

GROUNDWATER-SURFACE-WATER INTERACTIONS

Changes in invertebrate assemblage composition in benthic and hyporheic zones during a severe suprasedational drought

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Abstract: Droughts are unpredictable disturbances characterized in streams by declining flow, reduced habitat availability, and deteriorating abiotic conditions. Such events typically reduce benthic invertebrate taxon richness and modify assemblage composition, but little is known about how hyporheic invertebrate assemblages respond to drought or how these responses relate to changes in benthic assemblages. We hypothesized that taxon richness (α diversity) and variability (as within-site β diversity) in benthic assemblage composition would decline as drought proceeded, whereas concurrent changes in hyporheic assemblages would be lower in this more stable environment. We predicted that benthic assemblage composition between sites would converge as epigeal taxa were selectively eliminated, whereas between-site hyporheic β diversity would change little. We sampled benthic and hyporheic invertebrates concurrently from 4 sites along a groundwater-fed stream during the final stages of a severe suprasedational drought punctuated by a record heat wave. Abiotic conditions in benthic habitats deteriorated as flow declined, but changes were less pronounced in the hyporheic zone. Benthic α diversity declined during drought, whereas hyporheic α diversity changed little. However, benthic within-site β diversity increased as the drought progressed because of localized variation in the abundance of common taxa. Temporal trends in hyporheic β diversity were less consistent. Benthic assemblages at individual sites became more similar, especially during the heat wave, reflecting low α diversity and abundance. Hyporheic assemblages changed markedly because of temporary increases in abundances of epigeal and hypogean amphipods. These contrasting responses of benthic and hyporheic assemblages to drought should be recognized when developing management strategies for drought-impacted streams.

Key words: low flows, benthos, hyporheos, macroinvertebrate, alpha-diversity, beta-diversity, *Gammarus*, *Niphargus*

In all lotic ecosystems, suprasedational droughts are severe and unpredictable disturbances that gradually intensify over space and time (Lake 2003). In-stream changes during drought are complex and variable but typically include reduction in wetted habitat availability and heterogeneity, slowing and often cessation of flow, and an increase in the influence of groundwater and solar radiation on surface-water temperatures (Boulton 2003, Dewson et al. 2007). However, few investigators have examined the effects of these in-stream changes on aquatic biota during severe suprasedational droughts (Lake 2011) largely because of the challenges of capturing the

early stages of these unpredictable, slow-onset events (Fleig et al. 2010).

The few studies conducted were focused on benthic invertebrates in surface sediments (reviews in Dewson et al. 2007, Lake 2011). However, the hyporheic zone (HZ), between the surface sediments and phreatic groundwater, often supports a diverse invertebrate assemblage (Boulton et al. 1998), comprising groundwater and hyporheic specialists and taxa that typically inhabit the benthic zone (BZ) (Williams et al. 2010). Predominantly benthic taxa are proposed to migrate into the HZ during adverse con-

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ditions in the surface stream (Williams and Hynes 1974, Dole-Olivier 2011), including drought. These migrations may be triggered by intensified biotic interactions within contracting areas of wetted benthic habitat (Stubbington et al. 2011a) or by thermal stress during periods of elevated water temperature (Wood et al. 2010).

In addition to disturbance-related drivers, seasonal variability and multiple environmental variables influence the distribution and movements of invertebrates between the benthic and hyporheic zones, collectively resulting in a spatiotemporally variable community (Brunke and Gonsler 1999). Disturbances, such as drought or high-flow events, may have different effects on BZ and HZ habitats, eliciting different responses by their respective invertebrate faunas. However, few investigators have concurrently sampled invertebrate assemblages in the BZ and HZ (e.g., James et al. 2008, Young et al. 2011), and we are aware of only 4 studies in which paired benthic–hyporheic invertebrate samples were collected repeatedly during severe low flows or drying: Belaidi et al. (2004), Stubbington et al. (2011a), Datry (2012), and our study in the Little Stour, a groundwater-fed stream in southeastern England.

Severe low flows and drying of surface water may have greater effects on invertebrates in the BZ than in the HZ, reducing taxon richness (α diversity) and selectively eliminating surface species that require reliable flow and good water quality (Boulton 2003). As drought progresses, variation in benthic community composition among sites and over time (both spatial and temporal β diversity; sensu Anderson et al. 2011) also is likely to decline as conditions become progressively less favorable to most stream invertebrates. In other aquatic habitats, such as ponds, drought can reduce β diversity by acting as a strong ‘environmental filter’ (Chase 2007). Similar changes might be predicted in streams as a suprasedational drought proceeds (Lake 2011).

We concurrently sampled benthic and hyporheic invertebrate assemblages in riffle habitats at 2 perennial and 2 historically semiperennial sites along the Little Stour River, UK, at monthly intervals during the latter stages of a severe suprasedational drought to test 3 hypotheses: 1) benthic taxon richness (α diversity) would decline steadily as the drought proceeded, whereas hyporheic α diversities would change little because subsurface environmental conditions would be buffered in this groundwater-fed stream; 2) within-site variation in benthic community composition, as fine-scale patchiness among replicates (β diversity), would decline as the drought proceeded, especially at the 2 semiperennial sites (Wood and Petts 1999, Wood and Armitage 2004), whereas no significant temporal change in hyporheic β diversity would occur within sites because subsurface conditions would be buffered from drought; 3) benthic community composition would converge among sites over time as a result of the environmental filter of drought, whereas less convergence would occur in hyporheic

community composition over time, but some divergence would be possible because of site-specific movements of benthos into the HZ.

METHODS

Study site and drought characteristics

The Little Stour River (lat 51.275°N, long 1.168°E) is an 11.5-km-long lowland groundwater-dominated stream that drains a predominantly agricultural catchment of ~213 km². Geology in the headwaters is chalk overlain by alluvial gravels in the river’s middle and lower reaches. The sedimentary calcareous rocks result in relatively high conductivities (~580 $\mu\text{m}/\text{cm}$). Further details regarding the river and its catchment were provided by Wood and Petts (1999).

