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A review of the subterranean aquatic ecology of England and Wales

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Steve Killeen

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Head of Science

Executive Summary

Groundwater ecology has received very little attention in the UK, however the preamble to the new EU Groundwater Directive encourages further research on groundwater ecosystem function and protection. The well shrimp *Niphargus glenniei*, has recently been added to the UK Biodiversity Action Plan priority species list.

This report presents the results of a review of the distribution and ecological functions of subterranean aquatic fauna in England and Wales. It explores how water resource and other environmental management approaches could take more account of these subsurface assemblages, especially regarding the impact of water abstraction and pollution on aquifers. The report identifies significant gaps in the understanding of both the fauna and habitat function of groundwater, the hyporheic zone, and the roles these environmental compartments play in the wider integrated catchment.

Over 500 records of stygobites (invertebrates that live solely in subsurface aquatic habitats) were found for groundwater and hyporheic systems, which were obtained primarily from the Biological Records Centre, the Environment Agency's BIOSYS, caving records, published works and personal communications. In contrast to Europe (particularly karstic regions of France and the Balkans) there are very few stygobites recorded in England and Wales. They are typically found where the bedrock geology is fractured and calcareous, and usually in areas to the south of the Devensian (most recent) glaciation. Stygobites are slow moving and slow to disperse. Some species have been recorded from only one or two sites and it appears that they have not yet recolonised habitats affected by glaciation. Research suggests that stygobites are particularly vulnerable to anthropogenic disturbance due to their restricted distributions, poor dispersal, low reproductive rates and poor competitive ability.

Although species richness of stygobites is limited, the hyporheic and groundwater habitats make a unique contribution to biodiversity in the UK. There are also extensive assemblages of stygophile fauna occurring in both hyporheic and groundwater habitats; these may perform important functions such as modulating the activity of the hyporheic biofilm by grazing and bioturbation.

The report considers the ecological functions and services that hypogean fauna provide, and outlines options for their protection and enhancement, which are likely to be a part of the European Commission's review of the GW Directive in 2013.

A significant research effort is required to further knowledge about subterranean fauna, their habitats, ecological functions and management. Some priorities for research include:

- the responses of hypogean communities to contamination
- the development of monitoring methodologies for hyporheic/groundwater assemblages that could enhance existing river/groundwater quality surveys;
- an improved understanding of the distribution of hyporheic/groundwater assemblages in England and Wales especially in relation to the major aquifers and the glacial legacy;
- the impact of land use on groundwater and hyporheic assemblages;
- the relationships between hydrology, microbial processes and biodiversity in the hyporheic zone;
- the role of hyporheic zone microbes and meiofauna on river diversity and health.

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1 Introduction

This report describes the invertebrate hypogean communities found in the UK (principally England and Wales) and their ecological functions. It presents data on the known distribution of subterranean fauna, and summarises literature on similar taxa worldwide in order to:

1) identify the areas in England and Wales where subterranean aquatic fauna are most likely to be found (based on geological and geomorphological properties);
2) identify any likely differences in the types of fauna found in different geological conditions.

The report identifies gaps in existing knowledge and sets out recommendations for further research. It also suggests how environmental management approaches could be developed and how subterranean aquatic fauna could be used in the assessment of aquatic ecological health. This report focuses in particular on stygobites in hypogean environments. Although springs often contain stygobites and are areas where groundwaters and surface waters mix, these habitats are only briefly considered here.

Environmental management objectives for groundwater have traditionally focused on water resources and water quality (hydrochemistry). The Water Framework Directive (WFD) requires that the ecological health of groundwater-dependent systems, such as rivers, lakes and wetlands, is also protected; the Environment Agency must consider these ecological objectives when managing groundwater. More recently, explanatory text to the new EU Groundwater Directive encourages further consideration of groundwater ecosystems in groundwater management decisions. In the UK *Niphargus gleneii* is the first stygobite species to be listed in the UK Biodiversity Action Plan (UK BAP), designated June 2007 and consequently has an increased level of protection.

This report has been prepared to provide evidence to the Environment Agency and others in helping to inform policy and operational management decisions regarding the appropriate management of groundwater, having regard to the subterranean ecology that may be present.

Definiton box 1

Hypogean
The subsurface or subterranean environment as opposed to the surface (epigean) environment. The hypogean environment consists of three zones: the zone closest to the surface (the hyporheic zone); and groundwater in both shallow superficial deposits and deeper aquifers (including cave systems).

Hyporheos /hyporheic zone
A habitat and its biotic community occurring in the saturated interstices beneath the stream bed, and into the stream banks, that contain some proportion of channel water, or that have been altered by surface water and groundwater infiltration.

Stygobite
Obligate groundwater invertebrate

Stygophile
Facultative inhabitants of the hypogen domain. Normally completes life cycle in the epigean but is capable of completing the lifecycle in the hypogean as well.

Groundwaters are the largest hydrological unit after the worlds oceans, representing 97% of all global freshwaters (UNESCO, 1986). Groundwater is present in all rock formations, but is most important where the rocks have sufficient porosity and permeability to store and transmit water. These strata include karstic and porous-media aquifers. The fractured and porous nature of these deposits presents habitat opportunities for subterranean aquatic organisms.

Globally, these habitats contain a large number of stygobite species. Gibert and Culver (2004) suggested that about 7,700 aquatic stygobites were known in 2000; this number is rising as further geographic areas are explored. In some aquatic groups a high proportion of the total biodiversity is found in subterranean habitats. Crustaceans are especially well represented in groundwaters. For example, Sket (1999) found approximately 70% of harpacticoid and 60% of cyclopoid copepod species in Europe are stygobites and approximately 10% of all Malacostraca are stygobites (Sket, 2004). Furthermore there are other microcrustacean groups such as the Bathynellacea and Thermosbaenacea which are almost totally stygobitic. Assemblage composition of the hyporheos can also be extremely diverse. For example, over 300 species of meiofauna have been reported from the Oberer Seebach, a gravel bed stream in Austria (Schmid-Araya and Schmid, 1995; Schmid and Schmid-Araya, 1997). In the hyporheic zone of the upper Rhône, France, over 300 invertebrate taxa have been collected (Malard et al., 2002). Proudlove (2006) provides a comprehensive list of hypogean literature.

The diversity of groundwater/hypogean fauna has considerable spatial variability, with apparent biodiversity 'hotspots' (Culver and Sket, 2000). Areas of high diversity in Europe include the Dinaric (West Balkan) region and the Pyrenean-Aquitanian region (Sket, 2004, see Figure 2.2). High numbers of regional stygobitic species are mirrored in rich local fauna. For example, the Postojna-Planina cave system has 49 stygobites and the Vjetrenica cave has 40 stygobites;Both of these cave systems are in the Dinaric region (Culver and Sket, 2000).

Several theories have been advanced to explain the high species richness observed in groundwater assemblages. Stoch (1995) attributed the high species richness of copepods in northern Italy to strong niche specialization during an adaptive radiation process. Sket (1999) argues that the high crustacean biodiversity in Slovenian karstic groundwater is due both to the present day ecological conditions and the geological evolution of this area. Predation and competition may also be important determinants of subterranean assemblages, although there are contradictory views (Sket 1999).

The subterranean environment is unique compared to surface environments because it includes a large number of endemic (restricted distribution) and rare species. Many groundwater species are known from only one or two locations. For example, as many as 78% of the stygobitic taxa in the Dinaric region are endemic to that region (153,400 km^2) and 37-67% of the taxa may be endemic to one of its subregions, measuring only 3,500 – 51,000 km^2 (Sket, 2004). In the countries covered by the EU PASCALIS project[1] over 83% of the stygobitic species can be classified as strict endemics and over 69% are rare (Gibert et al., 2004).

Many groundwater invertebrates disperse so slowly that dispersal abilities set strong limits on their ranges. Numerous groundwater species appear not to have dispersed from their place of origin (e.g.Botosaneanu, 1986a). Similarly, many groundwater animals appear to be very slow to recolonise areas where populations were extirpated by catastrophic disturbances. The Pleistocene glaciations, for example, probably eliminated most or all of the groundwater fauna from glaciated regions (but see Holsinger, 1988; Kristjansson and Svavarsson, 2004; Lefebure et

[1] Protocols for the ASsessment and Conservation of Aquatic Life In the Subsurface. Main objectives are to 1) develop an evaluation procedure for estimating regional groundwater biodiversity throughout European countries; 2) identify potential biodiversity indicators in groundwater; 3) reinforce public and regional manager awareness of the need to conserve groundwater biodiversity; 4) propose recommendations and establish an action plan for the conservation of groundwater biodiversity at the European level.
http://serv-umr5023.univ-lyon1.fr/~pascalis/

al., 2007; Svavarsson and Kristjansson, 2006). Even though large areas of Europe and North America were free of ice around 10,000 years ago, present day distributions of groundwater organisms still reflect patterns of glaciation (Strayer, 1994). Such slow dispersal for many groundwater organisms suggests that the faunas of aquifers affected by anthropogenic pollution may recover extremely slowly and local extinctions by human activities might be irreversible (Strayer, 1994).

Groundwaters are considered to be extreme environments, with low oxygen conditions and low energy inputs. Stygobites are adapted to these conditions and typically have low metabolic rates and a high tolerance of hypoxia (Danielopol et al., 1994; Hervant and Mathieu, 1995; Malard and Hervant, 1999). They also tend to have low population densities, simple food chains, few trophic levels and unspecialized feeding (Danielopol et al., 2003). As an adaptation to energy-poor environments, stygobites typically show life histories involving delayed maturity, greater longevity, smaller clutch size, larger eggs and lower percentages of mature ovigerous females than related epigean species (Gibert et al., 1994). The low population numbers and slow reproduction of groundwater organisms may result in an increased vulnerability to anthropogenic change compared to epigean species. Their small distributional ranges compounds this vulnerability, particularly if stronger epigean competitors gain access (Sket, 1999).

Many groundwater organisms exhibit morphological convergence (e.g. loss of eyes, relative lengthening of appendages); this phenomenon probably biases the assessment of biodiversity in groundwater because until recently assessment of taxonomic diversity relied almost exclusively on morphologically based identification (Lefebure et al., 2004). However some studies have indicated that groundwater and subterranean habitats harbour remarkably high numbers of cryptic species (Lefebure et al., 2007; Stoch, 1995), another aspect of hypogean ecology that is largely unexamined in the UK. However, ongoing work in the UK by Proudlove and colleagues suggests that *Niphagus kochianus* comprises two separate species. Despite their morphological similarities, stygobites exhibit a diversity of responses to the environment (Rouch, 1986) and so may be used as environmental descriptors or 'sentinels', providing information about the state of groundwater ecosystems (Dole-Olivier et al., 1993).

The review presented here aims to provide an evidence-base that can underpin future Environment Agency policy and/or operational management decisions. It describes applied and 'blue-skies' research gaps that would improve understanding of the functions and importance of subterranean aquatic ecosystems. This knowledge should help to improve the assessment, protection and restoration of the UK's subterranean aquatic ecology.

2 Defining groundwater, the hyporheic zone and their biota

2.1 The hyporheic zone

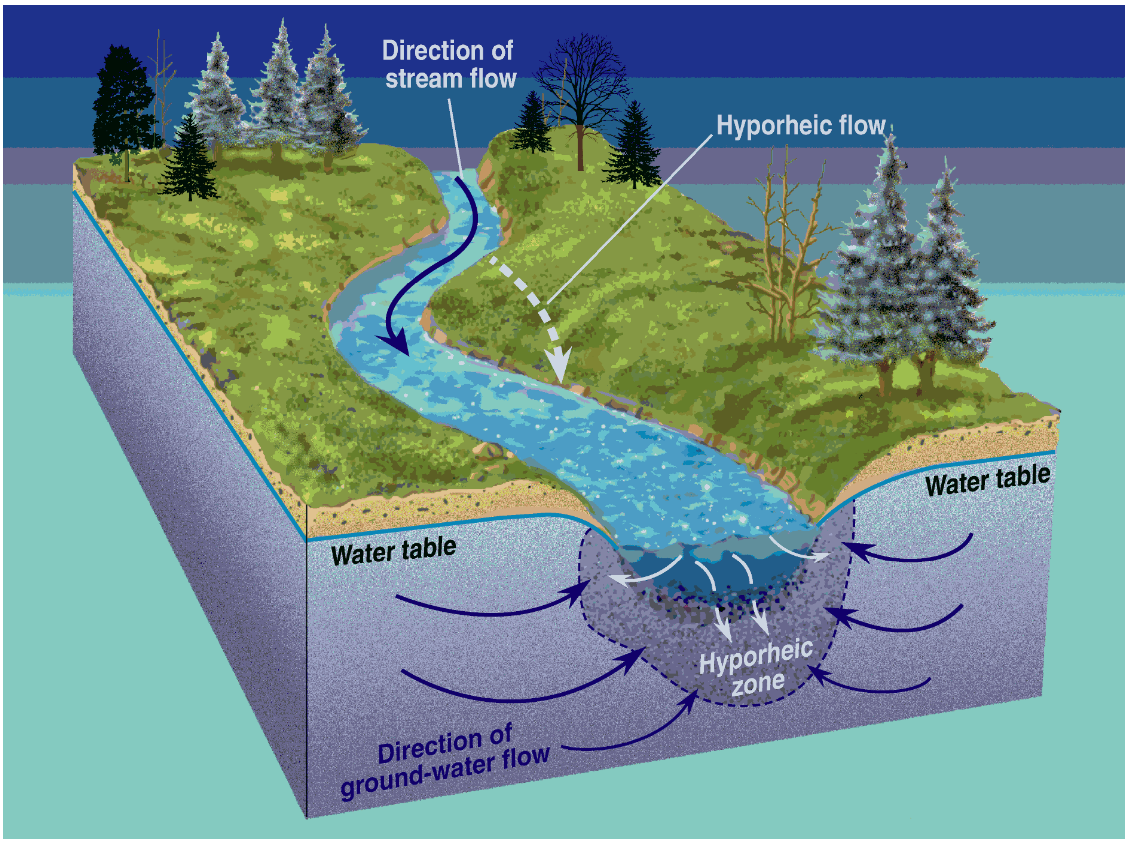
The hyporheic zone has been defined by White (1993) as 'the saturated interstices beneath the stream bed, and into the stream banks, that contain some proportion of channel water, or that have been altered by surface water infiltration'. The hyporheic zone is an ecotone connecting the groundwater with the surface river (Fig 2.1). It is a dynamic transition zone (Marmonier et al., 1993) and its nature varies widely in space and time as well as from system to system due to the heterogeneity of the substratum and discharge variability. It is this formation of gradients that confirms the hyporheic zone as an ecotone between two more uniform yet contrasting entities (Brunke and Gonser, 1997).

