

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

R. Stubbington,¹ P. J. Wood^{1*} and A. J. Boulton²

¹ Department of Geography, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK

² Ecosystem Management, University of New England, Armidale 2350, New South Wales, Australia

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 surface 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

* Correspondence to: Dr P. J. Wood, Department of Geography, Loughborough University, Loughborough, Leicestershire, LE11 3TU, UK.
E-mail: p.j.wood@lboro.ac.uk

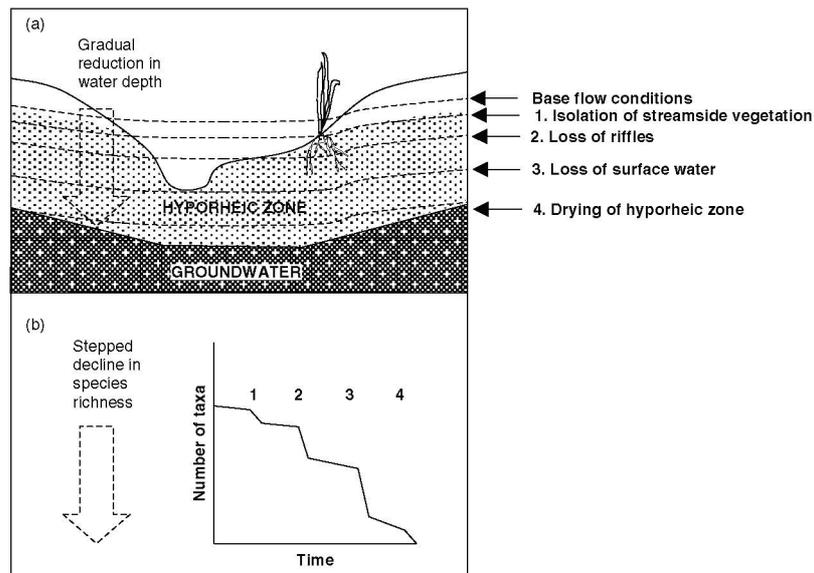


Figure 1. Changes in river stage and macroinvertebrate assemblage composition associated with supra-seasonal drought: (a) cross-section of a conceptualized channel during critical stages of drying; (b) hypothesized 'stepped' changes in species richness corresponding to these critical stages (adapted from Boulton, 2003)

1 response of lotic communities to drought and reduced
2 river discharge has been characterized by gradual (ramp)
3 changes punctuated by significant 'stepped' responses
4 as thresholds between critical levels are crossed (Boul-
5 ton, 2003). These steps reflect the gradual reduction in
6 river stage (water depth) coinciding with ecologically sig-
7 nificant threshold changes in discharge or the exposure
8 of particular habitats. Examples include the isolation of
9 streamside vegetation, cessation of flow, the isolation of
10 surface water into pools, loss of surface water and far
11 less studied the decline or loss of free water within the
12 hyporheic zone (Figure 1).

13 The functional significance of the hyporheic zone has
14 gained increasing prominence in recent years (Boulton
15 *et al.*, 1998; Boulton, 2007). This reflects the recognition
16 that the habitat supports a number of unique (obligate)
17 taxa and has wider linkages in the landscape with other
18 surface and groundwater habitats (Malard *et al.*, 2002).
19 There is increasing evidence that processes operating
20 within the hyporheic zone may significantly contribute
21 to maintaining ecosystem health (Tomlinson *et al.*, 2007;
22 Pinay *et al.*, 2009) through the provision of key ecosys-
23 tem services (Boulton *et al.*, 2008). It is now widely rec-
24 ognized that the hyporheic zone is a focal point for impor-
25 tant biogeochemical processes and the transient storage
26 of nutrients (Mulholland *et al.*, 2008; Pinay *et al.*, 2009).
27 In addition, the exchange of water within the hyporheic
28 zone may locally influence dissolved oxygen concentra-
29 tions, thermal properties and sedimentary characteristics
30 required to support salmonid fisheries (Malcolm *et al.*,
31 2005).

32 In this article, we synthesize the existing hydroecologi-
33 cal data available for the Little Stour River (Kent, UK) to
34 examine macroinvertebrate community responses to river
35 flow variability and drought-related low flows. The ben-
36 thic macroinvertebrate hydroecology of the river has been
37

extensively studied for over a decade in relation to flow
38 variability, in particular the influence of low flows asso-
39 ciated with droughts (Wood and Petts, 1999; Wood *et al.*,
40 2000; Wood and Armitage, 2004). We present data from
41 a long-term study of inter-annual variability of the ben-
42 thic community (1992–1999) and data collected as part
43 of a detailed monthly investigation of the benthic and
44 hyporheic invertebrate communities during a groundwa-
45 ter drought in 2006. In particular, we assess whether the
46 benthic and hyporheic fauna respond similarly to drought
47 and whether there is evidence of marked 'step responses'
48 to the ramp disturbance of drought in the hyporheic zone
49 where effects of drying are hypothesized to be buffered
50 by the saturated sediments. These results are used along
51 with other published information to develop a conceptual
52 model to demonstrate how interactions between surface
53 and groundwater influence hydrological processes within
54 the hyporheic zone which, in turn, may structure habitat
55 availability and the benthic and hyporheic zone commu-
56 nities.
57

STUDY SITE

61 The Little Stour River (Kent, UK) is a small lowland
62 chalk stream, 11.5-km long, draining a catchment area
63 of approximately 213 km² (51.275°N 1.168°E). The
64 highly permeable nature of the catchment results in a
65 low drainage density, which is typical of groundwater-
66 dominated streams. The sedimentary calcareous rocks
67 result in relatively high conductivities (*ca* 580 $\mu\text{S cm}^{-1}$).
68 Mean annual precipitation within the catchment is *ca*
69 650 mm per year (Wood and Petts, 1994). The river is
70 usually perennial below the spring head, although a 1-km
71 reach has been dewatered on three previous occasions
72 in the last century during supra-seasonal drought events
73 (1949, 1991–1992 and 1996–1997), with the latter two
74

1 events being studied in detail (Wood and Armitage,
2 2004). A subsequent drought event impacted the site
3 and much of southern England between 2004 and 2006
4 (Marsh, 2007), although the Little Stour maintained
5 perennial flow along its entire length throughout this
6 period.