Mean annual precipitation in the catchment is ~650 mm, which is usually sufficient to maintain perennial flow below the spring head (lat 51.265°N, long 1.153°E). However, a 1-km section within the study area dried during 3 previous suprasedational droughts in 1949, 1991–1992, and 1996–1997 (Wood and Armitage 2004). Our study was conducted during the latter stages of a severe (return period >1-in-100 y; Marsh 2007) suprasedational drought that affected southern and eastern England between 2004 and 2006. In the Little Stour, groundwater and surface-water levels fell during the extended period of rainfall deficit between November 2004 and October 2006 (Marsh 2007). Mean daily discharge between 2003 and the end of 2006 was 0.181 m³/s, but throughout 2006, discharge never reached this average (Fig. 1A). In July 2006, the rainfall deficit was accompanied by a heat wave that included the highest monthly mean air temperatures recorded in the 348-y Central England Temperature series (Prior and Beswick 2007; Fig. 1B). Sampling was done from April to October 2006, capturing the final months of this suprasedational drought and the 2 mo after the meteorological drought broke. Mean daily discharge then increased gradually until mid-December. The first winter storms in January 2007 caused a rapid rise in discharge to above the 2003–2006 average.

Each month, the benthic and hyporheic zones of 2 perennial sites (sites 1 and 4) and 2 semiperennial sites (sites 2 and 3) in the upper 5 km of the Little Stour were sampled. The semiperennial sites were in a 1-km reach that dried during 4 of the previous 16 y (Wood et al. 2000), but neither site dried completely during our study. Riffle crests were gradually exposed at both sites as flow declined, whereas sampling points remained inundated. All sites were predominantly riffle habitat, 5 to 10 m wide, and with a pebble–gravel bed (4–32 mm).

Invertebrate sampling and community characterization

At each site, 5 replicate sampling points were selected in riffles. The same points were used on each sampling oc-

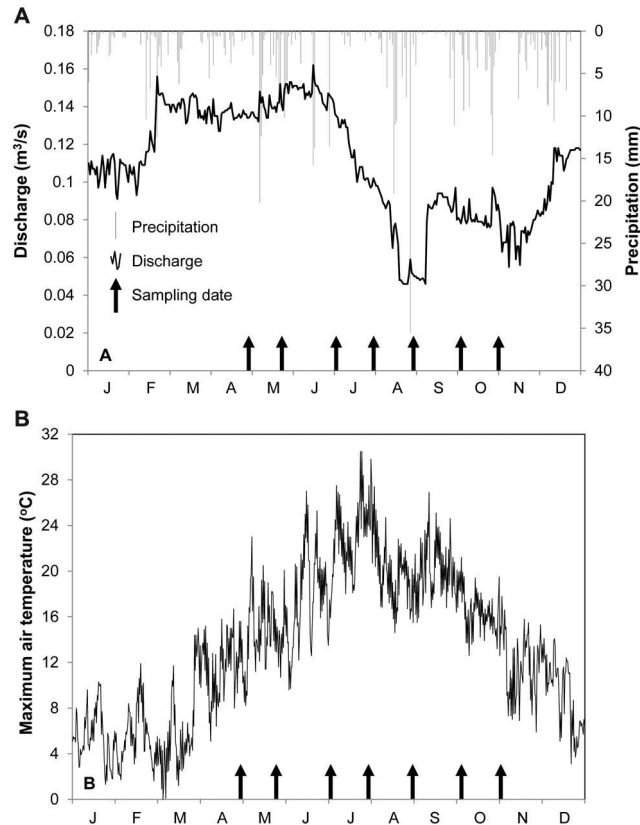


Figure 1. Environmental conditions in the Little Stour River in 2006. A.—Daily discharge and precipitation at Littlebourne (lat 51.277°N, long 1.167°E). B.—Twelve-hourly maximum temperatures at Manston (lat 51.344°N, long 1.369°E).

casation. Based on observations made during previous supra-seasonal droughts (Wood and Petts 1999, Wood and Armitage 2004), sampling points were in areas that would de-water last. Riffle crests and stream margins were avoided. Sampling points were ≥ 3 m apart to avoid overlap between the sediments sampled at 1 point with those at a neighboring point, particularly during hyporheic sampling. At each point, invertebrates were sampled from the BZ with a Surber sampler (0.1-m² frame, 250- μ m-mesh net) by manually disturbing the sediments to a depth of 5 cm for 30 s and inspecting larger clasts for attached invertebrates.

Hyporheic invertebrates were then sampled 1.5 to 2 m upstream of each benthic Surber sample. On the 1st sampling date, polyvinyl chloride (PVC) wells (25-mm internal diameter) were inserted 20 cm into the HZ at each of the 5 sampling points with a stainless steel T-bar. Each month, 6-L samples were extracted from the base of the well with a manual bilge pump following the procedure of Boulton and Stanley (1995). Six liters provides a standardized volumetric sample that previous investigators (Boulton et al. 2004, Stubbington et al. 2011b, Detry 2012) showed was adequate to characterize differences in hyporheic community composition among sites and sampling

points. Samples were passed through a sieve (90- μ m mesh) and preserved in 4% formaldehyde. For comparison with data from the benthic samples, only the invertebrates retained by a 250- μ m sieve are considered in our paper. The PVC wells were left in situ and sampled monthly, ensuring that repeated temporal sampling was not confounded by spatial variability.

Conductivity (μ S/cm), pH, dissolved O₂ (DO; mg/L) and water temperature ($^{\circ}$ C) were recorded in surface water and hyporheic water using standard meters (Hanna Instruments, Leighton Buzzard, UK). Water depth and mean flow velocity (at 0.6 \times depth) were recorded at each sampling point with an ADS SENSE-RC2 flow meter (ADS Environmental Services, Huntsville, Alabama). In the laboratory, most taxa were identified to species. However, larvae and adults of *Helophorus* (Coleoptera:Helophoridae) and *Hydraena* (Coleoptera:Hydraenidae) and larvae of *Riolus* (Coleoptera:Elmidae) were identified to genus; Planariidae (Tricladida), Sphaeriidae (Bivalvia), larval Dytiscidae and Haliplidae (Coleoptera), Baetidae (Ephemeroptera), and all Hemiptera and Diptera were identified to family; and Oligochaeta and Hydracarina were recorded at higher levels.

Data analysis

Two-way repeated-measures analysis of variance (rmANOVA) with month as the within-subjects factor and site as the between-subjects factor was used to compare hydrological and water-chemistry variables spatially and temporally for benthic and hyporheic habitats. For water-chemistry variables, rmANOVA tests using habitat (benthic vs hyporheic) as the between-subjects factor were conducted on a combined benthic–hyporheic data set. Mauchly's tests were used to verify the assumption of sphericity, and where this assumption was violated, p -values calculated by Greenhouse–Geisser tests were used to assess significance. Where rmANOVAs identified significant differences between groups, paired t -tests with Bonferroni adjustments were used to examine differences between individual months or sites. Where significant site \times month interactions were identified by rmANOVAs, temporal changes at individual sites were examined using 1-way ANOVAs with Tukey's post hoc tests. HZ and BZ assemblage analyses were undertaken separately because different sampling methods were used.

