Low flow controls on benthic and hyporheic macroinvertebrate assemblages during supra-seasonal drought

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Abstract:

Despite the widely accepted importance of the hyporheic zone as a habitat for stream macroinvertebrates during floods, few data exist regarding community composition and distribution during periods of low flow or drought in perennial streams. Integrating research on hyporheic invertebrates with results from a long-term study of a UK river provided the opportunity to examine how benthic and hyporheic macroinvertebrate communities respond to inter-annual variability in river flow and periods of groundwater drought. Changes in the riverine macroinvertebrate community associated with low flow included a reduction in species richness and the number of individuals per sample, particularly aquatic insects. The hyporheic community was characterized by a relatively homogeneous composition during a period of severe low flow, punctuated by short-term changes associated with variation in water temperature rather than changes in discharge. We present a conceptual model of the processes influencing benthic and hyporheic invertebrates under low-flow conditions. Previous studies have seldom integrated these two assemblages and their interactions. The model presented highlights the potential importance of surface water and hyporheic zone linkages for riverine invertebrate communities under a range of flow conditions. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS benthos; hyporheos; low flows; drought; hyporheic processes; invertebrates; groundwater

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INTRODUCTION

Natural low flows associated with droughts originate from a deficit of precipitation (Smakhtin, 2001). Droughts can occur in almost any biogeographical setting, although the onset of an individual event can be difficult to determine (Humphries and Baldwin, 2003; Smakhtin and Schipper, 2008). Following an initial deficit of precipitation (meteorological drought), river discharge and water levels in other surface water bodies decline leading to ‘hydrological drought’ within the drainage basin and/or wider region. Ultimately, without sufficient meteorological input (recharge), groundwater levels within aquifers will decline, resulting in a ‘groundwater drought’, the impact of which may be compounded by anthropogenic water resource requirements for agricultural, industrial and domestic uses (Tallaksen and van Lanen, 2004).

River flow regime variability and low flows associated with drought conditions have been widely studied in lotic systems (Smakhtin, 2001), and their role in structuring in-stream communities is now recognized (Lytle and Poff, 2004; Monk et al., 2008). However, due to the complexities of defining and determining the onset of events, hydroecological data documenting responses of in-stream communities to droughts, from their onset to recovery, are relatively limited compared with studies reporting the ecological responses to floods (Suren and Jowett, 2006; Lake, 2007). In addition, there are marked differences in the manifestation of drought between individual catchments and our understanding of how in-stream ecological communities respond varies regionally (Demuth and Young, 2004).

The response of in-stream organisms to drought largely reflects the predictability and severity, including the duration, of the event (Lake, 2003). The greatest understanding of the role of drought within lotic ecosystems is for those subject to predictable ‘seasonal’ droughts in semi-arid environments (Acuna et al., 2005; Bonada et al., 2006). Those communities experiencing regular drought, typical of Mediterranean environments, frequently display behavioural and physiological adaptations that enable them to withstand prolonged low flows or cessation of flow (Bonada et al., 2006). Ecological data available for droughts within temperate environments are comparatively limited (Wood and Armitage, 2004; Lake, 2007). Aquatic invertebrate communities in temperate zone perennial lotic ecosystems subject to irregular and/or high magnitude events are seldom adapted to withstand the extreme conditions and, as a result, are usually severely impacted when flow declines or ceases (Wright and Berrie, 1987; Caruso, 2002; Lake, 2007).

Droughts are ‘ramp disturbances’ (sensu Lake, 2003) that gradually increase in intensity over time. The
response of lotic communities to drought and reduced river discharge has been characterized by gradual (ramp) changes punctuated by significant ‘stepped’ responses as thresholds between critical levels are crossed (Boulton, 2003). These steps reflect the gradual reduction in river stage (water depth) coinciding with ecologically significant threshold changes in discharge or the exposure of particular habitats. Examples include the isolation of streamside vegetation, cessation of flow, the isolation of surface water into pools, loss of surface water and far less studied the decline or loss of free water within the hyporheic zone (Figure 1).