7 8 9 METHODS

10 The macroinvertebrate community of the river was sam-
11 pled annually (1992–1999) from nine sites along the
12 upper river. Macroinvertebrates were sampled during
13 base flow conditions (late August–early September)
14 using a semi-quantitative kick-sampling technique over
15 a 2-min period (Wood and Armitage, 2004). During
16 2006, both benthic and hyporheic invertebrate commu-
17 nities were sampled from four riffle sites on the river
18 between April 2006 and October 2006. This coincided
19 with the latter stages of a supra-seasonal drought result-
20 ing from below-average rainfall between November 2004
21 and June 2006 (Marsh *et al.*, 2007). For further details of
22 site locations and physical characteristics, including rela-
23 tive flow permanence, see Wood and Petts (1999) and
24 Wood *et al.* (2000).

25 During the intensive study in 2006, five benthic sam-
26 ples were collected at each of the four riffle sites on the
27 upper river each month using a Surber sampler (0.1 m²,
28 250- μ m mesh net) over a 30-s period, disturbing the
29 substratum to a depth of 50 mm. Associated with each
30 benthic sample, hyporheic invertebrate samples were col-
31 lected from 20-cm deep polyvinylchloride (PVC) wells
32 (25-mm internal diameter) following the procedure out-
33 lined by Boulton and Stanley (1995). PVC wells were
34 inserted into the riverbed using a stainless steel bar
35 and samples can be collected immediately. The primary
36 advantages of this technique over others, such as the
37 Bou-Rouch sampler (Bou and Rouch, 1967) are that:
38 (i) the small size of the well minimizes disturbance of
39 surrounding sediments and it can remain in place to allow
40 collection of subsequent samples; (ii) the sampler does
41 not require priming with water and as a result is fully
42 quantitative and (iii) the sample does not pass through the
43 mechanism of the pump and as a result specimens are less
44 prone to damage. Each sample comprised 6 l of hyporheic
45 water pumped from the base of the well using a bilge
46 pump. For each hyporheic water sample, pH, conductiv-
47 ity, dissolved oxygen concentration, and water tempera-
48 ture were measured (Hanna Instruments) before passing
49 the sample through a 90- μ m mesh sieve to isolate the
50 fauna. Benthic water characteristics (pH, conductivity,
51 dissolved oxygen concentration and water temperature)
52 were also recorded before the collection of faunal sam-
53 ples. Benthic and hyporheic invertebrate samples were
54 preserved in the field in 4% formaldehyde, and returned
55 to the laboratory for processing and identification. In the
56 laboratory, invertebrate taxa were identified to species
57 level except Baetidae (Ephemeroptera—mayfly larvae),
58 Chironomidae (non-biting midge larvae) and Oligochaeta
59 (worms).

To examine long-term temporal trends within the fau- 60
nal data, box-plots or error bar graphs were assessed. 61
The influence of inter-annual flow variability was investi- 62
gated using the number of individuals and the number 63
of taxa per sample (species richness). These two mea- 64
sures were standardized before analysis by calculating 65
z-scores for individual sample sites from 1992 to 1999 66
(site mean = 0 and standard deviation = 1). This method 67
of standardization does not alter the shape of the time- 68
series curves at individual sites or correlation coefficients 69
with independent variables, thus allowing comparisons 70
between the responses of multiple sites to the same 71
external factor (discharge variability). To examine the 72
influence of antecedent hydrological conditions on the 73
most common taxon recorded on the Little Stour, the 74
amphipod shrimp *Gammarus pulex* (L.), mean annual and 75
monthly discharge characteristics up to 12 months before 76
sample collection were examined using scatter plots and 77
by calculating correlation coefficients between river flow 78
(discharge) characteristics and the standardized number 79
of individuals per sample for the four riffle sites (also 80
used during the 2006 study period). One way analysis of 81
variance (ANOVA) was used to examine temporal differ- 82
ences between benthic and hyporheic invertebrate com- 83
munities during 2006 following application of Levene's 84
test to ensure that variances were homogeneous. Differ- 85
ences between individual months were examined using 86
Tukey's *post-hoc* multiple comparisons tests to identify 87
where significant differences occurred. All analyses were 88
undertaken using the package SPSS (Version 15). 89

90 91 92 RESULTS

93 *Benthic community response to inter-annual flow* 94 *variability*

95 The influence of three supra-seasonal droughts re- 96
corded during the study period (1992, 1996–1997 and 97
2005–2006) is clear on the long-term hydrograph of the 98
Great Stour River (Figure 2) for which a continuous flow 99
series is available and for which the Little Stour forms the 100
largest tributary. The influence of the drought periods is 101
evident for the Little Stour River between 1992 and 1999 102
(Figure 3a). However, the meteorological and hydrolog- 103
ical droughts marking the onset of the supra-seasonal 104
events (Summer, 1995 and Autumn, 2004) were charac- 105
terized by relatively high discharge on several occasions 106
due to high groundwater levels (H on Figure 2). Perennial 107
flow was maintained throughout the Great Stour during 108
the study period although a 1-km reach of the Little Stour 109
was dewatered during 1991–1992 and 1996–1997 when 110
extreme supra-seasonal groundwater drought conditions 111
prevailed. 112

113 A total of 87 taxa from 48 families were recorded dur- 114
ing the study period, ranging from only 42 taxa in 1992 115
to 60 taxa in 1995. The standardized number of individu- 116
als and species richness responded directly to changes in 117
the discharge regime (Figure 3). Supra-seasonal drought 118
conditions during 1992 and 1996–1997 resulted in low

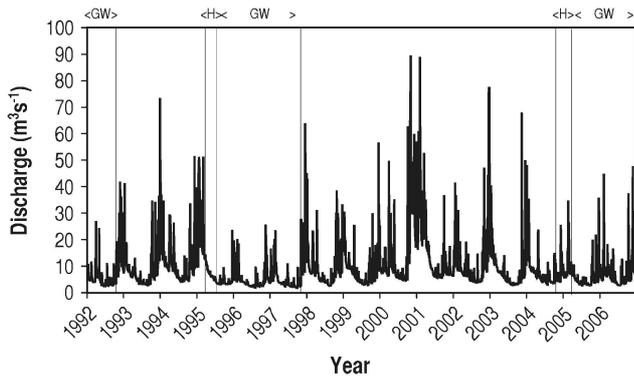


Figure 2. Hydrograph of mean daily discharge ($\text{m}^3 \text{s}^{-1}$) for the Great Stour River at Horton (1992–2006). GW indicates periods of supra-seasonal groundwater drought and H indicates the onset of meteorological and hydrological drought conditions