Studies in the Little Stour during the 2004–2006 drought showed significant changes in total taxon richness, total invertebrate abundance, and abundances of particular taxa in benthic and hyporheic zones (Stubbington et al. 2009, Wood et al. 2010). However, no site-level analysis of α diversity and β diversity has been conducted, nor have hypotheses about temporal changes in assemblage composition within sites and habitats been tested. Habitat-specific comparisons within and between sites over time can be explored in light of the differences in environmental conditions between the 2 zones as the drought proceeded.

To test our 1st hypothesis, site-level taxon richness (α diversity) was calculated for each sampling occasion as the mean of the 5 replicate samples and compared over time among sites with rmANOVAs. Where significant site \times month interactions were found, 1-way ANOVAs were conducted for individual sites, as described for environmental variables.

Many authors have argued that spatial and temporal variation in assemblage composition, expressed as β diversity (in both its spatial and temporal senses; Anderson et al. 2011), is a more informative measure of the effects of disturbances than changes in α diversity (review in Séguin et al. 2014). Therefore, to test our 2nd hypothesis, benthic and hyporheic β diversity were assessed at each site with the Index of Multivariate Dispersion (IMD) proposed by Anderson et al. (2006). The IMD expresses variation in assemblage composition as the average dissimilarity between individual samples and their group centroid in multivariate ordination space (see below). One-way ANOVAs were then used to detect temporal changes in β diversity (as IMD).

Our 3rd hypothesis was tested by plotting sequential sample centroids in 2-dimensional ordination space to reveal temporal trajectories of changes in assemblage composition at each site. Data from each zone (i.e., 5 replicates \times 7 sampling times \times 4 sites = 140 samples/zone) were ordinated with nonmetric multidimensional scaling (NMDS) of a Bray–Curtis similarity matrix with 100 restarts. We used analysis of similarities (ANOSIM) of site-level data followed by pairwise comparisons (10,000 permutations) to test whether assemblage composition differed between consecutive sampling dates (i.e., divergence) or not (i.e., convergence). The main taxa contributing to differences between sites and over time within each habitat were ascertained with similarity percentages (SIMPER). Pearson correlation coefficients were calculated to examine relationships between NMDS axis scores and environmental variables.

All univariate analyses were done with IBM SPSS Statistics (version 19; IBM Corporation, Armonk, New York). All multivariate analyses (NMDS, IMD, ANOSIM, SIMPER) were done using $\sqrt[4]{(x)}$ -transformed data in PRIMER (version 6; PRIMER-E, Ivybridge, UK).

RESULTS

Environmental conditions during the drought

River discharge was below the long-term average (0.181 m³/s) in April and May, decreased rapidly during June and July, and was lowest in August (Fig. 1A). Local management of weirs and in-stream macrophytes between August and October limited changes to mean water depth during this period (Table 1), but depths varied among sites while flow velocity remained locally variable. The greatest changes were declines of >5 cm at the semi-perennial sites, where riffle crests were exposed between July and September, although depth was never <2 cm at any sampling point. After a lagged response to increased rainfall during August, discharge began to recover during September and remained relatively stable until the end of the study (Fig. 1A).

Water temperatures were higher in the surface stream (15.7 \pm 0.3°C) than in the HZ (14.9 \pm 0.3°C; rmANOVA, p = 0.001) and peaked in July in both habitats (Table 1). In July, site-specific surface-water means varied from 20.0 to 21.9°C, and peak values reached 22.6°C, whereas in hyporheic water, site means were 19.3 to 21.3°C, and temperatures peaked at 21.7°C. Temperatures declined in August but experienced a 2nd, lower peak in September (Table 1, Fig. 1B). DO concentrations were lower in hyporheic (7.3 \pm 0.2 mg/L) than in surface water (9.4 \pm 0.1 mg/L, p < 0.001). Surface-water DO concentrations were higher in April (12.2 \pm 0.1 mg/L) than in subsequent months (p \leq 0.001), whereas hyporheic DO concentrations remained high in May before declining in June (rmANOVA, p < 0.001). This decline continued until August (Table 1). Surface and hyporheic water had similar pH (7.4–8.6, rmANOVA, p =

Table 1. Monthly mean (\pm 1 SE) values for hydrological and water chemistry variables (n = 5 site⁻¹ mo⁻¹) at 4 sites along the Little Stour River. SW = surface water, HW = hyporheic water.

Variable	SW/HW	April	May	June	July	August	September	October
Depth (cm)	SW	9.1 \pm 0.7	8.9 \pm 0.6	8.0 \pm 0.7	8.1 \pm 0.6	9.5 \pm 1.0	6.5 \pm 0.7	7.1 \pm 0.5
Velocity (cm/s)	SW	36 \pm 3	36 \pm 5	23 \pm 2	24 \pm 3	29 \pm 4	27 \pm 4	18 \pm 2
Temperature (°C)	SW	9.9 \pm 0.1	14.1 \pm 0.2	19.0 \pm 0.5	21.2 \pm 0.2	15.8 \pm 0.1	16.9 \pm 0.1	13.0 \pm 0.1
	HW	9.3 \pm 0.1	13.3 \pm 0.2	18.0 \pm 0.5	20.0 \pm 0.2	14.9 \pm 0.2	15.8 \pm 0.2	12.8 \pm 0.1
Dissolved O ₂ (mg/L)	SW	12.2 \pm 0.1	9.9 \pm 0.2	8.8 \pm 0.2	9.1 \pm 0.2	7.8 \pm 0.3	8.7 \pm 0.1	9.5 \pm 0.2
	HW	9.5 \pm 0.4	9.3 \pm 0.3	8.1 \pm 0.2	7.0 \pm 0.2	5.3 \pm 0.2	5.7 \pm 0.2	6.3 \pm 0.2
pH	SW	7.7 \pm 0.01	8.2 \pm 0.06	8.0 \pm 0.05	7.9 \pm 0.05	7.8 \pm 0.05	7.8 \pm 0.05	8.0 \pm 0.05
	HW	7.7 \pm 0.03	8.2 \pm 0.04	8.0 \pm 0.05	7.9 \pm 0.05	7.8 \pm 0.04	7.8 \pm 0.05	8.1 \pm 0.05
Conductivity (μ S/cm)	SW	649 \pm 7	526 \pm 2	556 \pm 3	560 \pm 1	562 \pm 3	563 \pm 3	563 \pm 2
	HW	662 \pm 5	539 \pm 1	563 \pm 3	565 \pm 1	567 \pm 3	572 \pm 2	565 \pm 2

0.952), and monthly means ranged from 7.7 to 8.2 in both zones (Table 1). Conductivity was higher in hyporheic (576 $\mu\text{S}/\text{cm}$) than in surface water (568 $\mu\text{S}/\text{cm}$, rmANOVA, $p < 0.001$) and was significantly higher in April than other months in both zones (rmANOVAs, $p < 0.001$; Table 1).