The functional significance of the hyporheic zone has gained increasing prominence in recent years (Boulton et al., 1998; Boulton, 2007). This reflects the recognition that the habitat supports a number of unique (obligate) taxa and has wider linkages in the landscape with other surface and groundwater habitats (Malard et al., 2002). There is increasing evidence that processes operating within the hyporheic zone may significantly contribute to maintaining ecosystem health (Tomlinson et al., 2007; Pinay et al., 2009) through the provision of key ecosystem services (Boulton et al., 2008). It is now widely recognized that the hyporheic zone is a focal point for important biogeochemical processes and the transient storage of nutrients (Mulholland et al., 2008; Pinay et al., 2009). In addition, the exchange of water within the hyporheic zone may locally influence dissolved oxygen concentrations, thermal properties and sedimentary characteristics required to support salmonid fisheries (Malcolm et al., 2005).

In this article, we synthesize the existing hydroecological data available for the Little Stour River (Kent, UK) to examine macroinvertebrate community responses to river flow variability and drought-related low flows. The benthic macroinvertebrate hydroecology of the river has been extensively studied for over a decade in relation to flow variability, in particular the influence of low flows associated with droughts (Wood and Petts, 1999; Wood et al., 2000; Wood and Armitage, 2004). We present data from a long-term study of inter-annual variability of the benthic community (1992–1999) and data collected as part of a detailed monthly investigation of the benthic and hyporheic invertebrate communities during a groundwater drought in 2006. In particular, we assess whether the benthic and hyporheic fauna respond similarly to drought and whether there is evidence of marked ‘stepped responses’ to the ramp disturbance of drought in the hyporheic zone where effects of drying are hypothesized to be buffered by the saturated sediments. These results are used along with other published information to develop a conceptual model to demonstrate how interactions between surface and groundwater influence hydrological processes within the hyporheic zone which, in turn, may structure habitat availability and the benthic and hyporheic zone communities.

STUDY SITE

The Little Stour River (Kent, UK) is a small lowland chalk stream, 11.5-km long, draining a catchment area of approximately 213 km² (51.275°N 1.168°E). The highly permeable nature of the catchment results in a low drainage density, which is typical of groundwater-dominated streams. The sedimentary calcareous rocks result in relatively high conductivities (ca 580 µs cm⁻¹). Mean annual precipitation within the catchment is ca 650 mm per year (Wood and Petts, 1994). The river is usually perennial below the spring head, although a 1-km reach has been dewatered on three previous occasions in the last century during supra-seasonal drought events (1949, 1991–1992 and 1996–1997), with the latter two events being studied in detail (Wood and Armitage,
2004). A subsequent drought event impacted the site and much of southern England between 2004 and 2006 (Marsh, 2007), although the Little Stour maintained perennial flow along its entire length throughout this period.

METHODS

The macroinvertebrate community of the river was sampled annually (1992–1999) from nine sites along the upper river. Macroinvertebrates were sampled during base flow conditions (late August–early September) using a semi-quantitative kick-sampling technique over a 2-min period (Wood and Armitage, 2004). During 2006, both benthic and hyporheic invertebrate communities were sampled from four riffle sites on the river between April and October. This coincided with the latter stages of a supra-seasonal drought resulting from below-average rainfall between November 2004 and June 2006 (Marsh et al., 2007). For further details of site locations and physical characteristics, including relative flow permanence, see Wood and Petts (1999) and Wood et al. (2000).

