The hyporheic zone as an invertebrate refuge: a review of variability in space, time, taxa and behaviour

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Abstract

The hyporheic zone is a potential refuge that can promote persistence of benthic invertebrates during adverse conditions in surface streams. For decades, changes in invertebrate depth distribution have been investigated in relation to flood, low flow and drying events, but evidence for use of the hyporheic refuge remains equivocal. This review examines the evidence for the hyporheic zone's refugial role during hydrological disturbances. Refuge potential is influenced by determinants in four categories. First, refuge use varies spatially in relation to physical habitat parameters, including sediment porosity and hydrologic exchange. Second, refuge use is temporally variable, and reflects disturbance characteristics including rate of onset. Third, refuge use is taxon-specific, depending on a range of morphological, behavioural and physiological traits. Fourth, the behaviours governing refuge use vary, with both active migrations and passive habitat use playing important roles in community persistence. These four determinants interact to influence refuge use; for example, the physical habitat providing an adequate refuge will vary between taxa. Despite this variability, the hyporheic zone is an important component in the suite of refuges that facilitate community resilience to disturbance events. As such, its ecological integrity should be safeguarded through sensitive management and effective rehabilitation schemes.

Additional keywords

Refugium, refugia, macro-invertebrate, hyporheic refuge hypothesis, epigean

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Introduction

In recent decades, the contribution of the hyporheic zone (HZ) to the ecological functioning of lotic ecosystems has become increasingly clear (Stanford and Ward 1993; Boulton *et al*. 1998; Krause *et al*. 2011). As an ecotone connecting the surface stream and groundwater, hydrologic exchange through the HZ allows water, nutrients, organic matter and organisms to move between ecosystem components (Brunke and Gonser 1997; Malard *et al*. 2002; Williams *et al*. 2010). Ecosystem services provided by the HZ include pollutant attenuation (Gandy *et al*. 2007; Domagalski *et al*. 2008), secondary production (Smock *et al*. 1992; Wright-Stow *et al*. 2006), and habitat provision for both spawning salmonids (Malcolm *et al*. 2004) and an invertebrate community comprising permanent hyporheic residents and transient migrants from the benthic zone.

A key ecological role proposed for the HZ is as a refuge that promotes persistence of benthos during disturbances in the surface stream (Orghidan 1959, 2010; Wood *et al*. 2010; Dole-Olivier in press), in particular during the hydrological extremes of floods (Williams and Hynes 1974; Marchant 1988; Dole-Olivier *et al*. 1997) and drying (Clifford 1966; Delucchi 1989; Clinton *et al*. 1996). At both extremes, some studies have recorded increases in the hyporheic abundance of invertebrates during a disturbance, providing evidence of refuge use, whilst other research has reported no significant changes in depth distributions (summarised in Tables 1 and 2). In addition, increased hyporheic abundance of benthos has been noted during low flows, due to submerged habitat contraction and a concurrent increase in biotic interactions (e.g. predation, competition) in the benthic zone (Covich *et al*. 2003; Stubbington *et al*. 2010, 2011a, 2011b). In contrast, other studies have observed no change in the depth distribution of benthic taxa as flow declines (James *et al*. 2008; James and Suren 2009; Table 3).

Whilst these inconsistent reports of refuge use can be explained in part by differences between sampling strategies (Dole-Olivier 2011), the equivocal evidence also indicates that vertical migrations depend on certain criteria being met. Refuge use is therefore likely to vary spatially at multiple scales. In addition, whilst the HZ is a more stable habitat than the benthic zone, its sediments vary temporally, and refuge use may therefore differ between disturbance events. Finally, the HZ poses challenges to interstitial inhabitation and resource availability, and refuge use may therefore be taxon-specific.

This review uses evidence presented for and against the hyporheic refuge hypothesis (HRH) to examine variability in the HZ as a benthic invertebrate refuge during adverse hydrological conditions. Published data is used to develop a conceptual model from which behavioural responses to adverse conditions can be inferred from changes in depth distribution. Conclusions drawn highlight the importance of ensuring the ecological integrity of the HZ through sensitive management and rehabilitation activities.

Hydrological conditions as invertebrate stressors

Hydrological variability is a key influence on instream habitat heterogeneity (Poff and Ward 1990; Monk *et al*. 2008) and has profound effects on invertebrate communities (Statzner and Higler 1986; Konrad *et al*. 2008). In particular, hydrological extremes (floods and streambed drying) can modify habitats and severely reduce both invertebrate abundance and taxon richness, regardless of whether conditions are unpredictable disturbance events (Resh *et al*. 1988; Death 2008; Sponseller *et al*. 2010) or occur within the typical flow regime (Poff 1992). In addition, low flows represent relatively moderate hydraulic conditions but have marked effects on instream communities due to reduced habitat availability (Wood and Petts 1999; Suren *et al*. 2003a, b; Dewson *et al*. 2007a), increased population densities and biotic interactions (Extence 1981; Malmqvist and Sackmann 1996), and changes in food resources (Englund and Malmqvist 1996) and water quality (Wood *et al*. 2010).

Invertebrates survive adverse conditions through resistance (an ability to persist) and/or resilience (an ability to recover afterwards; Webster *et al*. 1975; Lake and Barmuta 1986). Whilst biota may have evolved adaptations that confer resistance and/or resilience to predictable seasonal flow variation (Reice *et al*. 1990; Lytle and Poff 2004), community resistance to both floods and drying is typically low (Miller and Golladay 1996; Fritz and Dodds 2004). Despite this, invertebrates persist in frequently disturbed systems, with communities typically proving highly resilient (Miller and Golladay 1996; Kroon and Ludwig 2010). This resilience is facilitated by adaptations, which may be morphological, physiological, life history related, or behavioural (Townsend and Hildrew 1994; Lytle and Poff 2004; Watanabe 2006), the latter involving use of physical habitat refuges (Lake 2000, 2011).

Instream habitat heterogeneity causes invertebrate distribution and persistence to vary spatially (Robertson *et al*. 1995). Some habitats are refuges, where survival is enhanced due to reduced adverse impacts (Sedell *et al*. 1990; Lancaster and Belyea 1997). A habitat's ability to act as a refuge depends on the disturbance. During high flows, refuges are areas of low hydraulic stress, such as dead zones (Lancaster and Hildrew 1993; Lancaster 1999), inundated floodplains (Townsend *et al*. 1997; Matthaei and Townsend 2000), stable clasts (Cobb *et al*. 1992; Matthaei *et al*. 2000), woody debris (Palmer *et al*. 1996) and marginal vegetation (Robinson *et al*. 2004; Fig. 1a). In contrast, drying refuges retain free water or high humidity (Humphries and Baldwin 2003), for example crayfish burrows, woody debris, leaf packs, pools and spaces beneath large clasts (Boulton 1989; Boulton and Lake 2008; Stubbington *et al*. 2009a; Fig. 1b). There is therefore little overlap between high- and no-flow refuges, and many occur sporadically. The HZ is a potential exception to this; it may retain water after surface drying and may remain stable during floods (Boulton *et al*. 1998).

The hyporheic zone as a permanent habitat

The HZ is also a non-refugial habitat, with its location at the interface between surface and groundwater being reflected by the hyporheos, a fauna that comprises both permanent and occasional contingents (Williams and Hynes 1974). Species of permanent hyporheos complete their lifecycle in the HZ, and include a diverse assemblage of meiofauna (Dole-Olivier *et al*. 2000; Stead *et al*. 2004) and groundwater specialists (Dole-Olivier and Marmonier 1992a; Robertson *et al*. 2009). Occasional hyporheos move between benthic and hyporheic zones, this community being dominated by early-instar insect larvae (Williams 1984; Malard *et al*. 2001).