Groundwater and rivers have traditionally been viewed as distinct entities, but more recently many ecologists have recognised that longitudinal, lateral and vertical hydrological connectivity underpins many of the ecological patterns and processes occurring in rivers (Brunke and Gonser, 1997; Ward et al., 1998). This recognition is crucial if desired ecological improvements in rivers are to be achieved.

In comparison to surface waters, the hyporheic zone is characterized by a slower current velocity, a reduced range in daily and annual temperature, gradients of physicochemical parameters and a high stability of substrates that can be colonised (Brunke and Gonser, 1997). In comparison to the underlying groundwater, however, the hyporheic zone has a high current velocity, a greater temperature range and steeper gradients of physicochemical parameters (Table 2.1). Research, mainly over the last two decades, has confirmed that the hyporheic zone plays an important role in mediating exchange processes between surface and groundwater, for example, transferring water, nutrients and organic matter (Brunke and Gonser, 1997) – see section 3.2.

The hyporheic zone also has a lateral dimension that links riparian areas, palaeochannels and floodplain aquifers, thereby increasing the diversity of habitats within the catchment and thus its biodiversity.

Figure 2.1 Diagrammatic structure of a river-aquifer system, showing the hyporheic zone (USGS 2002)



2.2 Groundwater

Below the hyporheic zone lies 'true' groundwater, in this report we distinuish between two subterranean groundwater habitats: karstic and alluvial (coarse porous medium) aquifers. Karst is the term widely used to describe terrain shaped by the dissolution of a soluble layer or layers of bedrock, usually carbonate rock such as limestone or dolomite. These landscapes display distinctive surface features and underground drainage networks. Karst covers large areas of some European countries (see Fig. 2.2). It provides a heterogeneous habitat of interconnected cracks, fissures and drains, filled with air, water or both. Caves and their habitats are now considered to be parts, or subunits, of a broader and coherent physical unit. Today the term 'karstic system' is widely used, designating a functional unit involving organised flow pathways, storages and voids (Mangin, 1994).

Unlike the extensive karstic regions of southern Europe, Britain's karst is effectively limited to parts of the carboniferous limestone supergroup. However, it has been argued (Banks et al., 1995) that parts of the Chalk are sub-kastic and exhibit some of the features of a karstic aquifer, for example sink and swallow holes, macroscopic cave systems and high velocity groundwater flow.

The primary characteristic of subterranean environments is permanent darkness (Table 2.1), but there is also a general reduction in the diversity of habitats and a decrease in available space in comparison to surface water habitats. The lack of vegetation results in reduced habitat diversity, although physical heterogeneity still exists through variation in the size and shape of the voids.

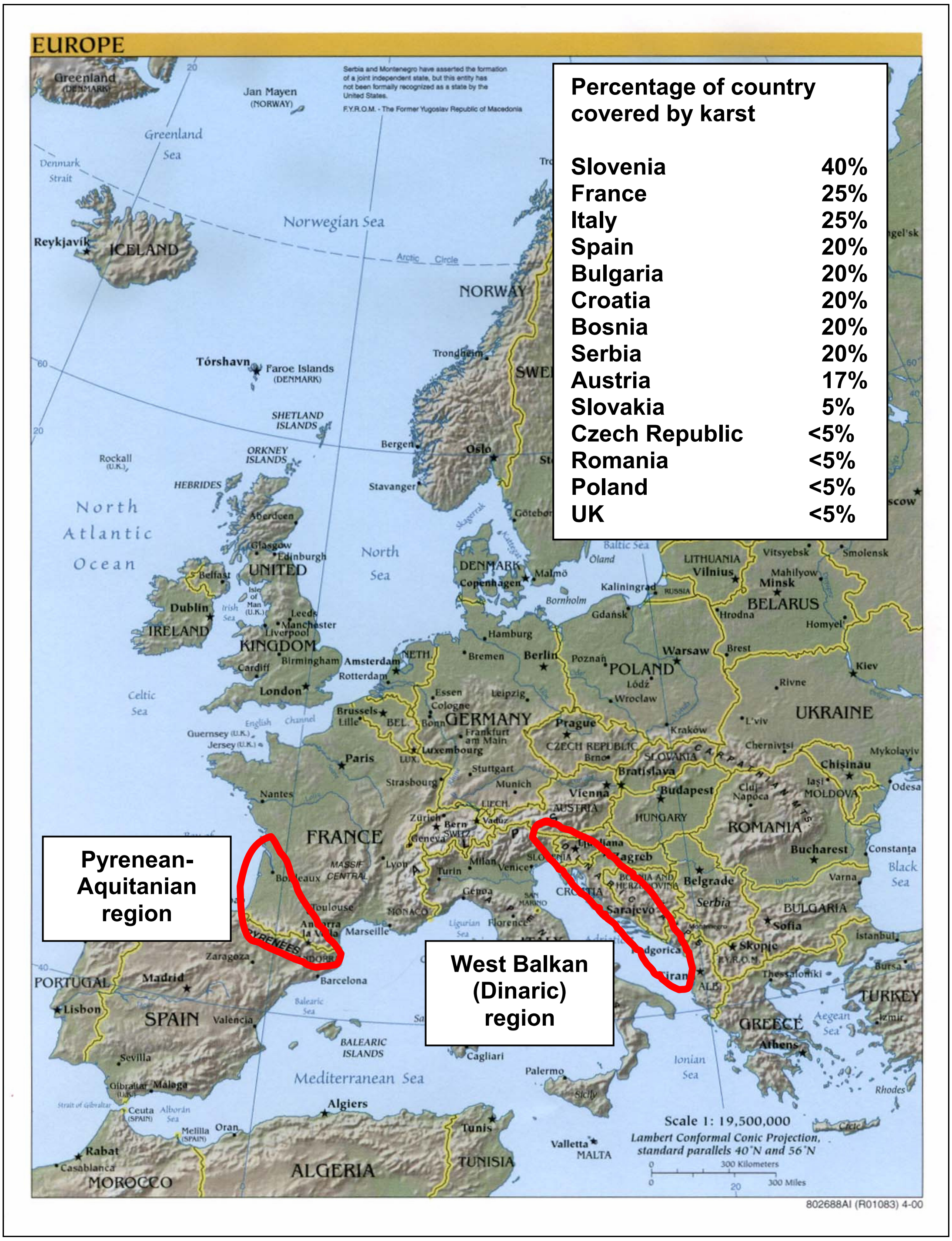
In the interstitial (alluvial) environment there is only one habitat type: the pore space. Yet pore space has considerable heterogeneity, for example in the arrangement of grains, pore size and physical and chemical characteristics (Gibert et al., 1994; Rouch, 1986; Ward, 1989).

The basic food resource in groundwaters is organic matter from external sources (Holsinger, 1988) and the seasonal cycles that are so important on the surface have a much reduced influence on subterranean ecosystems. Groundwater food webs are short and energy sources are weakly diversified (Marmonier et al., 1993).

Table 2.1 Summary of comparative physical and biological characteristics of groundwater, hyporheic and surface water environments.

Physical characteristic	Descriptive characteristic of environment in :		
	Groundwater	Hyporheos	Surface Water
Light	Constant darkness	Constant darkness	Daily light fluctuations
Current velocity	Low	Intermediate	High
Annual & daily temperature range	Strongly reduced	Reduced	High
Substrate stability	High	Intermediate	Low
Gradients of physico-chemical parameters	Low	Steep	Steep
Biological characteristics			
Habitat diversity	Low	Intermediate	High
Food webs	Short & simple	Intermediate	Long
Productivity	Low	Intermediate	High

Figure 2.2 Map of Europe indicating location of 'hotspots' of subterranean biodiversity. Insert shows the percentage of selected countries covered by karst (Juberthie, 2000).



2.3 The subterranean aquatic biota

A diverse array of organisms with varying affinities for groundwater inhabits the hyporheos and groundwater environments. There are many ways of classifying these organisms, typically based on their varying reliance on groundwater; this report adopts a functional classification scheme proposed by Gibert et al. (1994). This scheme is based on the morphological and physiological adaptations that invertebrates possess to a sub-surface existence, ranging from primarily surface dwelling stygoxenes to obligate groundwater invertebrates (stygobites).

Stygoxenes are organisms that have no affinities with groundwater systems (Gibert et al., 1994), although they may occur accidentally in alluvial sediments or caves and act as predators or prey of groundwater taxa.

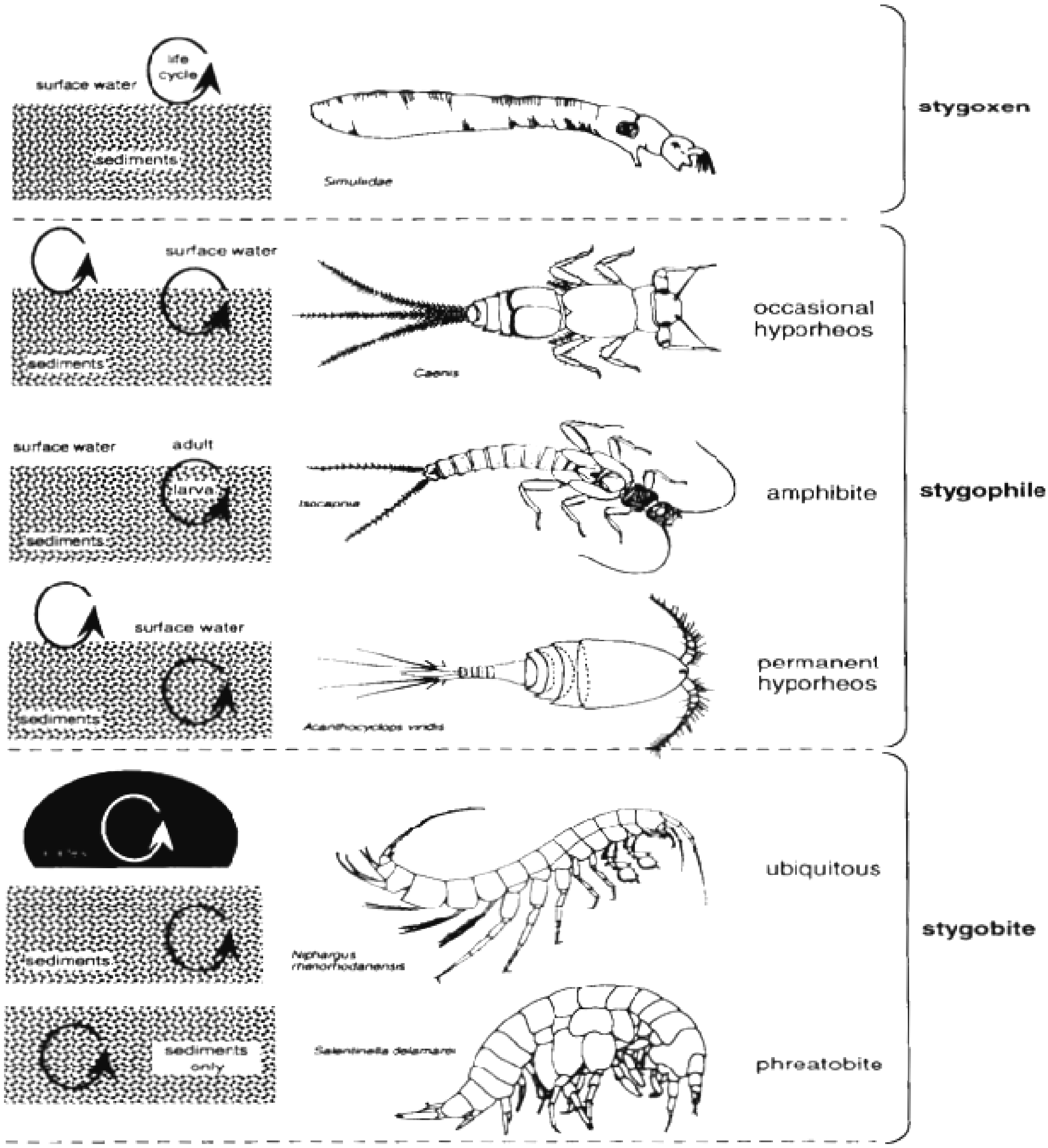
Stygophiles have a greater affinity for groundwaters. They appear to exploit resources actively and/or use the groundwaters as a refuge from surface events such as flooding or predation (Figure 2.3). In porous aquifers stygophiles are divided into three groups (Figure 2.3), namely:

- Occasional hyporheos comprising early instar larvae of epibenthic invertebrates that may reside in the hyporheos for a period of time.
- Partial hyporheos (amphibites), which covers organisms whose life cycle takes place in both surface water and groundwater ecosystems (e.g. some stonefly taxa in the Flathead River, Montana, live in the deep hyporheic zone for one or more years before returning to the river to emerge as terrestrial adults (Stanford and Ward, 1988));
- Permanent hyporheos, consisting of taxa that spend their entire life cycle in either the hyporheos or the epibenthos because they do not have an aerial adult stage, for example, specialised Copepoda, Ostracoda, and Cladocera.