During the intensive study in 2006, five benthic samples were collected at each of the four riffle sites on the upper river each month using a Surber sampler (0.1 m², 250-µm mesh net) over a 30-s period, disturbing the substratum to a depth of 50 mm. Associated with each benthic sample, hyporheic invertebrate samples were collected from 20-cm deep polyvinylchloride (PVC) wells (25-mm internal diameter) following the procedure outlined by Boulton and Stanley (1995). PVC wells were inserted into the riverbed using a stainless steel bar and samples could be collected immediately. The primary advantages of this technique over others, such as the Bou-Rouch sampler (Bou and Rouch, 1967) are that: (i) the small size of the well minimizes disturbance of surrounding sediments and it can remain in place to allow collection of subsequent samples; (ii) the sampler does not require priming with water and as a result is fully quantitative and (iii) the sample does not pass through the mechanism of the pump and as a result specimens are less prone to damage. Each sample comprised 6 l of hyporheic water pumped from the base of the well using a bilge pump. For each hyporheic water sample, pH, conductivity, dissolved oxygen concentration, and water temperature were measured (Hanna Instruments) before passing the sample through a 90-µm mesh sieve to isolate the fauna. Benthic water characteristics (pH, conductivity, dissolved oxygen concentration and water temperature) were also recorded before the collection of faunal samples. Benthic and hyporheic invertebrate samples were preserved in the field in 4% formaldehyde, and returned to the laboratory for processing and identification. In the laboratory, invertebrate taxa were identified to species level except Baetidae (Ephemeroptera—mayfly larvae), Chironomidae (non-biting midge larvae) and Oligochaeta (worms).

To examine long-term temporal trends within the faunal data, box-plots or error bar graphs were assessed. The influence of inter-annual flow variability was investigated using the number of individuals and the number of taxa per sample (species richness). These two measures were standardized before analysis by calculating z-scores for individual sample sites from 1992 to 1999 (site mean = 0 and standard deviation = 1). This method of standardization does not alter the shape of the time-series curves at individual sites or correlation coefficients with independent variables, thus allowing comparisons between the responses of multiple sites to the same external factor (discharge variability). To examine the influence of antecedent hydrological conditions on the most common taxon recorded on the Little Stour, the amphipod shrimp Gammarus pulex (L.), mean annual and monthly discharge characteristics up to 12 months before sample collection were examined using scatter plots and by calculating correlation coefficients between river flow (discharge) characteristics and the standardized number of individuals per sample for the four riffle sites (also used during the 2006 study period). One way analysis of variance (ANOVA) was used to examine temporal differences between benthic and hyporheic invertebrate communities during 2006 following application of Levene’s test to ensure that variances were homogeneous. Differences between individual months were examined using Tukey’s post-hoc multiple comparisons tests to identify where significant differences occurred. All analyses were undertaken using the package SPSS (Version 15).

RESULTS

Benthic community response to inter-annual flow variability

The influence of three supra-seasonal droughts recorded during the study period (1992, 1996–1997 and 2005–2006) is clear on the long-term hydrograph of the Great Stour River (Figure 2) for which a continuous flow series is available and for which the Little Stour forms the largest tributary. The influence of the drought periods is evident for the Little Stour River between 1992 and 1999 (Figure 3a). However, the meteorological and hydrological droughts marking the onset of the supra-seasonal events (Summer, 1995 and Autumn, 2004) were characterized by relatively high discharge on several occasions due to high groundwater levels (H on Figure 2). Perennial flow was maintained throughout the Great Stour during the study period although a 1-km reach of the Little Stour was dewatered during 1991–1992 and 1996–1997 when extreme supra-seasonal groundwater drought conditions prevailed.

A total of 87 taxa from 48 families were recorded during the study period, ranging from only 42 taxa in 1992 to 60 taxa in 1995. The standardized number of individuals and species richness responded directly to changes in the discharge regime (Figure 3). Supra-seasonal drought conditions during 1992 and 1996–1997 resulted in low
species richness and number of individuals per sample (Figure 3). As flow recovered following each event (1993–1994 and 1998–1999), the species richness and number of individuals per sample increased over the subsequent 2-year period (Figure 3b and c). The density of the most abundant taxon, the amphipod shrimp *G. pulex*, was significantly influenced by antecedent hydrological conditions before sampling (Table I). There was a clear positive relationship between discharge and the number of *G. pulex*, with periods of higher discharge (4–7 months before sampling) resulting in greater numbers.

