area, with acceptable environmental conditions potentially allowing concurrent population expansion (Death and Winterbourn, 1995). This suggestion is supported by the contrasting patterns of temporal change at perennial and intermittent sites, which could not be related to flow permanence but to channel morphology: at perennial sites, small declines in depth were sufficient

DOI: 10.1002/eco

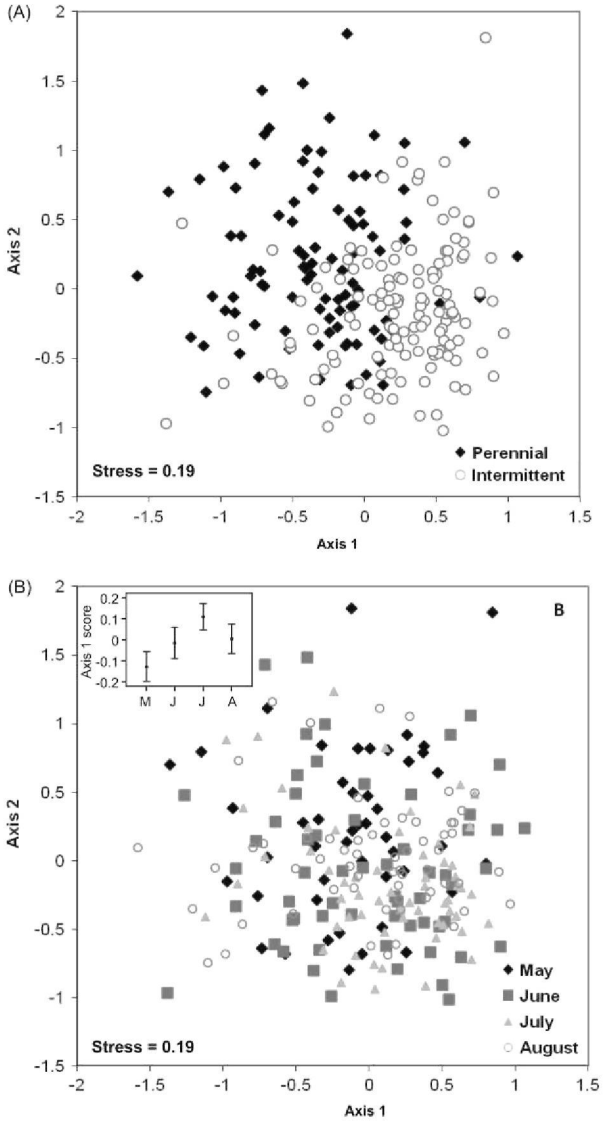

Figure 4. 2-D NMDS ordination of hyporheic invertebrate community composition during a 4-month flow recession: (A) historic flow permanence and (B) temporal change (inset: Mean ±1 SE temporal change in axis 1 score).

to expose considerable areas of mid-channel benthic sediments, resulting in an earlier increase in benthic *G. pulex* population densities. Boulton (2003) suggests that during a period of declining flow, a taxon will decrease in abundance only once a 'critical threshold' at which conditions becoming unfavourable is reached; increases in abundance suggests that this threshold was not reached for *G. pulex* in this study.

Benthic invertebrate use of the hyporheic zone

Some studies have found the hyporheic zone to act as a benthic invertebrate refugium during adverse conditions in the surface channel, in particular during floods (Dole-Olivier and Marmonier, 1992) and streambed drying (Cooling and Boulton, 1993). Of the few studies that have considered the hyporheic zone refugium during low flows (James *et al.*, 2008; James and Suren, 2009; Stubbington *et al.*, 2009b; Wood *et al.*, in press), only one (Stubbington *et al.* 2009b; Wood *et al.*, in press) has reported evidence supporting the hyporheic refuge hypothesis, but refugium use primarily corresponded to changes in the thermal regime. The absence of a refugium effect as discharge declines has been attributed to conditions in the benthic sediments remaining favourable, or at least preferable to the hyporheic zone (James *et al.*, 2008). In the River Lathkill, however, abundance of the benthic species *G. pulex* increased significantly in the hyporheic zone as flow declined, and a moderate increase in the proportion of the *G. pulex* population inhabiting the hyporheic sediments was also observed. Vertical migrations into the hyporheic sediments probably occurred in response to increasing biological interactions (e.g. cannibalism and competition) in the benthic sediments as *G. pulex* population densities increased in the contracting area of submerged habitat (Lake, 2003). This suggestion is supported by experimental work demonstrating a behavioural avoidance response in *Gammarus* exposed to chemicals released by conspecifics injured in cannibalistic attacks (Wisenden *et al.*, 2001), with avoidance responses including the preferential use of sediments with smaller interstitial spaces (McGrath *et al.*, 2007).

