

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

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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 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

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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

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1 and Armitage, 1999; Datry *et al.*, 2008), whilst increas- 60
 2 ing densities have been attributed to the concentration 61
 3 of individuals into a smaller submerged area (James 62
 4 *et al.*, 2008). Such habitat contraction can intensify bio- 63
 5 logical interactions including predation and competition 64
 6 (Covich *et al.*, 2003). Whilst these effects of low flows 65
 7 on benthic invertebrates are relatively well documented, 66
 8 little research has compared community response to flow 67
 9 recession at adjacent sites with contrasting historic flow 68
 10 permanence, although it has been suggested that the com- 69
 11 munities of intermittent sites should be more resistant 70
 12 to adverse environmental changes (Boulton, 2003; Lake, 71
 13 2003). 72

14 Several studies have noted the hyporheic zone as a 73
 15 refugium that promotes the survival of benthic inver- 74
 16 tebrates following streambed drying at sites with inter- 75
 17 mittent flow (Griffiths and Perry, 1993; Clinton *et al.*, 76
 18 1996). In contrast, few studies have considered how use 77
 19 of the hyporheic zone by benthic invertebrates changes 78
 20 during a gradual decline in discharge (James and Suren, 79
 21 2009; Stubbington *et al.*, 2009b; Wood *et al.*, in press). 80
 22 Of these, no study has linked changes in the benthic 81
 23 component of the hyporheic zone fauna to flow reces- 82
 24 sion, despite predictions that benthic invertebrates should 83
 25 become more abundant in the hyporheic zone as flow 84
 26 declines (James *et al.*, 2008; Wood *et al.*, in press). Mar- 85
 27 monier and Creuzé des Châtelliers (1991) compared the 86
 28 hyporheic community composition during spates and 87
 29 periods of constant low flow, and found occurrence of 88
 30 benthic invertebrates in the hyporheic sediments to be 89
 31 greatest during low flow in areas of downwelling water. 90
 32 It is not known, however, how such increases in benthic 91
 33 invertebrate abundance within the hyporheic zone affect 92
 34 the permanent hyporheic community. 93

35 Questions therefore remain regarding how benthic and 94
 36 hyporheic invertebrate communities respond to prolonged 95
 37 periods of declining discharge, how use of the hyporheic 96
 38 zone by benthic invertebrates is affected, and how historic 97
 39 flow permanence influences the community response. 98
 40 An uninterrupted 4-month flow recession on the River 99
 41 Lathkill (Derbyshire, UK) provided an opportunity to 100
 42 address these questions at adjacent sites with contrast- 101
 43 ing historic flow permanence regimes. We predicted that: 102
 44 (i) benthic invertebrate abundance in the hyporheic zone 103
 45 would increase if habitat availability declined in the ben- 104
 46 thic sediments, (ii) the permanent hyporheic community 105
 47 would be detrimentally affected by any increase in ben- 106
 48 thic invertebrates and (iii) community responses would 107
 49 be related to the historic flow permanence. 108

52 METHODS

53 *Study area*

54 The River Lathkill (Derbyshire, England; 53°11.2'N, 111
 55 1°43.1'W) flows through Lathkill Dale, a wooded valley 112
 56 in the Derbyshire Dales National Nature Reserve. Land 113
 57 use in the surrounding catchment is predominantly pas- 114
 58 tured. The region has a temperate climate, with a mean 115
 59 annual rainfall of ~1200 mm and a mean annual air tem- 116
 60 perature of 8.0 °C, ranging from 1.7 °C in January to 117
 61 14.5 °C in July (Wood *et al.*, 2005). 118

62

63 Lathkill Dale is underlain by Carboniferous limestone, 64
 65 and the river discharges autogenic water, which has only 66
 67 been in contact with carbonate rocks (Banks *et al.*, 2009). 68
 69 Whilst the limestone aquifer provides the river with 70
 71 significant baseflow, water is lost through the streambed 72
 73 to natural features of the karst bedrock, and transmission 74
 75 losses are exacerbated by underlying drainage levels 76
 77 and remnants of historic lead mining activity (James, 78
 79 1997). Consequently, some reaches within the study 80
 81 area typically lose all surface water during the summer 82
 83 months. 84

85 Five sites in the upper reaches were selected to 86
 87 represent the spatial variability in the river's flow regime. 88
 89 In terms of historic flow permanence, two sites (1 and 90
 91 2) were perennial (Figure 1) and three sites (3–5) were 92
 93 intermittent (Figure 1). The substrate consisted of mixed 94
 95 alluvial deposits dominated by sand- to cobble-sized 96
 97 clasts. Instream vegetation was dominated by mosses and 98
 99 liverworts, with scattered patches of reeds in the marginal 100
 101 areas. 102

103 *Hydrological and meteorological conditions*

104 The River Lathkill is almost entirely groundwater-fed, 105
 106 and the response to low-moderate rainfall events is there- 107
 108 fore subdued and flow recession is slow when compar- 109
 110 ed with surface water fed streams. Flow recession 111
 112 on the river usually begins in April/May and contin- 113
 114 ues until September/October. Reaches with intermittent 114
 115 flow typically begin to lose surface water in May and 115
 116 dry completely by late July. Downstream of the study 116
 117 area, groundwater is forced to the surface by a basalt 117
 118 barrier, and discharge is measured at a gauging station 118
 119 downstream of these perennial springs (Figure 1). 119