**Benthic and hyporheic community responses to supra-seasonal drought**

The hydrological conditions recorded during 2006 resulted from an extended supra-seasonal drought that started in late 2004. As a result of low winter rainfall during 2004–2005 and 2005–2006, recharge of the chalk aquifer was limited causing an extended supra-seasonal groundwater drought (Figure 4). Above-average rainfall occurred in the catchment during May 2006 (96–4 mm) and August 2006 (111–6 mm), although the low antecedent groundwater levels precluded recovery of surface flow. The lowest river flows were recorded between August 2006 and September 2006 (Figure 4), when the riffle crests were exposed at two study sites, although flow did not cease. In addition, maximum air temperatures during July 2006 were high, resulting in elevated surface and hyporheic water temperatures (Table II). The warm mean air temperatures recorded throughout July were nationally the highest recorded in the 348-year long Central England Temperature (CET) series (Prior and Beswick, 2007).

The abundance of benthic invertebrates recorded during the study differed significantly between months ($F_{6,140} = 6.18$, $P < 0.001$) and was particularly marked by a significant reduction during July (Tukey’s post-hoc test: all $P < 0.05$) (Figure 5a). Between April and July, the number of benthic macroinvertebrate taxa declined significantly ($F_{5,140} = 7.37$, $P < 0.001$) from an average of 23 to 13 taxa and was most marked during July (Tukey’s post-hoc test: all $P < 0.05$) (Figure 5b). This coincided with a significant reduction in the number of aquatic insect taxa ($F_{5,140} = 2.79$, $P = 0.01$) particularly mayflies (Ephemeroptera): Baetidae, *Serratella ignita* and *Caenis* spp. and caddisflies (Trichoptera): *Hydropsyche siltalai*, *Sericostoma personatum* and *Athripsodes bilineatus*. As a result, the percentage of aquatic insect larvae within the community (including mayflies, caddisflies and Diptera such as chironomid midge larvae) was significantly lower during both June

Figure 2. Hydrograph of mean daily discharge (m$^3$/s) for the Great Stour River at Horton (1992–2006). GW indicates periods of supra-seasonal groundwater drought and H indicates the onset of meteorological and hydrological drought conditions.

Figure 3. Time series of river flow and box-plots of macroinvertebrate assemblage indices 1992–1999 for the Little Stour River: (a) hydrograph of mean daily discharge (m$^3$/s) for the Little Stour River at West Stourmouth—see Figure 2 for definition of vertical lines; (b) standardized species richness and (c) standardized number of individuals per sample (log$_e$ transformed).
Table I. Pearson correlation coefficients between standardized loge-*Gammarus pulex* and lagged discharge variables for riffles sites (*n* = 4 sites) on the Little Stour River (1992–1999)

<table>
<thead>
<tr>
<th>Discharge variable</th>
<th>Correlation Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>August (M-1)</td>
<td>0.78**</td>
</tr>
<tr>
<td>July (M-2)</td>
<td>0.82**</td>
</tr>
<tr>
<td>June (M-3)</td>
<td>0.83**</td>
</tr>
<tr>
<td>May (M-4)</td>
<td>0.89**</td>
</tr>
<tr>
<td>April (M-5)</td>
<td>0.88**</td>
</tr>
<tr>
<td>March (M-6)</td>
<td>0.89**</td>
</tr>
<tr>
<td>February (M-7)</td>
<td>0.91**</td>
</tr>
<tr>
<td>January (M-8)</td>
<td>0.84**</td>
</tr>
<tr>
<td>December (M-9)</td>
<td>0.72**</td>
</tr>
<tr>
<td>November (M-10)</td>
<td>0.69**</td>
</tr>
<tr>
<td>October (M-11)</td>
<td>0.77**</td>
</tr>
<tr>
<td>September (M-12)</td>
<td>0.53*</td>
</tr>
<tr>
<td>3 months before sampling (Y-3)</td>
<td>0.47*</td>
</tr>
<tr>
<td>6 months before sampling (Y-6)</td>
<td>0.54*</td>
</tr>
<tr>
<td>9 months before sampling (Y-9)</td>
<td>0.51*</td>
</tr>
<tr>
<td>12 months before sampling (Y-12)</td>
<td>0.50*</td>
</tr>
</tbody>
</table>

