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

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Keywords: benthos, hyporheos, low flows, drought, hyporheic processes, invertebrates, groundwater.

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 river flow variability 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 characterised 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.

Keywords: benthos, hyporheos, low flows, drought, hyporheic processes, invertebrates, groundwater.

Introduction

Natural low flows associated with droughts originate from a deficit of precipitation (Smahktin 2001). Droughts can occur in almost any biogeographical setting, although the onset of an individual event can be difficult to determine (Humphries & Baldwin 2003; Smahktin & 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 & van Lanen 2004).

River flow regime variability and low flows associated with drought conditions have been widely studied in lotic systems (Smahktin 2001), and their role in structuring in-stream communities is now recognised (e.g., Lytle & 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 to studies reporting the ecological responses to floods (e.g., Lake 2007; Suren & Jowett 2006). 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 &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 limited in comparison (Wood & 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 & 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 characterised 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 recognised 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 paper, we synthesise 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 & 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 'step responses' to the ramp disturbance of drought in the hyporheic zone where effects of drying are hypothesised 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 km^2 (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 (c. 580 $\mu S\ cm^{-1}$). Mean annual precipitation within the catchment is c. 650 $mm\ yr^{-1}$ (Wood & 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 & Armitage 2004). A subsequent drought event impacted the site and much of southern England between 2004-2006 (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-minute period (Wood & Armitage 2004). During 2006, both benthic and hyporheic invertebrate communities were sampled from four riffle sites on the river between April and October 2006. 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 & 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 ($0.1m^2$, 250-μm mesh net) over a 30-second period, disturbing the substratum to a depth of 50 mm. Associated with each benthic sample, hyporheic invertebrate samples were collected from 20-cm deep PVC wells (25 mm internal diameter) following the procedure outlined by Boulton & Stanley (1995). PVC wells were inserted into the riverbed using a stainless steel bar and samples can be collected immediately. The primary advantages of this technique over others, such as the Bou-Rouch sampler (Bou & Rouch 1967) is that: i) the small size of the well minimises 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 prior to 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 standardised prior to analysis by calculating *z*-scores for individual sample sites 1992-1999 (site mean = 0 and standard deviation = 1. This method of standardisation 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 prior to sample collection were examined using scatter plots and by calculating correlation coefficients between river flow (discharge) characteristics and the standardised 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 among 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 1992-1999 (Figure 3a). However, the meteorological and

hydrological droughts marking the onset of the supra-seasonal events (Summer 1995 and Autumn 2004) were characterised 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 during 1992 to 60 taxa in 1995. The standardised 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 two-year period (Figure 3b and 3c). The density of the most abundant taxon, the amphipod shrimp *Gammarus pulex*, was significantly influenced by antecedent hydrological conditions prior to sampling (Table 1). There was a clear positive relationship between discharge and the number of *G. pulex*, with periods of higher discharge (4-7 months prior to sampling) resulting in greater numbers.

Benthic and hyporheic community response 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 2004-05 and 2005-06, 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 (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 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 2). The warm mean air temperatures recorded throughout July were nationally the highest recorded in the 348-year long Central England Temperature (CET) series (Prior & 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 ($F_{6, 140} = 7.37$, $P < 0.001$) 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 ($F_{6, 140} = 2.79$, $P = 0.01$) 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 (Tukey's post hoc test all $P < 0.05$) that 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 Spetember (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 increase in obligate hyporheic taxa including *Proasellus cavaticus*, *Niphargus aquilex* and *N. fontanus*.

Discussion

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 hypothesised by Boulton (2003), and summarised 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 adult) 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 & Armitage 2004; Lake 2007). Short duration meteorological or hydrological droughts may significantly modify benthic communities in naturally intermittent systems

(Boulton & 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 & Baldwin 2003; Lake 2003). Supra-seasonal groundwater droughts also lead to significant changes in water quality (Parr & Mason 2003; Suren et al. 2003), reduction of in-stream habitat availability and diversity, and changes to benthic community structure and composition (Extence 1981; Lake 2003; Dewson et al. 2007), particularly if the community is not adapted to extreme low flows or drying (Lytle & 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 & Symes 1999, Wood & 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 & 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 & Stanley 1995; Clinton et al. 1996; del Rosario & 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 during the 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 can not 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 prior to 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 hypothesised, drawing on sources from the hydrological, sedimentological and ecological literature. The conceptual model outlined in Figure 8 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 & 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 & 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 & Marmonier 1992; Davy-Bowker et al. 2006). Unimpaired hydrological exchanges 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 via microbial activity (Hendricks 1993; Marxen 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 (Meyer et al. 2008; Bo et al. 2007), 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 stabilised 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 become isolated within pools, although the hyporheic zone usually remains saturated (Figure 7c). As surface and groundwater levels decline, lateral interactions 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 conditions may exist (Smock et al. 1994). Water within the hyporheic zone will continue to travel downstream 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 become extremely limited, although refugia may exist in the form of moisture-retaining pockets of organic matter on the bed or at the margins, deeper burrows excavated by organisms such as crayfish, and hyporheic sediments that retain a high humidity (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 groundwater drought conditions, exchange processes within the hyporheic zone may all but cease until groundwater levels begin to recover.

A landscape perspective

Drought is a large-scale phenomenon (Lake 2003) and when the conceptual model outlined above is placed in a landscape perspective, the potential scale and significance of processes operating along the 'hyporheic corridor' (*sensu* Stanford & Ward 1993) or within the 'stygoscape' (*sensu* Datry et al. 2008) becomes apparent. The lateral connectivity of alluvial sediments and differential permeability associated with paleochannels and floodplain water bodies such as ponds, cutoffs and backwater channels provide corridors along which water and biota may be able to move (Figure 8). 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 'stygoscape' clearly extends into headwater streams and springs (Wood et al. 2005) and truly subterranean habitats including cave ecosystems (Gibert & 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 hypothesised 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 parafluvial zones. In most streams, recovery of flow and the aquatic invertebrate community will only occur once the aquifer, parafluvial 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.

Acknowledgements

The authors gratefully acknowledge the continued co-operation of the Environment Agency of England and Wales and particularly Ian Humpheryes, Shelagh Wilson and Kevin Grimmett. Part of this research was supported by a Natural Environment Research Council Urgency Grant (NE/E001769/1) entitled 'The response of aquatic invertebrate fauna to supra-seasonal drought and drying in a largely perennial chalk stream'. Meteorological data for Manston (Kent) were kindly supplied by the British Atmospheric Data Centre (BADC). Thanks to Sally Little for technical and laboratory support and

Mark Szegner (Department of Geography, Loughborough University) for assistance with the production of figures. We would like to thank two anonymous reviewers for their helpful and constructive comments on a draft of this manuscript which helped improve the clarity of the paper in a number of areas.