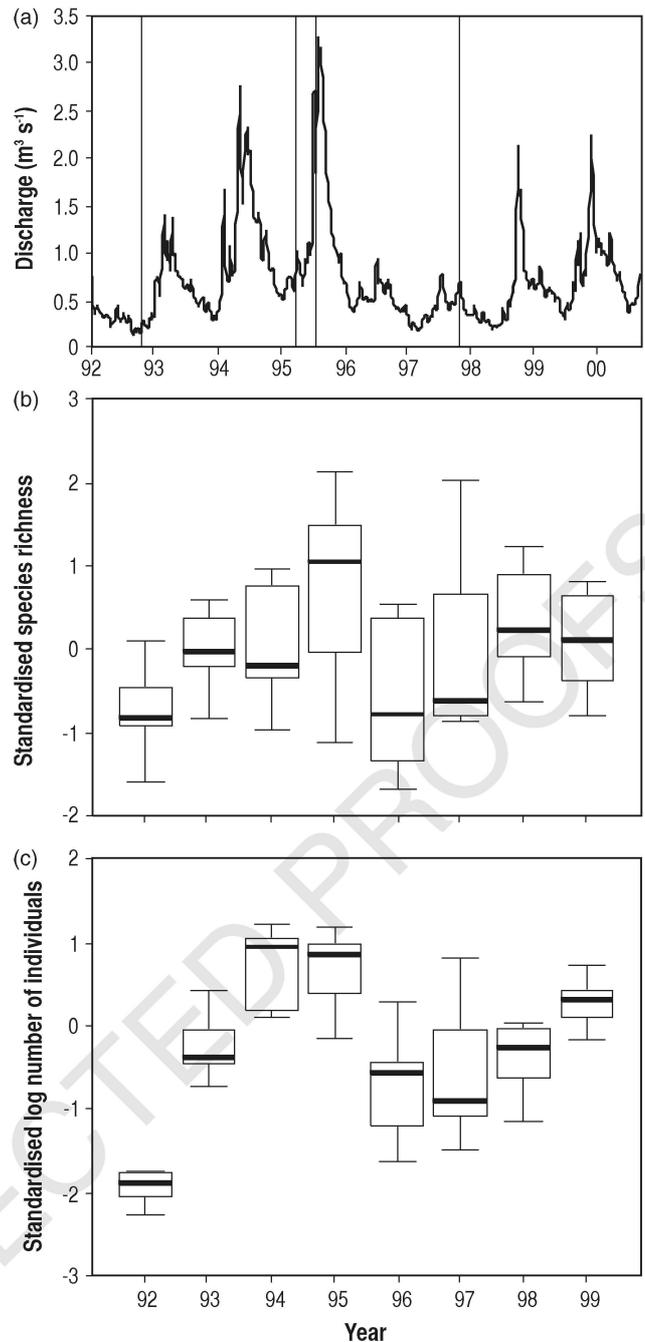


Figure 3. Time series of river flow and box-plots of macroinvertebrate assemblage indices 1992–1999 for the Little Stour River: (a) hydrograph of mean daily discharge ($\text{m}^3 \text{s}^{-1}$) for the Little Stour River at West Stourmouth—see Figure 2 for definition of vertical lines; (b) standardized species richness and (c) standardized number of individuals per sample (\log_e transformed)

1 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.

14 Benthic and hyporheic community responses to supra-seasonal drought

16 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).

35 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 ($F_{6,140} = 7.37$, $P < 0.001$) from an average of 23–13 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 ($F_{6,140} = 2.79$, $P = 0.01$) 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 and July

Table I. Pearson correlation coefficients between standardized \log_e -*Gammarus pulex* and lagged discharge variables for riffles sites ($n = 4$ sites) on the Little Stour River (1992–1999)

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

All samples collected from last week of August to the first week of September throughout the study period. *M*-*n* 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. * $P < 0.05$; ** $P < 0.005$.

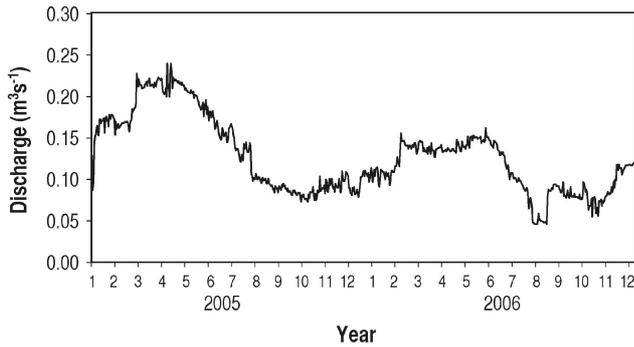


Figure 4. Hydrograph of mean daily discharge for the Little Stour River at Littlebourne (2005–2006)