Benthic assemblage composition

In total, 53,918 individuals from 89 taxa were recorded from 140 Surber samples. *Gammarus pulex* (Amphipoda: Gammaridae) dominated the assemblage (35% of total abundance), followed by Chironomidae larvae (Diptera, 14% of total abundance). Oligochaeta, *Agapetus fuscipes* (Trichoptera:Glossosomatidae), larval and adult *Elmis aenea* (Coleoptera:Elmidae), *Serratella ignita* (Ephemeroptera: Ephemerelellidae), and Baetidae (Ephemeroptera) each accounted for >3% of the assemblage (data not shown). Two hypogean amphipods (<0.02% of all invertebrates) occurred in the BZ: *Crangonyx subterraneus* (Amphipoda Crangonyctidae) (data not shown) and *Niphargus aquilex* (Amphipoda:Niphargidae) (Table 2).

Hyporheic assemblage composition

A total of 3140 invertebrates from 47 taxa were present in 140 hyporheic samples, with 1 to 13 taxa present per

sample. *Gammarus pulex* was the most abundant taxon (46% of total abundance; Table 2). Oligochaeta, Chironomidae, and *A. fuscipes* also were abundant (11.8–12.6% each). *Elmis aenea* larvae, Baetidae, and *N. aquilex* were common (2–4% each). Four other hypogean taxa (*C. subterraneus*, *Niphargus fontanus*, *N. kochianus kochianus*, and *Proasellus cavaticus* [Isopoda:Asellidae]) were uncommon (collectively 1.0% of total hyporheic abundance) (data not shown).

Temporal trends in site-level benthic and hyporheic taxon richness (α diversity)

Benthic taxon richness (α diversity) varied significantly over time and among sites (rmANOVA, $p < 0.001$), and was highest at perennial site 4 in all months except September (Fig. 2A). At all sites, α diversity declined gradually until July, when taxon richness was lowest at sites 2–4 (Fig. 2A). This decline was across multiple groups, including Diptera, Mollusca, and Trichoptera (Table 2). Taxon richness increased in August, mainly because of increases in Diptera, Coleoptera, Mollusca, and Trichoptera. A 2nd, moderate dip occurred in September at sites 1, 3, and 4 (Fig. 2A), reflecting minor reductions in the richness of several groups (Table 2). Temporal trends in α diversity

Table 2. Monthly mean (± 1 SE) total and taxon-specific invertebrate abundances and higher-level taxon richness on the Little Stour River. BZ = benthic zone, HZ = hyporheic zone. Values per sample are either /0.1 m²(BZ) or /6 L (HZ).

	Zone	April	May	June	July	August	September	October
Abundance								
All invertebrates	BZ	363 \pm 42	504 \pm 55	432 \pm 38	198 \pm 31	375 \pm 43	438 \pm 47	386 \pm 47
	HZ	14 \pm 2	13 \pm 2	19 \pm 3	38 \pm 5	11 \pm 1	51 \pm 5	13 \pm 2
<i>Erpobdella octoculata</i>	BZ	3.7 \pm 0.7	6.3 \pm 1.5	4.4 \pm 0.9	1.7 \pm 0.4	5.7 \pm 1.4	3.3 \pm 0.9	4.0 \pm 0.9
<i>Gammarus pulex</i>	BZ	80 \pm 8	154 \pm 30	204 \pm 26	117 \pm 21	122 \pm 22	129 \pm 30	125 \pm 13
	HZ	3.4 \pm 0.4	5.1 \pm 1.7	8.5 \pm 2.1	22.7 \pm 2.4	3.7 \pm 0.6	26.3 \pm 2.5	3.5 \pm 0.6
Gastropoda	BZ	1.9 \pm 0.5	2.5 \pm 0.9	1.5 \pm 0.4	0.3 \pm 0.1	2.5 \pm 0.5	1.8 \pm 0.5	0.8 \pm 0.4
<i>Niphargus aquilex</i>	HZ	0 \pm 0	0.3 \pm 0.1	0.2 \pm 0.1	3.0 \pm 0.8	0.05 \pm 0.05	0.1 \pm 0.1	0 \pm 0
Oligochaeta	BZ	43 \pm 10	51 \pm 14	51 \pm 14	8 \pm 2	35 \pm 7	66 \pm 20	43 \pm 12
	HZ	3.4 \pm 0.6	2.8 \pm 0.7	3.9 \pm 0.7	1.1 \pm 0.4	1.4 \pm 0.4	5.0 \pm 0.7	1.1 \pm 0.5
Planariidae	BZ	5.5 \pm 1.5	3.2 \pm 0.8	3.3 \pm 0.9	1.0 \pm 0.3	4.7 \pm 0.8	3.0 \pm 1.1	7.4 \pm 3.1
Higher-level taxon richness								
Coleoptera	BZ	3.4 \pm 0.3	3.3 \pm 0.3	3.1 \pm 0.4	2.5 \pm 0.3	3.3 \pm 0.3	3.0 \pm 0.4	2.9 \pm 0.3
	HZ	0.5 \pm 0.2	0.2 \pm 0.1	0.4 \pm 0.2	0.2 \pm 0.1	0.5 \pm 0.1	1.5 \pm 0.1	0.5 \pm 0.1
Crustacea	BZ	1.7 \pm 0.2	2.1 \pm 0.2	1.9 \pm 0.2	1.5 \pm 0.2	1.2 \pm 0.1	1.4 \pm 0.1	2.3 \pm 0.3
	HZ	1.1 \pm 0.1	1.4 \pm 0.2	1.3 \pm 0.1	2.2 \pm 0.2	1.1 \pm 0.1	1.4 \pm 0.2	1.2 \pm 0.1
Diptera	BZ	2.3 \pm 0.2	2.5 \pm 0.2	2.6 \pm 0.2	1.8 \pm 0.2	2.5 \pm 0.2	1.9 \pm 0.2	1.9 \pm 0.2
	HZ	1.0 \pm 0.2	1.1 \pm 0.1	1.1 \pm 0.2	0.9 \pm 0.2	0.8 \pm 0.1	1.3 \pm 0.1	1.0 \pm 0.1
Ephemeroptera	BZ	3.0 \pm 0.2	2.7 \pm 0.2	2.1 \pm 0.1	1.6 \pm 0.2	1.7 \pm 0.2	1.5 \pm 0.2	2.1 \pm 0.2
Hirudinea	BZ	1.8 \pm 0.2	1.8 \pm 0.2	1.9 \pm 0.2	1.4 \pm 0.2	1.9 \pm 0.2	1.6 \pm 0.2	1.7 \pm 0.3
Mollusca	BZ	1.9 \pm 0.2	1.0 \pm 0.2	1.4 \pm 0.3	0.3 \pm 0.1	2.1 \pm 0.4	1.3 \pm 0.4	0.6 \pm 0.2
Trichoptera	BZ	6.2 \pm 0.4	5.1 \pm 0.4	3.5 \pm 0.3	2.3 \pm 0.3	3.6 \pm 0.3	3.8 \pm 0.5	3.6 \pm 0.4
	HZ	0.9 \pm 0.2	0.3 \pm 0.1	0.4 \pm 0.1	0.7 \pm 0.2	0.6 \pm 0.1	1.4 \pm 0.2	0.7 \pm 0.2