All samples collected from last week of August to the first week of September throughout the study period. *M* refers to the mean daily discharge in the month (*M*) before sample collection (1–12). *Y*-n refers to the mean daily discharge in the 3, 6 and 12 months before samples collection. *P* < 0.05; **P** < 0.005.

Figure 4. Hydrograph of mean daily discharge for the Little Stour River at Littlebourne (2005–2006)

and July (Tukey’s post-hoc test: all *P* < 0.05) than all other months (Figure 5c).

The abundance of invertebrates within the hyporheic zone was significantly different between months (*F*~6,140~ = 21.02, *P* < 0.001). Hyporheic abundances increased significantly in July and September (Tukey’s post-hoc test: all *P* < 0.005) but were reduced during August and October (Figure 6a). The number of taxa recorded in hyporheic samples also differed significantly between months (*F*~6,140~ = 14.43, *P* < 0.001). This was almost exclusively due to a significant increase in the number of taxa recorded in September (Tukey’s post-hoc test: all *P* < 0.001) (Figure 6b) coinciding with an

Figure 5. Little Stour benthic assemblage response (April–October 2006) during the final stages of a supra-seasonal drought event (2004–2006). Mean (+/− 2 standard error) of: (a) abundance of macroinvertebrates, (b) number of taxa and (c) percentage of aquatic insect larvae within samples

Table II. Summary of mean monthly maximum and minimum daily temperature (with standard deviation in brackets) at Manston (Kent), and mean monthly benthic and hyporheic water temperature recorded at the study sites (April–October 2006)

<table>
<thead>
<tr>
<th></th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>September</th>
<th>October</th>
</tr>
</thead>
<tbody>
<tr>
<td>Max air temperature (°C)</td>
<td>14.2 (2.2)</td>
<td>13.5 (2.4)</td>
<td>17.2 (2.9)</td>
<td>21.9 (2.1)</td>
<td>17.7 (1.7)</td>
<td>18.8 (1.7)</td>
<td>15.1 (1.4)</td>
</tr>
<tr>
<td>Min air temperature (°C)</td>
<td>8.6 (2.3)</td>
<td>9.3 (1.9)</td>
<td>11.3 (2.7)</td>
<td>15.6 (1.7)</td>
<td>13.4 (1.4)</td>
<td>14.7 (1.7)</td>
<td>11.8 (2.5)</td>
</tr>
<tr>
<td>Water temperature (°C)</td>
<td>9.4 (0.5)</td>
<td>12.8 (1.8)</td>
<td>16.5 (2.5)</td>
<td>18.6 (3.1)</td>
<td>14.2 (1.2)</td>
<td>14.6 (1.1)</td>
<td>12.4 (0.8)</td>
</tr>
</tbody>
</table>

Benthic and hyporheic water samples were recorded at five locations from four sites (*n* = 20) each month.

Effects of drought on benthic and hyporheic invertebrate assemblages

The long-term data from the Little Stour clearly demonstrates that, on an inter-annual basis, the number of taxa and the number of individuals per sample appear to respond to the volume of discharge. Periods of supra-seasonal drought significantly reduced taxa richness and numbers of individuals over multiple events of varying duration. This corroborates the pattern predicted for benthic fauna hypothesized by Boulton (2003), and summarized in Figure 1, although the inter-annual response of hyporheic fauna to river flow variability remains unknown. The changes in benthic taxa richness and the number of individuals per sample may reflect differences in habitat availability within the channel during drought conditions and the loss or contraction of important habitats such as clean gravels and river margin habitats under low-flow conditions (Harrison, 2000), and also modified life history schedules (particularly emergence of adults) of aquatic insects during extended droughts (Lake, 2003).