Stygobites are specialized subterranean forms (Figure 2.3) such as the amphipod *Niphargus fontanus*. Some are ubiquitous in all types of groundwater systems (both cave systems and alluvial aquifers), for example the amphipod *Niphargus aquilex* in the UK. However, some are phreatobites, restricted to the deep groundwaters (the phreatic zone) of alluvial aquifers, for example *Niphargus kochianus kochianus* in the UK.

Stenothermic species are rather different organisms, capable of living and growing only within a limited range of temperatures. Some of these species appear to be normally restricted to groundwater, but may be found in surface waters when conditions are suitable. In the UK, species include the flatworms *Crenobia alpina* and *Phagocata vitta* and the beetles *Hydroporus obsoletus* and possibly *Agabus biguttatus*.

Figure 2.3 A classification of groundwater fauna based on its phenology and its presence or absence in various groundwater environments (Gibert et al., 1994)



3 Ecological functions provided by subterranean aquatic fauna

3.1 Introduction

The importance of the hyporheos to the whole river ecosystem is emphasised by the discovery that the hyporheic zone of rivers may contribute substantially to whole river metabolism and that extensive vertical transfer of energy may occur across the hyporheic zone (Ward et al., 1998). This report focuses on the role of invertebrates in hyporheic functioning, although it is undoubtedly true that microbes also play a fundamental role in this respect. In a study on the River Necker, Switzerland, the hyporheic zone contributed 76-96% of ecosystem respiration (Naegeli and Uehlinger, 1997), a similarly percentage (70%) was recorded for the hyporheic zone of Buzzard Branch, Viginia USA (Fuss and Smock, 1996).

The significance of hyporheic respiration to river ecosystem metabolism depends firstly on the proportion of the river's discharge traversing the hyporheic zone and secondly on the metabolic activity of the sediments (Findlay, 1995). Additionally Smock et al. (1992) demonstrated that the hyporheic zone accounted for 65% of invertebrate production in the channel of a sand-bottom stream. Although meiofauna may contribute a variable amount to total stream biomass due to their small body size (Hakenkamp and Morin, 2000; Stead et al., 2005a), their short life spans and rapid turnover probably result in a relatively high contribution to stream secondary productivity (Robertson et al., 2000).

Groundwater foodwebs are largely heterotrophic (Gibert *et al* 1994); the only primary producers are chemoautotrophic bacteria. Any secondary production depends on the transport of resources, such as detritus, from the surface. The amount available will depend on how the groundwater is connected with surface waters.

Most unpolluted groundwaters are characterised by scarce trophic resources. For example, Stanford and Ward (1988) observed that dissolved organic carbon concentrations were consistently low in the pristine unpolluted groundwaters of the Flathead River and that food webs were generally simple, with few trophic links. Microbial biofilms are the primary consumers in the hyporheos (see below) and probably constitute the major food base for interstitial organisms (Ward et al., 1998), although many interstitial animals are predatory (Schmid-Araya and Schmid, 1995) and many are polyphagous (Culver, 1985). Meiofauna form a major component of the diet of many stream macroinvertebrates, particularly the smaller instars (Schmid-Araya and Schmid, 2000). Some stream invertebrates are heavily reliant on the hyporheos for food, for example, 76% of the annual production of *Acanthophlebia cruentata* (a leptophlebid mayfly from the North Island, New Zealand) occurs in the hyporheic zone (Collier et al., 2004).

Boulton (2007) discusses a number of functional roles of hyporheic fauna in streams. These include; their physical impact on the porosity of the system, their alteration in the availability of nutrients, their impact on the breakdown of organic matter and participation in the transfer of material into, through or out of the hyporheic zone. These roles are described in the following sections.

3.2 Physical impact on porosity of substratum

Jones et al. (1994) coined the term 'ecosystem engineers' to describe the physical impact that organisms may have on their environment. In the hyporheic zone such impacts can occur via bioturbation or pelletisation. Although many hyporheic invertebrates, particularly the meiofauna, are small and elongate, some (e.g. peracarid Crustacea and tubificid worms) are large and robust enough to actively burrow in fine sediments (bioturbation). This physical activity in the hyporheos has been extensively demonstrated in microcosm experiments with asellid isopods, chironomid midge larvae and tubificid worms (see Mermillod-Blondin et al., 2003; Mermillod-Blondin et al., 2004; Mermillod-Blondin et al., 2001). In these studies, the organisms modified the distribution of sediment particles and water flux and indirectly stimulated aerobic and anaerobic activity by interstitial microbes by modulating the availability of resource flows (Mermillod-Blondin et al., 2003; Mermillod-Blondin et al., 2004). The galleries of tubificid worms and their egestion of faecal pellets stimulated denitrification and organic matter mineralisation and increased the penetration of surface pellets into the sediment (Mermillod-Blondin et al., 2001). Additionally, structures created by the tubificids increased solute exchange between sections of the sediment.

In the marine environment nematodes also carry out bioturbation, although this has yet to be studied in freshwaters (Traunspurger, 2000). Some stoneflies, in particular *Nemoura cambrica*, are able to excavate themselves when buried by sediment (Wood et al., 2005b) and thus may play a similar role to that described above following sedimentation.

Interstitial amphipods and isopods (e.g. *Proasellus* and *Niphargus*) egest large faecal pellets, reducing the quantity of fine organic particles which may subsequently promote hydraulic conductivity in the hyporheic zone (Danielopol, 1989; Palmer et al., 1997).

3.3 Alteration of the availability of nutrients and organic matter breakdown

Hyporheic metabolism, which can be appreciable, is thought to cause a fairly rapid renewal of organic carbon in deeper sediments. There are two likely mechanisms:

1) **The episodic burial of particulate organic carbon (POC) following a disturbance** (see Metzler and Smock, 1990).
The carbon is made available to hyporheic invertebrates capable of comminuting such material into fragments (Smith and Lake, 1993; Tillman et al., 2003). Smith and Lake (1993) found accelerated breakdown of buried eucalypt leaf packs relative to surface leaves in an Australian upland stream and suggested that the hyporheos of Australian streams may contribute significantly to decomposition of buried particulate organic matter. In contrast, buried leaves in a sand-bottom stream in Virginia did not break down quicker than surface leaves (Metzler and Smock, 1990; Stommer and Smock, 1989). Carbon liberated by leaf decomposition in the hyporheos may follow a number of paths: it may be scoured from the sediments during high flow; percolate into the stream via upwelling hyporheic flow paths (Marmonier et al., 1995); or fuel groundwater systems as a subsurface 'spiral' (Boulton, 2007).

2) **The transport of POC or dissolved organic carbon (DOC) into hyporheic sediments by streamwater or groundwater intrusions** (see Findlay et al., 1993).
In most cases interstitial flows are too slow to transport particulate matter more than a short distance into these sediments, thus DOC is probably the major source of carbon in the hyporheos. Few, if any, invertebrates can use DOC directly as a carbon source and thus the initial uptake of DOC is by microbes (Findlay, 1995). These heterotrophic

micro-organisms, including bacteria and fungi, play a fundamental role in the decomposition of particulate and dissolved organic matter in sediments because of their high metabolic rates and diverse array of carbon-degrading enzymes. They are likely to dominate many aspects of material and energy flow in hyporheic sediments (Findlay and Sobczak, 2000). It is also evident that hyporheic microbial processes are extremely important to the functioning of stream ecosystems (Chauvet et al., 1993; Findlay and Sobczak, 2000; Fischer et al., 1996).

In the hyporheic zone few micro-organisms are found suspended in pore water; most are associated with the sediment surfaces where they form biofilms (Griebler et al., 2002). These groundwater biofilms probably function in a similar manner to that of the epilithon in rivers (Ellis et al., 1998). Biofilms can be highly organised with distinct vertical layering of diverse microbial communities (Stevenson, 1997). Bacteria embedded in the biofilm may be temporarily buffered from fluctuating resource supply (Freeman and Lock, 1995). Relatively large pores may penetrate all sections of biofilms and influence the movement of dissolved constituents in and out of biofilms (Lock, 1993).

The complex biofilm community is strongly influenced by the physical characteristics of the environment. The available sediment surface area governs biofilm formation whilst hydraulic conductivity and interstitial water velocity determine the resupply and removal of dissolved gases, solutes, energy sources and essential inorganic nutrients (Findlay and Sobczak, 2000). As well as influencing hydraulic conductivity and interstitial water velocity, the grain size and porosity at a site will also affect whether meiofauna and macrofauna, which may feed on accumulated biofilms, have access (Findlay and Sobczak, 2000). Chironomids and copepods have been shown to assimilate bacterial carbon preferentially, compared to detrital particulate organic matter (Hall, 1995). Grazing by hyporheic invertebrates promotes the activity of microbial biofilms (Danielopol, 1989; Palmer et al., 1997; Traunspurger et al., 1997) by removing dead cells from the microbial community (for example, Montana, 1995). Nematodes may be particularly important in this respect due to their high densities in sediments (Traunspurger, 2000). Traunspurger et al. (1997) have shown that nematodes feeding on bacteria increased bacterial activity.

Hyporheic invertebrates may also increase microbial growth rates by increasing the supply of limiting resources such as essential nutrients (Alkemade et al., 1992). They may also alter the composition of the microbial community, consequently affecting rates of microbially mediated nutrient transformation. For example grazing by harpacticoid copepods reduced the number and size of attached bacteria in a small stream and were estimated to be more efficient at assimilating microbial production than macrofauna (Edler and Dodds, 1996; Perlmutter and Meyer, 1991).

Hyporheic invertebrates may also make detritus more accessible to bacteria by mechanically breaking it down into smaller pieces (Chauvet et al., 1993). Average levels of meiofaunal grazing on bioflms may exceed those of hyporheic macrofauna, given the higher densities and greater turnover of the former, although contributions vary widely across streams (Hakenkamp and Morin, 2000).

The hyporheic zone also plays an important role in the transformation and export of nitrogen (Brunke and Gonser, 1997).The high rates of metabolism in most hyporheic sediments often results in nutrient regeneration and the return of mineral nutrients to the open stream channel; water returning to the channel may have such elevated levels of N and P that localised algal periphyton blooms occur (Claret and Fontvielle, 1997; Valett et al., 1994). In contrast, hyporheic retention and subsequent remineralisation may also delay the loss of nutrients from a stream reach and this may, potentially, increase overall primary productivity and allow a more rapid recovery from disturbance (Findlay, 1995).

Many hyporheic systems are periodically anoxic and studies have shown that denitrification occurring in hyporheic sediments can be a major component of stream nitrogen budgets despite the apparent oxic nature of the system. Hyporheic sediments can thus remove nutrients, thereby ameliorating the downstream effects of high N loads to stream systems (Triska et al., 1993).

Several studies of burrowing bivalves have suggested that their excretory products may be used as a nutrient source by benthic algae. Vaughn and Hakenkamp (2001) and Marshall and Hall (2004) suggest that interstitial invertebrates can substantially alter biogeochemical processes in hyporheic zones.