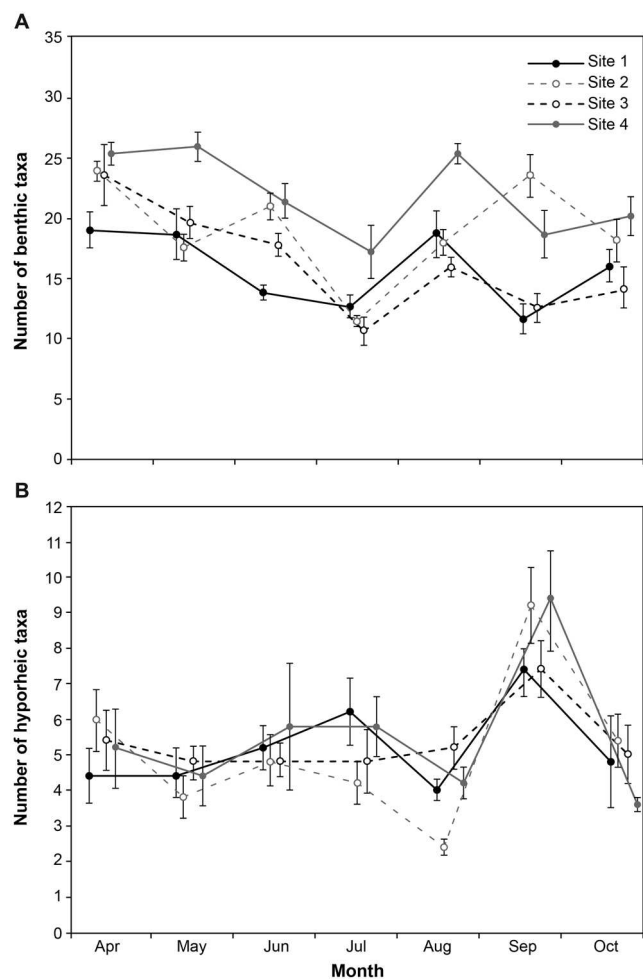


Figure 2. Mean (± 1 SE) taxon richness (α diversity) of 5 replicate samples from 2 perennial (1 and 4) and 2 semiperennial sites (2 and 3) in the benthic zone (A) and hyporheic zone (B) in the Little Stour River. Note the difference in vertical scales between panels.

varied among sites (rmANOVA interaction, $p < 0.001$). Semiperennial site 2 deviated from the overall pattern, largely because richness increased from July to a September peak (Tukey's test, $p < 0.001$) at this site.

Hyporheic α diversity did not differ among sites from April to July ($p = 1$ for all pairwise comparisons; Fig. 2B, Table 2). Taxon richness decreased in August, with a significant decline at site 2 (1-way ANOVA, $p < 0.001$) caused largely by the absence of 4 uncommon crustaceans. Richness then rose sharply at all sites in September (rmANOVA, $p < 0.001$, Fig. 2B), especially in the Trichoptera and Diptera, and also in the Coleoptera and Crustacea (Table 2). In October, richness at all sites had returned to levels similar to those recorded in April (Fig. 2B). Taxa present (at low abundance in all cases) in September but absent in August and October included *Glossiphonia complanata* (Hirudinea: Glossiphoniidae), *Asellus aquaticus*, *A. merianus*, *Proasellus cavaticus* (Crustacea:Asellidae), *N. fontanus*, the trichopter-

ans *Hydropsyche angustipennis* (Hydropsychidae), *Athripsodes cinereus* (Leptoceridae), and *Polycentropus flavomaculatus* (Polycentropodidae), and the dipteran family Empididae. The α diversity of semiperennial sites did not differ from that of perennial sites, nor was the time \times site interaction significant (rmANOVA, $p > 0.05$).