Temporal increases in *G. pulex* abundance and TIA in the hyporheic zone were more pronounced at historically intermittent sites compared with perennial sites. It is probably that these differences, rather than reflecting the flow permanence regime itself, reflect the *cause* of that regime, i.e. the relative contribution of upwelling groundwater to streamflow. Perennial sites had higher conductivity, lower DO concentrations and lower temperatures compared with intermittent sites, indicating that perennial sites were dominated by upwelling groundwater and intermittent sites by downwelling surface water (Malcolm *et al.*, 2003). Additional evidence of the dominant direction of hydrologic exchange includes a major upwelling groundwater spring at one perennial site (1, Figure 1; Wood *et al.*, 2005), obligate groundwater species at the second perennial site (2, Figure 1; Stubbington *et al.*, 2009c) and the mine drainage levels that cause transmission losses from reaches with intermittent flow. Downwelling surface water can facilitate passive and active migrations of benthic taxa (Datry *et al.*, 2008), and the direction of hydrologic exchange can influence use of the hyporheic zone refugium during spates (Dole-Olivier *et al.*, 1997). In the current investigation, the more pronounced increases in *G. pulex* abundance and TIA in the hyporheic zone of intermittent sites indicated that downwelling water can also promote hyporheic refugium use during low flow conditions.

Hyporheic community response to flow recession and benthic migrations

It was predicted that increased abundance of benthic taxa in the hyporheic zone would have detrimental effects on the permanent hyporheic community, due to increasing biotic pressures. However, the increase in *G. pulex* abundance in the hyporheic zone was not associated with changes in Berger-Parker dominance, hyporheic taxon richness increased, and no common taxon of