120 In 2008, the seasonal flow recession followed the 120
 121 usual pattern, with discharge decreasing sharply in April 121
 122 then continuing to decline slowly (Figure 2). When 122
 123 sampling commenced in mid-May, discharge had reached 123
 124 ~0.43 m³ s⁻¹. Flow recession continued uninterrupted 124
 125 throughout the study period, with the lowest hourly 125
 126 discharges, of 0.090–0.096 m³ s⁻¹, occurring during 126
 127 mid-August, in the days preceding the final sampling 127
 128 date. However, due to above-average rainfall inputs, 128
 129 particularly in July [190% of the 1971–2000 long-term 129
 130 average (LTA)] and August (150% LTA; Met Office, 130
 131 2009), the extent to which decline in flow was reduced 131
 132 compared to a typical year and all sites retained some 132
 133 surface water throughout the study. 133

134 Air temperature data from an automated weather 134
 135 station located 8 km from the River Lathkill indicated 135
 136 that the mean air temperature in the 28 days preceding 136
 137 sampling increased by approximately 2 °C each month, 137
 138 from 8.6 °C in May to 14.6 °C in August. Maximum 138
 139 hourly air temperature in the 28 days preceding sampling 139
 140 also increased during the study, from 21.3 °C in May to 140
 141 24.4 °C in August. 141

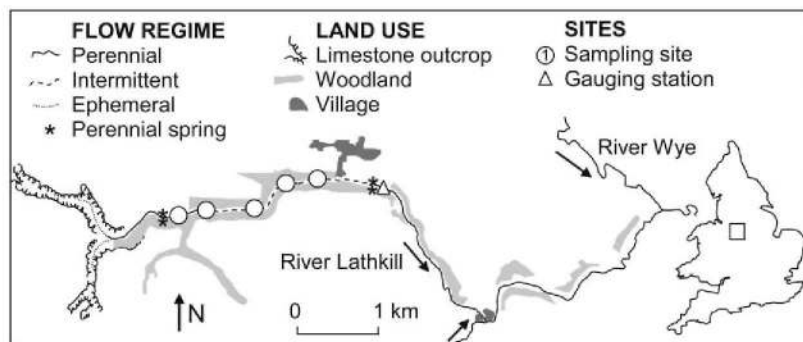


Figure 1. Location map of the River Lathkill, indicating sampling points.

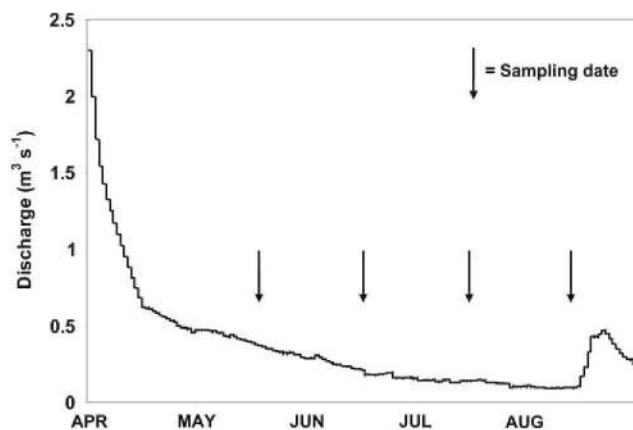


Figure 2. Hydrograph of mean hourly discharge on the River Lathkill, April-September 2008. Location of gauging station shown in Figure 1.

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 m², 250- μ m 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- μ m 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 $0.6 \times$ depth) and wetted width. Depth and velocity were measured using an ADS SENSE-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 Scirtidae (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,

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

4 To investigate the influence of antecedent hydrologi-
5 cal conditions on invertebrate community structure, mean
6 discharge at the downstream gauging station was calcu-
7 lated for the periods 24 h, 7 and 28 days prior to each
8 sampling date.

9 10 *Statistical analysis: invertebrate community data*

11 Non-metric multidimensional scaling (NMDS) was used
12 to examine spatial and temporal variability in invertebrate
13 community composition, using the program PC-ORD
14 (McCune and Mefford, 2006). NMDS is a robust ordina-
15 tion technique in which similarities between biotic assem-
16 blages are visualized by positioning the most similar
17 samples closest together in an *n*-dimensional ordination
18 space. Benthic and hyporheic invertebrate communities
19 at each depth were initially analysed separately. This
20 preliminary analysis indicated that similar patterns were
21 observed at each hyporheic depth, and all were there-
22 fore pooled. Prior to each analysis, data were square root
23 transformed to reduce skewness and reduce the influ-
24 ence of dominant taxa. NMDS was performed in two to
25 six dimensions on a Bray-Curtis distance matrix using a
26 random starting configuration and autopilot mode. Stress
27 functions were calculated for each dimension as a mea-
28 sure of goodness of fit, with a final stress of <0.2 con-
29 sidered ecologically interpretable (Clarke, 1993).

30 Three indices were calculated to describe the benthic
31 and hyporheic invertebrate communities: total inverte-
32 brate abundance (TIA), taxon richness (number of taxa),
33 and the Berger-Parker dominance index (a measure of
34 the proportion of the community accounted for by the
35 most common taxon). In addition, abundance of the
36 most common taxa (calculated separately for benthic and
37 hyporheic samples and defined as taxa accounting for
38 >1% of individuals present in all the samples) was deter-
39 mined for each sampling occasion. To examine use of the
40 hyporheic zone by benthic invertebrates, the proportion of
41 the total (benthic + hyporheic) population found within
42 the hyporheic zone (the hyporheic proportion) was cal-
43 culated for TIA and for selected common benthic taxa.
44 Using proportional data allows comparison of populations
45 sampled using different techniques.

46 All community metrics (NMDS axis scores, indices,
47 abundances and hyporheic proportions) were used as
48 dependent variables in subsequent analyses. Prior to
49 analysis, abundance data were square root transformed
50 and proportional data were arcsine square root trans-
51 formed to reduce skewness and reduce the influence
52 of dominant taxa. To assess spatial and temporal vari-
53 ability in these community metrics, two-way and one-
54 way RM ANOVA tests were conducted as described for
55 environmental variables.