Temporal trends in within-site variation in benthic and hyporheic assemblage composition (β diversity)

β diversity, as spatial variation of assemblage composition among replicate samples collected monthly at each site, was expressed by the IMD. Considering all sites, and despite relatively stable values at site 1, the IMD varied significantly over time in the BZ (1-way ANOVA, $p = 0.023$) with higher values occurring in September than in June (Tukey's test, $p = 0.038$; Fig. 3A). Some patterns were consistent across sites, particularly at sites 2, 3 and 4. Benthic IMD was generally low between April and June, increased considerably in July, and remained fairly high after July (Fig. 3A). Hyporheic β diversity also varied among months (1-way ANOVA, $p = 0.032$), but temporal changes were not consistent among sites until July (Fig. 3B). At Sites 1–3, hyporheic IMD increased between July and August,

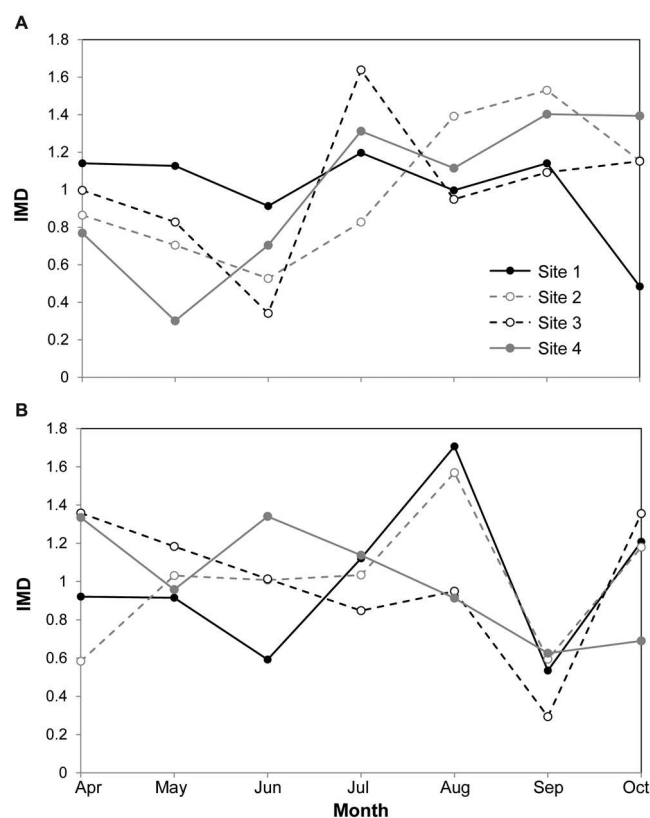


Figure 3. Temporal changes in Index of Multivariate Dispersion (IMD; β diversity) of 5 replicate samples from 2 perennial (1 and 4) and 2 semiperennial sites (2 and 3) in the benthic zone (A) and hyporheic zone (B) in the Little Stour River.

decreased significantly in September (Tukey's test, $p = 0.011$), and rose in October. A different pattern was observed at site 4, where a steady decline began in June and continued until September (Fig. 3B).

Temporal trends in between-site variation in benthic assemblage composition (β diversity)

NMDS ordination of benthic samples revealed marked differences in assemblage composition between sites 1, 4, and the 2 semiperennial sites (2 and 3), which overlapped slightly (Fig. 4A). Differences between all site pairs were significant (ANOSIM, global $R = 0.563$, $p < 0.001$) and reflected variation in the densities of *S. ignita*, Baetidae, *A. fuscipes*, and *E. aenea* larvae (SIMPER). Samples from site 4 had high axis-1 scores (Fig. 4A), which were significantly correlated ($p \leq 0.002$) with increasing depth and flow and declining pH. Semiperennial sites typically had higher axis-2 scores, which were significantly correlated ($p \leq 0.029$) with temperature and DO.

Temporal trajectories of change in benthic assemblage composition were broadly similar across sites, with NMDS axis-2 scores declining until month 4 (July), when centroids of sites 1–3 plotted in close proximity. This assemblage was characterized by low richness of insect and non-insect taxa and low abundance of common taxa, such as Oligochaeta (Table 2). After July, trajectories indicated a partial return to the assemblage composition seen in April (Fig. 4A). The pattern at perennial site 1 was the most variable mainly because of divergence in September. This divergence also was evident at semiperennial site 3. Nonetheless, β diversity over time (evident as the spread of the 7 centroids representing each site) was comparable at perennial sites 1 and 4 and was lower than at the semiperennial sites 2 and 3 (Fig. 4A).

Temporal change in assemblage composition was significant at site 1 (ANOSIM, global $R = 0.596$, $p < 0.001$), and the only significant overlap between consecutive months was for April and May ($p = 0.103$). Temporal change in assemblage composition also was significant at the other perennial site (4) ($R = 0.533$, $p < 0.001$), and the only significant overlap was between September and October ($p = 0.103$). At semiperennial site 2, assemblage composition changed over time ($R = 0.679$, $p < 0.001$), with no overlap between consecutive sampling dates. At semiperennial site 3, temporal changes were significant ($R = 0.518$, $p < 0.001$) with marked overlap between September and October. Despite the similar assemblage composition at sites 2 and 3 on the first 3 sampling dates (Fig. 4A), composition diverged at these sites after June.

Temporal trends in between-site variation in hyporheic assemblage composition (β diversity)

Hyporheic assemblage composition overlapped considerably among all sites (Fig. 4B), as indicated by nonsignificant ANOSIM scores between sites 1, 2, and 4 (pairwise