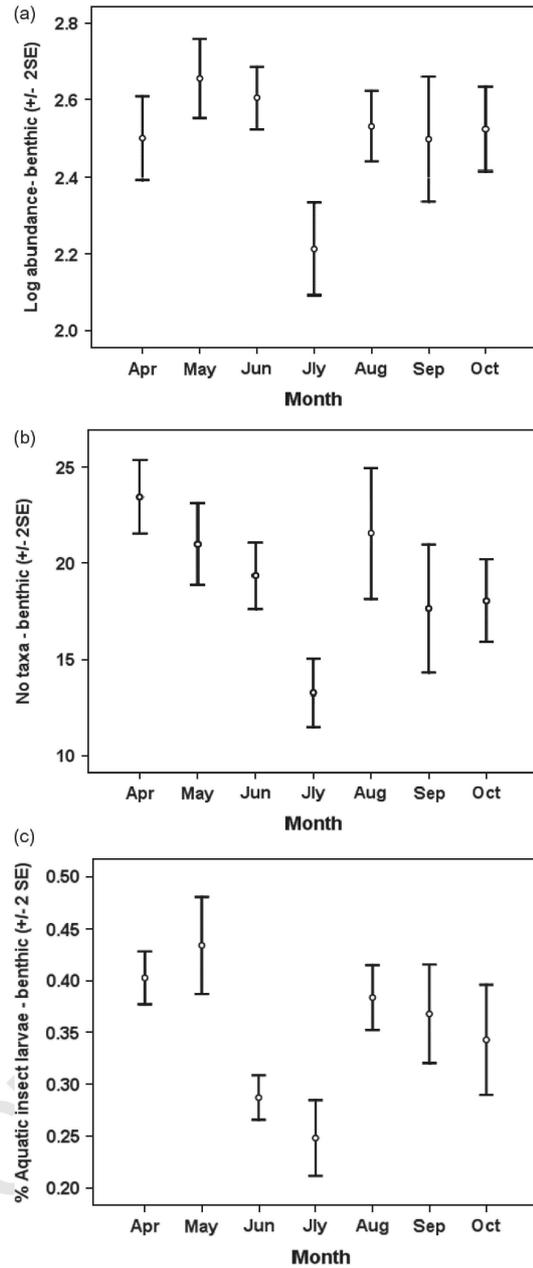


Figure 5. Little Stour benthic assemblage response (April–October 2006) during the final stages of a supra-seasonal drought event (2004–2006). Mean (+/-2 standard error) of: (a) abundance of macroinvertebrates, (b) number of taxa and (c) percentage of aquatic insect larvae within samples

1 (Tukey's *post-hoc* test: all $P < 0.05$) than all other
 2 months (Figure 5c).
 3 The abundance of invertebrates within the hyporheic
 4 zone was significantly different between months
 5 ($F_{6,140} = 21.02$, $P < 0.001$). Hyporheic abundances
 6 increased significantly in July and September (Tukey's
 7 *post-hoc* test: all $P < 0.005$) but were reduced during
 8 August and October (Figure 6a). The number of taxa
 9 recorded in hyporheic samples also differed significantly
 10 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

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)

	April	May	June	July	August	September	October
Max air temperature (°C)	14.2 (2.2)	13.5 (2.4)	17.2 (2.9)	21.9 (2.1)	17.7 (1.7)	18.8 (1.7)	15.1 (1.4)
Min air temperature (°C)	8.6 (2.3)	9.3 (1.9)	11.3 (2.7)	15.6 (1.7)	13.4 (1.4)	14.7 (1.7)	11.8 (2.5)
Water temperature (°C)	9.4 (0.5)	12.8 (1.8)	16.5 (2.5)	18.6 (3.1)	14.2 (1.2)	14.6 (1.1)	12.4 (0.8)
Hyporheic temperature (°C)	8.1 (0.5)	10.9 (1.7)	14.1 (2.2)	16.6 (2.1)	12.3 (1.1)	13.1 (1.0)	10.4 (0.7)

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

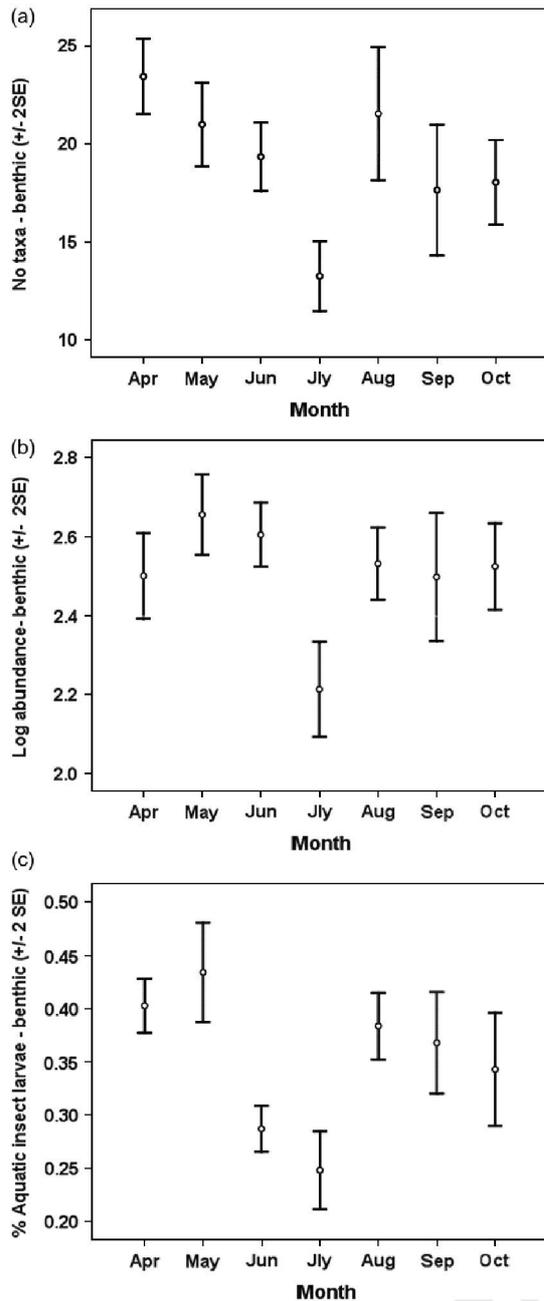


Figure 6. Little Stour hyporheic assemblage response (April–October 2006) during the final stages of a supra-seasonal drought event (2004–2006). Mean (± 2 standard error) of: (a) abundance of macroinvertebrates and (b) number of taxa

1 increase in obligate hyporheic taxa including *Proasellus*
 2 *cavaticus*, *Niphargus aquilex* and *N. fontanus*.