Periods of drought-related low flows have the potential to significantly modify in-stream communities in both naturally intermittent and perennial lotic systems (Boulton, 2003; Wood and Armitage, 2004; Lake, 2007). Short duration meteorological or hydrological droughts may significantly modify benthic communities in naturally intermittent systems (Boulton and Lake, 1992; Acuna et al., 2005) but may have limited or even undetectable impacts within perennial streams due to the buffering effect of baseflow from groundwater sources (Wood, 1998; Humphries and Baldwin, 2003; Lake, 2003). Supra-seasonal groundwater droughts also lead to significant changes in water quality (Parr and Mason, 2003; Suren et al., 2003), reduction of in-stream habitat availability and diversity, and changes to benthic community structure and composition (Exteve, 1981; Lake, 2003; Dewson et al., 2007), particularly if the community is not adapted to extreme low flows or drying (Lytle and Poff, 2004). However, it may take some time for the impact of drought on in-stream ecology to become apparent in groundwater-dominated systems (Wright and Symes, 1999; Wood and Armitage, 2004). Antecedent hydrological conditions are critical to determining the recession of flow during droughts (Marsh et al., 2007) and this, in turn, is a primary factor influencing the ability of in-stream communities to withstand the hydrological disturbance (Humphries and Baldwin, 2003; Lake, 2007).

Knowledge regarding the response of hyporheic communities to low flows and drought is limited and is largely confined to naturally intermittent systems where hyporheic communities have been monitored following the cessation of surface flows (Boulton and Stanley, 1995; Clinton et al., 1996; del Rosario and Resh, 2000; Hose et al., 2005). Only a single study has simultaneously considered the response of both benthic and hyporheic invertebrate communities to experimental low flows and this indicated no deleterious impacts on pool-dwelling invertebrates or on the abundance or vertical distribution of hyporheic macroinvertebrates as long as flow persisted (James et al., 2008).

The intensive short-term study associated with the final stages of the supra-seasonal drought in 2006 suggested that the response of the benthic fauna is governed by a range of factors in addition to flow (discharge) as the lowest species richness and abundance did not correspond with the period of lowest flows. These changes coincide with the emergence of many aquatic insect taxa from the benthos and means isolating the effect of drought from natural life history characteristics is not possible unless considered alongside long-term data (Lake, 2003), which indicates that emergence of many insects occurred earlier in 2006 drought than in non-drought years. The hyporheic community responded differently to the benthos to the
changes in flow and water level during the study period. Therefore, it cannot be assumed that the impact of low flow/drought upon benthic communities and the response of fauna inhabiting the hyporheic zone will be the same. This should not be unexpected because the reduction in the volume of water and the ultimate dewatering of the channel will occur within benthic habitats before water level changes within hyporheic habitats. The results of this study suggest that other abiotic parameters, such as thermal characteristics, may be significant factors structuring both communities during supra-seasonal drought.

A conceptual model of low flow and drought influences on ecologically significant processes and interactions between the benthic and hyporheic zones

The potential influences of changes in river flow and associated abiotic factors on benthic and hyporheic communities can be hypothesized, drawing on sources from the hydrological, sedimentological and ecological literature. The conceptual model outlined in Figure 7 specifically considers the processes and interactions that may influence invertebrate communities within the hyporheic zone during periods of low flow and stream bed drying associated with surface water and groundwater drought. To our knowledge, this is the first attempt that has been made to integrate abiotic drivers with likely responses by benthic and hyporheic stream invertebrates, and provides an insight into the potential impacts of anthropogenic activities on these subsystems and the hydrological linkages between them, especially during drought.