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List of Figures

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

Figure 2. Hydrograph of mean daily discharge ($m^3 s^{-1}$) for the Great Stour River at Horton (1992-2006). GW indicates periods of supra-seasonal groundwater drought and H indicates the onset of meterological 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 ($m^3 s^{-1}$) for the Little Stour River at West Stourmouth - see Figure 2 for definition of vertical lines; (b) standardised species richness; and (c) standardised number of individuals per-sample (log_e transformed).

Figure 4. Hydrograph of mean daily discharge($m^3 s^{-1}$) 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.

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.

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 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.

Table 1. Pearson correlation coefficients between standardised $\log_e$-*Gammarus pulex* and lagged discharge variables for riffles sites (n = 4 sites) on the Little Stour River (1992-1999).

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

Note: All samples collected during late 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) prior to sample collection (1-12). Y-n refers to the mean daily discharge in the 3, 6 and 12 months prior to samples collection. * = $P < 0.05$; ** = $P < 0.005$.

Table 2. 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)

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

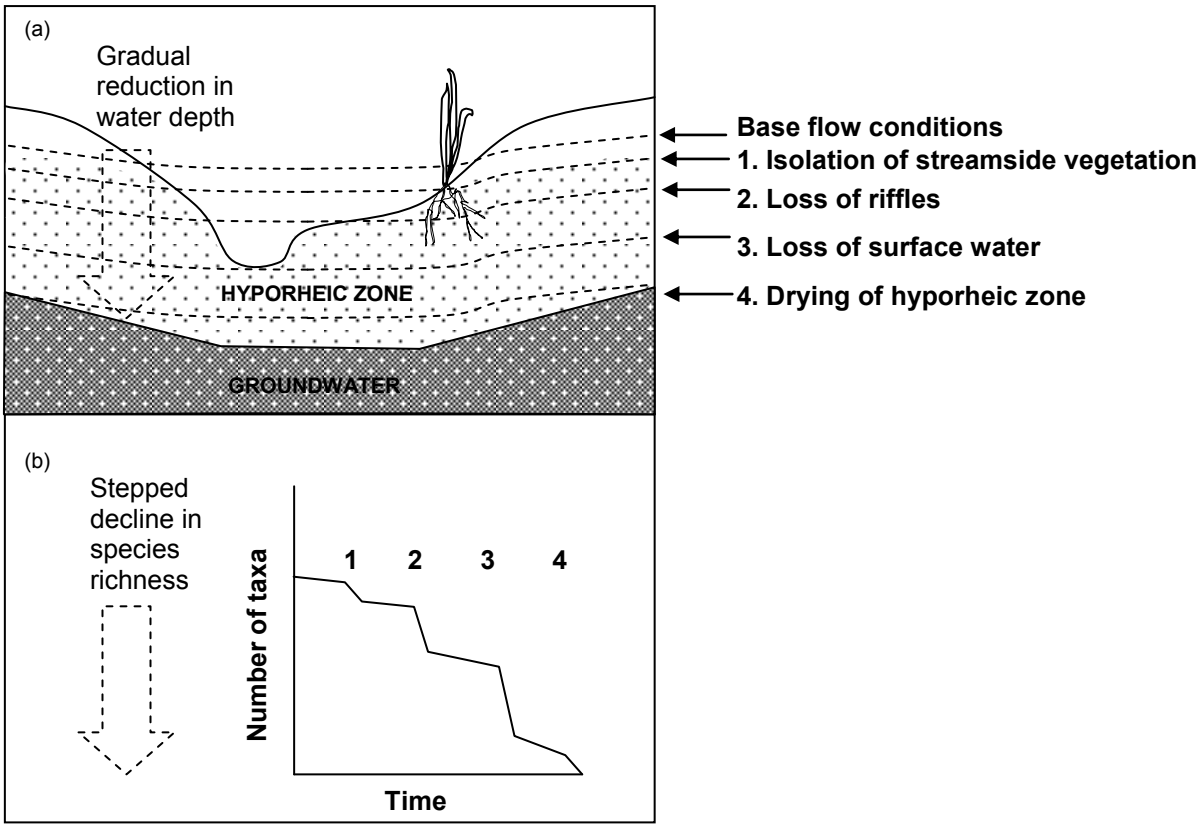
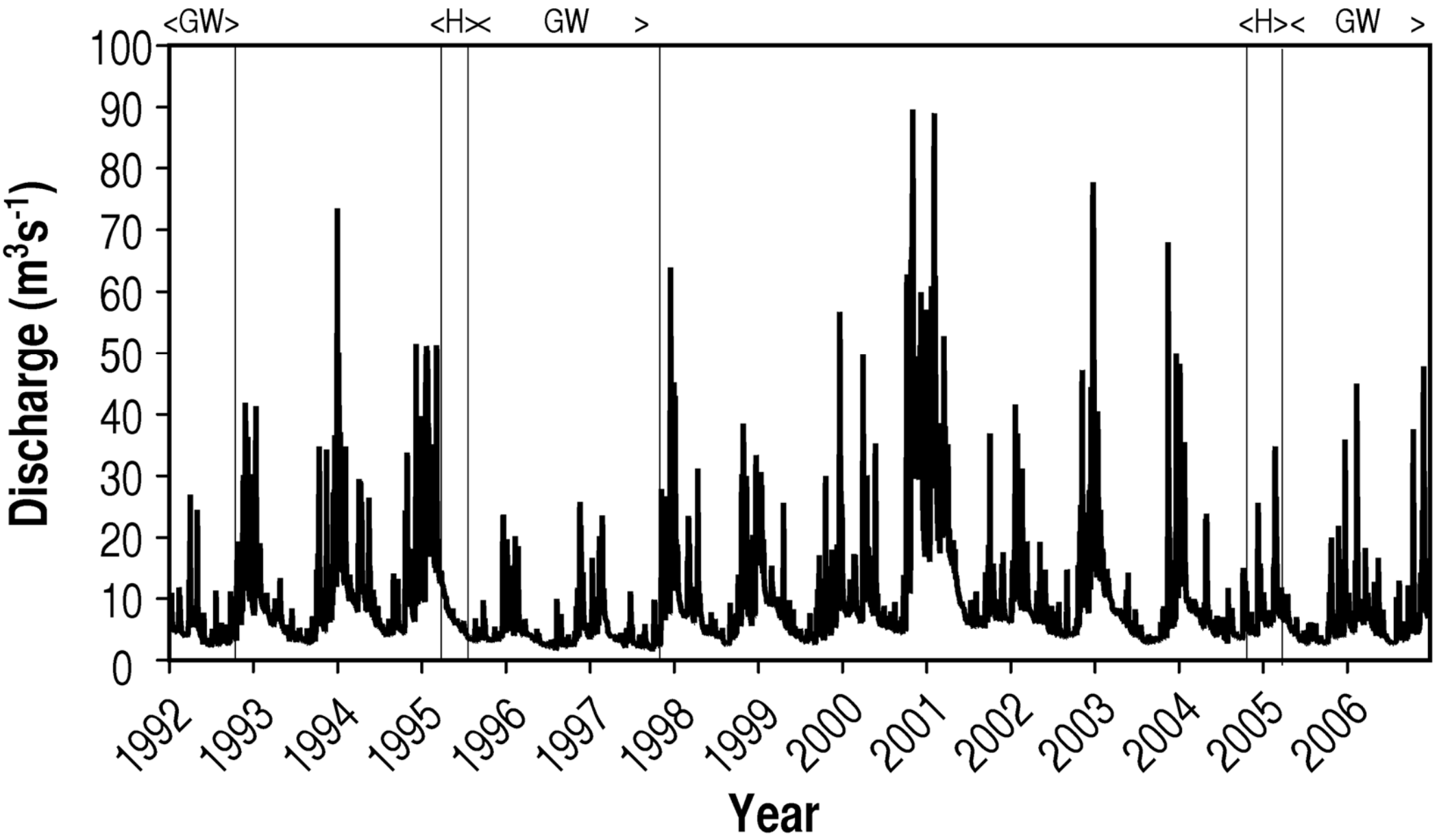