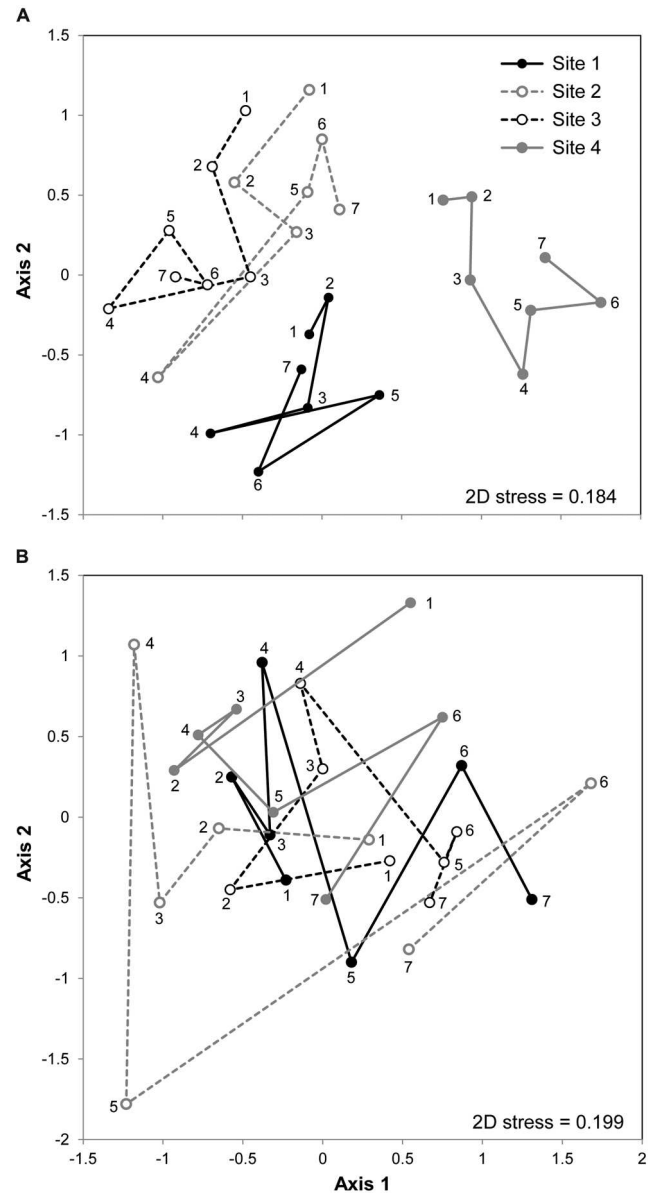


Figure 4. Two-dimensional plot of centroids derived from nonmetric multidimensional scaling ordination of benthic (A) and hyporheic (B) invertebrate assemblage composition from 2 perennial (1 and 4) and 2 semiperennial sites (2 and 3). Site-level centroids of 5 replicates for each month (April–October: 1–7) are linked by lines representing temporal trajectories of change during the final stages of drought (months 1–5) and after the drought broke (months 6 and 7).

global $R < 0.075$, Bonferroni-corrected $p > 0.05$). However, the temporal trajectories of change at individual sites were similar. Axis 1 scores decreased at all sites between April and May. In June, axis 1 scores increased slightly at sites 1, 3, and 4. When the heat wave occurred in July, all site centroids plotted in a single cluster with low axis 1 and high axis 2 scores (Fig. 4B) associated with relatively high densities of *G. pulex* and hypogean crustaceans, especially *N. aquilex*. Between July and August, axis 2 scores

declined considerably because many taxa, including *G. pulex* and *N. aquilex* became less abundant at both perennial and semiperennial sites. Scores then increased on both axes for all sites, and by September, samples had formed a distinct cluster with high axis 1 scores, associated with a 2nd peak in the abundance of *G. pulex* but not *N. aquilex*. Axis 2 scores then declined between September and October (Fig. 4B).

ANOSIM indicated significant temporal change in hyporheic assemblage composition at site 1 (global $R = 0.364$, $p < 0.001$), mainly between July and August and August and September ($p < 0.01$). These differences were associated with *N. aquilex*, *G. pulex*, *A. fuscipes*, and Chironomidae densities, all of which were considerably higher in July than August. The 2 amphipods and *A. fuscipes* were also more abundant in the HZ in September than October, although chironomid abundance increased during this period. Temporal changes also were significant in the HZ of perennial site 4 (global $R = 0.309$, $p < 0.001$), but only between the final 4 mo. Fluctuations in densities of oligochaetes, *A. fuscipes*, and larval *E. aenea* (particularly as September peaks) were primarily responsible for these significant differences (SIMPER).

Hyporheic assemblage composition also changed over time at the 2 semiperennial sites (global $R = 0.536$ for site 2, 0.355 for site 3, $p < 0.001$ for both), but assemblage composition did not differ among the first 3 sampling occasions within sites ($p \geq 0.151$). At site 3, a nonsignificant difference ($p = 0.357$) occurred between hyporheic assemblage composition in April and October, indicating potential convergence.

DISCUSSION

Benthic assemblage responses to suprasedasonal drought

Our results supported our 1st hypothesis that benthic taxon richness (α diversity) would decrease steadily as the drought proceeded, whereas hyporheic α diversities would change little. A general decrease in benthic α diversity during the final stages of the drought (April–July) was apparent despite site-specific fluctuations in richness. The loss of some taxa can be attributed to seasonal aquatic insect emergence (Wood et al. 2010), but other losses appear to pertain to drought-related environmental changes, including declining discharge and elevated water temperatures (Graeber et al. 2013). Gradual decline in α diversity is a common benthic invertebrate assemblage response to flow recession during drought and is caused by gradual reduction in habitat availability and heterogeneity (Wood and Armitage 2004, Dewson et al. 2007). Richness reductions reflect the loss of taxa susceptible to low flows and dewatering (Datry 2012).

Benthic α diversity was lowest in July because of low taxon richness of noninsect groups, such as Crustacea, Hirudinea, Mollusca (mainly gastropods), as well as many Insecta. This low richness coincided with the record heat

wave conditions, indicating that water temperatures exceeded the thermal tolerance of many lotic taxa (Woodward et al. 2010), including common eurytopic taxa, such as *G. pulex* (Maazouzi et al. 2011). Mouthon and Daufresne (2006) recorded similar significant reductions in gastropod and bivalve taxon richness in a large lowland river during a heat wave and suggested that these declines were caused by high water temperatures.

Benthic α diversity increased at all sites in August, coinciding with the lowest discharge and occurring after the heat wave ended. Groups contributing to this increase included multiple insect orders, Hirudinea, and Mollusca in particular. This rapid partial recovery after the heat wave is in contrast to the results of a study by Mouthon and Daufresne (2006), who noted poor recovery of the mollusk population after a more prolonged and severe heat wave, and implies persistence in refugia (Robertson 2000). Very few snails or leeches occurred in the HZ in the Little Stour, but our riffle-focused sampling design excluded cooler, deeper habitats, such as pools that may have served as sources of recolonists, as shown by Robson et al. (2011).

Our 2nd hypothesis, that within-site variation in β diversity of the benthic assemblage would decline as the drought proceeded, especially at semiperennial sites, was rejected. At all sites except perennial site 1, within-site β diversity (expressed as IMD) typically was higher from July to October than before the heat wave. These increases in benthic IMD values reflected variable within-site abundances of common taxa, such as *G. pulex* and *A. fuscipes*. These taxa reached high densities at some sampling points, possibly because of patches of preferred flow velocities or abundant food resources (Dewson et al. 2007, Stubbington et al. 2011b).

At the larger spatial scale of between-site β diversity, NMDS ordination revealed marked differences in benthic assemblage composition between each perennial site and the 2 semiperennial sites. Despite these differences among sites, temporal trajectories of assemblage change were broadly consistent across sites during the drought. In particular, during the July heat wave, assemblage composition of 3 sites converged in the same quadrant of the ordination because of shared declines in taxon richness and abundance. However, this convergence was not statistically significant, and support for our 3rd hypothesis is equivocal. Postdrought, temporal trajectories generally began to return to an assemblage composition resembling that of the 1st sample, reflecting the described recovery in α diversity and increases in abundance.