DOI: 10.1002/eco

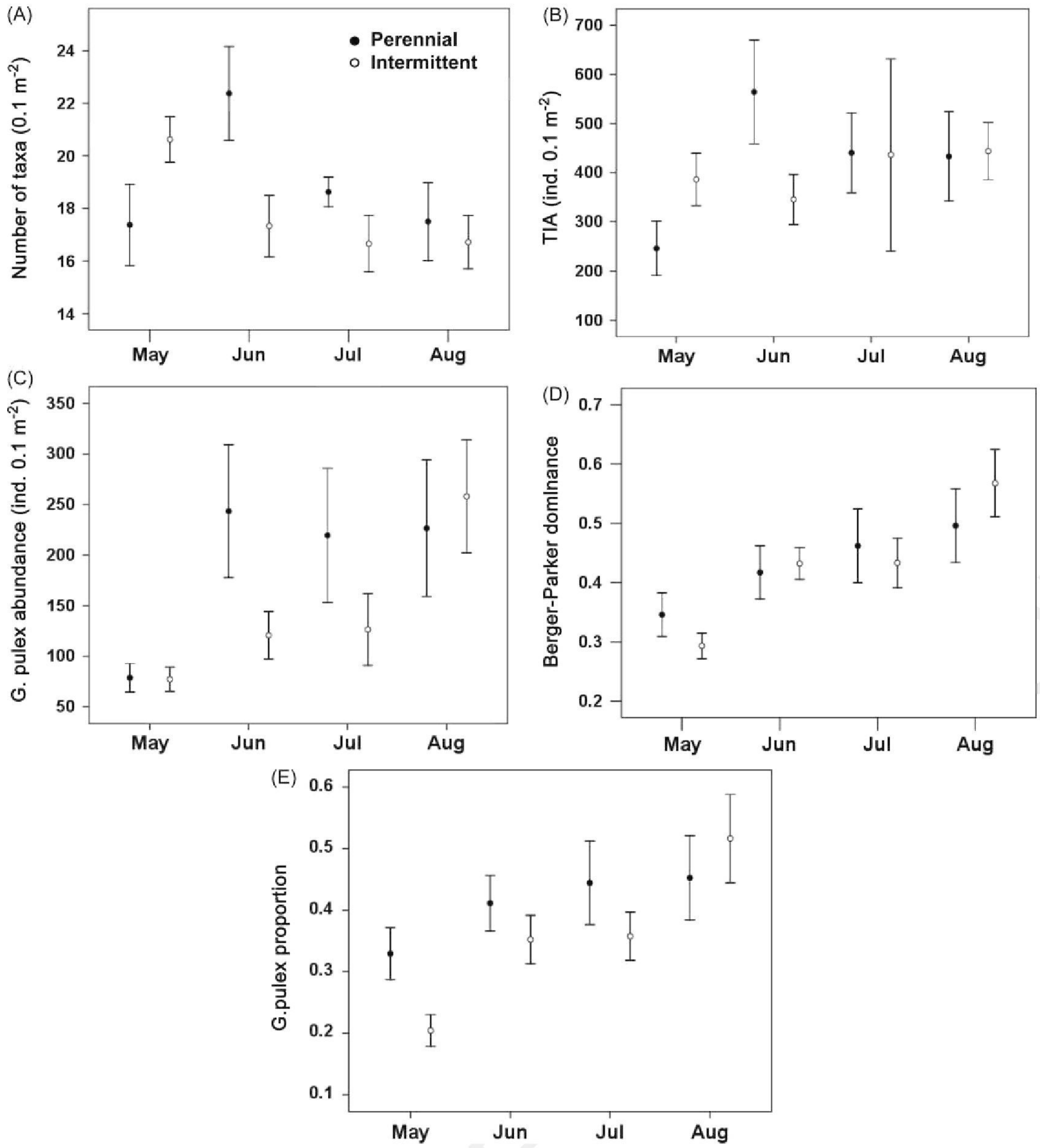

Figure 5. Mean ±1 SE benthic invertebrate community composition at sites with historically perennial and intermittent flow: (A) number of taxa ($0{\cdot}1\ m^{-2}$), (B) TIA (ind. $0{\cdot}1\ m^{-2}$), (C) *G. pulex* abundance (individuals $0{\cdot}1\ m^{-2}$), (D) Berger-Parker dominance index and (E) *G. pulex* abundance as a proportion of TIA.

the permanent hyporheic community (the Ostracoda, Cyclopoida, Oligochaeta and Nematoda) significantly decreased in abundance.

Although NMDS axis scores changed significantly during the flow recession, the ordination of hyporheic community composition indicated considerable variability both within and between months. Compositional shifts in response to changing environmental conditions are often less pronounced in hyporheic communities compared with benthic assemblages (Malard *et al.*, 2003), reflecting the overriding importance of relatively constant environmental parameters such as sediment composition (Olsen and Townsend, 2003), porosity (Maridet *et al.*, 1992) and the direction of hydrologic exchange (Franken *et al.*, 2001) in determining hyporheic community composition. Relationships between hyporheic communities and environmental parameters are therefore most apparent during extreme events (Storey and Williams, 2004), whilst the current study considered a period of moderate conditions.

CONCLUSIONS

Use of the hyporheic zone refugium during flow recession on the River Lathkill varied both between and within historic flow permanence groups. These differences were attributed in part to the dominant direction of hydrologic exchange and also to streambed morphology, which influenced the timing and extent of the reduction in habitat availability. To improve understanding of factors controlling refugium use during flow recession and low flows, future research should consider potentially important site-specific parameters in greater detail, including sediment composition and porosity, and the direction and strength of hydrologic exchange.