(a)
Gradual reduction in water depth
HYPORHEIC ZONE
GROUNDWATER
Base flow conditions
1. Isolation of streamside vegetation
2. Loss of riffles
3. Loss of surface water
4. Drying of hyporheic zone
(b)
Stepped decline in species richness
Number of taxa
1
2
3
4
Time

Figure 1


<GW>
<H>
GW
>
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GW
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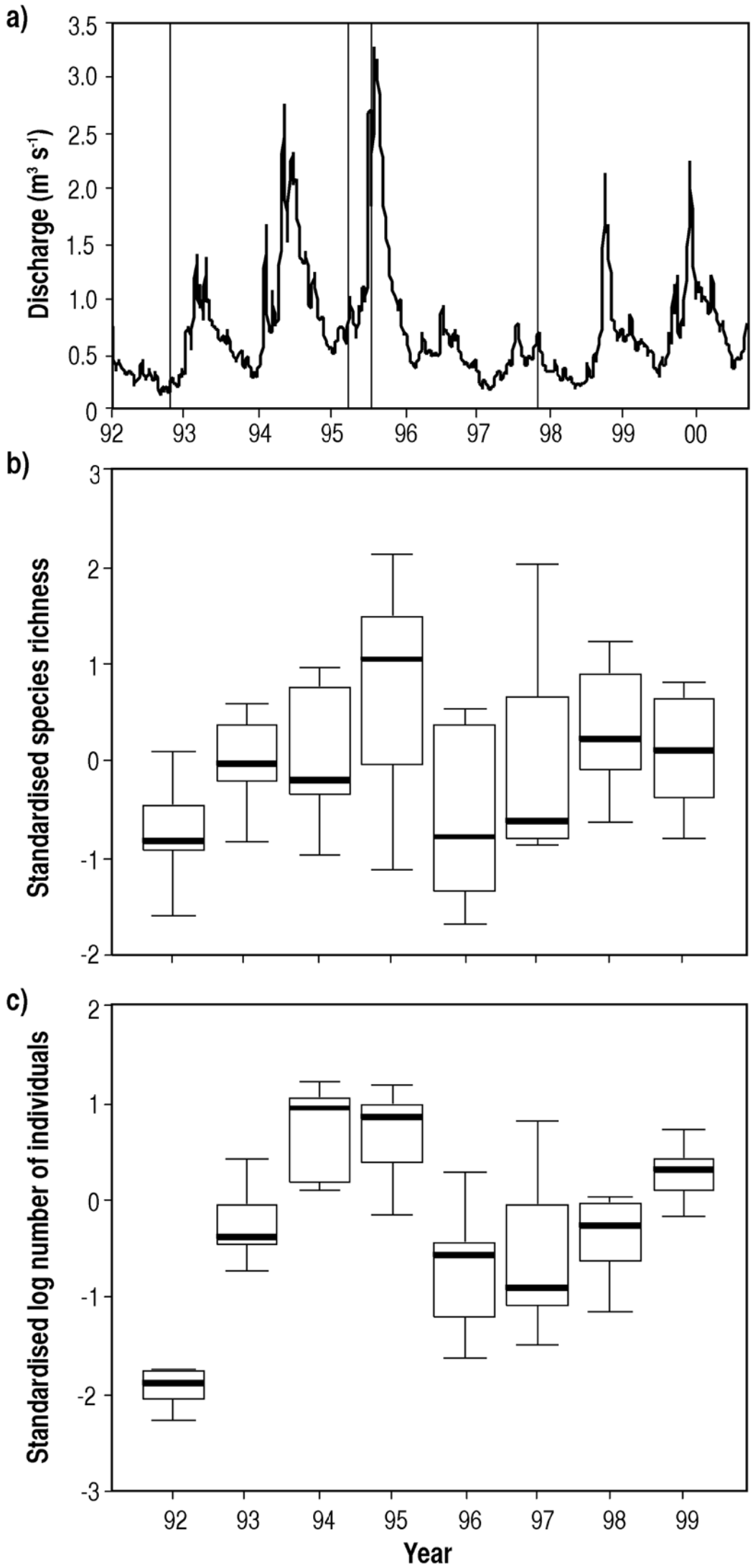
100
90
80
70
60
50
40
30
20
10
0
Discharge (m3s-1)
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
Year


a)
Discharge (m³ s⁻¹)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
92
93
94
95
96
97
98
99
00
b)
Standardised species richness
3
2
1
0
-1
-2
c)
Standardised log number of individuals
2
1
0
-1
-2
-3
92
93
94
95
96
97
98
99
Year