The physical habitat of the HZ is recognised as highly heterogeneous (Orghidan 1959, 2010), with several spatiotemporally variable parameters identified as influencing hyporheic community composition. These influences relate primarily to hydrology, sediment characteristics and the biotic suitability of the hydrological medium (i.e. water quality). The biotic effects of single habitat characteristics are often difficult to disentangle, due to both relationship complexity and the failure of many sampling techniques to characterise the fine scale at which biota experience their environment (Strayer *et al*. 1997; Storey and Williams 2004). Nonetheless, some relationships can be stated with confidence, as described below.

i) Sediment composition

A critical influence on the hyporheic community is sediment composition, which influences substrate porosity, permeability and interstitial architecture (Maridet *et al*. 1992; Schmid and Schmid-Araya 2010), and therefore determines the volume of inhabitable space and the network of movement pathways between clasts. Coarse substrata can support high-density diverse communities (Strayer *et al*. 1997), whilst meiofauna dominate sandy sediments (Malard *et al*. 2002), and a depauperate fauna resides within a colmated HZ (Richards and Bacon 1994; Wood and Armitage 1997). Several studies have demonstrated negative correlations between community metrics and the proportion of ‘fine’ sediment, variously defined as <150 µm (Richards and Bacon 1994), 63 µm to 1 mm (Olsen and Townsend 2003) and <2 mm (Weigelhofer and Waringer 2003). Sediment mobility is also important, with stable sediments supporting richer faunas than those prone to erosion (Marmonier *et al*. 2010).

ii) Hydrology

The direction and strength of hydrologic exchange is a crucial variable, with contrasting communities characterising upwelling and downwelling zones (Stanley and Boulton 1993; Franken *et al*. 2001; Olsen and Townsend 2003). Hypogean taxa, including microcrustaceans, Amphipoda and Isopoda, typically dominate upwelling groundwater zones (Dole-Olivier and Marmonier 1992b; Claret *et al*. 1999; Marmonier *et al*. 2010), which can elevate population densities and richness (Malard *et al*. 2003a; Datry *et al*. 2007). In contrast, downwelling surface water favours epigean occasional hyporheos, such as Ephemeroptera, Trichoptera and Coleoptera (Boulton and Foster 1998; Franken *et al*. 2001), which can also boost abundance and richness (Davy-Bowker *et al*. 2006). The influence of water movement along hyporheic flowpaths on the distribution of hyporheos is reviewed in detail by Dole-Olivier (2011).

Other hydrological influences on the hyporheos include flow velocities and flow permanence. Hyporheic velocities may be negatively correlated with meiofauna abundance, a faunal group that typically lack adaptations to resist displacement (Richardson 1992; Robertson *et al*. 1995). However, relationships between interstitial flow and macroinvertebrate distribution are complex and poorly quantified (Wagner and Bretschko 2002). Flow permanence also affects metrics including abundance, richness and stability, with intermittent sites typified by a depauperate community of desiccation resistant taxa (Datry *et al*. 2007). However, such relationships may be less apparent where drying occurs over small (sub-reach) areas or for short (days to weeks) durations (Stubbington *et al*. 2011a).

iii) Water quality

Dissolved oxygen has been identified as an influential water quality variable. Hyporheic concentrations are generally low compared with the surface stream and decrease with depth (Williams and Hynes 1974; Findlay 1995; Marmonier *et al*. 2010), reflecting penetration by oxygenated inputs (Fowler and Death 2001). Concentrations are typically highest in zones supplied by oxygen-rich stream water (Grimm and Fisher 1984; Jones *et al*. 1995), whilst groundwater inputs, slow exchange rates and long residence times reduce availability (Findlay 1995; Olsen and Townsend 2003; Marmonier *et al*. 2010; Fig. 2). Positive correlations between oxygen concentrations and invertebrate abundance (Williams and Hynes 1974; Franken *et al.* 2001), taxon densities (Boulton and Stanley 1995), taxon richness (Boulton *et al*. 1997; Franken *et al.* 2001) and biomass (Strommer and Smock 1989) have been documented. However, relationships may be weak (Strayer *et al*. 1997; Malard and Hervant 1999), particularly in well-oxygenated sediments, indicating that oxygen is only an important community determinant at low concentrations (Franken *et al*. 2001; Olsen and Townsend 2003).

Other potential influences on the invertebrate community include temperature, pH and nutrient concentrations (Boulton and Stanley 1995; Plenet *et al*. 1995; Davy-Bowker *et al*. 2006). However, relationships are typically complex and/or specific to certain systems (Malard *et al*. 2003b) and will not be considered further.

iv) Relationships between sediment composition, hydrology and water quality

These habitat variables are interdependent and interact to determine HZ habitat characteristics (Vervier *et al*. 1992; Fig. 2). Firstly, hydrologic exchange influences benthic and hyporheic sediment characteristics. During base flow, upwelling groundwater and high flow velocities may reduce siltation, whilst downwelling surface water introduces sediment into interstices, particularly where velocities are slow (Brunke and Gonser 1997; Fig. 2). Equally, sediment composition and porosity influence hydrologic exchange, with fine sediments reducing the strength of exchange whilst coarse substrata allow free water movement (Brunke 1999; Hancock 2002). Clogged sediments consequently receive a reduced oxygen supply whilst coarse sediments are well-oxygenated if flow velocities are sufficient (Findlay 1995; Wu 2000). The direction of exchange also influences oxygen content, with downwelling surface water typically being better oxygenated than upwelling groundwater (Grimm and Fisher 1984; Valett 1993; Franken *et al*. 2001; Fig. 2).

The suitability of the HZ as a habitat for benthic invertebrates is therefore a trade-off, with no single set of conditions being ideal. Downwelling zones have hydrological and water quality benefits but interstitial space may be limited whereas the unclogged interstices of upwelling zones may be resource-poor (Fig. 2).

The hyporheic zone as a refuge

The potential for the HZ to provide a refuge for benthic invertebrates was recognised by Orghidan (1959, 2010) following freezing in a surface stream. Other early evidence of this refugial role was provided by Clifford (1966) and Williams and Hynes (1974) who observed benthos in the HZ after surface drying and during a spate, respectively; other seminal research is described by Dole-Olivier (2011). The Hyporheic Refuge Hypothesis (HRH) was later formally stated by Palmer *et al.* (1992). By moving into the HZ, it is proposed that benthic invertebrates increase their probability of surviving an adverse condition in the surface stream. When conditions improve, refugees potentially recolonise benthic habitats from the HZ, thus facilitating community recovery.

The adverse conditions from which benthic refugees may seek shelter include both biotic and abiotic stresses. The HZ may be a protective nursery for early instar insect larvae (Giberson and Hall 1988; Puig *et al*. 1990; Jacobi and Cary 1996) and also a predation refuge for other vulnerable groups (e.g. moulting individuals; McGrath *et al*. 2007). In addition, the HZ is a potential shelter from environmental conditions including surface freezing (Orghidan 1959, 2010), low temperatures (Malard *et al*. 2001), high temperatures (Evans and Petts 1997; Wood *et al*. 2010) and pollution (Jeffrey *et al*. 1986; Belaidi *et al*. 2004). Most research considering the HRH, however, has focussed on the extremes of the hydrological continuum, namely floods and streambed drying. During high flows, the HZ reduces displacement, since flow velocities remain relatively slow and sediments relatively stable (Boulton *et al*. 2004). During drying, the HZ may retain free water, a necessity for most aquatic biota. However, despite receiving more attention than other potential refuges, evidence for the HRH remains equivocal during floods, drying, and low flows (Tables 1-3; Dole Olivier 2011).

Types of evidence for the hyporheic refuge hypothesis

The HRH remains contentious, in part due to differing interpretations of what constitutes refuge use. Therefore, before presenting the evidence itself, a conceptual model (Fig. 3) will be used to assess these contrasting interpretations, and a definition of acceptable evidence will be outlined.

Evidence type 1: Presence of benthic invertebrates in the hyporheic zone

Some studies have simply observed benthic invertebrates in the HZ during adverse surface conditions, without knowledge of temporal change in depth distribution (Imhof and Harrison 1981; Fenoglio *et al*. 2006). Others have noted that, despite declining hyporheic abundance, a few benthic individuals persist in the HZ during both drying (Griffith and Perry 1993; del Rosario and Resh 2000) and spates (Boulton *et al*. 2004; Bruno *et al*. 2009). Such data provide no evidence of active shelter-seeking behaviour, but demonstrate passive refuge inhabitation (Box 2, Fig. 3), which is also an important mechanism promoting invertebrate survival.

Evidence type 2: An increase in abundance in the hyporheic zone

Other studies have reported an increase in a benthic taxon's abundance in the HZ as evidence of refuge use (Dole-Olivier and Marmonier 1992a; Marchant 1995; Dole-Olivier *et al*. 1997). However, if densities concurrently increase in the benthic zone, then the proportion of a population in the HZ may be unchanged or may decline, indicating range extension but not shelter-seeking behaviour (Box 1, Fig. 3). Both floods and drying are, in fact, likely to decimate benthic populations (Hynes 1958;

Wood and Armitage 2004; Death 2008) and even if benthic densities are unknown, an increase in the hyporheic proportion can often be assumed to accompany an increase in hyporheic abundance (Dole-Olivier and Marmonier 1992a; Clinton *et al*. 1996; Dole-Olivier *et al*. 1997). In contrast, low flows may cause benthic population densities to increase as habitats contract (Extence 1981; Dewson *et al*. 2007b). In such cases, an increase in hyporheic abundance may be outweighed by rising benthic densities, causing the hyporheic proportion of a population to fall (Stubbington *et al*. 2011b). As such, only vertical range extension of the benthic population can be inferred (Box 1, Fig. 3).