When river flow and bed integrity are unimpaired, the hyporheic zone and the adjacent parafluvial zone (sensu Boulton et al., 1998) will be saturated, allowing both vertical and lateral hydrological exchange (Stanford and Ward, 1993; Malard et al., 2002). The nature of physical and biogeochemical interactions occurring within the hyporheic zone will be strongly influenced...
by the direction of hydrological exchange (upwelling groundwater or downwelling surface water) and the flow velocity (Figure 7a). Local differences in the nature of these exchanges will be influenced by floodplain and channel morphology (Stanford and Ward, 1993) and at smaller scales by individual riffle, pool and bar sequences (Lefebvre et al., 2006) and even individual bed elements (Boulton, 2007) which may result in micro-scale patch variability in faunal distributions (Dole-Olivier and Marmonier, 1992; Davy-Bowker et al., 2006). Unimpaired hydrological exchange within the hyporheic zone promotes thermal exchange (Hannah et al., 2008), the maintenance of hyporheic interstitial permeability, porosity and flow velocities (Malcolm et al., 2005) and in-stream storage or export of nutrients (Figure 7a). As a result, the hyporheic zone may be one of the primary locations for the processing of nutrients and dissolved and particulate organic matter within some systems (Mulholland et al., 2008; Pinay et al., 2009) particularly through microbial activity (Hendricks, 1993; Marxsen, 2006).

As flow declines as a drought proceeds, exchange processes and connectivity between the hyporheic zone and the adjacent parafluvial will be reduced (Figure 7b). Riparian vegetation may begin to experience water stress, and marginal and in-stream vegetation will become partially or even fully exposed. Depending on whether water is locally upwelling or downwelling, the hyporheic zone may still function as a transient store or source of solutes (Stofleth et al., 2008), although the rate of exchange is likely to be significantly reduced. In the absence of flushing flows, fine sediments (<2 mm in size) may be deposited onto the bed, infiltrating and potentially clogging the interstices within the benthic and hyporheic zones (Brunke, 1999). This reduces the competency of exchange processes and the porosity and permeability of the sediments (Bo et al., 2007; Meyer et al., 2008), with consequences for the supply of dissolved solutes and hyporheic oxygen (Youngson et al., 2004). It also reduces living space for larger hyporheic invertebrates as well as sediment-associated benthos. The fine sediments may also be stabilized by the development of autochthonous biofilms and algal mats, further exacerbating the situation (Battin, 2000).

In many naturally intermittent rivers (in semi-arid and temperate regions) or during high magnitude supra-seasonal droughts within environments where surface
flow is usually perennial, flow may almost cease and
water becomes isolated within pools, although the
hyporheic zone usually remains saturated (Figure 7c). As
surface and groundwater levels decline, lateral interac-
tions with the parafluvial zone may diminish or cease.
Riparian and marginal vegetation typically experience
significant water stress and aquatic macrophytes may
be eliminated (Westwood et al., 2006). Fine sediments
often form a relatively impermeable crust over the
substratum of the bed, beneath which anoxic condi-
tions may exist (Smock et al., 1994). Water within
the hyporheic zone will continue to travel down-
stream and local upwelling may supply free water,
maintaining a limited interstitial habitat and thermal
regime within the tolerance limits of some fauna (Hose
et al., 2005). However, the chemical characteristics
of this hyporheic water are likely to be altered by
the reduced interaction with surface waters as well
as the deteriorating water quality typical of drying
streams.

If drought conditions persist, levels of water within
the hyporheic zone may decline, ultimately leading to
the desiccation of benthic then hyporheic sediments
(Figure 7d). The habitat available for aquatic organisms
will then become extremely limited, although refugia
may exist in the form of moisture-retaining pock-
ets of organic matter on the bed or at the margins,
deeper burrows excavated by organisms such as cray-
fish, and hyporheic sediments that retain a high humid-
ity (Boulton, 1989; Fenoglio et al., 2006). Some aquatic
taxa, particularly in systems with predictable periods of
stream bed drying, display life-cycle adaptations such
as diapause to withstand the desiccation (Boulton, 2003;
Williams, 2006). Under extreme supra-seasonal ground-
water drought conditions, exchange processes within the
hyporheic zone may all cease until groundwater levels
begin to recover.