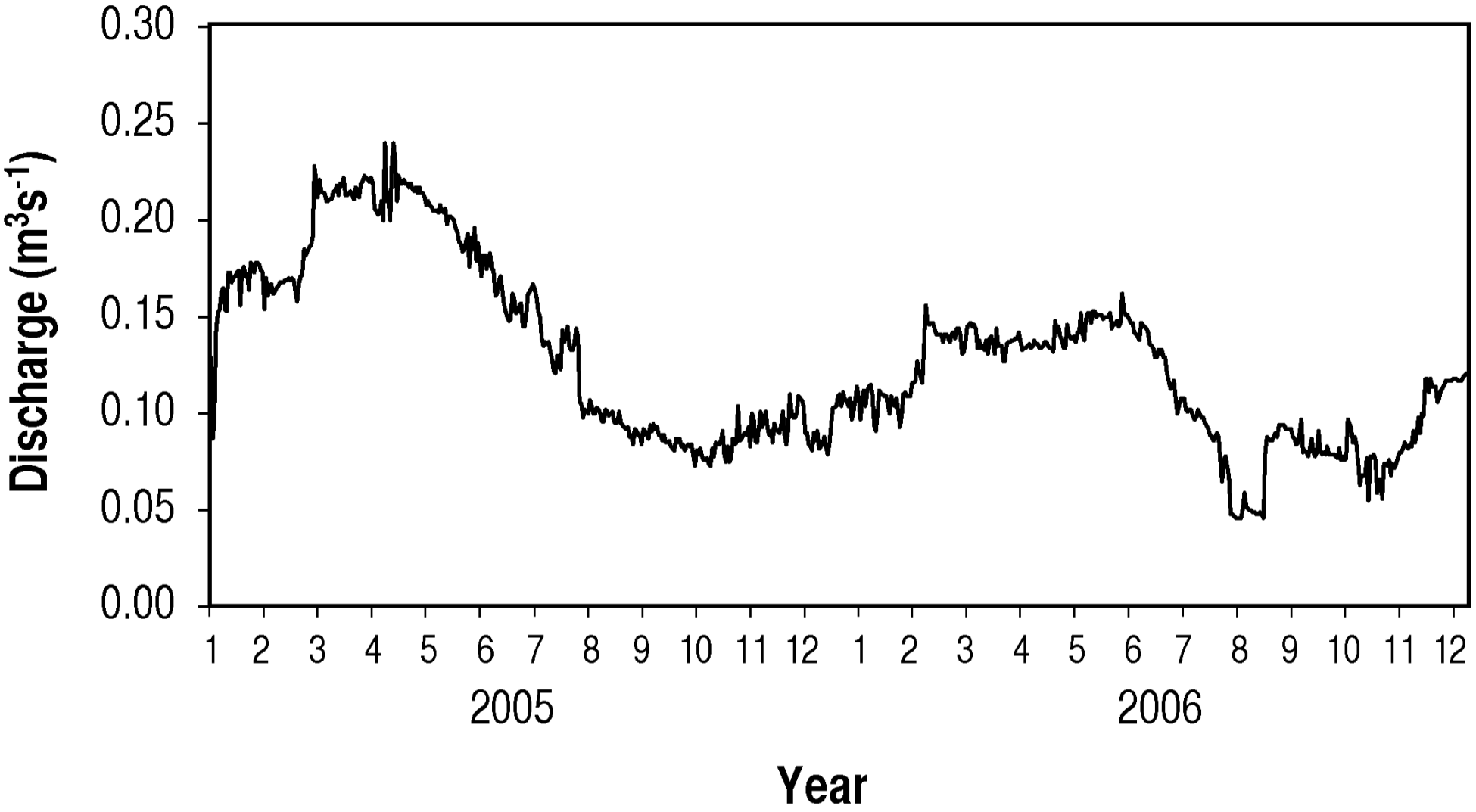
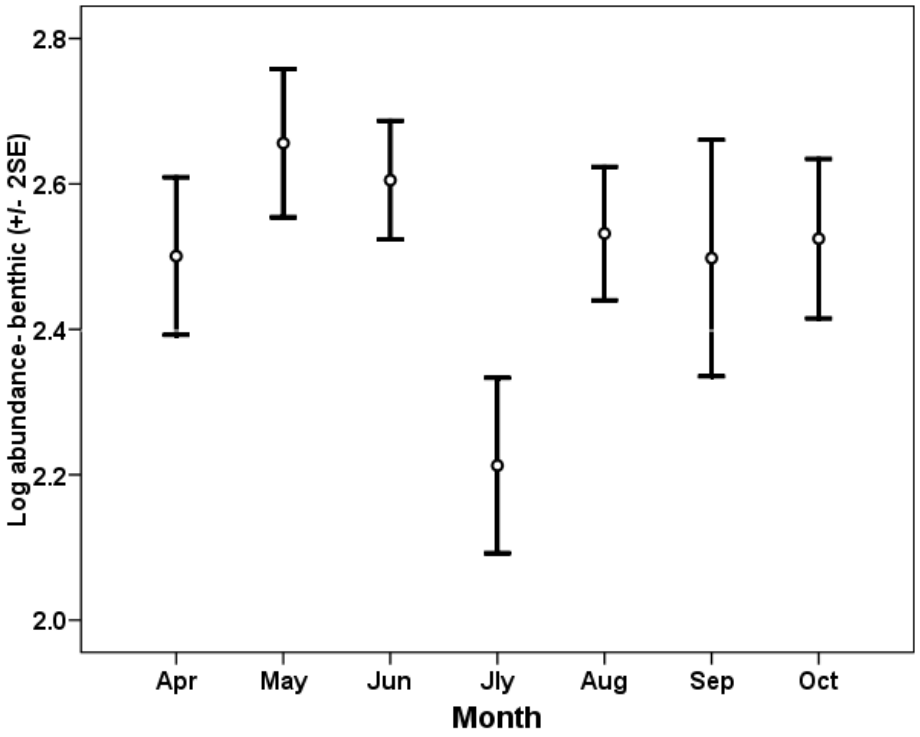

Discharge (m^3s^{-1})
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12
2005
2006
Year