Evidence type 3: An increase in a population's hyporheic proportion

Other research has posited an increase in the hyporheic proportion of a taxon's total (benthic + hyporheic) population as evidence for the HRH. However, an increase in proportion may accompany a reduction in hyporheic abundance, so long as the decline is of a lesser magnitude than occurs in the benthic zone (Giberson and Hall 1988; Palmer *et al*. 1992; Olsen and Townsend 2005). Whilst survival may be enhanced for those animals in deeper sediments when a disturbance commences, such studies indicate passive refuge use (Box 2, Fig. 3), not active migrations.

Evidence type 4: Concurrent increases in hyporheic abundance and proportion

Evidence types 1-3 demonstrate that, regardless of how benthic abundance changes, simultaneous increases in the hyporheic abundance and proportion of a population provide the most convincing evidence of active migrations (Fig. 3). Such evidence is required for refuge use to be considered 'active' in Tables 1-3.

The active-passive refuge distinction

The distinction between active and passive refuge use has long been recognised with reference to the HZ (Robertson *et al*. 1995; Robertson and Wood 2010) and other refuges (Ward 1989; Lake 2000). Robertson *et al*. (1995) described models of refuge use including a 'catastrophe avoided' model of active migration, and 'incomplete catastrophe' and 'refuge as habitat' models, in which refuge inhabitants are passively protected. Lancaster and Belyea (1997) refined these models, their 'directed flux between microhabitats' scheme equating to active refuge use whilst in their 'no flux' and 'undirected flux' models, passive refuge use reduces disturbance impacts.

Robertson and Wood (2010, p. 284) suggest that "as long as survivorship in the HZ is [proportionally] higher than that in benthic habitats, then it will act as a refugium". However, passive refuge use can have an even simpler condition attached: as long as survival *occurs* in the HZ, it may promote invertebrate persistence.

Both active and passive movements may therefore promote invertebrate survival, for example in downwelling zones during low-magnitude spates (Dole-Olivier *et al*. 1997). However, active refuge use increases the potential of the HZ to protect a greater range of taxa during a greater range of disturbance types. Active migrations are necessary, for example, during slow-onset drying events in which flow velocities are insufficient to move macroinvertebrates, and during high-flow events in which the direction of hydrologic exchange opposes migratory movements.

Despite the earlier models (Robertson *et al*. 1995; Lancaster and Belyea 1997; Robertson and Wood 2010), inferring the behaviours behind refuge use from field or experimental data remains problematic. To address this, the model presented in Fig. 3 provides a framework to guide interpretation of data collected during HRH research, as outlined above. However, although Fig. 3 can be used to *infer* behaviour, the model cannot distinguish between active migrants and refugees passively carried into the HZ (Dole-Olivier *et al*. 1997; Lancaster and Belyea 1997). Indeed, whilst laboratory experiments (Holomuzki and Biggs 2000) and field sampling campaigns (Palmer *et al*. 1992) may provide compelling evidence of active migrations, conclusive proof of whether individual movements are intentional or involuntary remains elusive. It is theoretically possible that an increase in the hyporheic abundance and proportion of a population may result entirely from passive displacement by downwelling water; equally, a decrease in hyporheic abundance may mask active migrations of a few individuals. As such, it is recognised that the changes in distribution taken as evidence of refuge use may result from a combination of active and passive movements (Robertson *et al*. 1995; Dole-Olivier *et al*. 1997; Lancaster 2000). Inferred behaviours should therefore be considered as the dominant, but not the only, behaviours influencing a population's distribution (Fig. 3).

Evidence for active use of the HZ refuge

i) Refuge use during floods

It was the early observations of changes in invertebrate depth distributions after flood events that sparked interest in the HZ as a refuge (Clifford 1966; Williams and Hynes 1974), and this has since been formalised in the Flood Refuge Hypothesis (Boulton *et al*. 2004). This hypothesis posits vertical migration as a behavioural response to an increase in flow velocity or other hydraulic stress (Boulton *et al*. 2004).

Evidence of active migrations has been reported by at least eight studies (Table 1, Section A), encompassing natural spates (Williams and Hynes 1974; Dole-Olivier and Marmonier 1992a; Dole-Olivier *et al*. 1997), prolonged high flows (Marchant 1988, 1995), and their experimental equivalents (Holomuzki and Biggs 2000). Williams and Hynes (1974), for example, noted increased invertebrate abundance at and below 30 cm after a flood, accompanied by equivalent reductions in shallower sediments, whilst total abundance remained stable. Supporting evidence from laboratory simulations is provided by Holomuzki and Biggs (2000) who observed shifts in the depth distribution of one mayfly, one snail and two caddisfly genera in response to short-term, high-magnitude increases in discharge.

Other studies have found no evidence of active migrations during floods (Table 1, Section B). In many cases, this has been attributed to inadequate habitat (e.g. sediment-clogged interstices), substrate instability and/or upwelling water (Palmer *et al*. 1992; Dole-Olivier *et al*. 1997; Olsen and Townsend 2005). In other cases, disturbance-related factors appear responsible, including rapid spate onset (Gayraud *et al*. 2000; Imbert and Perry 1999), and spate magnitude being too low to elicit a response (Boulton *et al*. 2004) or high enough to mobilise HZ sediments and fauna (Dole-Olivier *et al*. 1997; Stubbington *et al*. 2010). The importance of disturbance characteristics is also demonstrated by events that reduce the abundance of permanent hyporheos (Dole-Olivier and Marmonier 1992a; Olsen and Townsend 2005; Hancock 2006). However, even when impacts are severe, benthic invertebrates are routinely present in HZ after a disturbance, albeit at low abundance (Table 1). This highlights the importance of passive refuge use in promoting community resilience, with the few survivors acting as potential recolonists of benthic sediments (Table 1, Section B). Such recolonisation is particularly important if the HZ has come to support a higher proportion of the total community (Giberson and Hall 1988; Stubbington *et al*. 2010).

ii) Refuge use following streambed drying

The HZ's potential as a refuge after streambed drying hinges on the availability of free water, or at least high humidity. The principal impetus for invertebrate migration is therefore to remain submerged, although stresses such as increasing surface water temperatures may also be involved (Wood *et al*. 2010).

Where free water is retained, changes in depth distribution have indicated that invertebrates can actively follow the receding water table into deeper sediments (Delucchi 1989; Clinton *et al*. 1996; Table 2, Section A). Many other studies have found passive inhabitation to facilitate population persistence (Table 2, Section B), with the diverse assemblage surviving in moist interstices including Isopoda, Amphipoda (Clifford 1966), Trichoptera (Imhof and Harrison 1981), and adult Coleoptera (Fenoglio *et al*. 2006). However, where the criterion of water availability is not fulfilled, the HZ fails as a refuge (Boulton and Stanley 1995). Therefore, whilst research into the HZ flood refuge has always found a small proportion of benthos to persist (Table 1), drying can eliminate virtually all benthic invertebrates, including both active and passive refugees (Table 2, Section C). However, as these studies have not considered dormant life stages present in dry sediments, community persistence may have been underestimated (Stubbington *et al*. 2009a; T. Datry unpublished data).

Refugial capacity may be reduced during drying if fine sediments are deposited in interstices as flow declines; sediment compaction and baking may then cause interstitial hypoxia (Gagneur and Chaoui-Boudghane 1991; Smock *et al*. 1994; Belaidi *et al*. 2004). Such habitat characteristics are invariably held responsible for the failure of the hyporheic refuge during drying events (Table 2), which, as gradual onset disturbances (Lake 2000, 2003), favour a behavioural response. The quality of the HZ refuge is, however, relative to other microhabitats, and vertical migrations may be reduced if alternative refuges exist. Boulton (1989), for example, found more refugee taxa and individuals in receding pools and nearby perennial waters than in the HZ of intermittent streams.

iii) Refuge use during low flows

Few studies have considered use of the HZ refuge during low flows (Table 3), with relatively benign hydrological conditions being a less obvious migration trigger.