DOI: 10.1002/eco

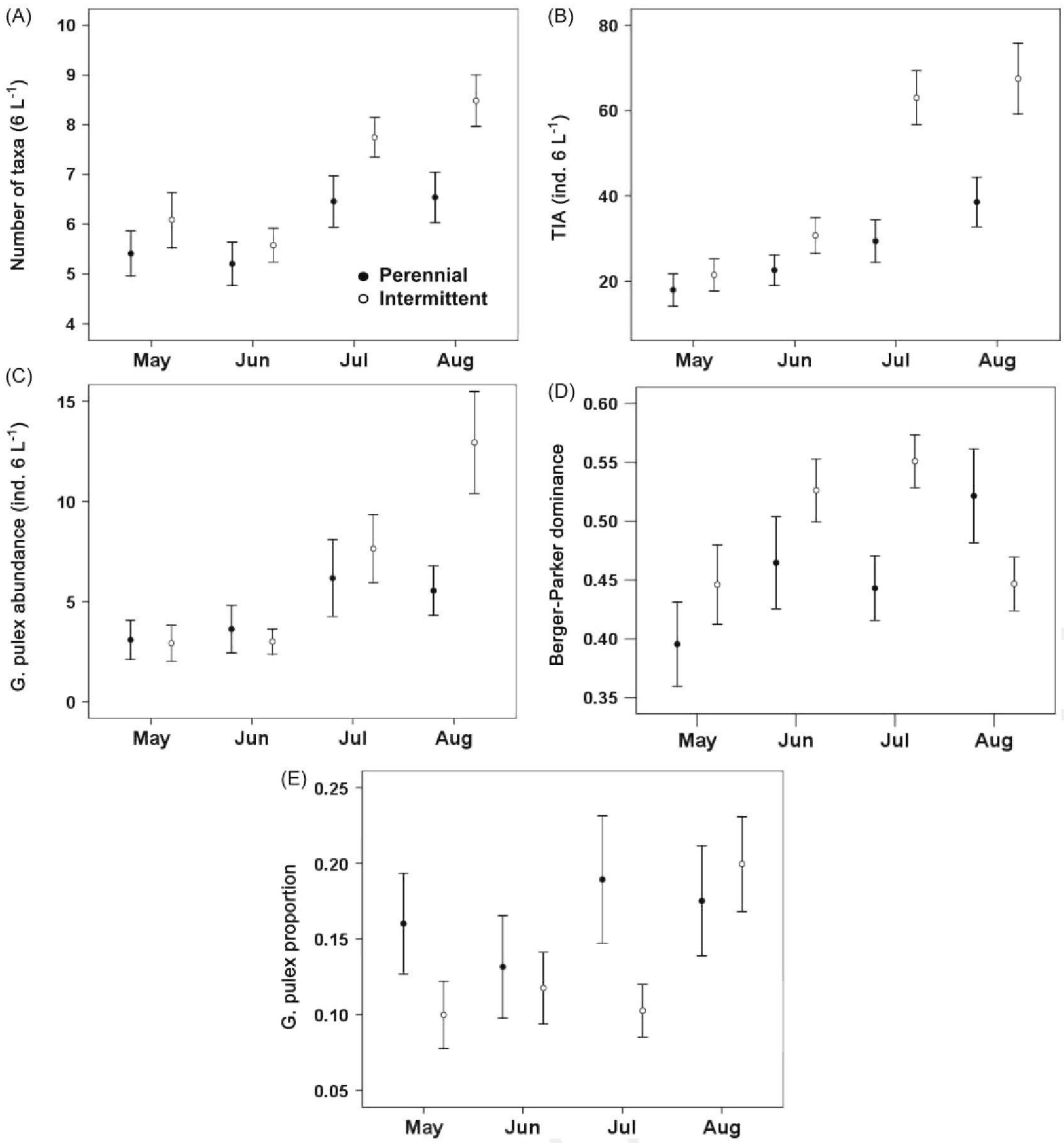

Figure 6. Mean ±1 SE hyporheic community composition at sites with historically perennial and intermittent flow: (A) number of taxa (6 l^{-1}), b) TIA (ind. 6 l^{-1}), c) *G. pulex* abundance (individuals 6 l^{-1}), (D) Berger-Parker dominance index and (E) *G. pulex* abundance as a proportion of TIA.

There is increasing recognition of the importance of the hyporheic zone in stream ecosystem functioning, with its potential as a refugium for invertebrates being one key ecological role (Boulton *et al.*, 1998). Whilst many studies have considered the hyporheic zone as a refugium, previous work has focussed on adverse hydrological conditions, namely spates (Dole-Olivier *et al.*, 1997) and streambed drying (e.g. Clinton *et al.*, 1996). In contrast, refugium use on the River Lathkill was observed during a gradual decline in discharge, which coincided with a substantial increase in the abundance of a competitive taxon, from which an intensification of biotic interactions could be inferred. Recognition that the hyporheic zone may function as a refugium during flow recession in temperate streams is of particular relevance in the face of continuing climatic variability; much research indicates lower summer rainfall, with a consequent increase in the magnitude and duration of low flows likely in some regions of the UK (Hannaford and Marsh, 2006). The hyporheic zone may therefore increase in importance as a refugium that promotes invertebrate survival during flow recession and low flows. However, many anthropogenic activities threaten the ecological integrity of the hyporheic zone by depositing fine sediments which clog interstitial spaces, compromising hydrologic exchange processes and limiting refugial potential (Boulton, 2007; Stubbington *et al.*, 2009b). This study, therefore, adds weight to call for freshwater ecological monitoring programmes and restoration schemes to recognize and explicitly consider the hyporheic zone as an integral ecosystem component.