Figure 5

a


Log abundance- benthic (+/- 2SE)
2.8
2.6
2.4
2.2
2.0
Apr
May
Jun
Jly
Aug
Sep
Oct
Month

b

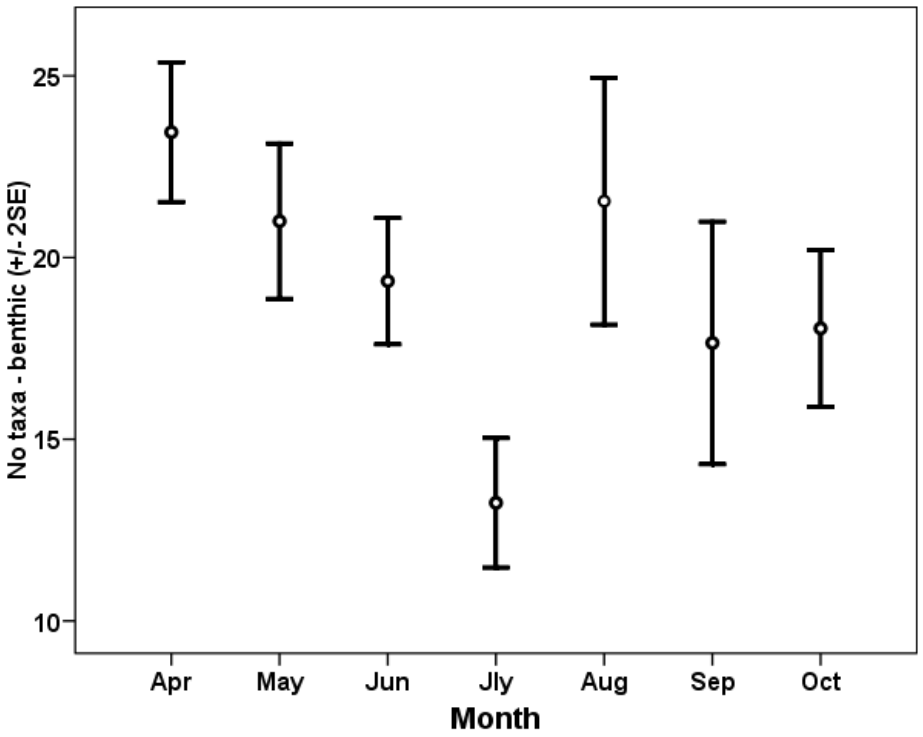

No taxa - benthic (+/- 2SE)
25
20
15
10
Apr
May
Jun
Jly
Aug
Sep
Oct
Month

Figure 5 Continued

c

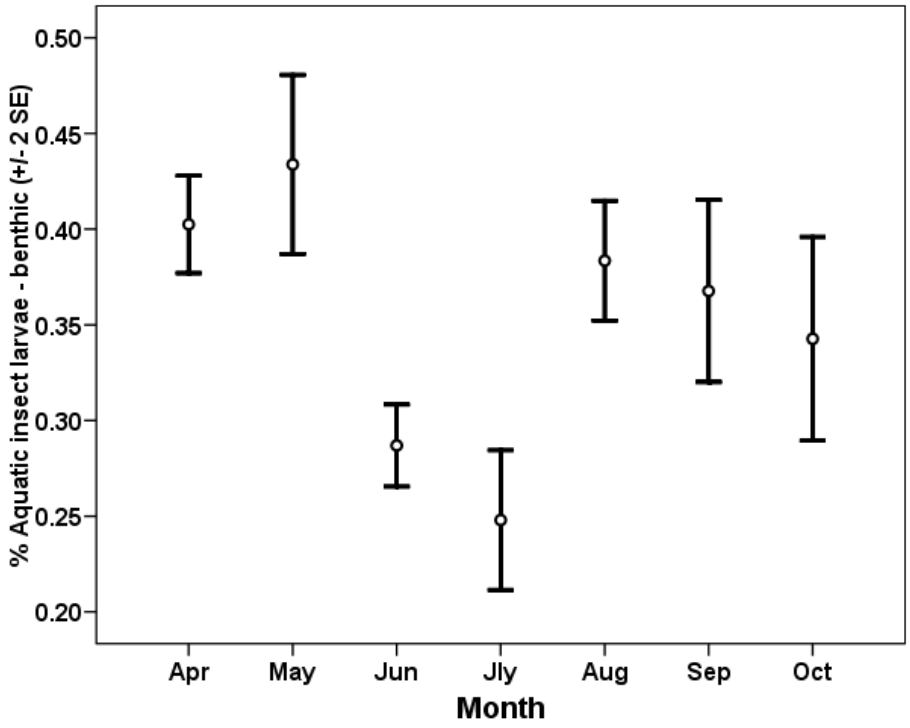
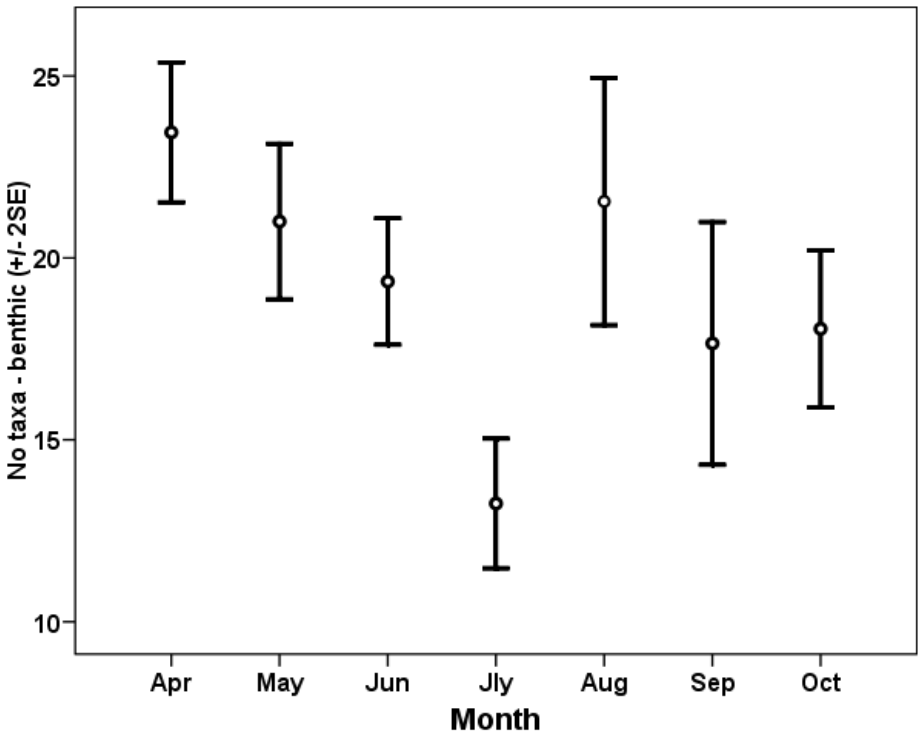