DISCUSSION

6 *Effects of drought on benthic and hyporheic invertebrate*
 7 *assemblages*

8 The long-term data from the Little Stour clearly
 9 demonstrates that, on an inter-annual basis, the num-
 10 ber of taxa and the number of individuals per sample
 11 appear to respond to the volume of discharge. Periods of
 12 supra-seasonal drought significantly reduced taxa rich-
 13 ness and numbers of individuals over multiple events

of varying duration. This corroborates the pattern pre- 60
 dicted for benthic fauna hypothesized by Boulton (2003), 61
 and summarized in Figure 1, although the inter-annual 62
 response of hyporheic fauna to river flow variability 63
 remains unknown. The changes in benthic taxa richness 64
 and the number of individuals per sample may reflect dif- 65
 ferences in habitat availability within the channel during 66
 drought conditions and the loss or contraction of impor- 67
 tant habitats such as clean gravels and river margin habi- 68
 tats under low-flow conditions (Harrison, 2000), and also 69
 modified life history schedules (particularly emergence of 70
 adult) of aquatic insects during extended droughts (Lake, 71
 2003). 72

Periods of drought-related low flows have the poten- 73
 tial to significantly modify in-stream communities in 74
 both naturally intermittent and perennial lotic systems 75
 (Boulton, 2003; Wood and Armitage, 2004; Lake, 2007). 76
 Short duration meteorological or hydrological droughts 77
 may significantly modify benthic communities in natu- 78
 rally intermittent systems (Boulton and Lake, 1992; 79
 Acuna *et al.*, 2005) but may have limited or even unde- 80
 tectable impacts within perennial streams due to the 81
 buffering effect of baseflow from groundwater sources 82
 (Wood, 1998; Humphries and Baldwin, 2003; Lake, 83
 2003). Supra-seasonal groundwater droughts also lead 84
 to significant changes in water quality (Parr and Mason, 85
 2003; Suren *et al.*, 2003), reduction of in-stream habitat 86
 availability and diversity, and changes to benthic com- 87
 munity structure and composition (Extence, 1981; Lake, 88
 2003; Dewson *et al.*, 2007), particularly if the commu- 89
 nity is not adapted to extreme low flows or drying (Lytle 90
 and Poff, 2004). However, it may take some time for 91
 the impact of drought on in-stream ecology to become 92
 apparent in groundwater-dominated systems (Wright and 93
 Symes, 1999; Wood and Armitage, 2004). Antecedent 94
 hydrological conditions are critical to determining the 95
 recession of flow during droughts (Marsh *et al.*, 2007) 96
 and this, in turn, is a primary factor influencing the ability 97
 of in-stream communities to withstand the hydrologi- 98
 cal disturbance (Humphries and Baldwin, 2003; Lake, 99
 2007). 100

Knowledge regarding the response of hyporheic com- 101
 munities to low flows and drought is limited and is 102
 largely confined to naturally intermittent systems where 103
 hyporheic communities have been monitored following 104
 the cessation of surface flows (Boulton and Stanley, 1995; 105
 Clinton *et al.*, 1996; del Rosario and Resh, 2000; Hose 106
et al., 2005). Only a single study has simultaneously 107
 considered the response of both benthic and hyporheic 108
 invertebrate communities to experimental low flows and 109
 this indicated no deleterious impacts on pool-dwelling 110
 invertebrates or on the abundance or vertical distribution 111
 of hyporheic macroinvertebrates as long as flow persisted 112
 (James *et al.*, 2008). 113

The intensive short-term study associated with the final 114
 stages of the supra-seasonal drought in 2006 suggested 115
 that the response of the benthic fauna is governed by 116
 a range of factors in addition to flow (discharge) as the 117
 lowest species richness and abundance did not correspond 118

1 with the period of lowest flows. These changes coincide
 2 with the emergence of many aquatic insect taxa from the
 3 benthos and means isolating the effect of drought from
 4 natural life history characteristics is not possible unless
 5 considered alongside long-term data (Lake, 2003), which
 6 indicates that emergence of many insects occurred earlier
 7 in 2006 drought than in non-drought years. The hyporheic
 8 community responded differently to the benthos to the
 9 changes in flow and water level during the study period.
 10 Therefore, it cannot be assumed that the impact of
 11 low flow/drought upon benthic communities and the
 12 response of fauna inhabiting the hyporheic zone will
 13 be the same. This should not be unexpected because
 14 the reduction in the volume of water and the ultimate
 15 dewatering of the channel will occur within benthic
 16 habitats before water level changes within hyporheic
 17 habitats. The results of this study suggest that other
 18 abiotic parameters, such as thermal characteristics, may
 19

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 litera-
 27 ture. The conceptual model outlined in Figure 8 specifi-
 28 cally considers the processes and interactions that may
 29 influence invertebrate communities within the hyporheic
 30 zone during periods of low flow and stream bed drying
 31 associated with surface water and groundwater drought.
 32 To our knowledge, this is the first attempt that has been
 33 made to integrate abiotic drivers with likely responses by
 34 benthic and hyporheic stream invertebrates, and provides
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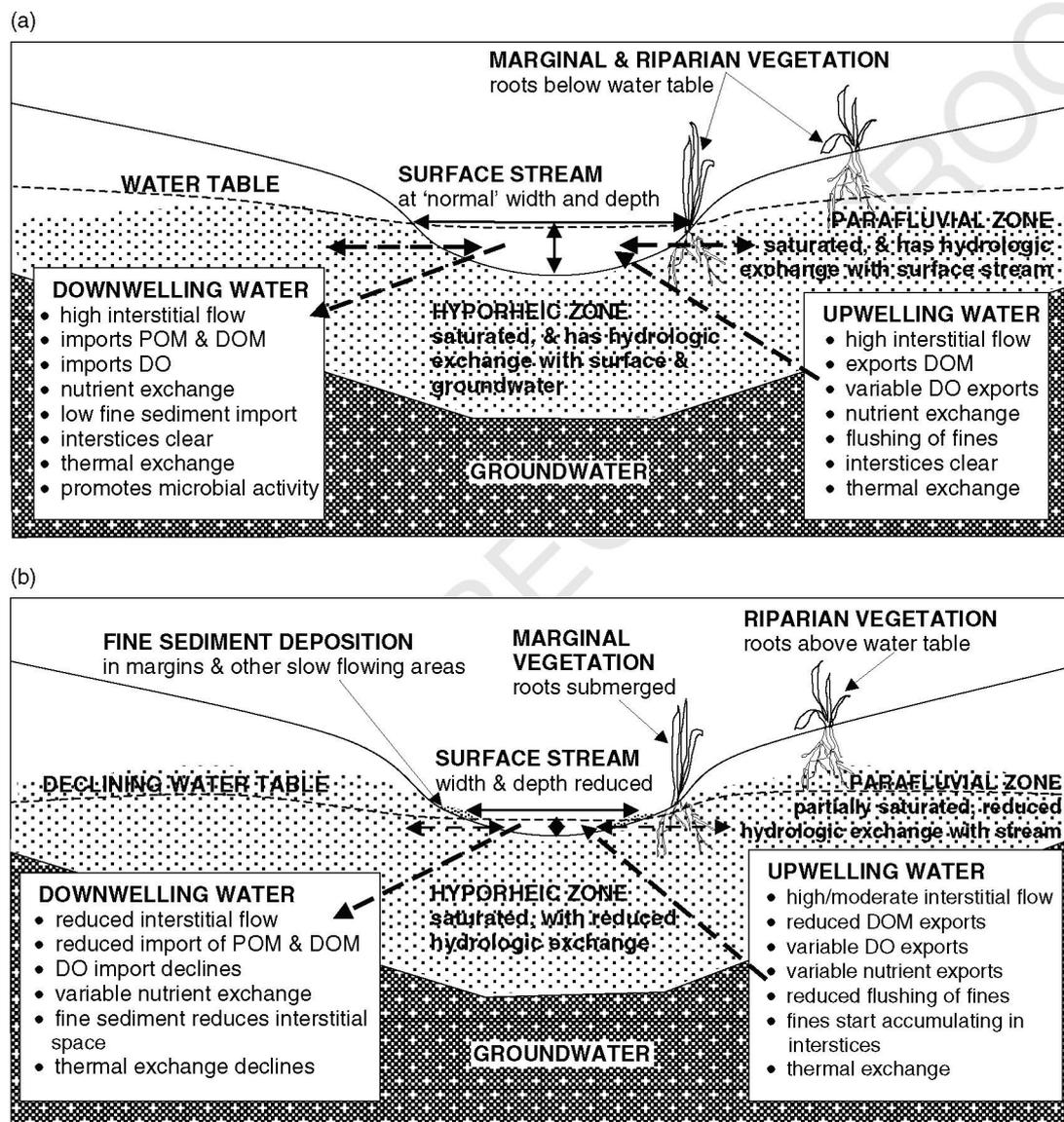