However, James *et al*. (2008) hypothesized that vertical migrations would occur as flow receded if habitat contraction forced invertebrates into a smaller area, thus increasing biotic interactions. Such predictions are supported by observations that mobile taxa such as the amphipod *Gammarus pulex* migrate into smaller interstices in response to an increased risk of cannibalism (McGrath *et al*. 2007). However, only Stubbington *et al*. (2011a, 2011b) have inferred refuge use during flow recession, with *G. pulex* migrating into the HZ following habitat contraction and a concurrent increase in benthic densities (Table 3). In addition, Wood *et al*. (2010) noted active migrations of *G. pulex* during low flows, these migrations being linked to thermal, but not hydrological drivers. In other studies, surface sediments appear a preferable habitat, even if benthic population densities do increase (James *et al*. 2008; James and Suren 2009).

Variability in the hyporheic refuge

The preceding discussion has identified use of the HZ refuge as very variable. Spatial variability depends on habitat characteristics whilst temporal variability reflects disturbance type. Additional variation is biotic; refuge use is restricted to certain taxa, and although poorly understood, biotic interactions may also affect active migrations.

Spatial variability in the hyporheic refuge

Use of the hyporheic refuge is spatially variable, depending on the fulfilment of certain environmental criteria (Townsend 1989; Lancaster and Belyea 1997; Robertson and Wood 2010). Whilst refuges can promote population persistence at multiple spatial scales (Townsend and Hildrew 1994; Robertson *et al*. 1995; Robson *et al*. 2011), individual invertebrates always act at the smallest scales (Lancaster 2008), and patch-scale variation is therefore particularly relevant to refuge use. The dependence of refuge use on the fulfilment of habitat-related criteria has been termed “refugial effectiveness” (Robertson and Wood 2010) and “refugial potential” (Stubbington *et al*. 2011b), the latter term recognising that sediments with suitable characteristics may nonetheless not be used as a refuge (Fig. 4). The habitat characteristics that influence the permanent hyporheos are also principal determinants of refuge potential: hydrologic exchange and sediment characteristics, which are interdependent and also influence water quality.

i) Hydrologic exchange

Despite recognition that downwelling zones promote refuge use during both high and low flows, the vital features of infiltrating water have not been isolated, and several factors may be relevant (Davy-Bowker *et al*. 2006). Movement of downwelling water is assumed to facilitate active and passive transport of benthos into the HZ, and this assumption may be valid at high flow velocities (Dole-Olivier *et al*. 1997). However, during flow recession, surface velocities may decline (Wright and Berrie 1987; Dewson *et al*. 2007a) and whilst rarely measured, velocities are probably even slower in the HZ (Angradi and Hood 1998). Therefore, it is unlikely that upwelling water prevents downwards migrations of mobile taxa during low flows.

However, water chemistry also varies depending on the direction of hydrologic exchange. Downwelling water typically resembles surface water in terms of oxygen, temperature, chemistry and organic matter content, whilst groundwater inputs have a distinct chemistry and are often oxygen- and resource-poor (Brunke and Gonser 1997; Datry *et al*. 2005, 2007). Such variables may influence migrations during low-magnitude disturbances such as flow recession (Stubbington *et al*. 2011b), but are of secondary importance to habitat stability during spates and to free water after drying. Equally, whilst the presence of free water may suffice for tolerant taxa and during short drying events (Williams and Hynes 1974; Danielopol 1989), as dry phase duration increases, long residence times and the absence of surface inputs affect water quality, with consequences for the survival of an increasing proportion of the community. Upwelling zones providing high-quality groundwater inputs may therefore have the highest refugial potential during drying events (Dole-Olivier 2011). Dole-Olivier (2011) provides greater detail on hydrological variables influencing refuge use.

ii) Sediment characteristics

No refuge use is possible without connectivity between the HZ and the surface stream, hence the central role of sediment composition in determining refuge potential. The most fundamental requirement is that a HZ exists, which is not the case in channels with impermeable strata (White 1993; Dole-Olivier 2011). The size of the HZ is also important and hyporheic sediments may be limited in spatial extent, as in many headwater streams (Stubbington *et al*. 2009a; Chester and Robson 2011).

Regardless of spatial extent, shallower sediments are more likely to be encountered by migrants (Williams and Hynes 1974; Marmonier *et al*. 2010), but the availability of deeper layers potentially increases survival due to reduced scour at high flows, and increased water availability after surface drying.

Once the basic criterion of a sufficiently voluminous HZ is met, then the same characteristics that support a speciose hyporheos also encourage refuge use, with coarse-grained, porous sediments facilitating both active and passive movements. The detrimental effects of fine sediment may, however, be exacerbated by a disturbance. Firstly, during spates, finer sediments are more easily mobilised, thus displacing any resident refugees (Palmer *et al*. 1992; Olsen and Townsend 2005). Equally, during drying, fine sediments may form a surficial crust which separates the HZ from atmospheric oxygen inputs and restricts invertebrate movements (Gagneur and Chaoui-Boudghane 1991; Belaidi *et al*. 2004).

Temporal variability in the hyporheic refuge

Whilst the refugial role of the HZ depends in part on its stability, it is nonetheless a temporally dynamic habitat (Stanford and Ward 1993). Many determinants of refuge potential may be altered by the conditions triggering refuge use, especially high flows. If the effects of bed-mobilising floods extend into the HZ, refugial potential may be severely compromised (Matthaei *et al*. 1999; Wondzell and Swanson 1999); equally, sediment deposition may bury refugees, providing additional protection during a disturbance but impeding later recolonisation of the surface (Olsen *et al*. 2010). In the longer term, sediments reworked by high flows may have higher or lower fine sediment content (McKenzie-Smith *et al*. 2006; Olsen *et al*. 2010), influencing their refugial potential during future events. The direction and strength of hydrologic exchange may also be altered by changes in surface flow and disturbance-related changes in sediment composition (Baker and Vervier 2004; Boulton *et al*. 2004).

Despite this temporal variability in refuge potential, few studies have considered changes in refuge use over extended periods. Notable exceptions include Dole-Olivier and Marmonier (1992a) and Dole-Olivier *et al*. (1997), who considered a period of base flow interrupted by multiple spates in a regulated channel. These studies highlighted temporal variability in refuge use, with migrations depending on both spate amplitude and habitat features. Similarly, Wood *et al*. (2010) considered a 7-month period of stable then declining discharge, finding evidence of active migrations in response to increasing surface water temperatures, but not flow recession. In addition, Smock *et al*. (1994) and Stubbington *et al*. (2010) have considered refuge use during consecutive, contrasting disturbances. Smock *et al*. (1994) recorded no refuge use during a storm or drying, due to hyporheic anoxia. In contrast, Stubbington *et al*. (2010) observed migrations of *G. pulex* during a flow recession, the species' hyporheic abundance then plummeting during a spate, thus demonstrating inter-disturbance variability in refuge potential.

Spatiotemporal variability in biotic interactions

As well as being reduced by deteriorations in environmental quality relating to disturbance onset, long-term survival in refuges may be limited by unfavourable biotic conditions that develop as a consequence of refuge use (Lancaster and Belyea 1997). In particular, any increase in population densities causes biotic interactions to intensify, including competition for limited resources (such as space, food and oxygen) and predation (Lancaster 1996). Active refuge use involves movement into a habitat that is usually less desirable than the benthic sediments, and increased biotic interactions may further reduce the attractiveness of the HZ. Individual invertebrate migrations may therefore be density-dependent as well as reflecting environmental conditions. However, whilst increased predation has been observed in surface refuges (Lancaster 1996), little evidence relates specifically to the HZ, and routine use of the zone as a predation refuge by vulnerable life stages (Jacobi and Cary 1996; McGrath *et al*. 2007) indicates that biotic pressures do not intensify significantly due to refugee influxes. This may be due to interstitial space limiting hyporheic densities of larger predatory macroinvertebrates (Franken *et al*. 2006), reductions in predation efficiency in interstices (Schmid and Schmid-Araya 1997) and/or reduced predator activity in a resource-limited habitat (Stubbington *et al*. 2009a; Robson *et al*. 2011).

Variability in benthic refugee taxa

Whilst evidence for the HRH relates to a diverse assemblage, active migrations are often restricted to certain taxa (Table 4), indicating that morphological and/or behavioural taxon-specific characteristics influence refuge use. Robertson and Wood (2010) used the trait analysis of Poff *et al*. (2006) to identify features of active migrants (Table 5). To assess the validity of this analysis, taxa identified as active migrators (Table 4) are compared to proposed traits (Table 5). All migrant taxa share one trait, *no attachments* (Table 5), suggesting this as a prerequisite for migration. However, evidence of active migration has been observed in Simuliidae larvae (pers. obs.), which attach to substrata using anal hooks. Simuliids can, however, move to the streambed using silk anchor threads and then use looping movements to enter the HZ (Wotton 1979). *No attachments* is therefore not a prerequisite for refuge use, so long as release can be achieved swiftly at the onset of a disturbance.