Figure 6

a


No taxa - benthic (+/- 2SE)
25
20
15
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Apr
May
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Aug
Sep
Oct
Month

b

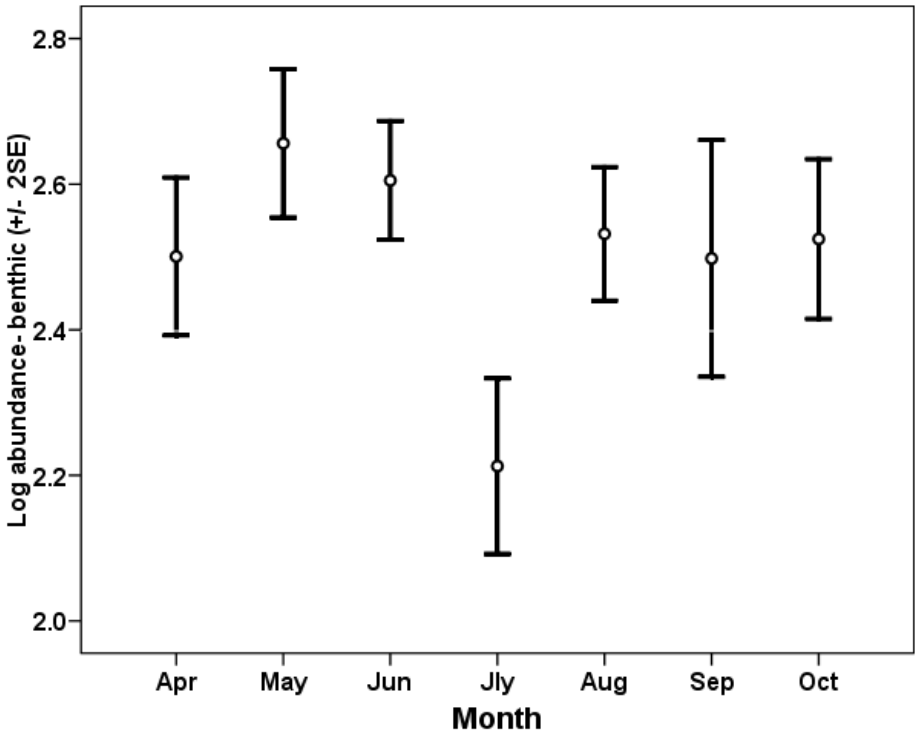

Log abundance- benthic (+/- 2SE)
2.8
2.6
2.4
2.2
2.0
Apr
May
Jun
Jly
Aug
Sep
Oct
Month

Figure 6 continued

c

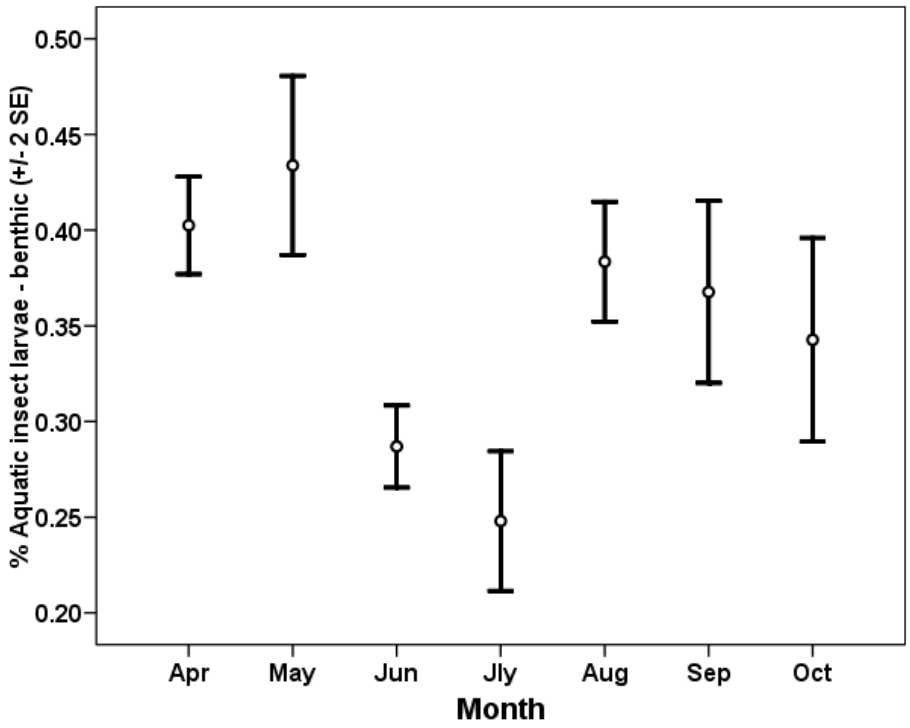
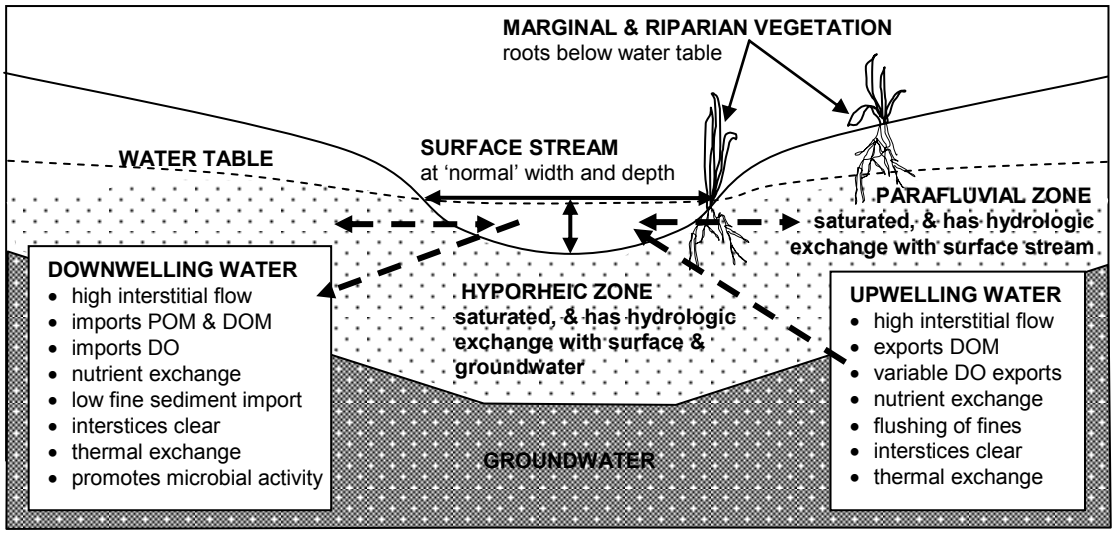
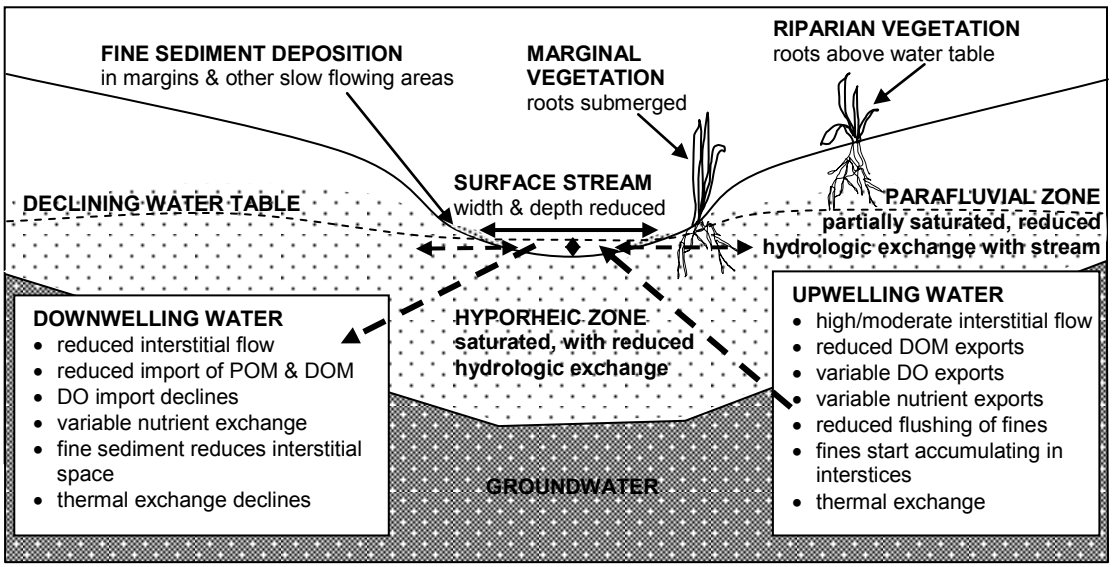