56 Pearson's product-moment correlation coefficients
57 were calculated to examine relationships between all the
58 community metrics and hydrological and water chemistry
59

60 variables. Prior to analysis, abundances and indices were
61 standardized by calculating z-scores for each sampling
62 site. This method of standardization re-scales data from
63 individual sites to allow comparison of the responses of
64 multiple sites to the same external factor.

65 66 67 RESULTS

68 69 *Environmental conditions*

70 Significant reductions in water depth, flow velocity
71 and wetted width occurred between May and August,
72 although these general declines were interrupted by
73 minor increases in depth and wetted width between
74 June and July, and a small increase in velocity between
75 July and August (Table I). Surface and hyporheic water
76 at historically perennial sites had significantly higher
77 conductivity and lower pH, temperature and DO (%
78 saturation) compared with intermittent sites ($p < 0.05$).
79 Surface and hyporheic water underwent similar changes
80 during flow recession, with significant linear changes
81 being observed in DO (mg l^{-1}), pH and conductivity
82 (Table I).

83 84 *Invertebrate communities*

85 A total of 30 812 individuals from 79 taxa were recorded
86 from 75-benthic Surber samples. The freshwater shrimp,
87 *G. pulex* (L.) (Amphipoda: Crustacea), dominated the
88 benthic community accounting for 40.8% TIA. The Chi-
89 ronomidae (Diptera) were also abundant, and comprised
90 17.8% TIA. Eight other taxa made up 1-10% TIA: the
91 flatworm *Polycelis felina*, the Oligochaeta, two mayflies
92 (*Serratella ignita*, *Baetis* spp.), a stonefly (*Leuctra* spp.),
93 a caddisfly (*Agapetus fuscipes*) and two riffle beetle lar-
94 vae (*Elmis aenea*, *Riolus subviolaceus*).

95 A total of 8840 invertebrates were recorded from
96 226-hyporheic samples collected from depths of 10, 20
97 and 30 cm. The Ostracoda, Chironomidae and *G. pulex*
98 dominated at all depths. The Ostracoda accounted for 19-
99 29% TIA at each depth and decreased in abundance with
100 increasing depth. The Chironomidae accounted for 18.9%
101 TIA at 10 cm increasing to 30.3% at 30 cm, and occurred
102 at similar densities at each depth. *G. pulex* decreased
103 slightly in both abundance and dominance with increasing
104 depth, from 17.1% TIA at 10 cm, to 14.2% TIA at 20 and
105 30 cm. Other taxa comprising 1-10% TIA were similar
106 at all depths and included the Oligochaeta, Cyclopoida,
107 Nematoda, *P. felina* and three insect taxa (*Nemoura* spp.,
108 *Leuctra* spp., and *S. ignita*).

109 110 *Community ordination*

111 NMDS of the benthic community data yielded a three-
112 dimensional (3D) solution (final stress = 0.15, final insta-
113 bility = 0, Monte Carlo test $p = 0.004$; Figure 3).
114 Separation of samples along axis 2 indicated clear dif-
115 ferences in community composition at sites with historic
116 intermittent and perennial flow ($p < 0.001$; Figure 3(A)).
117 Separation along axis 1 was more variable; however, axis
118

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 ± 0.66	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 except 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.

1 scores were positively correlated with all discharge vari- 32
 2 ables (Table II) and underwent linear temporal change, 33
 3 decreasing each month as the flow recession progressed 34
 4 ($p < 0.001$; inset, Figure 3(B)). 35

5 NMDS ordination of the hyporheic community data 36
 6 yielded a 3-D solution (final stress = 0.19, final insta- 37
 7 bility = 0.0228, Monte Carlo test $p = 0.004$; Figure 4). 38
 8 Community composition could be distinguished accord- 39
 9 ing to historic flow permanence on both axis 1 ($p =$ 40
 10 0.033) and axis 2 ($p < 0.001$; Figure 4(A)). Despite con- 41
 11 siderable variability and overlap between months, tempo- 42
 12 ral change was also significant on both axes, with axis 1 43
 13 scores rising to a peak in July then declining moderately 44
 14 in August ($p < 0.001$; inset, Figure 4(B)) and the oppo- 45
 15 site pattern being observed for axis 2 scores ($p < 0.001$; 46
 16 Figure 4(B)); both axes had weak but significant correla- 47
 17 tions with all discharge variables as well as wetted width 48
 18 (Table II). 49

20 Temporal change in benthic community composition

21 Mean taxon richness was comparable at historically inter- 50
 22 mittent sites (17.6 ± 0.56 taxa 0.1 m^{-2}) and perennial 51
 23 sites (19.0 ± 0.77 taxa 0.1 m^{-2} ; $p = 0.412$) and varied 52
 24 little during the flow recession ($p = 0.070$; Figure 5(A)). 53
 25 The interaction with flow permanence was significant, 54
 26 due to taxon richness peaking in May at intermittent sites 55
 27 and in June at perennial sites ($p = 0.010$). 56