The trait *burrowing habit* indicates a predisposition towards interstitial inhabitation, which would seem vital for vertical migration. Evidence of refuge use in taxa lacking this trait is restricted to the caddisfly larvae of Leptoceridae (which Holomuzki and Biggs (2000) note as equally likely to remain on the surface as migrate) and Hydropsychidae and Polycentropodidae, regarding which Dole-Olivier and Marmonier (1992a) provide no details. The trait *high crawling rate* indicates a capacity to respond quickly at disturbance onset, which may be crucial during spates. Accordingly, two of three taxa lacking this trait (*Gammarus*, Leptophlebiidae) are instead strong swimmers, and some chironomids are also capable of vigorous movement to enter preferred habitats (Palmer *et al*. 1992; Armitage *et al*. 1995). This trait should therefore be broadened to *high movement rate*, because locomotory mode is less important than mobility (Claret *et al.* 1999); equally, this feature may be of little relevance during slow-onset events. Following migration, the trait *depositional rheophily* implies adaptation to sediment-depositing habitats, which the HZ may be during any hydrological disturbance. Eight of nine *burrowing* taxa also exhibited this trait, whilst chloroperlid stonefly nymphs did not; this taxon prefers erosional zones and its burrowing, and thus refuge use, may occur only in coarse gravels (Baumann *et al*. 1977).

Two morphological traits are suggested by Robertson and Wood (2010) as migrant attributes: *small size at maturity* (<9 mm) and *vermiform shape.* However, only four migrant taxa may be small when mature, with late instar Ephemeroptera, Plecoptera and Trichoptera (EPT) and *Gammarus* reaching sizes that could inhibit interstitial inhabitation (Robertson and Wood 2010). Indeed, HZ residents are typically small, irrespective of the ultimate size a taxon achieves (Cooling and Boulton 1993; Malard *et al*. 2003b). Size *at maturity* is therefore less important than the occurrence of small instars within the life cycle, so long as the time taken to reach maturity exceeds disturbance duration. Maximum size will also relate to pore-size distribution, and will be influenced by morphology and behaviour, including the capacity to alter pore sizes through physical activity (Claret *et al*. 1999).

The trait *vermiform shape* is also only partly supported (Table 5), with flattened, blunt, robust, and/or streamlined forms also allowing HZ inhabitation. Williams and Hynes (1974) suggested two morphologies as suiting the HZ: long and flexible, to move between grains, and blunt and well-protected, to bludgeon past them. *Vermiform* should thus be replaced by a rather general attribute: *morphologically suited*. Even then, morphological features of some migrants, such as mayflies with delicate gills, appear ill-suited to the HZ (Marchant 1988), emphasizing the influence of habitat characteristics on taxon-specific refuge use. Gilled EPT are also amongst refugees limiting support for the trait *tegument respiration*; mode of gas exchange does not appear to influence refuge use.

Relationships between spatial, temporal and taxonomic variability

For any individual inhabiting the benthic zone, migration into the HZ at disturbance onset is concurrently determined by factors in the four categories discussed: habitat characteristics, disturbance features, biotic interactions and migrant traits (Fig. 4). First, the HZ must provide an adequate habitat, with sufficient interstitial space, favourable water quality and adequate resources, as well as acceptably low biotic interactions (C1, Fig. 4). Second, disturbance characteristics must be conducive to refuge use, for example having a gradual onset, and not causing biotic risks to increase to intolerable levels in the HZ (C2, Fig. 4). Third, the invertebrate itself must be inclined to migrate in response to disturbance triggers (C3, Fig. 4); suitable habitat and disturbance characteristics do not automatically elicit a response.

All three criteria must be fulfilled for any individual to actively migrate (Fig. 4). For example, the HZ habitat may be suitable and disturbance characteristics may favour a response, but a taxon may employ an alternative survival strategy, such as entrance into the drift (Perry and Perry 1986) or use of other refuges (Boulton 1989; Cooling and Boulton 1993; Rempel *et al*. 1999). Alternatively, a taxon known to migrate may be prevented from moving into suitable habitat by a disturbance characteristic, such as rapid onset (Imbert and Perry 1999; Gayraud *et al*. 2000; Stubbington *et al*. 2011b). This same potential refugee's vertical migration may be thwarted during a slow-onset disturbance by an inappropriate habitat feature (Olsen and Townsend 2005); features of importance and tolerance thresholds will differ between taxa.

Fig. 4 can be used to predict refuge use by a particular taxon if habitat and disturbance characteristics are known. However, whilst an initial migration can be predicted, HZ habitat quality may change as a disturbance progresses. In particular, water quality and resource availability may decline during drying events, with oxygen becoming limited as hyporheic water residence times increase. Therefore, an initial migration is only the first step in exploiting the HZ refuge (Dole-Olivier in press), and does not guarantee long-term survival.

Directions for future research

Whilst recent research has continued to ask if the HZ is a refuge, the variable nature of refuge use means that the answer is never clear-cut. The HZ can be a refuge, but only for certain taxa, if the habitat fulfils their requirements, and if the disturbance has certain characteristics. This complexity of determinants leaves many questions concerning the occurrence of migrations remain unanswered, and further research is needed to elucidate the habitat characteristics that allow refuge use in particular taxa. In particular, Dole-Olivier (2011) argues that future research should seek to characterise hydrologic exchange patterns in greater detail to clarify the influence of upwelling and downwelling water on refuge use.

For the model presented in Fig. 3 to be employed as a framework for the inference of invertebrate behaviour, essential criteria for future research into the HRH include the collection of paired benthic-hyporheic samples (e.g. Belaidi *et al*. 2004; Wood *et al*. 2010; Stubbington *et al*. 2011b) using non-destructive methods which allow repeated collection of quantitative samples from the same locations during a temporal sequence (Stubbington *et al*. 2009b). Variation in sampling efficiency between methods should be recognised (Fraser and Williams 1997; Scarsbrook and Halliday 2002; Kibichii *et al*. 2009), but the model remains valid where benthic and hyporheic sampling techniques differ, so long as each is employed consistently. Such studies will provide valuable information to guide the rehabilitation of impacted systems.

Other pertinent questions relate to the long-term prospects of migrants. As the HZ remains connected to non-refugial areas when a disturbance ends, there is scope for benthic recolonisation. Accordingly, shifts from shallow to deeper layers and subsequent return to the original depth distribution have been observed in response to both spates (Williams and Hynes 1974; Dole-Olivier *et al*. 1997) and flow-related temperature changes (Wood *et al*. 2010). Such apparent shifts in migration direction highlight the importance of active migrations. However, experimental work is needed to confirm that individual vertical migrations are reversed, and that the HZ is a true, not a transient, refuge (Dole-Olivier 2011).

In particular, whilst downwelling water may facilitate initial refuge use, it is not known how this direction of exchange affects refugees attempting to exit the HZ (Dole-Olivier *et al*. 1997; Stubbington *et al*. 2011b). Hyporheic flowpaths are spatio-temporally variable and occur at multiple spatial scales (Jones and Holmes 1996; Montgomery and Buffington 1997; Dole-Olivier 2011), and both spatial and temporal changes in exchange direction may facilitate the return of migrants to the surface. Such pathways may be particularly important in redistributing passive refugees, for which the HZ is otherwise a trap (Marmonier and Creuzé des Châtelliers 1991). The active-passive distinction is thus highly relevant to long-term refugee survival.

Implications for river management and restoration

A refugial habitat is one of many contributions the HZ makes to stream ecosystem functioning. This role may become increasingly important, given predictions of climatic shifts involving increased drought and flood severity (IPCC 2007; Larned *et al*. 2010; Aldous *et al*. 2011). However, anthropogenic deposition of fine sediment and channel modifications that reduce geomorphological complexity threaten the HZ refuge, by impeding hydrologic exchange and blocking the interstitial pathways upon which refuge use depends (Hancock 2002; Kondolf *et al*. 2006). The HZ therefore requires protection through environmental policy and legislative instruments such as the European Union Water Framework Directive (WFD; CEC 2000). The WFD requires a holistic approach to catchment management, including integrated management of groundwater and surface waters (Environment Agency 2002, 2009), but does not explicitly consider the HZ. Indeed, in Europe and elsewhere the ecological integrity of the HZ is rarely addressed by either monitoring programmes or rehabilitation schemes (Boulton 2007; Kasahara *et al*. 2009; Tomlinson and Boulton 2010; but see Kasahara and Hill 2006a, 2006b, 2007). There is therefore scope for regulators to ensure meaningful implementation of legislation to maximise ecological benefits for total river ecosystems.