Figure 7. Conceptual model of ecologically significant processes and interactions between the benthic and hyporheic zones as a result of low flow and supra-seasonal drought: (a) unimpaired flow; (b) low/base flow; (c) loss of surface water and (d) decline of water level within the hyporheic zone

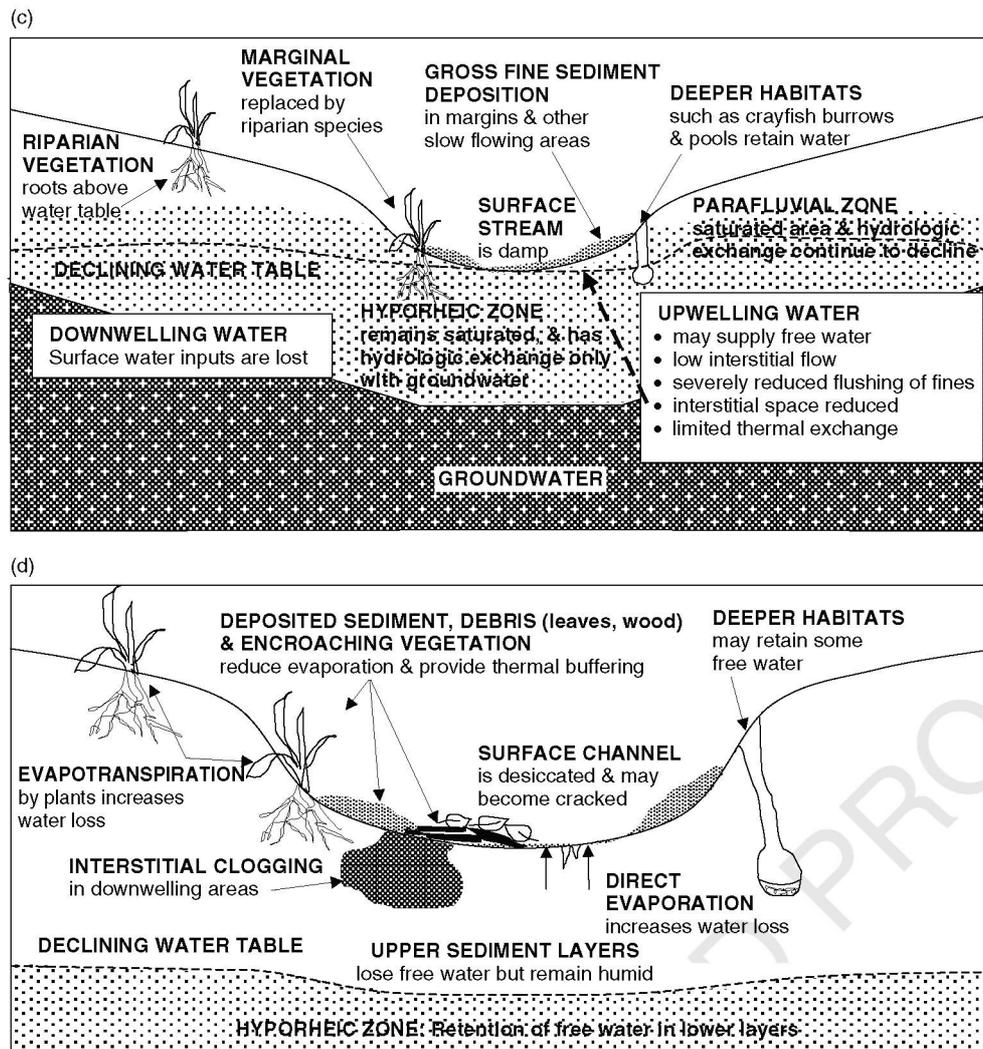


Figure 7. (Continued)

1 an insight into the potential impacts of anthropogenic
2 activities on these subsystems and the hydrological link-
3 ages between them, especially during drought.