28 Mean TIA was similar at sites with historically inter- 57
 29 mittent and perennial flow ($p = 0.503$) and increased 58
 30 moderately between May (316.1 ± 41.2 individuals (ind.) 59
 31 0.1 m^{-2}) and June (432.8 ± 56.2 ind. 0.1 m^{-2}), then 60
 61
 62

stabilized ($p = 0.150$; Figure 5(B)). The interaction be- 32
 33 tween TIA and historic flow permanence was not sig- 34
 35 nificant ($p = 0.391$). Mean abundance of the dominant 36
 37 benthic taxon, *G. pulex*, was similar at historically inter- 38
 39 mittent and perennial sites ($p = 0.936$). *G. pulex* abun- 40
 41 dance increased significantly between May (78 ± 8.9 42
 43 ind. 0.1 m^{-2}) and August (244.9 ± 41.9 ind. 0.1 m^{-2} ; 44
 45 $p < 0.001$; Figure 5(C)) and was negatively correlated 46
 47 with all discharge and hydrological variables (Table II). 48
 49 The interaction between *G. pulex* abundance and his- 50
 51 toric flow permanence was significant ($p = 0.01$), with 52
 53 abundance at perennial sites increasing between May and 54
 55 June then remaining stable ($p = 0.011$), whilst abun- 56
 57 dance at intermittent sites increased between May and 58
 59 June and again between July and August ($p = 0.002$; 60
 61 Figure 5(C)). 62

Berger-Parker dominance was comparable at sites with 49
 50 historically intermittent and perennial flow ($p = 0.498$). 51
 52 Dominance increased throughout the flow recession ($p <$ 53
 54 0.001; Figure 5(D)), and was negatively correlated with 55
 56 all discharge and hydrological variables (Table II). The 57
 58 increase in community dominance occurred as the pro- 59
 60 portion of *G. pulex* rose from 0.27 TIA in May to 61
 62 0.49 TIA in August ($p < 0.001$; Figure 5(E)). The inter-
 action 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)).

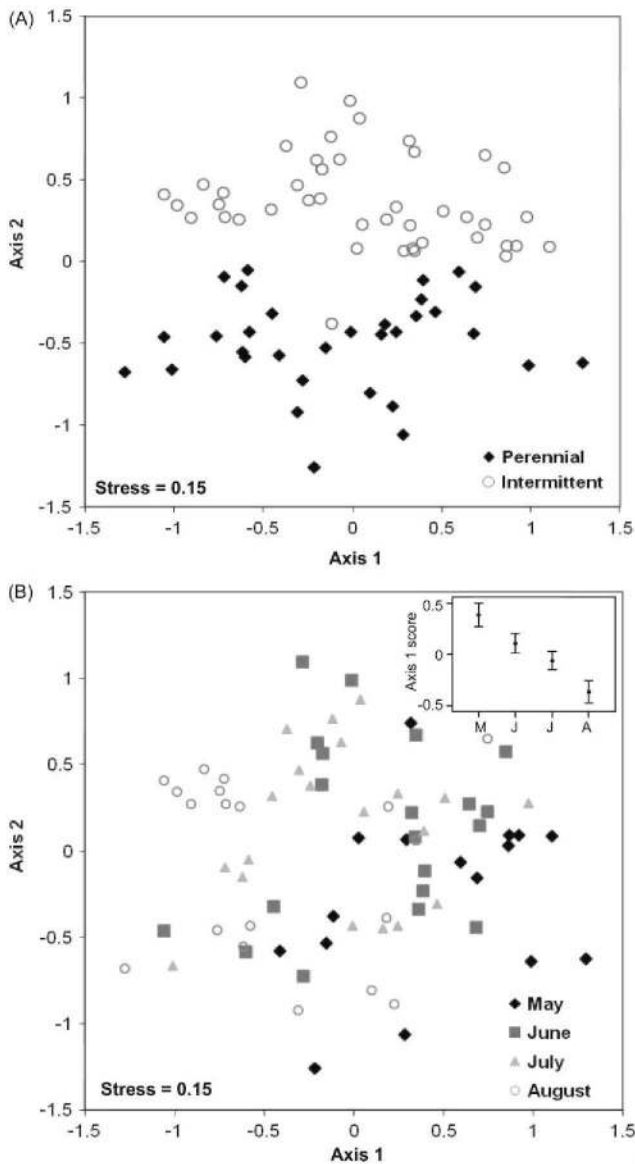


Figure 3. Two-dimensional (2D) NMDS ordination of benthic invertebrate community composition during a 4-month flow recession: (A) historic flow permanence and (B) temporal change (inset: mean \pm 1 SE temporal change in axis 1 score).

1 Temporal change in hyporheic community composition

2 Mean taxon richness was comparable at historically inter-
 3 mittent sites (7.1 ± 0.3 taxa 6 l^{-1}) and perennial sites
 4 (5.9 ± 0.3 taxa 6 l^{-1} ; $p = 0.368$), and was lower in May
 5 (5.7 ± 0.4 taxa 6 l^{-1}) and June (5.4 ± 0.3 taxa 6 l^{-1})
 6 than in July (7.3 ± 0.3 taxa 6 l^{-1}) and August ($7.7 \pm$
 7 0.4 taxa 6 l^{-1} ; $p < 0.001$; Figure 6(A)). The interaction
 8 between taxon richness and historic flow permanence
 9 was not significant ($p = 0.559$), although the increase
 10 in richness was more pronounced at intermittent sites
 11 (Figure 6(A)). Increased richness reflected the occurrence
 12 of several insect taxa which were common in the benthos
 13 in all months but only occurred in the hyporheic zone in
 14 July and/or August [i.e. *Silo nigricornis*, *Chaetopteryx*
 15 *villosa* and *Drusus annulatus* (Trichoptera), *Elmis aenea*
 16 and *Riolus subviolaceus* (Coleoptera)].