3.4 Transfer of material into, through or out of the hyporheic zone

Hyporheic invertebrates can undergo substantial movements vertically, laterally and downstream and so may transfer matter and energy in the hyporheic zone (for example, Ward et al., 1998). One of the most notable demonstrations of this is the amphibite stoneflies of some alluvial rivers that travel several kilometres from the stream channel. The entire nymphal stage of this group occurs in the hyporheic zone; mature nymphs only return to the river channel to emerge, mate and oviposit (Stanford and Ward, 1988). Emerging amphibites export energy and nutrients from the hyporheic zone and provide substantial food resources for epigean predators because productivity in the hyporheos can be high and stoneflies may dominate the drift during emergence (Perry and Perry, 1986).

Interstitial invertebrates also may be washed out of the hyporheic zone during floods (Marmonier and Creuzé des Châtelliers, 1991; Palmer, 1990) and they may also be displaced to the surface in upwelling zones (Brunke and Gonser, 1997); in both cases they may become prey for epigean predators.

The hyporheos may act as a refuge for epigean fauna during times of disturbance such as high flows (flooding) or low flows (drought) (e.g.Dole-Olivier et al., 1997a). Some animals actively burrow down into the sediments and/or a proportion of the population may already be located deeper within the sediment. By surviving surface high flows they can then recolonise the surface sediments after the disturbance has passed. Thus the hyporheos may enhance the resilience of the epigean community to disturbance and influence river recovery following perturbations. This emphasises the fact that the hyporheos is a dynamic area and that it is important to consider the whole river ecosystem and not just selected sub-units.

4 Subterranean aquatic assemblages in England & Wales

4.1 Introduction

Scientific publications concerning hypogean and groundwater ecology in England and Wales are sparse compared to those concerning hypogean ecology in continental Europe, North America and Australia/New Zealand. However, the Biological Records Centre holds a database on the distribution of subterranean aquatic Crustacea within the British Isles (see Appendix 1), much of this data being obtained from the Cave Research Group of Great Britain. One publication has resulted from this data (Proudlove et al., 2003). Additional records come from the Environment Agency database BIOSYS and scientific publications.

4.2 Stygobites and stygophiles of England and Wales

4.2.1 Stygobites

There are few stygobites in England and Wales[2] in comparison to continental Europe. These are listed below (see also Table 4.1).

Crustacea
- Amphipoda
  - Niphargidae
    - *Niphargus aquilex* Schiodte, 1855
    - *Niphargus fontanus* Bate, 1859
    - *Niphargus glenniei* Spooner 1952
    - *Niphargus kochianus kochianus* Bate, 1859
  - Crangonyctidae
    - *Crangonyx subterraneus* Bate, 1859
- Isopoda
  - Asellidae
    - *Proasellus cavaticus* (Leydig, 1871)
- Syncarida
  - Bathynellidae
    - *Antrobathynella stammeri* (Jakobi, 1954)
- Copepoda
  - Cyclopoida
    - *Acanthocyclops sensitivus* (Graeter & Chappuis, 1914)
- Ostracoda
    - *Pseudocandona eremita* (Vejdovsky, 1882

[2] Two further species, *Niphargus wexfordensis* and *Niphargus kochianus irlandicus* are endemic to Ireland. *N. wexfordensis* is known from a single location, a well at Kerloge, county Wexford. *N.k. irlandicus* occurs in caves, the interstitial and Lough Mask. It is found in areas fully glaciated in Devensian times and may be a preglacial relict species, surviving the glaciation in sub-glacial refugia (Costello 1993).

Arachnida
Acari
Hydrachnellae
Panisellus thienemanni (Viets)
Thyasella mandibularis (Lundblad)
Wandesia racovitzai Gledhill
Torrenticola andrei (E. Angelier)
Monatractides madritensis (Viets)
Atractides denticulatus (Walter)
Atractides latipalpis (Motas & Tanasachi)
Atractides acutirostris (Motas & Angelier)
Feltria cornuta Walter
Feltria denticulata E. Angelier
Feltria subterranea Viets
Feltria (Azugofeltria) motasi (Schwoerbel)
Barbaxonella angulata (Viets)
Lethaxona cavifrons Szalay
Kongsbergia clypeata Szalay
Stygomomonia latipes Szalay
Neoacarus hibernicus Halbert
Hungarohydracarus subterraneus Szalay

Niphargus aquilex
The majority of records are to the south of the Devensian glacial limit although there are a few records to the north of this limit ((Proudlove et al., 2003). This species is the most superficial of the *Niphargus* species, for example it has been frequently recorded in Environment Agency kick samples (Appendix 1). It is also found in interstitial samples and in caves and is a ubiquitous stygobite (see section 3.3). Outside Britain this species is known from central and southern Europe (Botosaneanu, 1986b).

Niphargus fontanus
This species is found in caves, interstitial samples and wells in the UK, and does not extend as far north as *N. aquilex* (Gledhill et al., 1993). Proudlove et al. (2003) notes that specimens from interstitial sites are routinely smaller than those from caves. It is possible that this species comprises a suite of cryptic forms (see Section 2). This species is also found in France, Belgium, Germany and Austria (Botosaneanu, 1986b).

Niphargus glenniei
This species is endemic to England and is currently listed as a priority species in the UK BAP and will require monitoring at new and known sites. This species has been collected from 24 sites comprising caves, mines and the interstitial in Devon and Cornwall (Knight, 2001). *N. glenniei* is much smaller than the other British *Niphargus,* with the exception of *N. wexfordensis,* attaining sexual maturity at around 3mm whereas the other species are sexually mature at a minimum size of 4-6mm (Spooner, 1952). It is thought to be an interstitial form (phreatobite) that gets washed into pools in caves and mines after heavy rainfall (Proudlove et al., 2003).

Niphargus kochianus kochianus
This subspecies occurs in wells, springs and interstitial groundwater and in three caves in England and Wales. It is predominantly a phreatobite and is closely associated with outcrops of the Cretaceous Chalk in southern England (Proudlove et al., 2003), an association previously reported for this subspecies in France (Vonk, 1988). It has also been recorded occasionally from Carboniferous, Jurassic and Devonian limestones in England (Proudlove et al., 2003). A large

scale study of the distribution of this species, together with environmental data, has been carried out in the Lee, Colne and Rickmansworth valleys by Arietti and Edwards (in preparation).

Crangonyx subterraneus
This species is found in two caves and in interstitial sites in southern England and Wales and has been recorded in one site (Ceridigion, Wales) which is approximately 100km north of the Devensian limit in South Wales and 100km west of the limit in the border area of England and Wales (Proudlove et al., 2003). This species is also found in western and central Europe (Botosaneanu, 1986b).

Proasellus cavaticus
A species found in wells, caves, mines and interstitial sites in karstic and non-karstic rocks and alluvial sediments. There are two size morphs of this species, one of approximately 4mm in length occurring in Mendip vadose passages and the other of 8mm occurring in different locations (Proudlove et al., 2003). It is possible that this species may also harbour one or more cryptic species. *P. cavaticus* is also found in The Netherlands, Germany, Belgium, Switzerland, Austria and France.

Antrobathynella stammeri
These small (~1mm) organisms have been found at 15 interstitial sites in Britain (Proudlove et al., 2003). Many records of this species are from north of the Devensian limit e.g. from Scotland and from Yorkshire (Gledhill and Driver, 1964; Proudlove et al., 2003; Serban and Gledhill, 1965). *A. stammeri* is also known from Germany, Austria, Italy, Romania and the Czech Republic (Botosaneanu, 1986b).

Acanthocyclops sensitivus
Records for this species in England and Wales are only from Ringwood in Hampshire (Harding and Smith, 1974). The species has also been recorded from Switzerland, France, Austria and Germany.

Hydrachnellae (water mites)
None of these species is endemic to the British Isles. Nearly all of these water mites were collected from the hyporheic zone of rivers and streams in highland areas of Britain using the Karaman- Chappuis method (Gledhill, 1974). Most water mite larvae are phoretic and parasitic on the flying adults of aquatic insects and consequently are more widely dispersed than other stygobites.

4.2.2 Stygophiles

The stygophile species occurring in England and Wales are too numerous to name individually. However, some species, although also found in surface waters, have a particular association with the interstitial and hypogean groundwater habitats and these are listed here.

Platyhelminthes
    Planariidae
        Crenobia alpine (Dana)
        Phagocitta vitta (Dugés)

Oligochaeta

Several species are probably stygophilic (Piearce 1975, Gidman 1975, Piearce and Wells 1977)

Crustacea

Copepoda

Cyclopoida

Graeteriella unisetigera (Graeter, 1908)
Speocyclops demetiensis (Scourfield, 1932)
Eucyclops serrulatus (Fischer, 1851)
Paracyclops fimbriatus (Fischer, 1853)
Megacyclops viridis (Jurine, 1820)
Acanthocyclops venustus (Norman and Scott, 1906)
Diacyclops bicuspidatus (Claus, 1857)
Diacyclops hypnicola (Gurney, 1927)

Ostracoda

Cavernocycpris subterranean (Wolf 1920)
Eucypris pigra (Fischer, 1851)
Fabaeformiscandona breuili (Paris 1920)
Nannocandona faba Ekman, 1914
Potamocypris pallida Alm 1914
Potamocypris zschokkei (Kaufmann, 1900)
Psychodromus olivaceus (Brady & Norman, 1889)
Psychodromus robertsoni (Brady & Norman 1889)

Cladocera

Alona quadrangularis

Amphipoda

Gammarus pulex

Insecta

Coleoptera

Dytiscidae

Hydroporus obsoletus Aubé 1838
Hydroporus ferrugineus Stephens 1829
Agabus biguttatus (Olivier, 1795)
Agabus guttatus (Paykull 1798)

Stygophile species comprise both macroinvertebrates (particularly the smaller instars) and meiofauna such as copepods, ostracods and cladocerans (see Appendix 1).

Hydroporus ferugineus

This beetle appears to be strongly stygophilic although the adult is widely distributed in England and Wales (Alarie et al., 2001; Wood and Sadler, 1997). The larvae have only been found in the Peak-Speedwell cavern system and are adapted to a subterranean existence in that they lack pigment and have small eyes (Alarie et al., 2001). The adult is thought to be flightless due to the poor development of its wing muscles (Jackson, 1958).

Gammarus pulex
This species is a very common stygophile in England and Wales (Piearce, 1975; Piearce and Cox, 1977; Proudlove et al., 2003). Eyeless specimens of this species have been recorded from springs rising from caves in Lathkill Dale (P.J. Wood *pers. Comm.*).

Crenobia alpina and *Phagocita vitta*
These cold stenothermic flatworms are a rather special case as their range is limited by temperature. *Crenobia alpina* can only reproduce at temperatures below 12°C and is thought to be a glacial relict (Wright, 1974). They are found in cool springs but also occur in other suitable habitats. BIOSYS records indicate that both species occur widely in England and Wales.

Taxa occurring in the hyporheos and groundwaters are a subset of those occurring in the epibenthos. Although most stygobites are found to the south of the glacial limit (see above and section 5.2.1), stygophiles are found in the hyporheos of rivers both south and north of the glacial limit and so the hyporheic processes that they mediate (see Chapter 3) occur in all rivers. Few data exist on the composition and distribution of stygophile hyporheic assemblages in the UK (see section 5) and there are significant knowledge gaps regarding the role that they play in hyporheic processes such as biogeochemical transformations.

Table 4.1 Summary of stygobites species occurring in England and Wales

Scientific name	Common name	Description	Typical habitat
Niphargus aquilex *N. fontanus* *N. glenniei* *N. kochianus kochianus*	Well shrimps	amphipods	Caves, wells, mines and the interstices of alluvial gravels. Mostly to the south of the glacial limit in Chalk and limestone strata.
Crangonyx subterraneus	Well shrimp	amphipod	Interstitial sites mainly to the south of the glacial limit.
Proasellus cavaticus	Water hog louse	Isopod. May be more than one species.	Caves and interstitial sites mainly to the south of the glacial limit.
Antrobathynella stammeri	None	Syncarid. ~ 1mm long.	Interstitial and phreatic. Many records to the north of the glacial limit.
Acanthocyclops sensitivus	Water flea	Copepod	Very limited information but has been found only once in a well at Ringwood.
Panisellus thienemanni *Thyasella mandibularis* *Wandesia racovitzai* *Torrenticola andrei* *Monatractides madritensis* *Atractides denticulatus* *Atractides latipalpis* *Atractides acutirostris* *Feltria cornuta* *Feltria denticulata* *Feltria subterranea* *Feltria (Azugofeltria) motasi* *Barbaxonella angulata* *Lethaxona cavifrons* *Kongsbergia clypeata* *Stygomomonia latipes* *Neoacarus hibernicus* *Hungarohydracarus subterraneus*	Water mites	An extensive suite of species, often found to the north of the glacial limit.	All species found in interstitial water in alluvial gravels.

4.3 Research on subterranean aquatic ecology in the UK

Few hypogean aquatic communities have been studied in any detail in the UK although there are many records for the occurrence of individual species (see Appendix 1).[3] Some very recent work, as yet unpublished, has been undertaken on the River Little Stour, Kent (Paul Wood, pers comm.) and in the catchment of the River Don, South Yorkshire (Anna Ritchie, pers comm.).