Figure 7

a


MARGINAL & RIPARIAN VEGETATION
roots below water table
WATER TABLE
SURFACE STREAM
at 'normal' width and depth
PARAFLUVIAL ZONE
saturated, & has hydrologic exchange with surface stream
DOWNWELLING WATER
high interstitial flow
imports POM & DOM
imports DO
nutrient exchange
low fine sediment import
interstices clear
thermal exchange
promotes microbial activity
HYPORHEIC ZONE
saturated, & has hydrologic exchange with surface & groundwater
UPWELLING WATER
high interstitial flow
exports DOM
variable DO exports
nutrient exchange
flushing of fines
interstices clear
thermal exchange
GROUNDWATER

b


FINE SEDIMENT DEPOSITION
in margins & other slow flowing areas
MARGINAL VEGETATION
roots submerged
RIPARIAN VEGETATION
roots above water table
SURFACE STREAM
width & depth reduced
DECLINING WATER TABLE
PARAFLUVIAL ZONE
partially saturated, reduced hydrologic exchange with stream
DOWNWELLING WATER
reduced interstitial flow
reduced import of POM & DOM
DO import declines
variable nutrient exchange
fine sediment reduces interstitial space
thermal exchange declines
HYPORHEIC ZONE
saturated, with reduced hydrologic exchange
UPWELLING WATER
high/moderate interstitial flow
reduced DOM exports
variable DO exports
variable nutrient exports
reduced flushing of fines
fines start accumulating in interstices
thermal exchange
GROUNDWATER