60 Mean TIA was moderately higher at historically inter-
 61 mittent sites (42.1 ± 3.0 ind. 6 l^{-1}) than at perennial sites
 62 (27.7 ± 2.3 ind. 6 l^{-1} ; $p = 0.07$), increased between May
 63 (19.8 ± 2.7 ind. 6 l^{-1}) and August (54.9 ± 5.7 ind. 6 l^{-1} ;
 64 $p < 0.001$; Figure 6(B)), and had highly significant nega-
 65 tive correlations with all discharge variables as well as
 66 velocity (Table II). The interaction between TIA and his-
 67 toric flow permanence was not significant ($p = 0.319$),
 68 despite the increase in TIA being more pronounced at
 69 intermittent sites (Figure 6(B)). The Ostracoda and *G.*
 70 *pulex* were the principal taxa responsible for the increase
 71 in TIA. Ostracods were particularly abundant at histor-
 72 ically intermittent sites ($p = 0.010$), where mean abun-
 73 dance increased from 1.9 ± 0.5 ind. 6 l^{-1} in May to
 74 14.2 ± 3.0 ind. 6 l^{-1} in July ($p < 0.001$). Mean *G. pulex*
 75 abundance was similar at historically intermittent and
 76 perennial sites ($p = 0.614$) and increased between May
 77 (3.0 ± 0.65 ind. 6 l^{-1}) and August (10.0 ± 1.67 ind.
 78 6 l^{-1} ; $p < 0.001$; Figure 6(C)), as reflected by the nega-
 79 tive correlations with all discharge and hydrological
 80 variables (Table II). Although, there was no significant
 81 interaction between month and historic flow permanence
 82 ($p = 0.227$), the increase in *G. pulex* abundance was only
 83 significant at intermittent sites ($p = 0.004$; Figure 6(C)).

84 Berger-Parker dominance was moderately higher at
 85 historically intermittent sites compared with perennial
 86 sites ($p = 0.098$), and a significant interaction was also
 87 observed with the flow permanence ($p = 0.012$). At sites
 88 with historically perennial flow, dominance increased
 89 between May and June and again between July and
 90 August ($p = 0.03$; Figure 6(D)); this was associated
 91 with the Chironomidae between May and July, then
 92 with *P. felina* in August. At sites with intermittent
 93 flow, increasing dominance between May and July and
 94 a subsequent decrease in August ($p = 0.003$) reflected
 95 seasonal changes in the Chironomidae (Figure 6(D)). A
 96 moderate increase in the proportion of TIA accounted
 97 for by *G. pulex* also occurred between June (0.12) and
 98 August (0.19; $p = 0.108$; Figure 6(E)).

101 Interactions between benthic and hyporheic communities

102 The hyporheic proportion of total TIA was moderately
 103 higher at historically intermittent sites (0.30 ± 0.03) than
 104 at perennial sites (0.20 ± 0.02 ; $p = 0.394$). Considering
 105 all sites, an increase in the hyporheic proportion of
 106 TIA between May (0.19 ± 3.2) and August (0.30 ± 4.6)
 107 was not significant ($p = 0.280$; Figure 7(A)); neither was
 108 the interaction with historic flow permanence significant
 109 ($p = 0.081$).

110 The hyporheic proportion of the *G. pulex* population
 111 was also moderately higher at historically intermittent
 112 sites (0.17 ± 0.03) compared with perennial sites ($0.11 \pm$
 113 0.02 ; $p = 0.692$), and also increased during the flow
 114 recession, from 0.11 in May to 0.19 in August ($p =$
 115 0.263 ; Figure 7(B)). There was no interaction with flow
 116 permanence ($p = 0.998$), although the increase was more
 117 pronounced at intermittent sites (Figure 7(B)).

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

	NMDS axis score		TIA ^a	Taxon richness ^a	Berger-Parker dominance ^b	<i>G. pulex</i> abundance ^a
	Axis 1	Axis 2				
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.* $p < 0.05$.** $p < 0.01$.

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

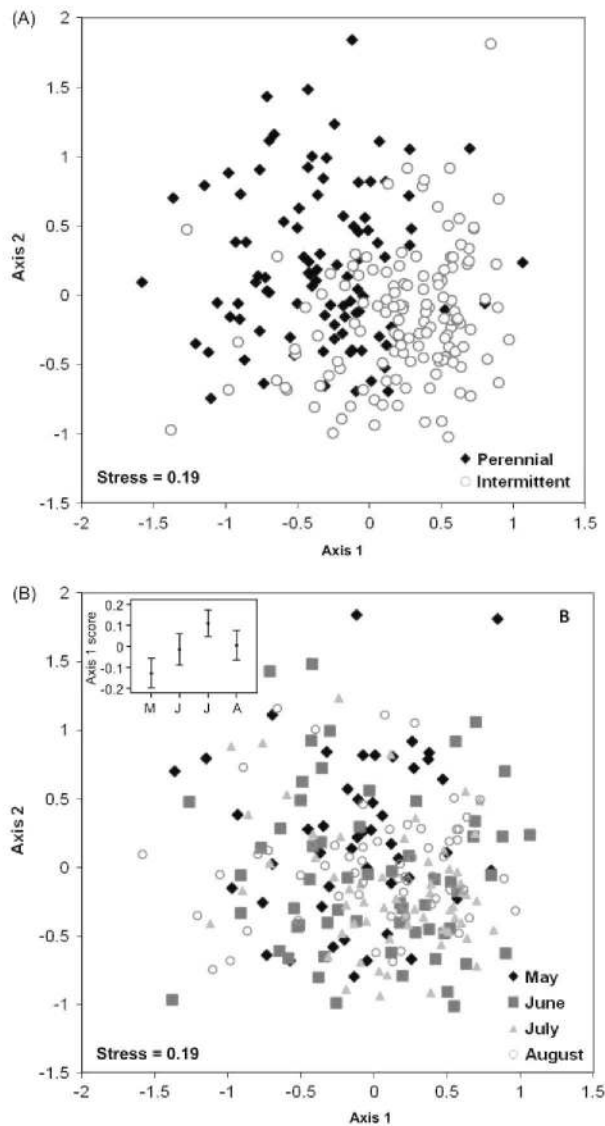


Figure 4. 2-D NMDS ordination of hyporheic invertebrate community composition during a 4-month flow recession: (A) historic flow permanence and (B) temporal change (inset: Mean \pm 1 SE temporal change in axis 1 score).