Hyporheic assemblage responses to suprasedasonal drought

Our hypothesis that hyporheic taxon richness (α diversity) would be stable over time was largely supported because no overall significant change in richness occurred between April and August (the last month before the

drought broke). We expected little change in hyporheic α diversity because drought-induced environmental extremes would be dampened in the HZ of the groundwater-fed Little Stour. Hyporheic water temperatures were cooler than in the surface stream, and hyporheic DO concentrations remained within the tolerance of most hypogean taxa until August (Malard and Hervant 1999, Issartel et al. 2005). In September, a marked but temporary peak in richness was observed because of the occurrence of multiple taxa at low abundance, including epigeal and hypogean insect and noninsect taxa. The presence of epigeal insects may reflect transient use of the HZ as a nursery for early instars (Malard et al. 2003), but the influx of the epigeal isopods *A. aquaticus* and *A. meridianus* is unexplained. Hypogean crustaceans (*P. cavaticus*, *N. fontanus*) probably were carried into the upper HZ by an increase in the strength of upwelling groundwater concurrent with the increase in river discharge, as described by Plénet et al. (1995).

Hyporheic β diversity (as IMD) varied significantly over time at all sites but, as hypothesized, did not show any consistent response as the drought proceeded. As for α diversity, the environmental conditions in the HZ of this groundwater-fed stream apparently ameliorated the stressful extremes of water temperature (Robertson and Wood 2010, Stubbington and Wood 2013). In predominantly downwelling surface-fed streams, effects on the hyporheic invertebrate assemblage would be expected to be greater than observed in our study because of the higher temperature of downwelling water (Malard et al. 2002) and the greater influxes of benthic refugees (Davy-Bowker et al. 2006, Stubbington et al. 2011a). These predictions acknowledge the importance of the predominant direction of vertical hydrological exchange in determining likely interactions between the surface stream and the underlying HZ (Brunke and Gosner 1997).

Our 3rd hypothesis was that little or no convergence would occur in hyporheic assemblage composition over time. This hypothesis was rejected. The NMDS plot of the temporal trajectories of monthly centroids representing site-level assemblage composition showed that despite the significant overlap in assemblage composition at sites 1, 2, and 4, some convergence was evident during the heat wave in July, when centroids from all 4 sites shared low axis-1 and high axis-2 scores. This convergence was associated with high hyporheic densities of the epigeal amphipod *G. pulex* and the hypogean amphipod *N. aquilex* in July (Wood et al. 2010). The influx of predominantly benthic amphipods indicated that the HZ served as a thermal refuge when water temperatures were $\geq 3.0^{\circ}\text{C}$ cooler than in the BZ, a result supporting the concept of the HZ as a refuge for benthos during multiple disturbance types (Dole-Olivier 2011, Stubbington 2012). The influx of the hypogean *N. aquilex* into the shallow HZ may reflect declining O_2 availability in deeper sediments and groundwater. Hyporheic sediments are typi-

cally more highly oxygenated than underlying aquifers, and reduced flows that increased groundwater residence times may have further depleted O_2 concentrations during drought (Malard and Hervant 1999, McGuire et al. 2002). As a result, vertical migrants escaping either thermally stressful surface water or poorly oxygenated groundwater colonized the intervening HZ. This result elegantly illustrates the complexity of faunal responses to drought disturbances in benthic, hyporheic, and phreatic habitats, and the importance of interhabitat connectivity in allowing migrations between adjacent ecosystem components (Dole-Olivier 2011, Stubbington 2012). Experiments in which benthic and hyporheic invertebrates are tagged with nontoxic biochemical markers and tracked along migration pathways within the sediments would permit direct observation of movements and refuge use during disturbances, such as drought.

In August, discharge was at its lowest, and temporal trajectories of hyporheic assemblage composition diverged widely from the July cluster as epigeal and hypogean refugees returned to their respective principal habitats when the heat wave ended. After the drought broke, the centroids of all sites converged and had high axis-1 scores associated with a 2nd peak in *G. pulex* abundance, which, unlike the first peak, cannot be attributed to thermal stress or any other recorded environmental variable. Ordination scores then declined along axis 2 between the last 2 months of sampling. In October, the centroids for both semiperennial sites plotted near their April equivalents, indicating resilience of these assemblages to drought disturbance. In contrast, trajectories of assemblage composition continued to diverge from the initial composition at both perennial sites. However, the suprasedonal drought we studied in 2006 had its origins in a winter rainfall deficit in 2004–2005 (Marsh 2007), and changes to invertebrate assemblages had almost certainly taken place prior to the onset of our sampling.

Implications for river ecosystem management

Management of lotic ecosystems in the face of increasing climatic extremes typically has focused on flooding because of its dramatic impacts on human societies (Jones 2013). However, effective management also must preserve ecological resistance and resilience to the ‘creeping disaster’ of drought, especially in parts of the world where temperatures are rising and precipitation is declining (Lake 2005, Robson et al. 2011). Such management strategies should encompass protection of all in-stream components, including the fauna and biogeochemical processes occurring in hyporheic habitats. This protection is especially important because the HZ can act as a source of propagules for recolonization after floods and droughts (Dole-Olivier 2011, Stubbington and Datry 2013) and is a major site for the microbially mediated transformation of nutrients and other materials in lotic ecosystems.

Our demonstration of the contrasting responses of benthic and hyporheic invertebrate assemblages to extreme drought, even in a groundwater-fed stream, highlights the need to consider the entire lotic assemblage—benthic and hyporheic—across a range of sites with differing flow histories when planning adaptation strategies for mitigating the effects of climate change or restoration programs following anthropogenic disturbances. Researchers and managers should not assume that benthic assemblage responses will resemble those of the hyporheos or other stream biota. Instead, these assemblages are likely to be connected and to share taxa that migrate between zones and seek different refugia at different times depending on the type and magnitude of a given disturbance. Therefore, we urge river managers to adopt strategies that explicitly recognize the vertical linkages connecting benthic biota and associated ecological processes to those in the underlying HZ and adjacent alluvial aquifers. For example, plans for the restoration of impaired river reaches should include specific predictions about recovering damaged hyporheic linkages and processes (Boulton 2007), especially where the effects of anthropogenic changes to streams are superimposed on large natural disturbances, such as suprasedasonal drought.

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