Rehabilitation schemes are typically focussed on the surface stream (Bannister *et al*. 2005; Boulton 2007), and whilst such efforts may benefit the subsurface (Boulton *et al*. 2010), hydrologic exchange must also be targeted if the HZ refuge is to be safeguarded (Jansson *et al*. 2007; Boulton 2007; Hester and Gooseff 2010). To date, HZ-specific rehabilitation has involved increasing geomorphological complexity, for example by introducing wood into streams (Kasahara and Hill 2006a, 2006b; Mika *et al*. 2008). Such schemes promote hydrologic exchange (Kasahara and Hill 2006b), and patterns of exchange (an upwelling zone shortly downstream of a downwelling zone) may favour HZ refuge use and subsequent benthic recolonisation (Boulton 2007). Such schemes potentially have only localised effects, but since refuge use is patch-specific in heterogeneous habitats, localised refugial hot-spots may support enough individuals for subsequent recruitment and recolonisation of the surface (Robertson *et al*. 1995). Nonetheless, the HZ is a refuge only for certain taxa in certain circumstances, and rehabilitation schemes should therefore aim to create heterogeneous habitats incorporating a suite of potential refuges (Fig. 1).

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Table 1: Evidence of active and passive use of the hyporheic refuge by benthic invertebrate taxa during high flows (modified from Robertson and Wood 2010).

Evidence of active refuge use is provided by concurrent increases in the HZ abundance and proportion of a population; the proportion is inferred from observed or assumed changes in BZ abundance; evidence of passive refuge use is provided by the occurrence of benthic invertebrates in the HZ. HZ = hyporheic zone; BZ = benthic zone; EPT = Ephemeroptera, Plecoptera and Trichoptera.

Section A. Studies providing evidence of active refuge use			
Site description / location	**Evidence**	**Explanation for lack of migrations**	**Reference**
Riffle in headwaters of Speed River, Canada	Peak abundance of benthos at greater depth 1 day after spate; concurrent decrease in BZ abundance	-	Williams and Hynes 1974
Three forested sites, Thomson River, Victoria, Australia	Abundance of benthos lower at 0-10 cm and higher at 10-30 cm during high flows (at 1 of 3 sites)	-	Marchant 1988
Bypassed section of River Rhône River, France	More benthos (EPT, chironomids, flatworms) at 50 cm after spate, at upwelling sites	-	Marmonier and Creuzé des Châtelliers 1991
Bypassed section of River Rhône River, France	Benthos (*Gammarus*, ostracods) abundance increased in deeper sediments 1 day after spate, then decreased	-	Dole-Olivier and Marmonier 1992
Sand-bottomed stream, Virginia, USA	Rotifer abundance increased in HZ and decreased in BZ after flood.	-	Palmer et al 1992
Upland sites, Acheron River, Victoria, Australia	Chironomid, elmid, mite and copepod (but not EPT) abundance higher in HZ (10-30 cm) in high flow months.	-	Marchant 1995
Bypassed section of Rhône River, France	*Gammarus* and chironomids at greater depths after small / medium spates in downwelling zones	-	Dole-Olivier *et al*. 1997
Experimental flow tank	Hydrobiidae, Leptophlebiidae and Leptoceridae occurred in deeper layers during experimental flow increases	-	Holomuzki and Biggs 2000
Section B. Studies providing evidence of passive refuge use			

Site description / location	Evidence	Explanation for lack of migrations	Reference
Uniform riffle, Brazos River, Texas, USA	Increased HZ proportion of benthos (hydropsychids, elmid larvae, leptophlebiids); HZ abundance not known	None stated; active migrations possible	Poole and Stewart 1976
Pool-riffle downstream lake outflow, Ontario, Canada	HZ simuliid abundance stable during spate whilst BZ abundance declined. Other taxa present at low density.	Other refuges used (stable substrates)	Giberson and Hall 1988
Bypassed section of River Rhône River, France	Increase in HZ proportion but reduced HZ abundance for chironomids, oligochaetes and copepods after spate	Sandy substrate; “wash out” effect	Marmonier and Creuzé des Châtelliers 1991
Upland sites, Acheron River, Victoria, Australia	Evidence of active migrations (Section A) not observed during 1 of 2 high flow events	Possibly sediment compaction	Marchant 1995
Bypassed section of Rhône River, France	Little or no increase in HZ abundance of benthos after small/medium spates in upwelling zones	Stable hydrology	Dole-Olivier *et al*. 1997
Bypassed section of Rhône River, France	Benthos drifted rather than entering the HZ during high magnitude floods in downwelling zones	Spate magnitude; mobile substrate	Dole-Olivier *et al*. 1997
Gravel-bed experimental streams, USA	Non-significant increase in HZ abundance following abrupt/stepped flow increases	Rapid onset/ low spate magnitude	Imbert and Perry 1999
Cobble-bed sub-Alpine stream, France	Densities of benthos were stable in HZ before and after an experimental flow increase	Rapid spate onset	Gayraud *et al*. 2000
Subtropical river, Australia	Benthic mite abundance stable in HZ before and after experimental spates	Low spate magnitude	Boulton *et al*. 2004
Kye Burn, New Zealand	HZ abundance of all benthos lower after spate, but reduction in BZ abundance greater	Fine sediments	Olsen and Townsend 2005
Alpine stream, Italy	Hyporheic abundance/diversity of benthos reduced at hydropeaking-impacted sites	Disturbance frequency	Bruno *et al*. 2009
Second order karst stream, England	HZ abundance of benthos lower after spate, but reduction in BZ abundance greater	Mobile sediments/ rapid spate onset	Stubbington *et al*. 2010

Table 2: Evidence of active, passive, minimal and no use of the hyporheic zone as a refuge by benthic invertebrates during streambed drying (modified from Wood *et al*. 2010).

See Table 1 caption for additional details.

Section A. Studies providing evidence of active refuge use

Site description and location	**Evidence**	**Explanation for lack of migrations**	**Reference**
Temporary stream, New York, USA	Directional cages traps indicate migration of chloroperlids and leptophlebiids into HZ of riffles	-	Delucchi 1989
Intermittent desert stream, Arizona, USA	Abundance of permanent hyporheos decreased at 30 and 50 cm and increased at 1 m as water table fell	-	Clinton *et al*. 1996

Section B. Studies providing evidence of passive refuge use

Site description and location	**Evidence**	**Explanation for lack of migrations**	**Reference**
Intermittent stream, Indiana, USA	Isopods, amphipods and coleopterans present in moist interstitial spaces	Migrations not studied	Clifford 1966
2 intermittent creeks, Ontario, Canada	Chironomids, oligochaetes, amphipods, coleopterans and others recolonised surface sediments from HZ	Not studied; may have occurred	Williams 1977
Intermittent headwater stream, Ontario, Canada	Hydropsychids, rhyacophilids and nemouriids observed in moist interstices after surface drying	None suggested	Imhof and Harrison 1981
Intermittent streams, Australia	A few taxa (1 isopod, oligochaete, flatworm, mite, and leptophlebiid) occurred in the HZ of a dry stream	High streambed temperature	Boulton 1989
Intermittent wadi headwaters, Algeria	A few benthic taxa survived the dry phase at low abundance in the HZ	Compaction/baking of fine sediments	Gagneur and Chaoui-Boudghane 1991
Intermittent streams, Arizona, USA and Australia	35-69 % of benthic taxa present in HZ during dry phase	Migrations not studied	Boulton *et al*. 1992
Arid-zone intermittent stream, Australia	Benthos including mites, EPT, chironomids and simuliids found in HZ below dry streambed	-	Cooling and Boulton 1993

2nd order Appalachian headwater streams, USA	Suggested that 2 stonefly genera more abundant in deeper HZ layers due to earlier drying	-	Griffith and Perry 1993
2 intermittent creeks, California, USA	Abundance of most temporary hyporheos decreased in the HZ during the dry phase	Water lost from HZ above 0.6 m	Del Rosario and Resh 2000
Sub-Alpine river, Italy	*Agabus paludosus* (Dytiscidae: Coleoptera) present in deep sediments during the dry phase	Migrations not studied	Fenoglio *et al*. 2006
Intermittent lowland stream, England	Abundance of benthos in BZ and HZ decreased after repeated short-term drying	Fine sediment, water loss/ hypoxia	Stubbington *et al*. 2012
Normally perennial 5th order river, SE Australia	Oligochaetes, dipterans, a hydroptilid, mites, elmids and dytiscids present in HZ after surface drying	Migrations not studied	Young *et al*. in press