1 to expose considerable areas of mid-channel benthic sedi-
 2 ments, resulting in an earlier increase in benthic *G. pulex*
 3 population densities. Boulton (2003) suggests that during
 4 a period of declining flow, a taxon will decrease in abun-
 5 dance only once a 'critical threshold' at which condi-
 6 tions becoming unfavourable is reached; increases in
 7 abundance suggests that this threshold was not reached
 8 for *G. pulex* in this study.

10 Benthic invertebrate use of the hyporheic zone

11 Some studies have found the hyporheic zone to act as
 12 a benthic invertebrate refugium during adverse condi-
 13 tions in the surface channel, in particular during floods
 14 (Dole-Olivier and Marmonier, 1992) and streambed dry-
 15 ing (Cooling and Boulton, 1993). Of the few studies
 16 that have considered the hyporheic zone refugium during
 17 low flows (James *et al.*, 2008; James and Suren, 2009;
 18 Stubbington *et al.*, 2009b; Wood *et al.*, in press), only
 19 one (Stubbington *et al.* 2009b; Wood *et al.*, in press)

60 has reported evidence supporting the hyporheic refuge
 61 hypothesis, but refugium use primarily corresponded to
 62 changes in the thermal regime. The absence of a refugium
 63 effect as discharge declines has been attributed to condi-
 64 tions in the benthic sediments remaining favourable, or
 65 at least preferable to the hyporheic zone (James *et al.*,
 66 2008). In the River Lathkill, however, abundance of the
 67 benthic species *G. pulex* increased significantly in the
 68 hyporheic zone as flow declined, and a moderate increase
 69 in the proportion of the *G. pulex* population inhabiting the
 70 hyporheic sediments was also observed. Vertical migra-
 71 tions into the hyporheic sediments probably occurred in
 72 response to increasing biological interactions (e.g. cannibal-
 73 ism and competition) in the benthic sediments as *G.*
 74 *pulex* population densities increased in the contracting
 75 area of submerged habitat (Lake, 2003). This sugges-
 76 tion is supported by experimental work demonstrating
 77 a behavioural avoidance response in *Gammarus* exposed
 78 to chemicals released by conspecifics injured in cannibal-
 79 istic attacks (Wisenden *et al.*, 2001), with avoidance
 80 responses including the preferential use of sediments with
 81 smaller interstitial spaces (McGrath *et al.*, 2007).

82 Temporal increases in *G. pulex* abundance and TIA
 83 in the hyporheic zone were more pronounced at histori-
 84 cally intermittent sites compared with perennial sites. It
 85 is probably that these differences, rather than reflecting the
 86 flow permanence regime itself, reflect the *cause* of that
 87 regime, i.e. the relative contribution of upwelling ground-
 88 water to streamflow. Perennial sites had higher conduc-
 89 tivity, lower DO concentrations and lower temperatures
 90 compared with intermittent sites, indicating that peren-
 91 nial sites were dominated by upwelling groundwater and
 92 intermittent sites by downwelling surface water (Malcolm
 93 *et al.*, 2003). Additional evidence of the dominant direc-
 94 tion of hydrologic exchange includes a major upwelling
 95 groundwater spring at one perennial site (1, Figure 1;
 96 Wood *et al.*, 2005), obligate groundwater species at the
 97 second perennial site (2, Figure 1; Stubbington *et al.*,
 98 2009c) and the mine drainage levels that cause transmis-
 99 sion losses from reaches with intermittent flow. Down-
 100 welling surface water can facilitate passive and active
 101 migrations of benthic taxa (Datry *et al.*, 2008), and the
 102 direction of hydrologic exchange can influence use of
 103 the hyporheic zone refugium during spates (Dole-Olivier
 104 *et al.*, 1997). In the current investigation, the more pro-
 105 nounced increases in *G. pulex* abundance and TIA in the
 106 hyporheic zone of intermittent sites indicated that down-
 107 welling water can also promote hyporheic refugium use
 108 during low flow conditions.

109 Hyporheic community response to flow recession 110 and benthic migrations

111 It was predicted that increased abundance of benthic taxa
 112 in the hyporheic zone would have detrimental effects on
 113 the permanent hyporheic community, due to increasing
 114 biotic pressures. However, the increase in *G. pulex*
 115 abundance in the hyporheic zone was not associated
 116 with changes in Berger-Parker dominance, hyporheic
 117 taxon richness increased, and no common taxon of
 118