UK hypogean communities can be divided into those containing obligate stygobites and those comprising a subset of the epigean community with no stygobites present. Many (but not all) of the former are in caves or in alluvial deposits to the south of the maximum extent of the Pleistocene glaciation (see Appendix 1).

4.3.1 Cave habitats

The Ogof Ffynnon Dhu cave system (Tawe Valley, Powys, South Wales), which lies to the south of the glacial limit, is one of the largest in Great Britain and is one of the best studied; its invertebrate community was detailed by Jefferson et al. (2004) (see also Appendix 1). There are four stygobites – *Proasellus cavaticus, Crangonyx subterraneus, Niphargus fontanus* and *Cavernocycpris subterranea,* the latter being possibly only a local stygobite. The fauna of Dan Yr Ogof, in the Swansea valley opposite Ogof Ffynnon Ddu, was studied by Edington (1977). Species collected included the stygobites *Proasellus cavaticus*, *Niphargus fontanus* and *Niphargus aquilex*, and the stygophile *Gammarus pulex*. Two species of flatworm, *Dendrocoelum lacteum* and *Phagocata vitta*, were recorded. There were three species of copepod, *Megacyclops viridis*, *Acanthocyclops vernalis* and *A. viridis*. Edington made an early attempt to construct a food web for the cave. The basal resources were detritus and chemoorganotrophic bacteria. These were grazed by *Proasellus cavaticus* which in turn was predated by *Niphargus fontanus*, *Gammarus pulex* and the flatwoms. The flatworms and *G. pulex* probably also preyed on the *Niphargus* and *Gammarus*.

In contrast, the invertebrate community of the Peak-Speedwell cave system in the English Peak District, Derbyshire (to the north of the glacial limit) contained no stygobites (Gunn et al., 2000). A total of 28 invertebrate taxa were recorded from this system; most were also recorded from adjacent epigean habitats with the notable exception of the larvae of the aquatic beetle *Hydroporus ferrugineus* (this species appears to be intimately associated with subterranean environments with a possible obligatory subterranean larval stage). Changes in the community were strongly associated with seasonal variations and natural hydrological variability (Gunn et al., 2000). In two rare studies on the effects of pollution on a subterranean ecosystem in England, Wood et al. (2002 and in press) found that the first episode of organic pollution significantly decreased invertebrate diversity and abundance, whereas the second episode actually resulted in an increase of organisms within the cave, associated with increased availability of trophic resources.

Chapman (1979) studied Otter Hole near Chepstow. He recorded 53 taxa including the stygobites *Proasellus cavaticus* and *Niphargus fontanus* and the common stygophile *Gammarus pulex.*

[3] These studies are detailed in the following publications: Baker, 2006; Davy-Bowker J, 2006; Gilvear et al., 2006; Gledhill, 1967a; Gledhill, 1967b; Gledhill, 1970; Gledhill, 1971a; Gledhill, 1971b; Gledhill, 1974; Gledhill, 1977; Gledhill, 1982; Gledhill, 1983; Gledhill, 1985; Gledhill and Ladle, 1969; Gunn et al., 2000; Hynes et al., 1976; Jefferson et al., 2004; Proudlove et al., 2003; Rundle, 1990; Stead et al., 2003; Stead et al., 2004; Stead et al., 2005a; Stead et al., 2005b; Williams, 1991; Williams, 2003; Williams and Hynes, 1974; Wood et al., 2002; Wood et al., 2005a.

Piearce (1975), (see also Gidman, 1975; Piearce and Cox, 1977; Piearce and Wells, 1977) studied the fauna of Ingleborough Cave, Yorkshire. No stygobites were recorded but there was a strong suggestion that an isolated population of *Gammarus pulex* was present within the system. These animals were unpigmented and differed in their reaction to light from epigean animals from a stream nearby.

4.3.2 Shallow groundwater habitats

The Waterstone Cress beds, located on alluvial deposits above the Chalk on the River Piddle, Dorset, have a well described assemblage of subterranean amphipods (Gledhill, 1977; see also Appendix 1 and below). Four stygobitic amphipods were found here: *Niphargus aquilex, N. fontanus, N.k. kochianus* and *Crangonyx subterraneus. N. aquilex* was always the most abundant species.

Population fluctuations of these species were followed over a five year period and were found to be closely related to the variations in water levels within the site. *C. subterraneus, N. fontanus and N.k.kochianus* usually thought to inhabit deeper subterranean water; their numbers generally rose in association with rising water levels within the site as water was drawn up from deeper levels. The abundance of *N. aquilex,* usually an inhabitant of the more superficial water-filled interstices of the gravel bed, generally increased during periods of decreasing water levels (Gledhill, 1977).

Gledhill & Ladle (1969) undertook a detailed study of the life history of *Niphargus aquilex* in the gravel beds of the River Oberwater in the New Forest. This particular population had at least two generations per year and the mean number of eggs carried per female was 2.87 (larger females carried more eggs). Gledhill has published prolifically on the hyporheic water mites found in England and Wales (Gledhill, 1967a; Gledhill, 1970; Gledhill, 1971a; Gledhill, 1971b; Gledhill, 1974; Gledhill, 1982; Gledhill, 1983; Gledhill, 1985) and has identified a suite of species found in the interstitial habitat of alluvial gravels.

Hynes et al. (1976) and Williams (1991; 2003) studied the hyporheos of streams in mid- and North Wales (Afon Hirnant in mid-Wales and Yr Ogof and Afon Aber in North Wales). In each case stygobites were absent and the fauna collected were epigean in nature. Rundle (1990) working in the Ashdown Forest of southern England examined the interstitial communities of 10 streams with an underlying sandstone geology. He found that stygobites were absent and that the hyporheic and epibenthic communities could not be differentiated clearly. Two cyclopoid copepods, *Diacyclops languidus* and *Diacyclops languidoides*, were restricted to the hyporheos at circumneutral sites. A further in-depth study of the metazoan community of an Ashdown Forest stream with a restricted hyporheos (15 cm) was undertaken by Stead and colleagues (Stead, 2002; Stead et al., 2003; Stead et al., 2004; Stead et al., 2005a; Stead et al., 2005b). Most taxa were found throughout the depth profile of this stream. However, the assemblage of relatively few large individuals near the surface was replaced by a suite of numerous small-bodied organisms in the deeper sediments. Invertebrate density and biomass in the subsurface sediments always exceeded that of the surface sediments (Stead et al., 2004).

Baker (2006) examined the hyporheos of the Jubilee River (a new flood alleviation channel of the River Thames in the Windsor/ Maidenhead area) and the adjacent River Thames, using standpipe traps, in order to document colonisation and succession in this new channel. He recorded 22 invertebrate taxa in the River Jubilee and 23 taxa in the Thames over a two-year period including one stygobite species (*Niphargus aquilex*). Successional patterns were not evident in the data and there were minimal seasonal changes in hyporheic species diversity and abundance. Baker (2006) concluded that the hyporheos could be a useful refuge during times of epibenthic disturbance.

Davy-Bowker et al. (2006) studied invertebrate assemblages in the River Frome, Dorset in order to test the hypothesis that benthic and hyporheic macroinvertebrate assemblages would differ between riffle heads (downwelling zones) and riffle tails (upwelling zones) and that benthic and hyporheic numbers and family richness would be greater in downwelling zones compared to upwelling zones. In the hyporheic zone there was no significant difference between total numbers of invertebrates in the riffle heads and tails although species richness was higher at the downwelling zone at the shallower depth. Overall there was a gradual breakdown in the distinction between riffle head and tail communities with increasing hyporheic depth (Davy-Bowker et al., 2006). These findings differ from previous studies which have found that taxonomic diversity/ richness was higher in upwelling areas (Malard et al., 2003; Olsen and Townsend, 2003). Pepin and Hauer (2002) suggested two mechanisms that might account for these differences in composition: nutrient rich upwelling promotes periphyton production and so herbivore abundance; and/or upwelling water favours taxa with strong habitat affinities.

Gilvear et al. (2006) undertook a preliminary study of the hyporheos in four Scottish rivers, the Feshie, Spey, Tummel and Dee. In total 50 meiofaunal taxa were recorded in all hyporheic and surface samples. Fifteen meiofauna taxa were found only in the hyporheos, emphasising the potential importance of this zone in river biodiversity. The authors suggest that there may be a distinctive community beneath the bed of Scottish gravel bed rivers and one that is controlled by differing environmental controls to the benthic community (Gilvear et al., 2006). No stygobite species were recorded. None of the meiofaunal taxa were new to the UK but one (*Paracyclops poppei*) had not previously been described from Scotland. This probably reflects the fact that previous sampling of riverine meiofaunal taxa in Scotland has been extremely limited and restricted to surface dwelling taxa.

Springs are the outlet of subterranean waters and are areas where groundwaters and surface waters mix. They contain characteristic assemplages including stygobites and stygophiles washed out of the groundwaters (for review see Botosaneanu 1998). There are few studies of spring systems in England and Wales. Smith and Wood (2002) and Smith et al. (2003), working in the Peak District, found that springs supported distinct communities with some taxa recorded exclusively at the source or within the spring brook (for example, *Agabus guttatus* and *Micropterna lateralis*).

4.3.3 Deep groundwater (phreatic) habitats

Very little work has been undertaken in deep phreatic groundwater habitats, possibly because sampling is difficult. Many of the details of this habitat remain unknown; further studies are certainly needed, given that some of these aquifers are important for supplying water. Arietti and Edwards (unpublished) sampled 60 boreholes within the area of the Three Valleys Water Company. Common species were *Niphargus fontanus* (13 sites) and *N, kochianus* (40 sites), *Crangonyx subterraneus* was found at 12 sites. Copepoda were also common.

5 Distribution of subterranean aquatic fauna in England and Wales

5.1 Introduction

Groundwater systems, including karstic, porous-medium and riverine alluvial aquifers, are dynamic ecosystems that respond to a range of processes similar to those experienced by surface ecosystems (Gibert et al., 1994). The complex processes that determine the structure and function of groundwater ecosystems occur at the microscale and macroscale over a range of time periods. This nested hierarchy of different spatial and temporal scales (Gibert et al., 1994) ranges from the microhabitat (1 - 10 years; mm – metres) through to regional or continental drainage basins (greater than 100,000 years; greater than 10,000km).

Each level in this hierarchy integrates all the patterns and processes that occur at lower levels; each is linked to the next larger scale. The regional/continental domain ranges from regional to global and is measured in geological time. Thus geology and climate (including glaciation) have exerted control on the nature and distribution of aquifers which in turn have influenced the biotic colonisation of the groundwaters.

Processes at the intermediate scale in this hierarchy encompass the flow of material and energy and can be affected by the impact of humans, for example, the degradation of groundwater quality (eutrophication, clogging of interstices, altered productivity and loss of ecosystem resilience) that may only be detected decades later. At this scale short-term succession of the biota occurs in response to disturbances and changes in environmental gradients. Thus the ecosystem at this scale is dynamic but is probably resilient and stable in the longer term unless damaged by human pollution.

Microhabitats are only the size of a pore, fissure or channel; significant events take place over the course of a year. The local constraints on biota include water velocity, grain size, temperature and available energy resources.

5.2 Regional / continental controls on groundwater and hyporheic assemblages

A database of UK and Ireland records of subterranean assemblages (groundwater and hyporheic) was constructed to examine regional or continental controls on groundwater and hyporheic assemblages. The database was used to identify areas where hypogean and groundwater fauna are most likely to be found (based on geological and geomorphological properties) and to determine any likely differences in the types of fauna found in different geological conditions (Appendix 1). Records were obtained primarily from the Biological Records Centre, the Environment Agency's BIOSYS[4], caving records held by Graham Proudlove of the Department of Zoology,Manchester Museum, and Lee Knight, the subterranean Crustacea recorder, together with published works and personal communications. There were a total of 529 records, of which 513 contained stygobites. Records for England and Wales were then entered into a GIS to examine the relationship of subterranean and hyporheic assemblages with outcrops

[4] Note that there is no requirement to record taxa such as *Niphargus* in the BMWP score, however we recommend that, where possible, Ecological Appraisal Teams within the Environment Agency should record all hypogean non-scoring families/ species.

of selected bedrock geology (principally those associated with the major aquifers), superficial deposits, the glacial legacy and the degree of fissuring in the bedrock.

A review of international literature identified records of subterranean assemblages (groundwater and hyporheic) on a global scale and related the geologies (i.e. records from areas with close geological proxies in the UK)

5.2.1 Glacial legacy

The great majority of current UK records lie to the south of, or close to, the maximum limit of the Devensian glaciation, which reached its maximum extent between 25,000 and 15,000 years ago (Figure 5.1). This finding is consistent with the published literature (e.g. Proudlove et al., 2003; Strayer, 1994) which suggests that hypogean assemblages would be extirpated during glaciations.