ACKNOWLEDGEMENTS

We are grateful to Natural England, and in particular Philip Bowler, for supporting research on the River Lathkill and granting site access. We thank Matthew

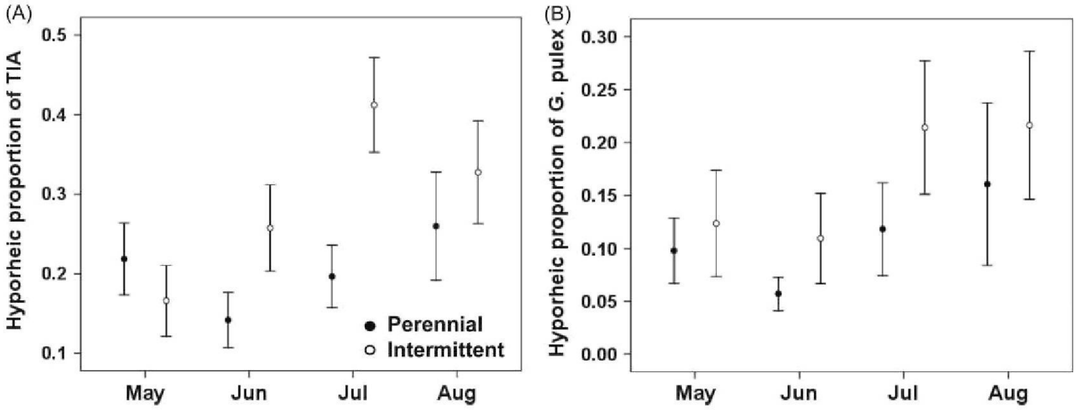

Figure 7. Mean ±1 SE hyporheic proportion of the total invertebrate community, at sites with historically perennial and intermittent flow: (A) TIA and (B) *G. pulex* abundance.

Mohammed, Matt Johnson, Antonia Liversidge and Tom Worrall for assistance in the field. RS acknowledges the support of a Faculty of Social Sciences and Humanities Research Studentship provided by Loughborough University. We thank two anonymous reviewers for constructive comments which helped to improve the manuscript.

REFERENCES

Banks VJ, Gunn J, Lowe DJ. 2009. Stratigraphical influences on the limestone hydrogeology of the Wye catchment, Derbyshire. *Quarterly Journal of Engineering Geology and Hydrogeology* **42**: 211–225. DOI: 10.1144/1470-9236/07-046.

Boulton AJ. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology* **48**: 1173–1185. DOI: 10.1046/j.1365–2427.2003.01084.x.

Boulton AJ. 2007. Hyporheic rehabilitation in rivers: restoring vertical connectivity. *Freshwater Biology* **52**: 632–650. DOI: 10.1111/j.1365–2427.2006.01710.x.

Boulton AJ, Findlay S, Marmonier P, Stanley EH, Valett HM. 1998. The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* **29**: 59–81. DOI: 10.1146/annurev.ecolsys.29.1.59.

Boulton AJ, Valett HM, Fisher SG. 1992. Spatial distribution and taxonomic composition of the hyporheos of several Sonoran Desert streams. *Archiv für Hydrobiologie* **125**: 37–61.

Caruso BS. 2002. Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *Journal of Hydrology* **257**: 115–133. DOI: 10.1016/S0022-1694 (01) 00546-7.

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecology* **18**: 117–143. DOI: 10.1111/j.1442–9993.1993.tb00438.x.

Clinton SM, Grimm NB, Fisher SG. 1996. Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. *Journal of the North American Benthological Society* **15**: 700–712.

Cooling MP, Boulton AJ. 1993. Aspects of the hyporheic zone below the terminus of a South Australian arid-zone stream. *Australian Journal of Marine and Freshwater Research* **44**: 411–426. DOI: 10.1071/MF9930411.

Covich AP, Crowl TA, Scatena FN. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology* **48**: 1199–1206. DOI: 10.1046/j.1365–2427.2003.01093.x.

Datry T, Larned ST, Scarsbrook MR. 2007. Responses of hyporheic invertebrate assemblages to large-scale variation in flow permanence and surface-subsurface exchange. *Freshwater Biology* **52**: 1452–1462. DOI: 10.1111/j.1365–2427.2007.01775.x.