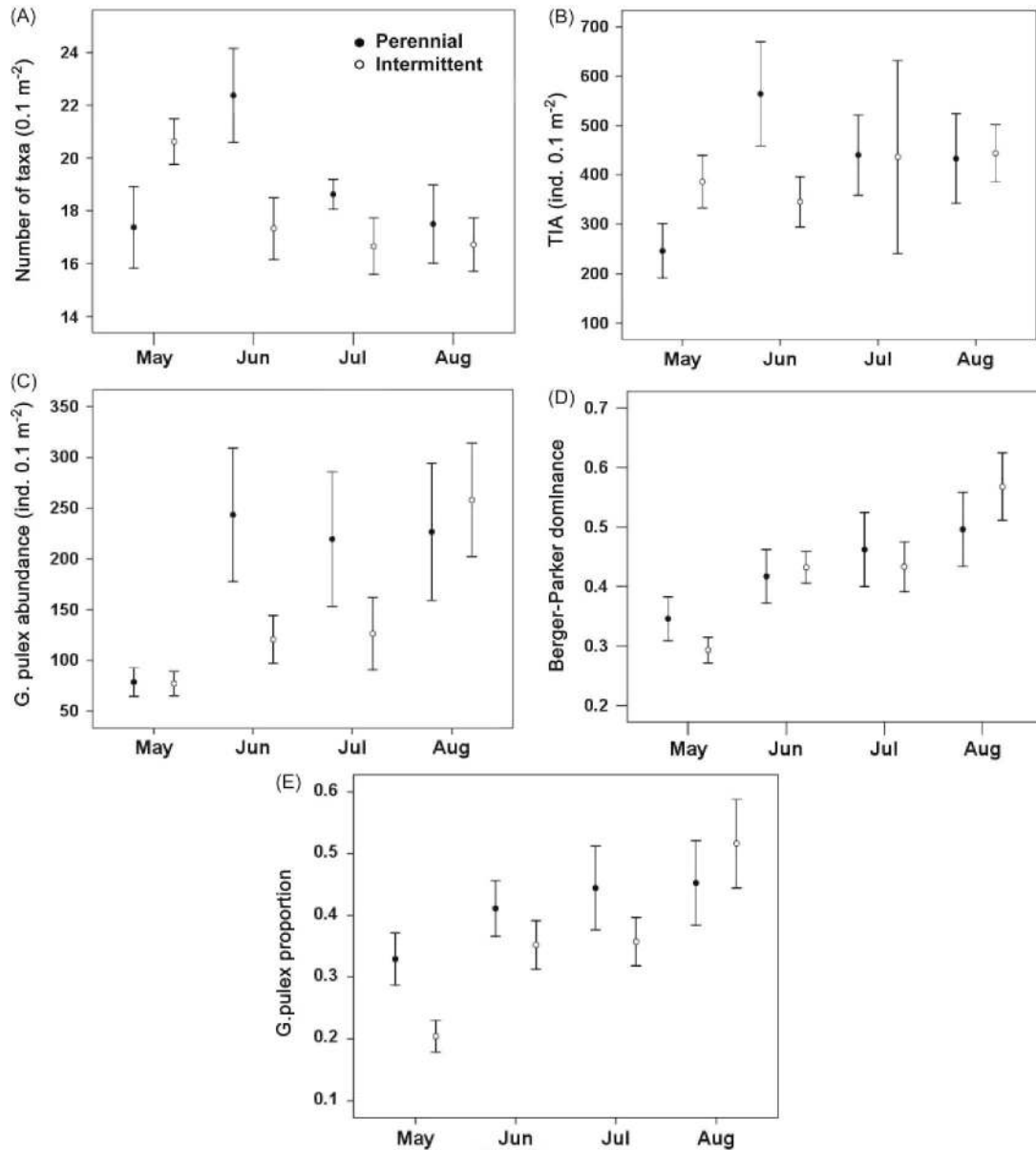


Figure 5. Mean ± 1 SE benthic invertebrate community composition at sites with historically perennial and intermittent flow: (A) number of taxa (0.1 m^{-2}), (B) TIA (ind. 0.1 m^{-2}), (C) *G. pulex* abundance (individuals 0.1 m^{-2}), (D) Berger-Parker dominance index and (E) *G. pulex* abundance as a proportion of TIA.

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

4 Although NMDS axis scores changed significantly dur-
5 ing the flow recession, the ordination of hyporheic com-
6 munity composition indicated considerable variability
7 both within and between months. Compositional shifts in
8 response to changing environmental conditions are often
9 less pronounced in hyporheic communities compared
10 with benthic assemblages (Malard *et al.*, 2003), reflecting
11 the overriding importance of relatively constant environ-
12 mental parameters such as sediment composition (Olsen
13 and Townsend, 2003), porosity (Maridet *et al.*, 1992)
14 and the direction of hydrologic exchange (Franken *et al.*,
15 2001) in determining hyporheic community composition.
16 Relationships between hyporheic communities and envi-
17 ronmental 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.