Caution, however, must be exercised in this interpretation. It is possible that stygobites are widespread to the north of the glacial limit but have not yet been detected due to a limited sampling effort. This possibility should be addressed in future research efforts.

Certainly Figure 5.1 indicates that there are a few records to the north of the Devensian glacial limit in England and Wales – a finding that is in agreement with Proudlove et al. (2003). For example, there are several records of *Antrobathynella stammeri* in the Lake District and in mid-west Yorkshire (Great Douk and White Scar caves) and this species has also been recorded in a tributary of the River Endrick in Scotland (Appendix 1). Similarly *Niphargus fontanus* and *Proasellus cavaticus* occur in the North Crop limestone of South Wales which was glaciated in the Devensian (Figure 5.1).

There are two possible explanations for the origins of these populations. First, they may be descended from animals that arrived here from unglaciated areas following the last glaciation; second, they may have survived in refugia either in unfrozen groundwater within the tundra (tundral refugia) or in groundwaters below the ice sheet (sub-glacial refugia) (Proudlove et al., 2003). There is a considerable body of evidence suggesting that some species have indeed survived past glaciations in sub-glacial refugia. One of the best documented examples is Castleguard Cave, Canada, which is approximately 500km north of the last glacial limit and has been ice free for at least 700,000 years. Several stygobitic Crustacea are found in this cave (Bousfield and Holsinger, 1981; Holsinger, 1981; Holsinger et al., 1983). More recently two new stygobite amphipod species (*Crymostygius thingvallensis* and *Crangonyx islandicus*) have been described from Iceland. These are the northernmost records of stygobite species in Europe and have apparently survived Pliocene and Pleistocene glaciations in the groundwater of a porous lava, persisting in Iceland for several million years (Kristjansson and Svavarsson, 2004; Svavarsson and Kristjansson, 2006)

In England and Wales, *Antrobathynella stammeri* is probably one of the best candidates for survival in sub-glacial refugia (Proudlove et al., 2003) as syncarids have little capacity for dispersal (Guil and Camacho, 2000).

5.2.2 Influence of geology

The UK database (Appendix 1) indicates that the majority of groundwater records in England and Wales are found where the bedrock geology can be classed as calcareous, mainly chalk or limestone (Figure 5.2 and Figure 5.3), with most records from the Chalk Group (Figure 5.4). These results are consistent with our review of global stygobite records which show that the majority of groundwater stygobite records occurred on bedrock geology whose closest UK proxy was limestone. Groundwater records in England and Wales also closely tracked the location of strata with extensive fissuring (Figure 5.5).

Fissuring is strongly correlated with the occurrence of Chalk and limestone outcrops. Strata with extensive fissuring could perhaps provide the greatest availability of habitat for groundwater fauna. These geologies are also rich in calcium, which may be important as this element is an essential component of the carapaces of Crustacea (Rukke, 2002). However, *Niphargus glenniei* and *Antrobathynella stammeri* are also found in acidic geologies (Appendix 1).

The majority of records of groundwater fauna from caves and mines came from areas where the underlying geology was limestone, whereas most of the records of groundwater fauna from boreholes and wells were obtained from areas of Chalk geology (Figure 5.6 and Figure 5.4). This pattern reflects the different groundwater habitats available in these strata. The distribution of some stygobite taxa also follow this pattern of habitat availability, for example *Niphargus kochianus kochianus* is most often obtained from boreholes/wells in Chalk indicating a more phreatic groundwater existence (Appendix 1).

Perhaps unsurprisingly, records of streambed hyporheic fauna in the UK were closely associated with areas where the superficial geology was alluvium (Figure 5.7). Most records of streambed hyporheic fauna came from areas where the underlying geology was Chalk (Figure 5.8).

Despite the apparently clear findings of this analysis, the results should be interpreted with caution. There are relatively few records and these are dominated by records collected by members of the caving community. Thus results may be biased towards limestone because this is the geology where most caves are found. Bias towards the Chalk is more likely to be the result of historical sampling effort in relation to drinking water supplies. There is a clear need for research to collect records from non-Chalk/limestone geologies with significant secondary fissuring, such as the Permo-Triassic sandstones, Greensands and Namurian grits, and from alluvial terrace gravels associated with large rivers such as the Thames and Severn.

Figure 5.1 Stygobite records in England and Wales on a map indicating outcrop of the major aquifers. Southern limit of Devensian glaciation after Clark et al. (2004).

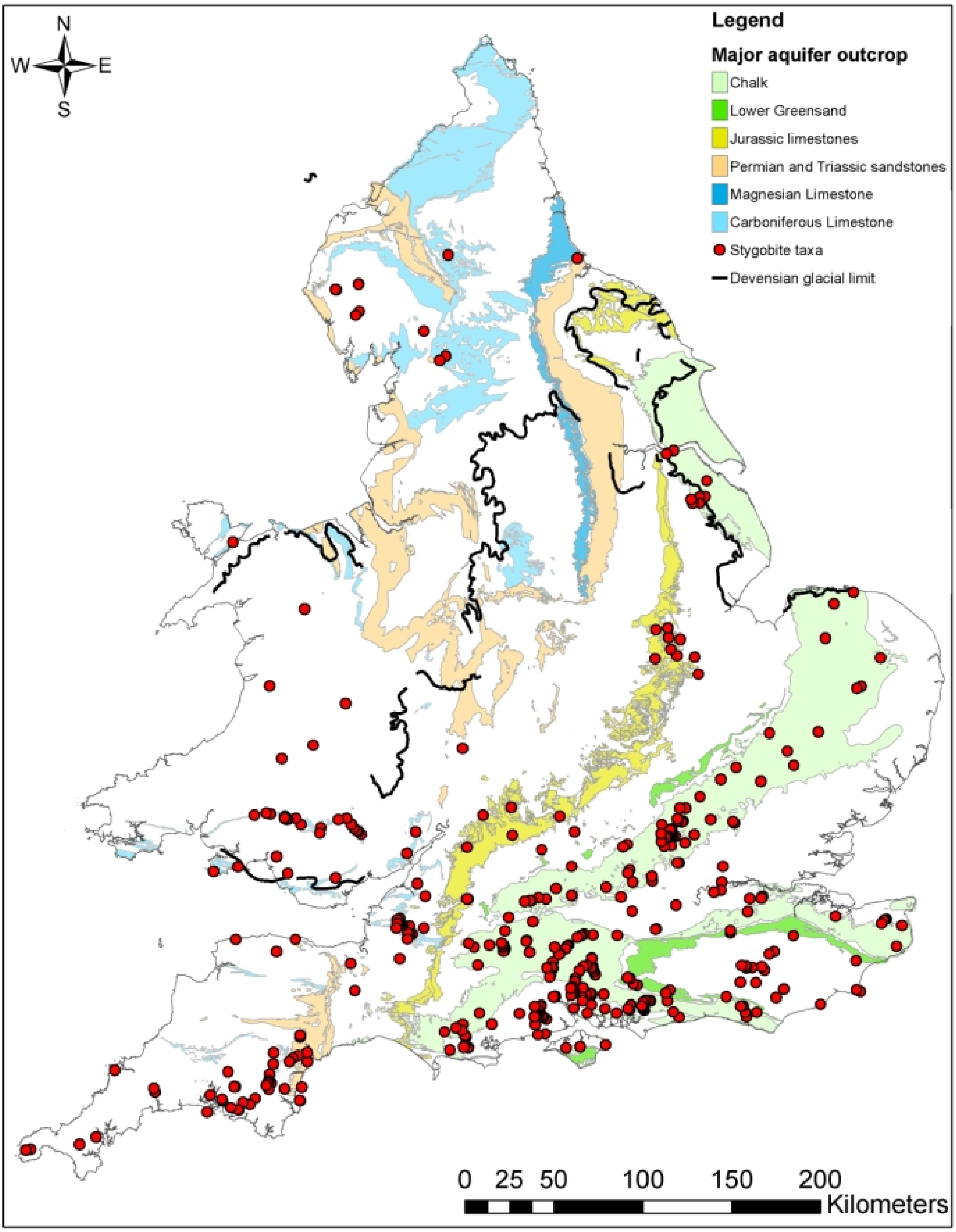


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Figure 5.2 Records of stygobites deferentiated between groundwater and hyporheic records in England and Wales overlain on a map showing major aquifer outcrops. Southern limit of Devensian glaciation after Clark et al. (2004).

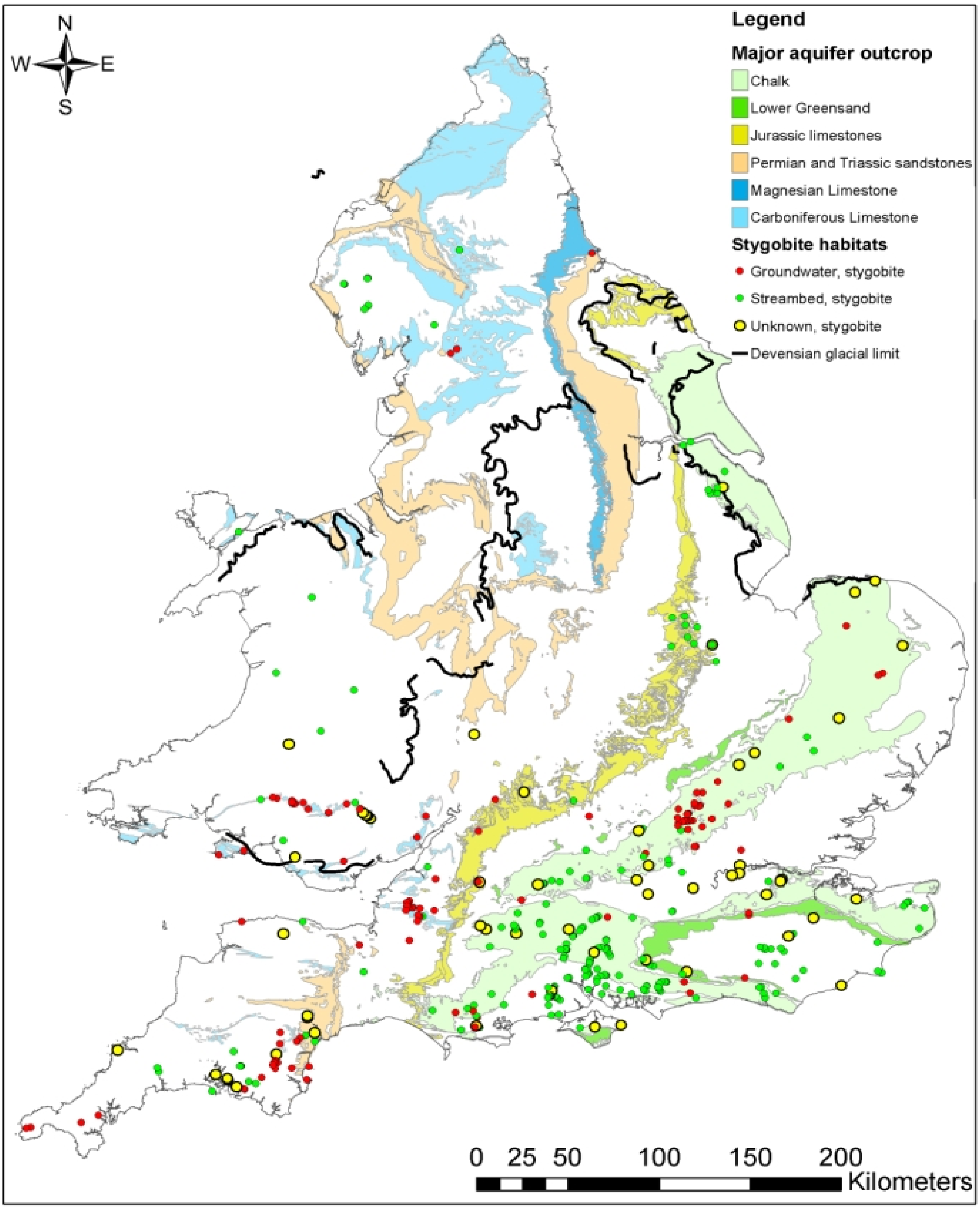


Figure 5.3 All stygobite records in England and Wales overlain on a map showing the location of calcareous strata. Southern limit of Devensian glaciation after Clark et al. (2004).