Section C. Studies providing minimal or no evidence of refuge use

Site description and location	Evidence (lack thereof)	Explanation for no refuge use	Reference
Headwater stream, coastal forest, South Carolina, USA	No active invertebrates present after flow ceased	Anoxia/dry, sandy substrate	Smock *et al*. 1994
Sycamore Creek, intermittent Sonoran desert stream, USA	Ceratopogonids abundant at 0-10 cm immediately after flow resumption	Hypoxia/small interstices	Stanley *et al*. 1994
Sycamore Creek, intermittent Sonoran desert stream, USA	Very few benthic taxa survive dry phase in HZ	HZ dried	Boulton and Stanley 1995
Regulated intermittent wadi, NW Algeria	Very few benthic invertebrates present in HZ during dry phase	Baking of fine sediments; anoxia	Belaidi *et al*. 2004
Normally perennial 5th order river, SE Australia	Virtually no active invertebrates present in the HZ during dry phase	HZ dried to depth of 0.4 m	Young *et al*. in press

Table 3: Evidence of active and passive use of the hyporheic refuge by benthic invertebrates during reduced flows (modified from Wood *et al*. 2010).

See Table 1 caption for additional details.

Section A. Studies providing evidence of active refuge use

Site description / location	Evidence	Explanation for lack of migrations	Reference
Lowland chalk stream, England	Decreased BZ abundance/increased HZ abundance of benthos linked to temperature, not discharge	-	Stubbington *et al*., 2009; Wood *et al.* 2010
Two small limestone streams, England	Increase in HZ abundance and HZ proportion observed for *Gammarus* at downwelling sites	-	Stubbington *et al*. 2011; Stubbington *et al*. 2012

Section B. Studies providing evidence of passive refuge use

Site description / location	Evidence	Explanation for lack of migration	Reference
Three small cobble-bottom streams, North Island, New Zealand	Benthos present in HZ; vertical distribution similar before and after 88-96 % flow reductions	BZ preferable	James *et al*. 2008
Experimental channels in a New Zealand lowland river	15 % of benthos present in HZ both before and after 25-98 % flow reductions	Stable submerged area; BZ preferable	James and Suren 2009
Two small limestone streams, England	HZ abundance stable whilst BZ abundance increased for *Gammarus* at upwelling site	Water movement/ water chemistry	Stubbington *et al*. 2011; Stubbington *et al*. 2012
Normally perennial 5th order river, SE Australia	Many taxa present in HZ at sites with 80% bed exposure, but assemblage similar to that at sites with greater flow	BZ preferable	Young *et al*. in press

Table 4: Taxon-specific evidence of active migrations by benthic macroinvertebrate into the hyporheic zone. Studies noting active migrations identified using Tables 1-3; only taxa recorded as actively migrating by some studies are noted.

Class	**Taxon**	**Active migrator?**	**References**
Tricladida	Planariidae	Yes	Marmonier and Creuzé des Châtelliers 1991
Gastropoda	*Potamopyrgus*	Yes	Holomuzki and Biggs 2000
Amphipoda	*Gammarus*	Yes	Dole-Olivier and Marmonier 1992; Dole-Olivier *et al*. 1997; Wood *et al.* 2010; Stubbington *et al*. 2012
		No	Dole-Olivier *et al*. 1997 Gayraud *et al*. 2000
Ephemeroptera	Not specified	Yes	Marmonier and Creuzé des Châtelliers 1991
		No	Marchant 1995; Gayraud *et al*. 2000 (Heptageniidae)
	Leptophlebiidae	Yes	Delucchi 1989; Holomuzki and Biggs 2000
Plecoptera	Not specified	Yes	Marmonier and Creuzé des Châtelliers 1991
		No	Marchant 1995
	Chloroperlidae	Yes	Delucchi 1989; Dole-Olivier and Marmonier 1992
	Leuctridae	Yes	Dole-Olivier and Marmonier 1992
Trichoptera	Not specified	Yes	Marmonier and Creuzé des Châtelliers 1991
		No	Marchant 1995
	Hydropsychidae	Yes	Dole-Olivier and Marmonier 1992
	Leptoceridae	Yes	Holomuzki and Biggs 2000
	Polycentropodidae	Yes	Dole-Olivier and Marmonier 1992
	Sericostomatidae	Yes	Holomuzki and Biggs 2000
Coleoptera	Elmidae larvae	Yes	Marchant 1988; Dole-Olivier and Marmonier 1992; Marchant 1995
Diptera	Chironomidae	Yes	Marchant 1988, 1995; Dole-Olivier *et al*. 1997
		No	Gayraud *et al*. 2000

Table 5: Evidence for proposed traits of taxa identified as active migrants Traits proposed by Robertson and Wood (2010). Active migrants identified in Table 4. Trait assignment requires some, not all, members of a taxon to have the trait.

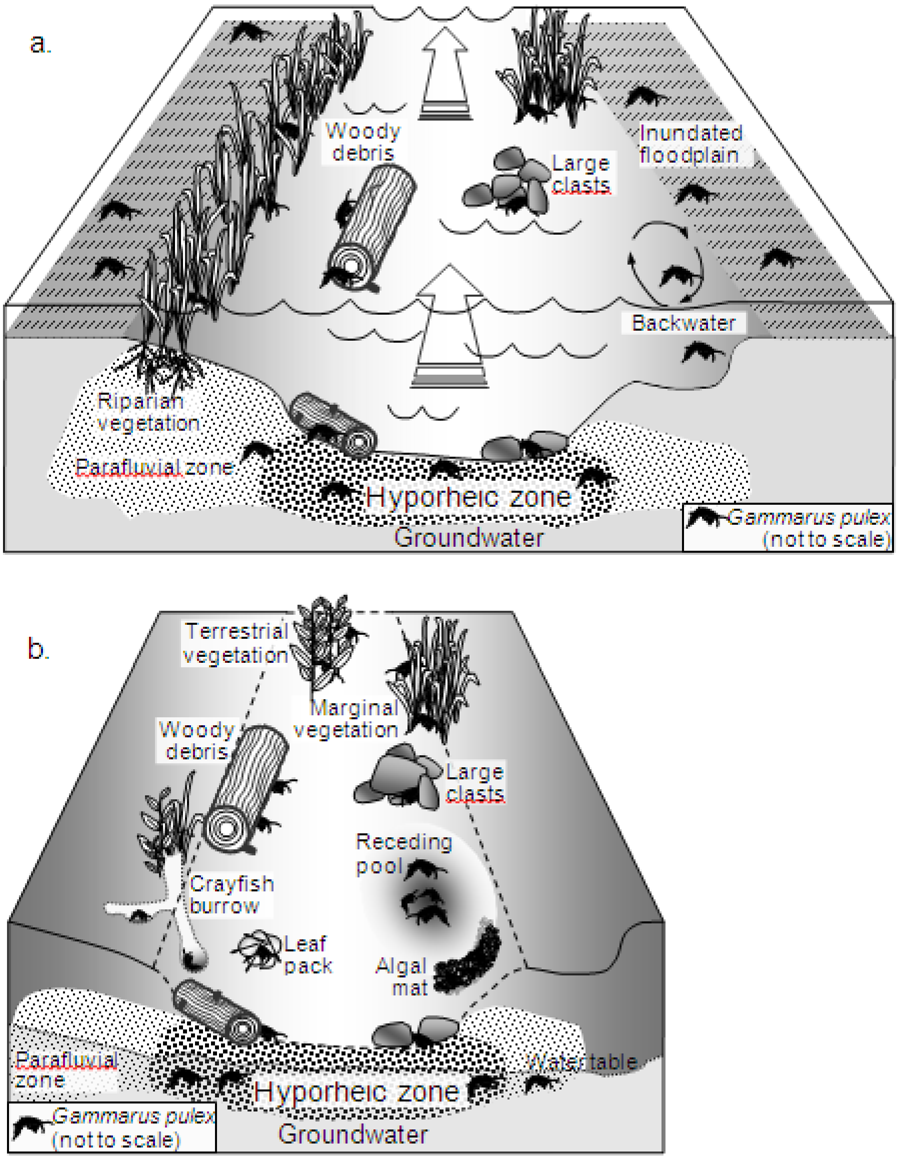
		Proposed traits of active migrants							
		No attachments	Burrowing habit	Depositional rheophily	High crawling rate	Small (<9 mm) at maturity	Tegument respiration	Vermiform shape	Total traits (max. 7)
Taxa identified as active migrants	Chironomidae	✓	✓	✓	✗	✓	✓	✓	6
	Planariidae	✓	✓	✓	✓	✓	✓	✗	6
	Potamopyrgus	✓	✓	✓	✓	✓	✗	✗	5
	Elmidae (larvae)	✓	✓	✓	✓	✓	✗	✓	5
	Gammarus	✓	✓	✓	✗	✗	✗	✗	3
	Chloroperlidae	✓	✓	✗	✓	✗	✗	✗	3
	Leuctridae	✓	✓	✓	✓	✗	✗	✗	3
	Leptoceridae	✓	✗	✓	✓	✗	✗	✗	3
	Sericostomatidae	✓	✓	✓	✓	✗	✗	✗	3
	Hydropsychidae	✓	✗	✗	✓	✗	✗	✗	2
	Leptophlebiidae	✓	✓	✓	✗	✗	✗	✗	2
	Polycentropodidae	✓	✗	✗	✓	✗	✗	✗	2
	Total taxa (max. 12)	12	9	9	8	4	2	2	