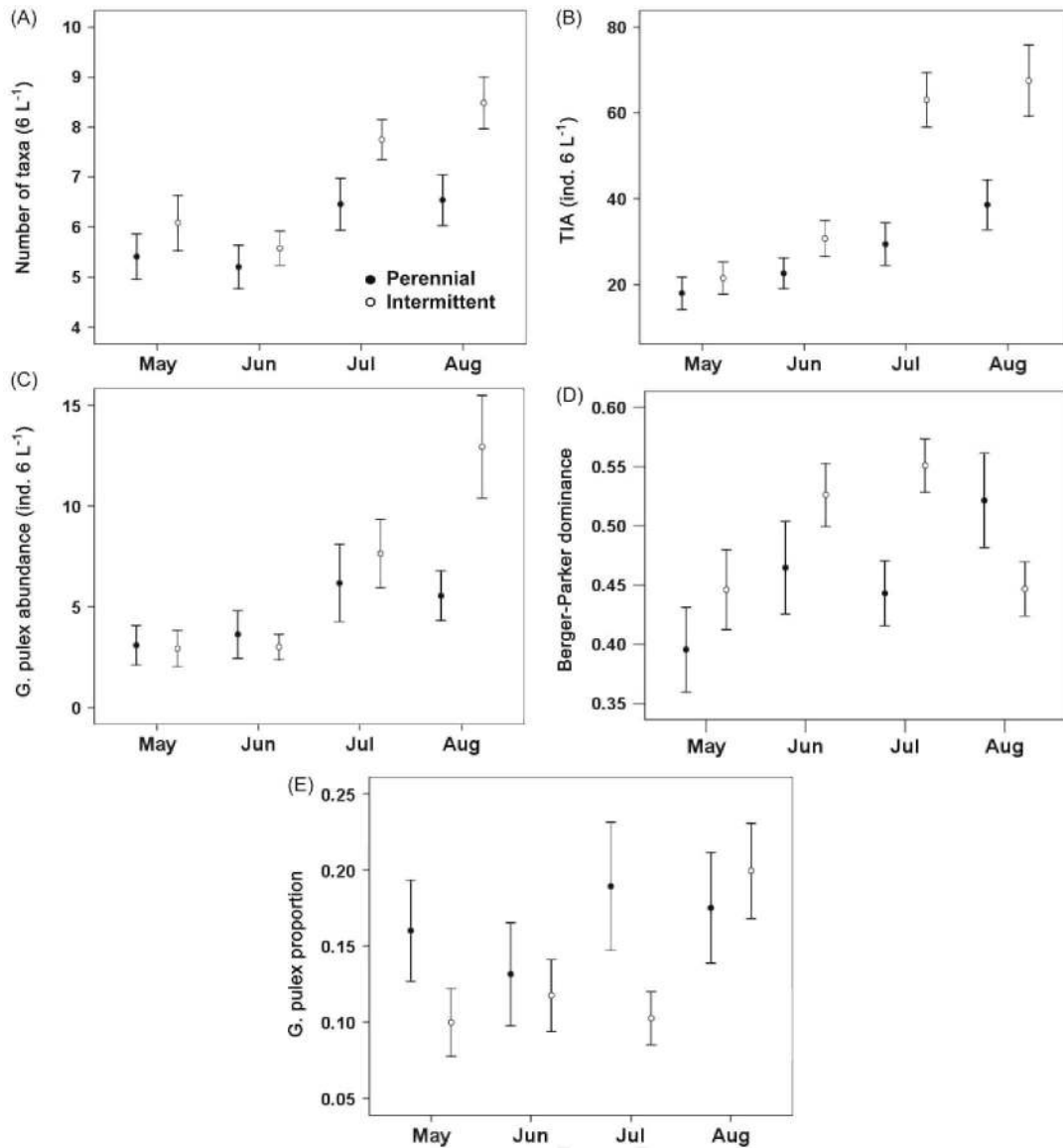


Figure 6. Mean ± 1 SE hyporheic community composition at sites with historically perennial and intermittent flow: (A) number of taxa (6 L^{-1}), (B) TIA ($\text{ind. } 6\text{ L}^{-1}$), (C) *G. pulex* abundance (individuals 6 L^{-1}), (D) Berger-Parker dominance index and (E) *G. pulex* abundance as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

1 There is increasing recognition of the importance
 2 of the hyporheic zone in stream ecosystem function-
 3 ing, with its potential as a refugium for invertebrates
 4 being one key ecological role (Boulton *et al.*, 1998).
 5 Whilst many studies have considered the hyporheic
 6 zone as a refugium, previous work has focussed on
 7 adverse hydrological conditions, namely spates (Dole-
 8 Olivier *et al.*, 1997) and streambed drying (e.g. Clinton
 9 *et al.*, 1996). In contrast, refugium use on the River
 10 Lathkill was observed during a gradual decline in dis-
 11 charge, which coincided with a substantial increase in
 12 the abundance of a competitive taxon, from which an
 13 intensification of biotic interactions could be inferred.
 14 Recognition that the hyporheic zone may function as
 15 a refugium during flow recession in temperate streams
 16 is of particular relevance in the face of continuing cli-
 17 matic variability; much research indicates lower summer
 18 rainfall, with a consequent increase in the magnitude
 19 and duration of low flows likely in some regions of

the UK (Hannaford and Marsh, 2006). The hyporheic 20
 zone may therefore increase in importance as a refugium 21
 that promotes invertebrate survival during flow recession 22
 and low flows. However, many anthropogenic activities 23
 threaten the ecological integrity of the hyporheic 24
 zone by depositing fine sediments which clog interstitial 25
 spaces, compromising hydrologic exchange processes 26
 and limiting refugial potential (Boulton, 2007; Stubbington 27
et al., 2009b). This study, therefore, adds weight to 28
 call for freshwater ecological monitoring programmes 29
 and restoration schemes to recognize and explicitly 30
 consider the hyporheic zone as an integral ecosystem 31
 component. 32

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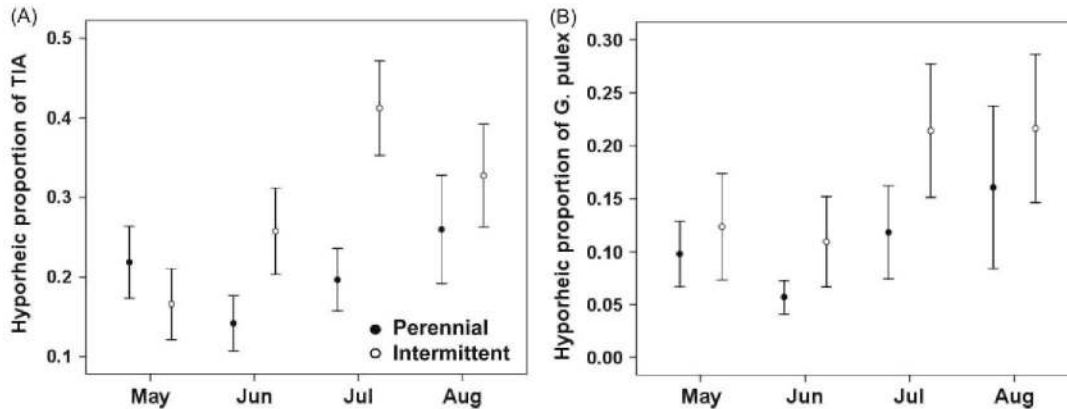


Figure 7. Mean ± 1 SE hyporheic proportion of the total invertebrate community, at sites with historically perennial and intermittent flow: (A) TIA and (B) *G. pulex* abundance.

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