Datry T, Scarsbrook M, Larned S, Fenwick G. 2008. Lateral and longitudinal patterns within the stygoscape of an alluvial corridor. *Fundamental and Applied Limnology* **171**: 335–347. DOI: 10.1127/1863-9135/2008/0171-0335.

Death RG, Winterbourn MJ. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* **76**: 1446–1460.

Dewson ZS, Death RG, James ABW. 2003. The effect of water abstractions on invertebrate communities in four small North Island streams. *New Zealand Natural Sciences* **28**: 51–65. DOI: 10.1899/07-003R.1.

Dewson ZS, James ABW, Death RG. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* **26**: 401–415. DOI: 10.1899/06-110.1.

Dole-Olivier MJ, Marmonier P. 1992. Effects of spates on the vertical distribution of the interstitial community. *Hydrobiologia* **230**: 49–61. DOI: 10.1007/BF00015114.

Dole-Olivier MJ, Marmonier P, Beffy JL. 1997. Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? *Freshwater Biology* **37**: 257–276. DOI: 10.1046/j.1365–2427.1997.00140.x.

Franken RJM, Storey RG, Williams DD. 2001. Biological, chemical and physical characteristics of downwelling and upwelling zones in the hyporheic zone of a north-temperate stream. *Hydrobiologia* **444**: 183–195. DOI: 10.1023/A:1017598005228.

Griffith MB, Perry SA. 1993. The distribution of macroinvertebrates in the hyporheic zone of two small Appalachian headwater streams. *Archiv für Hydrobiologie* **126**: 373–384.

Hannaford J, Marsh T. 2006. An assessment of trends in UK runoff and low flows using a network of undisturbed catchments. *International Journal of Climatology* **26**: 1237–1253. DOI: 10.1002/joc.1303.

Hannah DM, Malcolm IA, Bradley C. 2009. Seasonal hyporheic temperature dynamics over riffle bedforms. *Hydrological Processes* **23**: 2178–2194. DOI: 10.1002/hyp.7256.

James R. 1997. Mine drainage and water resources. *Mining History: The Bulletin of the Peak District Mines Historical Society* **13**: 74–82.

James ABW, Dewson ZS, Death RG. 2008. Do stream macroinvertebrates use instream refugia in response to severe short-term flow reduction in New Zealand streams? *Freshwater Biology* **53**: 1316–1334. DOI: 10.1111/j.1365–2427.2008.01969.x.

James ABW, Suren AM. 2009. The response of invertebrates to a gradient of flow reduction—an instream channel study in a New Zealand lowland river. *Freshwater Biology* **54**: 2225–2242. DOI: 10.1111/j.1365–2427.2009.02254.

Lake PS. 2003. Ecological effects of perturbation by drought in running waters. *Freshwater Biology* **48**: 1161–1172. DOI: 10.1046/j.1365–2427.2003.01086.x.

Langan SJ, Johnston L, Donaghy MJ, Youngson AF, Hay DW, Soulsby C. 2001. Variation in river water temperatures in an upland stream over a 30-year period. *Science of the Total Environment* **265**: 195–207. DOI: 10.1016/S0048-9697(00)00659-8.

Malard F, Galassi D, Lafont M, Dolédec S, Ward JV. 2003. Longitudinal patterns of invertebrates in the hyporheic zone of a glacial river. *Freshwater Biology* **48**: 1709–1725. DOI: 10.1046/j.1365–2427.2003.01118.x.

Malcolm IA, Soulsby C, Youngson AF, Petry J. 2003. Heterogeneity in ground water-surface water interactions in the hyporheic zone of a salmonid spawning stream. *Hydrological Processes* **17**: 601–617. DOI: 10.1002/hyp.1156.

Malcolm IA, Soulsby C, Youngson AF, Hannah DM, McLaren IS, Thorne A. 2004. Hydrological influences on hyporheic water quality: implications for salmon egg survival. *Hydrological Processes* **18**: 1543–1560. DOI: 10.1002/hyp.1405.

Maridet L, Wasson JG, Philippe M. 1992. Vertical distribution of fauna in the bed sediment of three running water sites: influence of physical and trophic factors. *Regulated Rivers-Research & Management* **7**: 45–55. DOI: 10.1002/rrr.3450070107.