4 When river flow and bed integrity are unimpaired,
5 the hyporheic zone and the adjacent parafluvial zone
6 (*sensu* Boulton *et al.*, 1998) will be saturated, allowing
7 both vertical and lateral hydrological exchange (Stan-
8 ford and Ward, 1993; Malard *et al.*, 2002). The nature
9 of physical and biogeochemical interactions occurring
10 within the hyporheic zone will be strongly influenced
11 by the direction of hydrological exchange (upwelling
12 groundwater or downwelling surface water) and the flow
13 velocity (Figure 7a). Local differences in the nature of
14 these exchanges will be influenced by floodplain and
15 channel morphology (Stanford and Ward, 1993) and at
16 smaller scales by individual riffle, pool and bar sequences
17 (Lefebvre *et al.*, 2006) and even individual bed elements
18 (Boulton, 2007) which may result in micro-scale patch
19 variability in faunal distributions (Dole-Olivier and Mar-
20 monier, 1992; Davy-Bowker *et al.*, 2006). Unimpaired
21 hydrological exchanges within the hyporheic zone pro-
22 motes thermal exchange (Hannah *et al.*, 2008), the main-
23 tenance of hyporheic interstitial permeability, porosity

and flow velocities (Malcolm *et al.*, 2005) and in-stream
24 storage or export of nutrients (Figure 7a). As a result, the
25 hyporheic zone may be one of the primary locations for
26 the processing of nutrients and dissolved and particulate
27 organic matter within some systems (Mulholland *et al.*,
28 2008; Pinay *et al.*, 2009) particularly through microbial
29 activity (Hendricks, 1993; Marxsen, 2006).
30

31 As flow declines as a drought proceeds, exchange
32 processes and connectivity between the hyporheic zone
33 and the adjacent parafluvial will be reduced (Figure 7b).
34 Riparian vegetation may begin to experience water stress,
35 and marginal and in-stream vegetation will become
36 partially or even fully exposed. Depending on whether
37 water is locally upwelling or downwelling, the hyporheic
38 zone may still function as a transient store or source
39 of solutes (Stoffleth *et al.*, 2008), although the rate of
40 exchange is likely to be significantly reduced. In the
41 absence of flushing flows, fine sediments (<2 mm in size)
42 may be deposited onto the bed, infiltrating and potentially
43 clogging the interstices within the benthic and hyporheic
44 zones (Brunke, 1999). This reduces the competency of
45 exchange processes and the porosity and permeability
46 of the sediments (Bo *et al.*, 2007; Meyer *et al.*, 2008),

1 with consequences for the supply of dissolved solutes and
 2 hyporheic oxygen (Youngson *et al.*, 2004). It also reduces
 3 living space for larger hyporheic invertebrates as well
 4 as sediment-associated benthos. The fine sediments may
 5 also be stabilized by the development of autochthonous
 6 biofilms and algal mats, further exacerbating the situation
 7 (Battin, 2000).
 8 In many naturally intermittent rivers (in semi-arid
 9 and temperate regions) or during high magnitude supra-
 10 seasonal droughts within environments where surface
 11 flow is usually perennial, flow may almost cease and
 12 water becomes isolated within pools, although the
 13 hyporheic zone usually remains saturated (Figure 7c). As
 14 surface and groundwater levels decline, lateral interac-
 15 tions with the parafluvial zone may diminish or cease.
 16 Riparian and marginal vegetation typically experience
 17 significant water stress and aquatic macrophytes may be
 18 eliminated (Westwood *et al.*, 2006). Fine sediments often
 19 form a relatively impermeable crust over the substratum
 20 of the bed, beneath which anoxic conditions may exist
 21 (Smock *et al.*, 1994). Water within the hyporheic zone
 22 will continue to travel downstream and local upwelling
 23 may supply free water, maintaining a limited interstitial
 24 habitat and thermal regime within the tolerance limits of
 25 some fauna (Hose *et al.*, 2005). However, the chemical

26 characteristics of this hyporheic water are likely to be
 27 altered by the reduced interaction with surface waters as
 28 well as the deteriorating water quality typical of drying
 29 streams.

30 If drought conditions persist, levels of water within
 31 the hyporheic zone may decline, ultimately leading to
 32 the desiccation of benthic then hyporheic sediments
 33 (Figure 7d). The habitat available for aquatic organisms
 34 will become extremely limited, although refugia may
 35 exist in the form of moisture-retaining pockets of organic
 36 matter on the bed or at the margins, deeper burrows
 37 excavated by organisms such as crayfish, and hyporheic
 38 sediments that retain a high humidity (Boulton, 1989;
 39 Fenoglio *et al.*, 2006). Some aquatic taxa, particularly in
 40 systems with predictable periods of stream bed drying,
 41 display life-cycle adaptations such as diapause to with-
 42 stand the desiccation (Boulton, 2003; Williams, 2006).
 43 Under extreme supra-seasonal groundwater drought con-
 44 ditions, exchange processes within the hyporheic zone
 45 may all cease until groundwater levels begin to recover.
 46