c

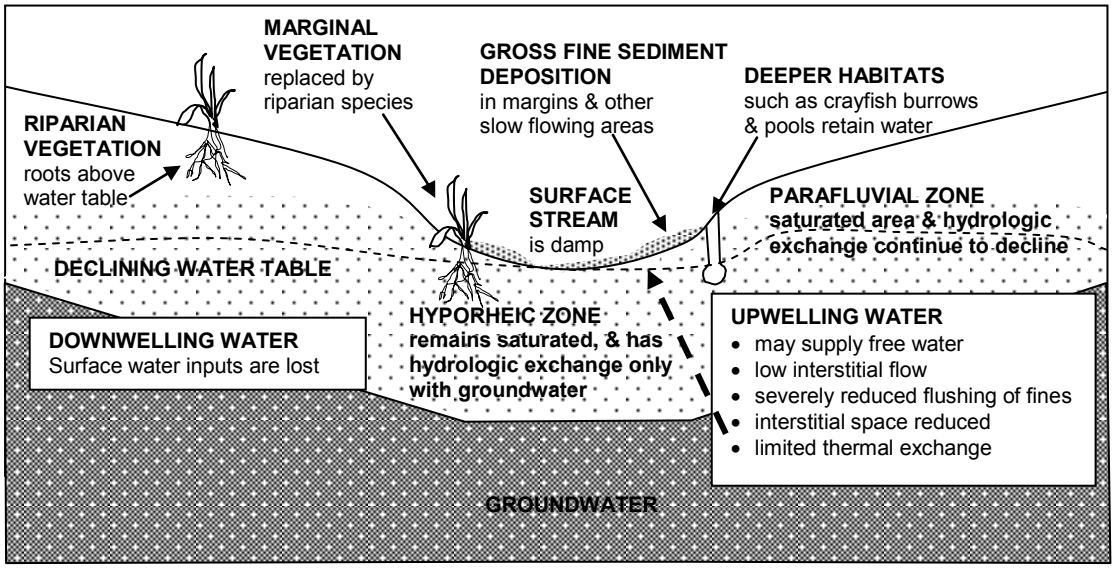
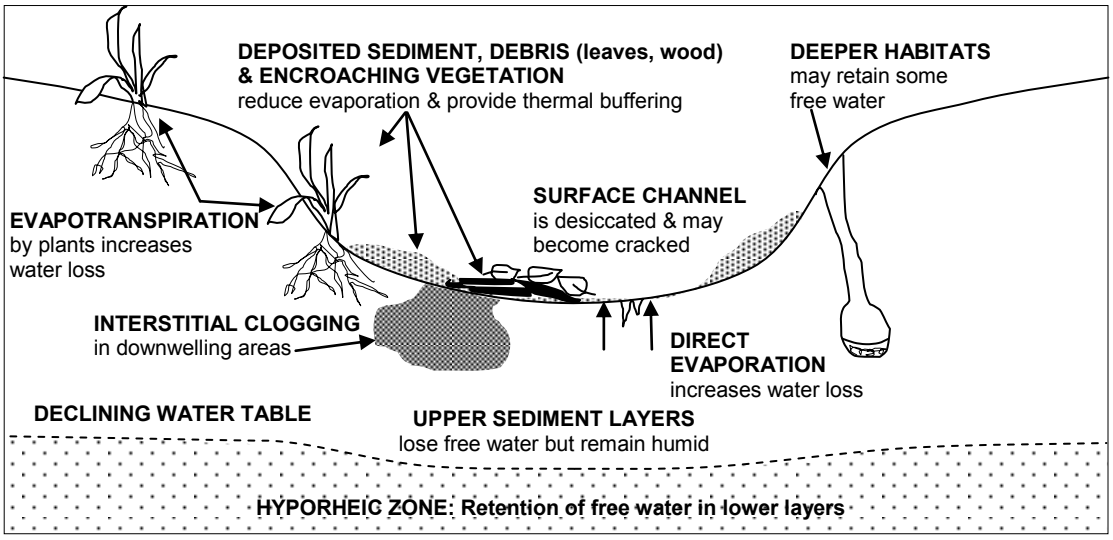
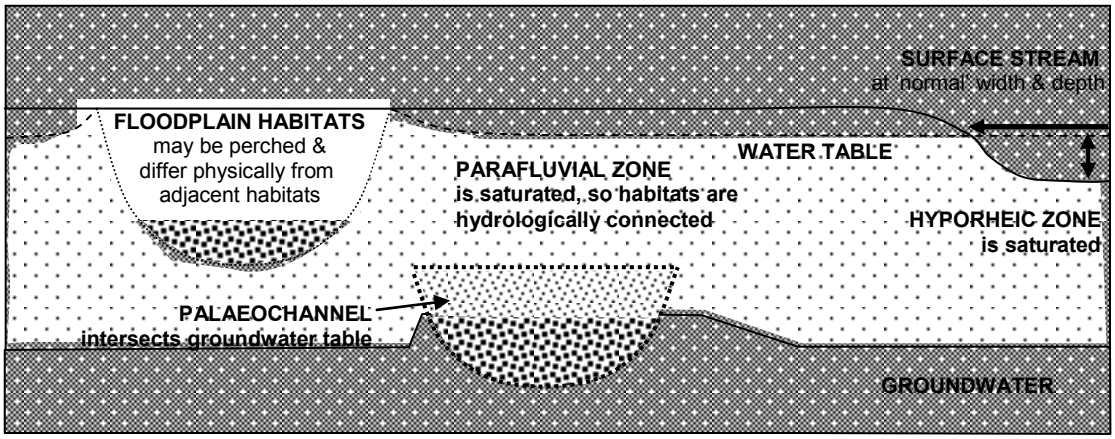

MARGINAL VEGETATION
replaced by riparian species
GROSS FINE SEDIMENT DEPOSITION
in margins & other slow flowing areas
DEEPER HABITATS
such as crayfish burrows & pools retain water
RIPARIAN VEGETATION
roots above water table
SURFACE STREAM
is damp
PARAFLUVIAL ZONE
saturated area & hydrologic exchange continue to decline
DECLINING WATER TABLE
DOWNWELLING WATER
Surface water inputs are lost
HYPORHEIC ZONE
remains saturated, & has hydrologic exchange only with groundwater
UPWELLING WATER
may supply free water
low interstitial flow
severely reduced flushing of fines
interstitial space reduced
limited thermal exchange
GROUNDWATER

Figure 7 Continued

d



a


SURFACE STREAM
at 'normal' width & depth
FLOODPLAIN HABITATS
may be perched &
differ physically from
adjacent habitats
WATER TABLE
PARAFLUVIAL ZONE
is saturated, so habitats are
hydrologically connected
HYPORHEIC ZONE
is saturated
PALAEOCHANNEL
intersects groundwater table
GROUNDWATER

b

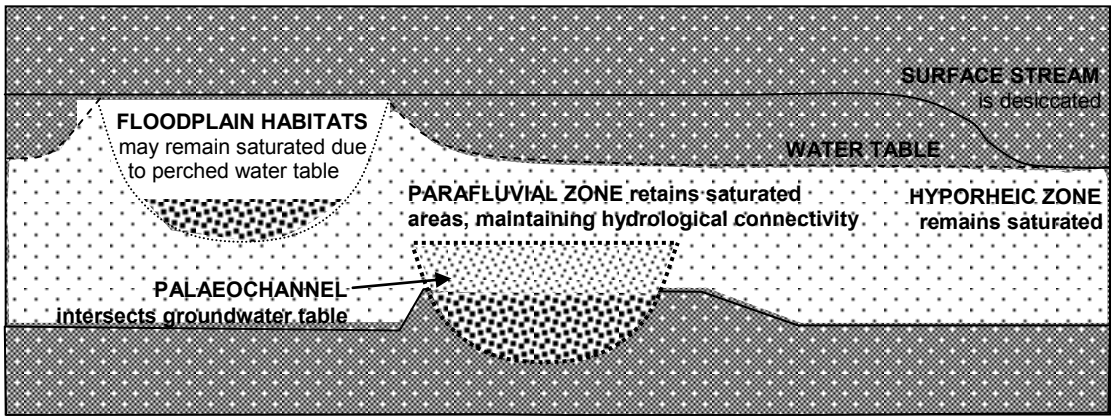

SURFACE STREAM
is desiccated
FLOODPLAIN HABITATS
may remain saturated due
to perched water table
WATER TABLE
PARAFLUVIAL ZONE retains saturated
areas, maintaining hydrological connectivity
HYPORHEIC ZONE
remains saturated
PALAEOCHANNEL
intersects groundwater table

Figure 8