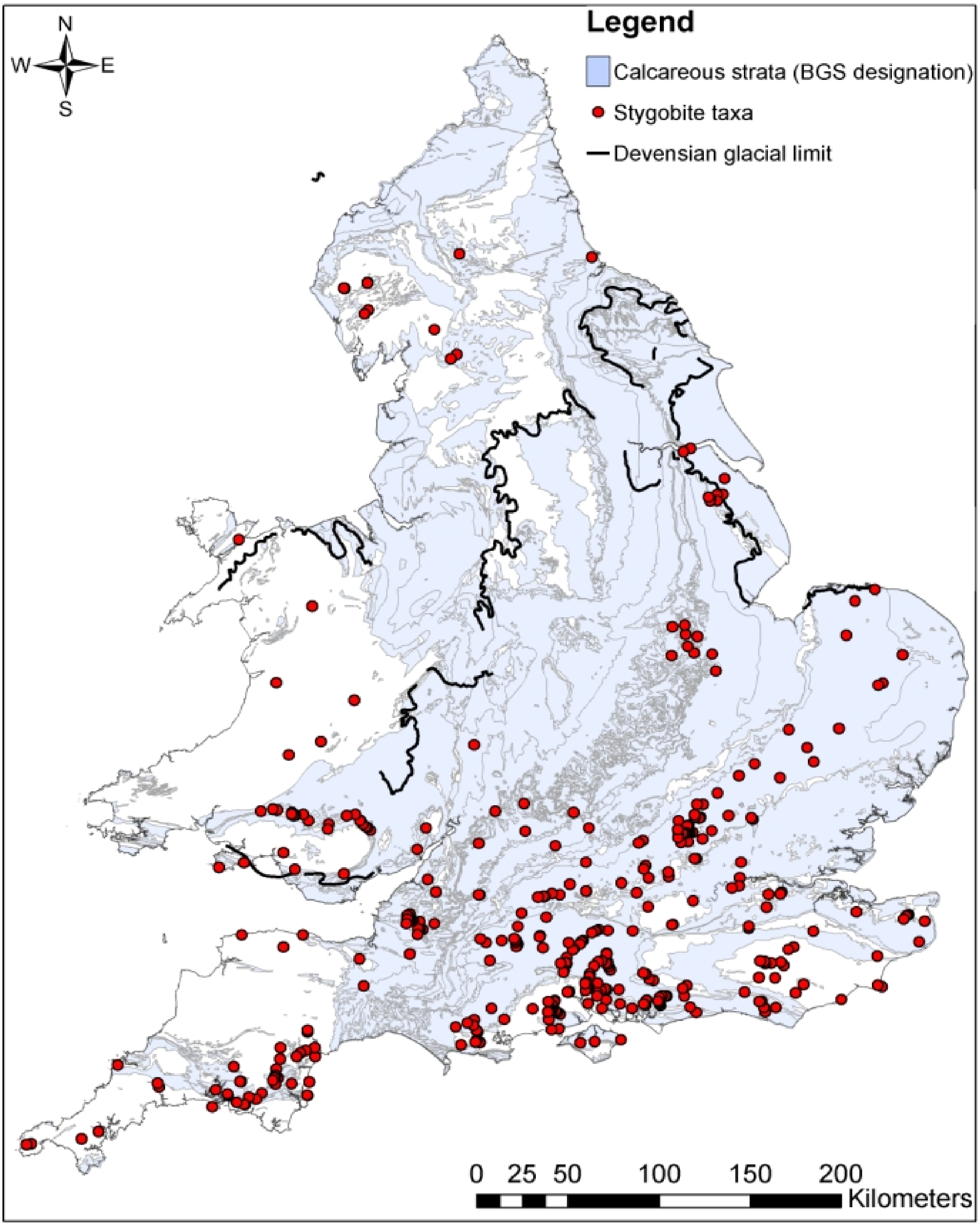


Figure 5.4 Numbers of sites where stygobites have been recorded from boreholes/wells and caves/mines, in geological strata in England and Wales.

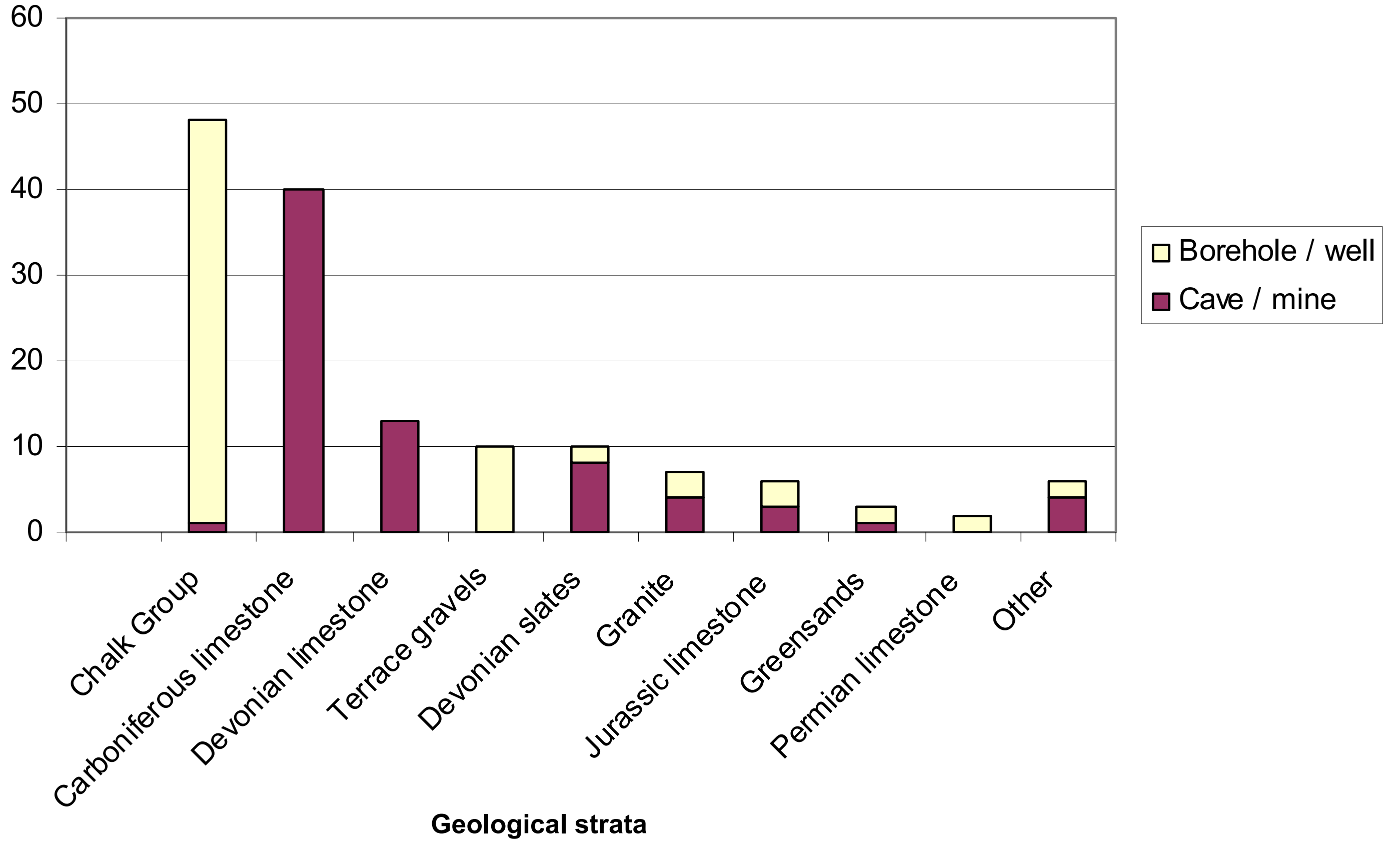


Figure 5.5 Records of groundwater stygobites in England and Wales overlain on a map showing the location of strata with extensive fissuring. Southern limit of Devensian glaciation after Clark et al. (2004).

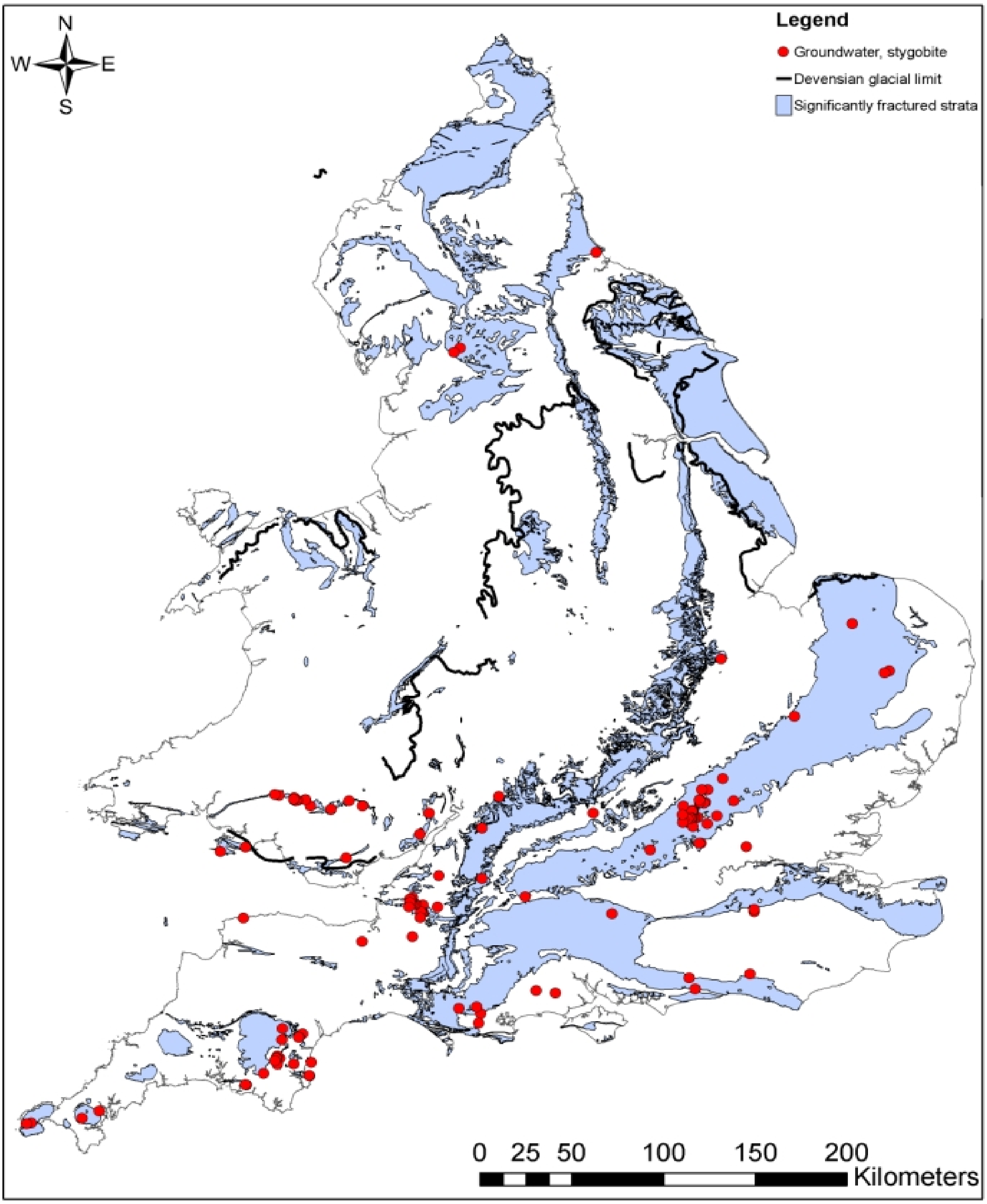


Figure 5.6 Records of groundwater samples collected from boreholes/wells and caves/mines overlain on a map showing the location of major aquifer outcrops.