47 *A landscape perspective*

48 Drought is a large-scale phenomenon (Lake, 2003) and
 49 when the conceptual model outlined earlier is placed in
 50

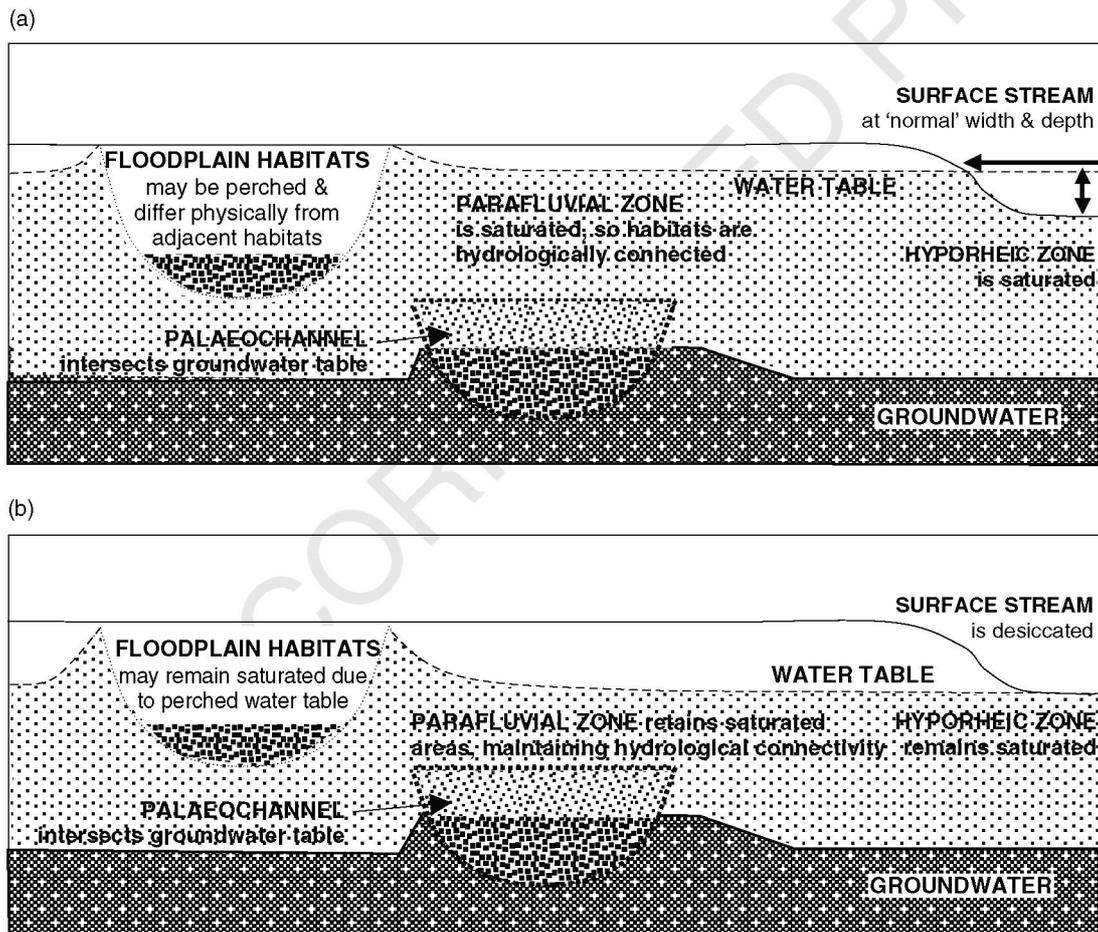


Figure 8. Conceptual model of the 'hyporheic corridor' from a landscape perspective indicating floodplain habitats such as ponds, pools, oxbow lakes and palaeochannels: (a) lateral connectivity of the hyporheic corridor during unimpaired flow and (b) lateral connectivity when surface flow in the river channel has ceased

1 a landscape perspective, the potential scale and signifi- 60
 2 cance of processes operating along the 'hyporheic cor- 61
 3 ridor' (*sensu* Stanford and Ward, 1993) or within the 62
 4 'stygoscape' (*sensu* Datry *et al.*, 2008) becomes appar- 63
 5 ent. The lateral connectivity of alluvial sediments and 64
 6 differential permeability associated with paleochannels 65
 7 and floodplain water bodies, such as ponds, cutoffs and 66
 8 backwater channels, provide corridors along which water 67
 9 and biota may be able to move (Figure 8). These dif- 68
 10 ferences in sedimentary characteristics may lead locally 69
 11 to elevated (perched) water tables (Malard *et al.*, 2002), 70
 12 which may provide small areas of surface water that 71
 13 persist even when flow in adjacent rivers has ceased 72
 14 (Figure 8b). This landscape perspective also demon- 73
 15 strates the refugial potential of the 'hyporheic corridor' 74
 16 for both hypogean and surface water fauna, respectively 75
 17 (Harris *et al.*, 2002). When this landscape perspective 76
 18 is extended to consider the wider drainage basin, the 77
 19 'stygoscape' clearly extends into headwater streams and 78
 20 springs (Wood *et al.*, 2005) and truly subterranean habi- 79
 21 tats including cave ecosystems (Gibert and Deharveng, 80
 22 2002). The potential influence of supra-seasonal ground- 81
 23 water drought upon subterranean ecosystems has not been 82
 24 widely considered to date due to the widely perceived 83
 25 stability of these environments and communities they 84
 26 support. However, the pervasive vertical hydrological 85
 27 linkages across the drainage basin, via hyporheic zones 86
 28 and shallow aquifers clearly have potential to structure 87
 29 communities in these habitats and affect refugial areas 88
 30 for surface communities. These environments and their 89
 31 fauna may not be so stable after all, especially during 90
 32 hydrological and groundwater droughts. 91
 33
 34

35 CONCLUSION

36
 37 In-stream faunal responses to low flows and drought are 92
 38 frequently overlooked or only considered once the event 93
 39 has proceeded for many months or seasons. By which 94
 40 time, significant changes have often already occurred. 95
 41 To compound these problems, the extended and 'creep- 96
 42 ing' nature of groundwater droughts do not easily fit 97
 43 the timeframe of most research projects (Lake, 2003). 98
 44 The results of this research demonstrate the temporal 99
 45 impact of groundwater drought on surface and subsurface 100
 46 faunal assemblages at scales of individual in-stream habi- 101
 47 tats (riffles) to the landscape perspective hypothesized in 102
 48 our conceptual models. The research also illustrates the 103
 49 importance of considering lagged effects in response to 104
 50 hydrological inputs (precipitation) both during and fol- 105
 51 lowing periods of drought. This is particularly important 106
 52 in areas subject to extended supra-seasonal groundwater 107
 53 droughts as the response of the aquatic faunal commu- 108
 54 nity is a function of the conditions within the underlying 109
 55 aquifer, hyporheic and parafluvial zones. In most streams, 110
 56 recovery of flow and the aquatic invertebrate commu- 111
 57 nity will only occur once the aquifer, parafluvial and 112
 58 hyporheic zones are fully saturated. 113
 59

Until stream hydrologists, ecologists and river man- 60
 agers fully appreciate the interactions between ground- 61
 water, the hyporheic zone and the surface stream, our 62
 understanding of the effects of drought on microbial pro- 63
 cesses and the invertebrates inhabiting the hyporheic and 64
 benthic zones will be severely constrained. We contend 65
 that disappearance or reappearance of surface water is 66
 only part of the dynamic in-streams subject to drought 67
 and we urge further integrated research on surface and 68
 subsurface habitats to test hypotheses derived from our 69
 conceptual model. Currently, the model is a static one and 70
 as we learn more about the effects of antecedent condi- 71
 tions, we will be able to add the crucial temporal compo- 72
 nent that could predict the effects of 'drought history' on 73
 surface and hyporheic assemblages, with obvious impli- 74
 cations for understanding the effects of climate change 75
 and anthropogenic modifications of flow regime. 76
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