Fig. 1. Conceptualisation of the hyporheic zone as one of a suite of invertebrate refuges available during (*a*) high flows, and (*b*) streambed drying. *Gammarus pulex* (Crustacea: Amphipoda) is depicted (not to scale), as a representative benthic invertebrate.

Fig. 2. Interactions between sediment characteristics, hydrologic exchange (HE), flow velocity and dissolved oxygen concentrations in the hyporheic zone. Italics indicate high refuge potential.

Fig. 3. Behaviour inferred from changes in absolute and relative abundance of benthic and hyporheic invertebrates. HZ = hyporheic zone; BZ = benthic zone. Examples: [1]Stubbington *et al*. 2011, 2012; [2]Pers. obs., River Glen (Lincolnshire, UK) during habitat contraction; [3]Stubbington *et al*. 2012; [4]James *et al*. 2008; [5]Williams and Hynes 1974, Marchant 1988, Wood *et al*. 2010; [6] Giberson and Hall 1988, Palmer *et al*. 1992, James and Suren 2009; [7, 8, 9]No known examples.

Fig. 4. Flow chart for predicting use of the hyporheic zone (HZ) as a refuge. C1-3 indicate three criteria that must be met for active refuge use to occur.



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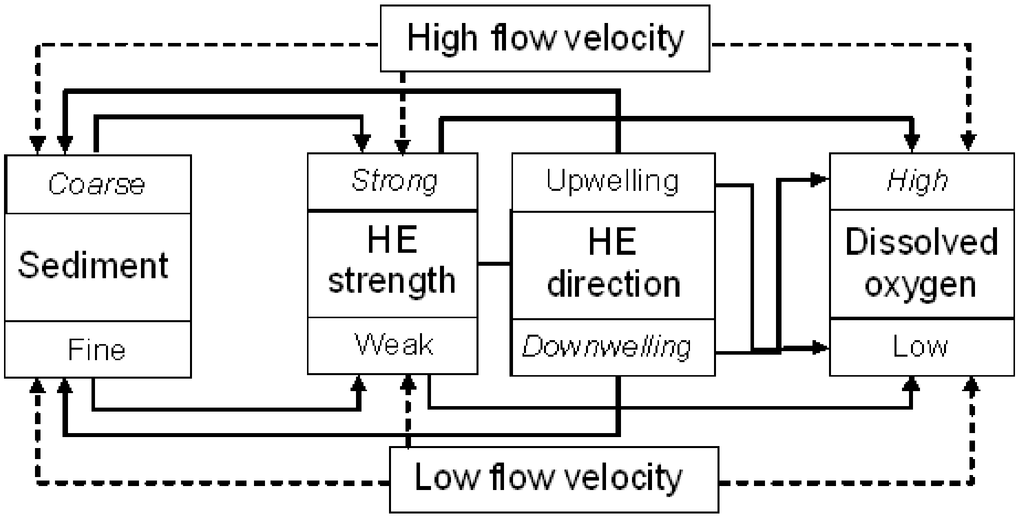

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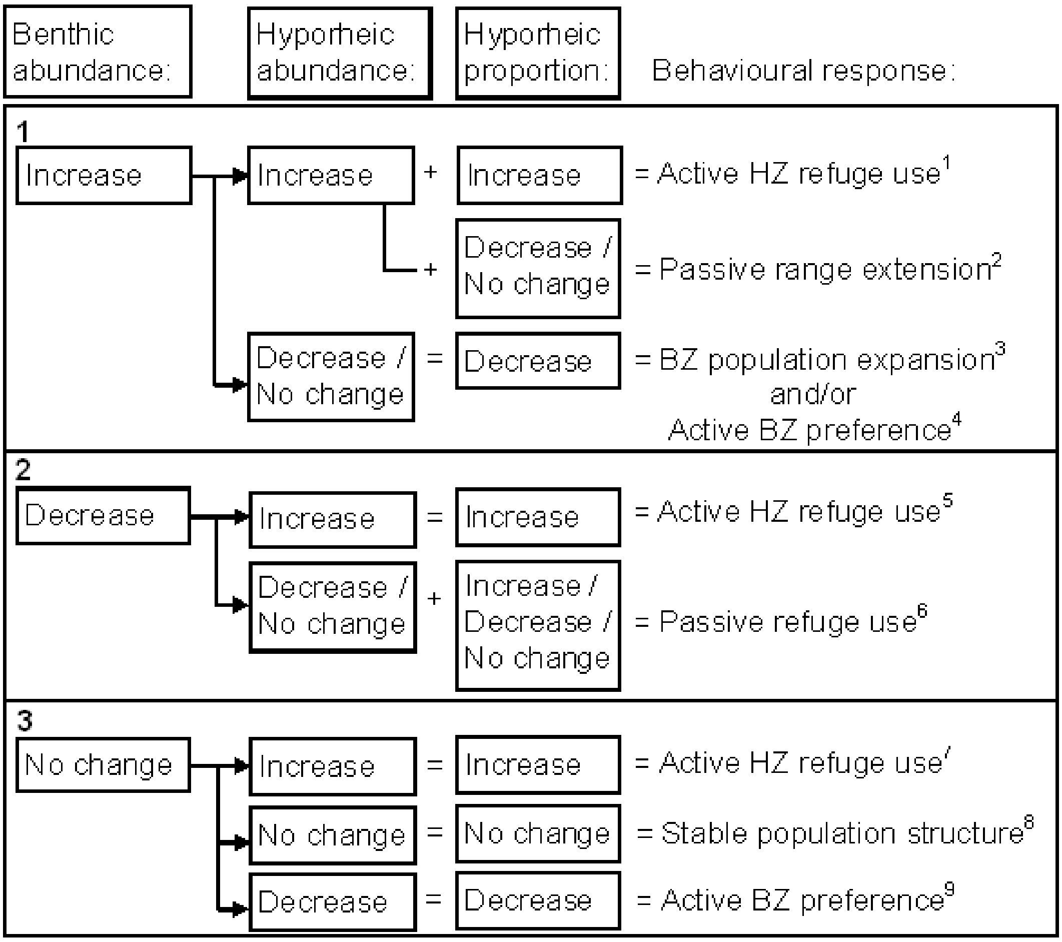

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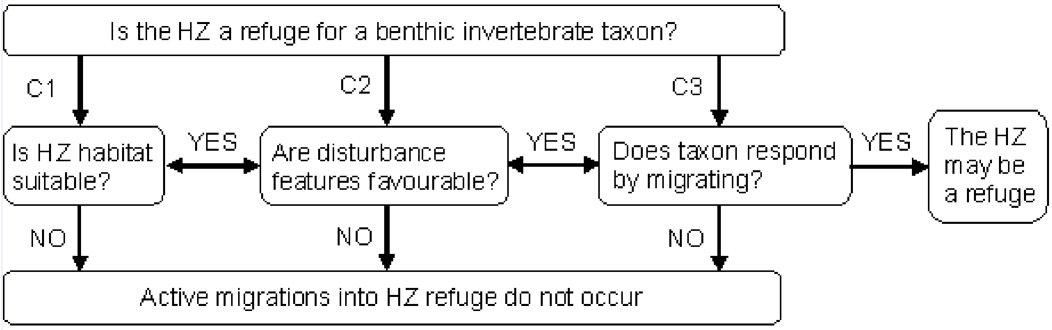

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