Marmonier P, Creuzé des Châtelliers M. 1991. Effects of spates on interstitial assemblages of the Rhône River. Importance of spatial heterogeneity. *Hydrobiologia* **210**: 243–251. DOI: 10.1007/BF00034683.

McCune B, Mefford MJ. 2006. PC-ORD multivariate analysis of ecological data version 5.10. MjM Software, Gleneden Beach, Oregon, USA.

McGrath KE, Peeters ETHM, Beijer JAJ, Scheffer M. 2007. Habitat-mediated cannibalism and microhabitat restriction in the stream invertebrate *Gammarus pulex*. *Hydrobiologia* **589**: 155–164. DOI: 10.1007/s10750-007-0731-5.

McIntosh MD, Benbow ME, Burky AJ. 2002. Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications* **18**: 569–581. DOI: 10.1002/rra.694.

Met Office, 2009. 2008 weather summaries—Regional values. http://www.metoffice.gov.uk/climate/uk/2008/index.html. Accessed 01/06/09.

Monk WA, Wood PJ, Hannah DM, Wilson DA. 2008. Macroinvertebrate community response to inter-annual and regional river flow regime dynamics. *River Research and Applications* **24**: 988–1001. DOI: 10.1002/rra.1120.

Murdoch PS, Baron JS, Miller TL. 2000. Potential effects of climate change on surface-water quality in North America. *Journal of the American Water Resources Association* **36**: 347–366. DOI: 10.1111/j.1752-1688.2000.tb04273.x.

Olsen DA, Townsend CR. 2003. Hyporheic community composition in a gravel-bed stream: influence of vertical hydrological exchange, sediment structure and physicochemistry. *Freshwater Biology* **48**: 1363–1378. DOI: 10.1046/j.1365–2427.2003.01097.x.

Storey RG, Williams DD. 2004. Spatial responses of hyporheic invertebrates to seasonal changes in environmental parameters. *Freshwater Biology* **49**: 1468–1486. DOI: 10.1111/j.1365–2427.2004.01284.x.

Stubbington R, Greenwood AM, Wood PJ, Armitage PD, Gunn J, Robertson AL. 2009a. The response of perennial and temporary headwater stream invertebrate communities to hydrological extremes. *Hydrobiologia* **630**: 299–312. DOI: 10.1007/s10750-009-9823-8.

Stubbington R, Wood PJ, Boulton AJ. 2009b. Low flow controls on benthic and hyporheic macroinvertebrate assemblages during supra-seasonal drought. *Hydrological Processes* **23**: 2252–2263. DOI: 10.1002/hyp.7290.

Stubbington R, Dunscombe MP, Gledhill T. 2009c. Occurrence of Antrobathynella stammeri (Jakobi, 1954) (Crustacea: Syncarida: Bathynellidae) in the hyporheic zone of two English karst rivers. *Cave and Karst Science* **35**: 59–62.

Webb BW, Clack PD, Walling DE. 2003. Water-air temperature relationships in a Devon river system and the role of flow. *Hydrological Processes* **17**: 3069–3084. DOI: 10.1002/hyp.1280.

Wisenden B, Pohlman SG, Watkin EE. 2001. Avoidance of conspecific injury released chemical cues by free-ranging Gammarus lacustris (Crustacea: Amphipoda). *Journal of Chemical Ecology* **27**: 1249–1258. DOI: 10.1023/A:1010376215052.

Wood PJ, Armitage PD. 1999. Sediment deposition in a small lowland stream—management implications. *Regulated Rivers-Research & Management* **15**: 199–210. DOI: 10.1002/(SICI)1099–1646(199901/06)15:1/3<199::AID-RRR531>3.0.CO; 2-0.

Wood PJ, Armitage PD. 2004. The response of the macroinvertebrate community to low flow variability and supra-seasonal drought within a groundwater dominated stream. *Archiv für Hydrobiologie* **161**: 1–20. DOI: 10.1127/0003-9136/2004/0161-0001.

Wood PJ, •Boulton AJ, Little S, Stubbington R. Is the hyporheic zone a refugium for macroinvertebrates during severe low flow conditions? *Fundamental and Applied Limnology* in press.

Wood PJ, Gunn J, Smith H, Abas-Kutty A. 2005. Flow permanence and macroinvertebrate community diversity within groundwater dominated headwater streams and springs. *Hydrobiologia* **545**: 55–64. DOI: 10.1007/s10750-005-2213-y.