A landscape perspective

Drought is a large-scale phenomenon (Lake, 2003) and
when the conceptual model outlined earlier is placed
in a landscape perspective, the potential scale and sig-
ificance of processes operating along the ‘hyporheic corridor’ (sensu Stanford and Ward, 1993) or within the ‘stygoscape’ (sensu Datry et al., 2008) becomes
apparent. The lateral connectivity of alluvial sediments
and differential permeability associated with paleochan-
nels and floodplain water bodies, such as ponds, cut-
offs and backwater channels, provide corridors along
which water and biota may be able to move (Figure 8).

Figure 8. Conceptual model of the ‘hyporheic corridor’ from a landscape perspective indicating floodplain habitats such as ponds, pools, oxbow lakes
and palaeochannels: (a) lateral connectivity of the hyporheic corridor during unimpaired flow and (b) lateral connectivity when surface flow in the
river channel has ceased.
These differences in sedimentary characteristics may lead locally to elevated (perched) water tables (Malard et al., 2002), which may provide small areas of surface water that persist even when flow in adjacent rivers has ceased (Figure 8b). This landscape perspective also demonstrates the refugial potential of the ‘hyporheic corridor’ for both hypogean and surface water fauna, respectively (Harris et al., 2002). When this landscape perspective is extended to consider the wider drainage basin, the ‘stygoscpe’ clearly extends into headwater streams and springs (Wood et al., 2005) and truly subterranean habitats including cave ecosystems (Gibert and Deharveng, 2002). The potential influence of supra-seasonal groundwater drought upon subterranean ecosystems has not been widely considered to date due to the widely perceived stability of these environments and communities they support. However, the pervasive vertical hydrological linkages across the drainage basin, via hyporheic zones and shallow aquifers clearly have potential to structure communities in these habitats and affect refugial areas for surface communities. These environments and their fauna may not be so stable after all, especially during hydrological and groundwater droughts.

CONCLUSION

In-stream faunal responses to low flows and drought are frequently overlooked or only considered once the event has proceeded for many months or seasons, by which time significant changes have often already occurred. To compound these problems, the extended and ‘creeping’ nature of groundwater droughts do not easily fit the timeframe of most research projects (Lake, 2003). The results of this research demonstrate the temporal impact of groundwater drought on surface and subsurface faunal assemblages at scales of individual in-stream habitats (riffles) to the landscape perspective hypothesized in our conceptual models. The research also illustrates the importance of considering lagged effects in response to hydrological inputs (precipitation) both during and following periods of drought. This is particularly important in areas subject to extended supra-seasonal groundwater droughts as the response of the aquatic faunal community is a function of the conditions within the underlying aquifer, hyporheic and parfluval zones. In most streams, recovery of flow and the aquatic invertebrate community will only occur once the aquifer, parfluval and hyporheic zones are fully saturated.

Until stream hydrologists, ecologists and river managers fully appreciate the interactions between groundwater, the hyporheic zone and the surface stream, our understanding of the effects of drought on microbial processes and the invertebrates inhabiting the hyporheic and benthic zones will be severely constrained. We contend that disappearance or reappearance of surface water is only part of the dynamic in-streams subject to drought and we urge further integrated research on surface and subsurface habitats to test hypotheses derived from our conceptual model. Currently, the model is a static one and as we learn more about the effects of antecedent conditions, we will be able to add the crucial temporal component that could predict the effects of ‘drought history’ on surface and hyporheic assemblages, with obvious implications for understanding the effects of climate change and anthropogenic modifications of flow regime.

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