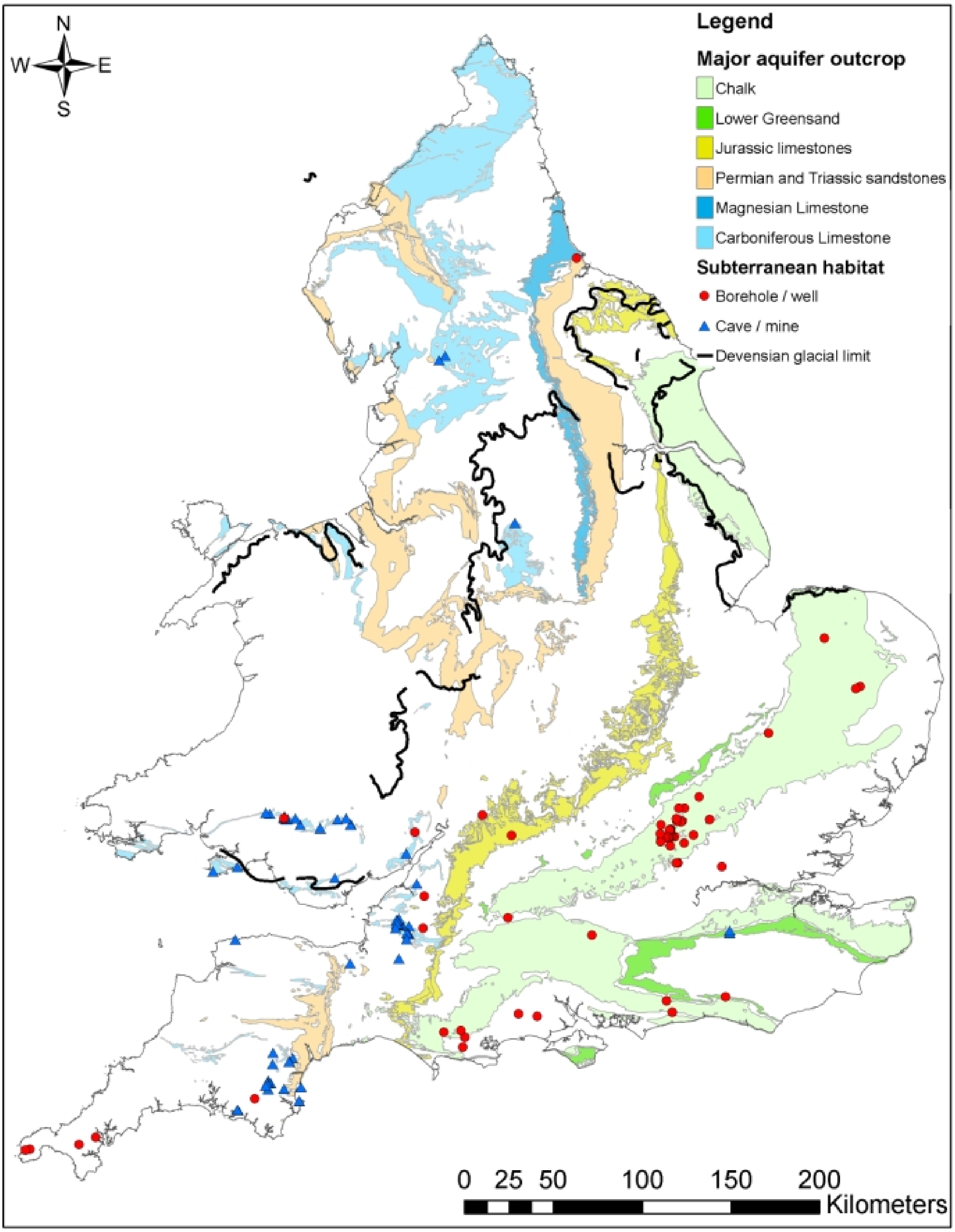


Figure 5.7 Records of hyporheic zone samples in England and Wales overlain on a map indicating superficial deposits. Southern limit of Devensian glaciation after Clark et al. (2004).

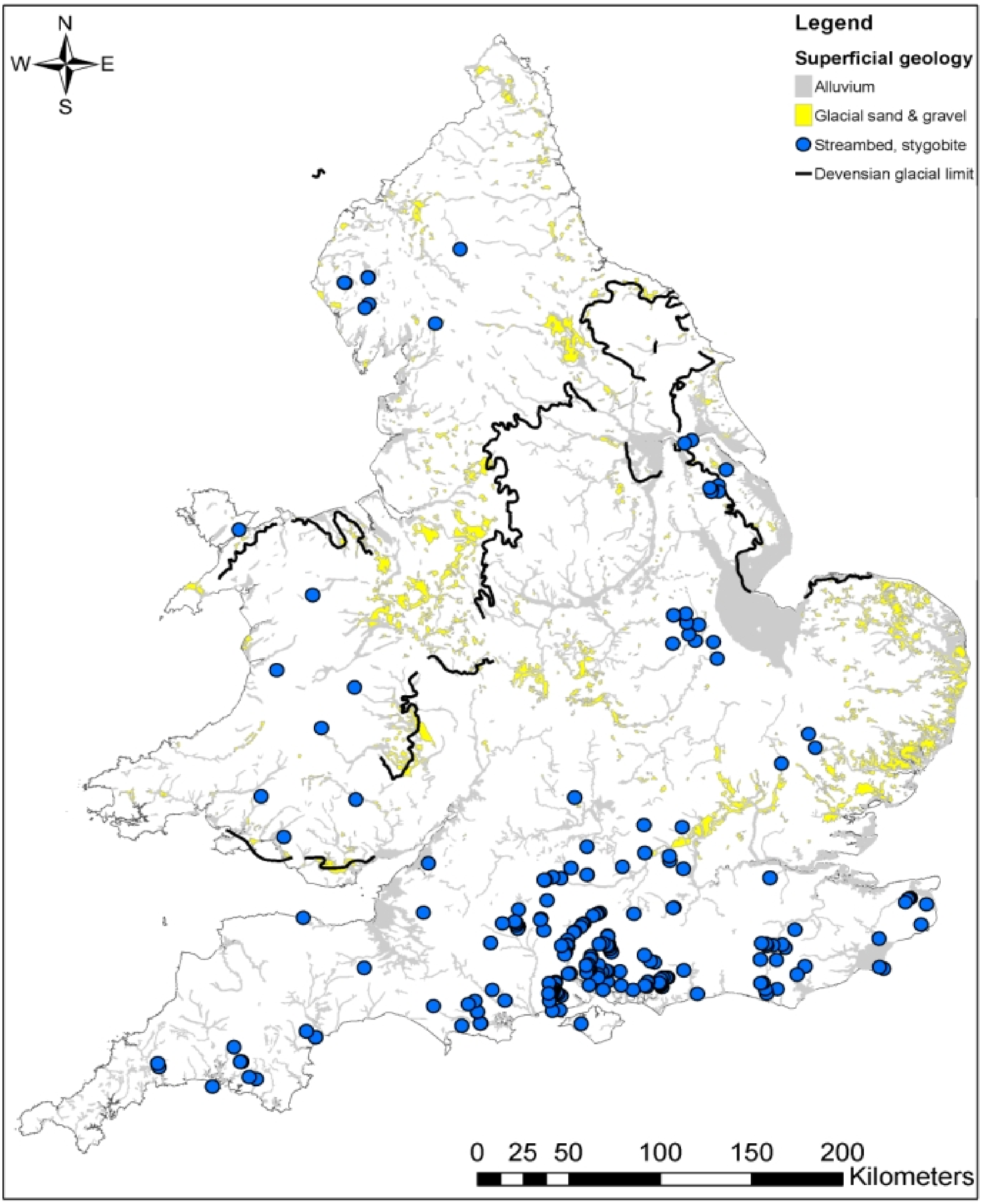
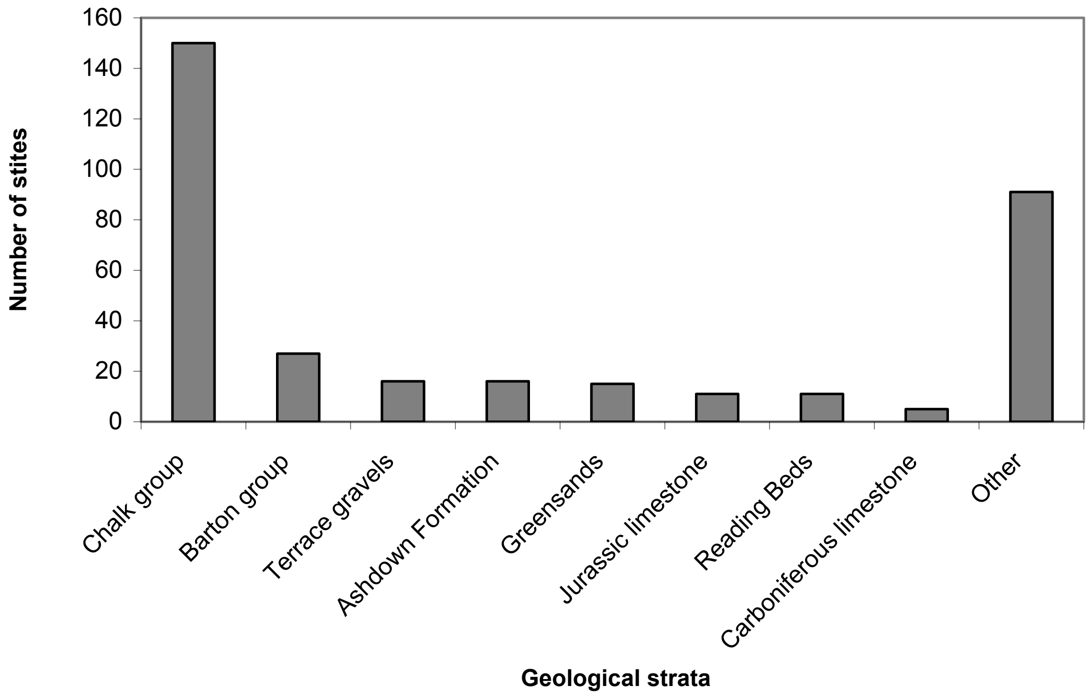


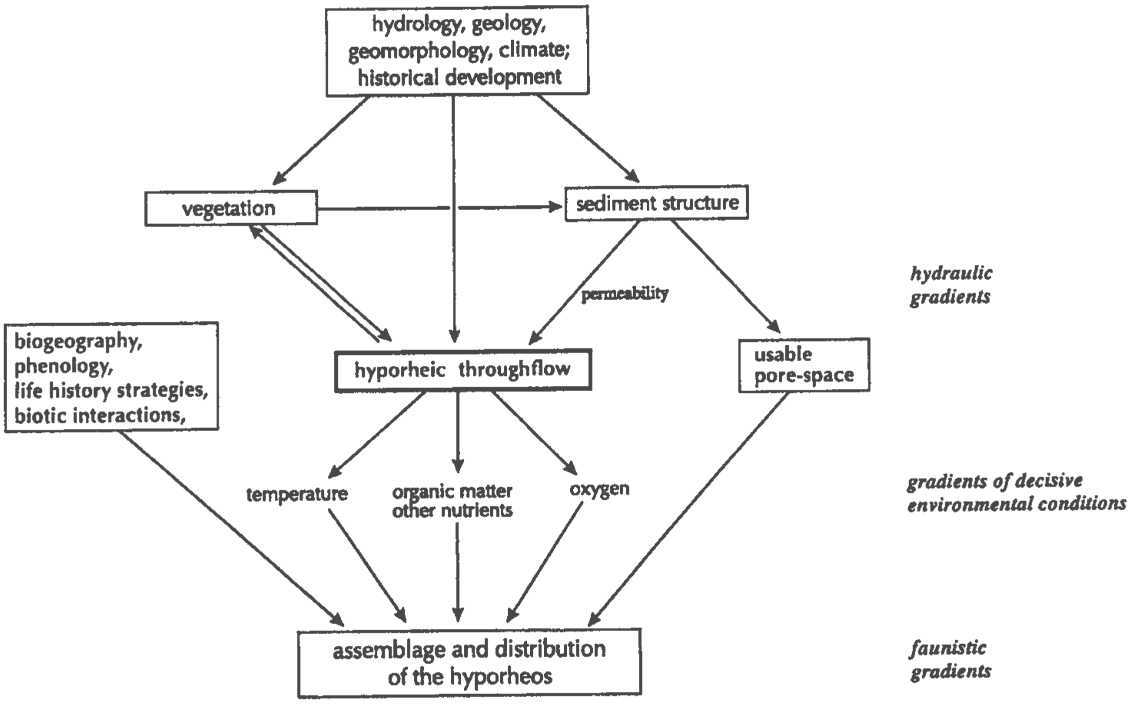
Figure 5.8 Number of sites in England and Wales recording stygobite fauna in hyporheic sediments, against their underlying geological strata.



5.3 Microscale controls

The composition and distribution of the hyporheos at the microscale is controlled abiotically by the usable pore space, interstitial flow rates and hydrological exchange processes. Many of these variables are directly or indirectly controlled by hydrological connectivity, water residence time and substratum composition (Boulton, 2000; Boulton, 2007; Brunke and Gonser, 1997; Strayer, 1994) (Figure 5.9). A critical process in this respect is the clogging of the top layers of the substratum with fine sediment. This clogging has been shown to be detrimental to a range of organisms that use the hyporheic zone including the endangered pearl mussel, *Margaritifera margaritifera,* (Geist and Auerswald, 2007), salmonids (for example, Grieg et al., 2007) and macroinvertebrates (for example, Bo et al., 2007). Sedimentation (also known as colmation) can be exacerbated by land management practices, such as felling of riparian trees that might otherwise act as sediment traps.

Figure 5.9. Factors influencing the biotic composition of the hyporheos. From (Brunke and Gonser, 1997)



Downwelling zones in coarse sediments have higher densities of epigean organisms, whereas upwelling zones are often typified by high proportions of stygobites and low numbers of epigean taxa (Dole-Olivier and Marmonier, 1992; Oslen and Townsend, 2003; Strayer et al., 1997; Ward et al., 1998).

Other factors also influence the fine scale patchiness of the hyporheos. Dissolved oxygen is a key environmental parameter in interstitial habitats as most metazoans inhabiting interstitial habitats are aerobes (Malard and Hervant, 1999; Ward et al., 1998). Dissolved oxygen in subsurface sediments depends on the permeability and porosity of the sediments, the saturation of pore spaces with water and the intensity of sediment respiration (the latter largely results from microbial metabolism). Sediment respiration is related to bacterial activity, itself dependent on the amount of available carbon present in the habitat.

Oxygen diffuses slowly in the aqueous phase and sediments with low porosity and permeability generally have low oxygen concentrations. This is the case in alluvial sediments of floodplains where pore spaces between gravels and cobbles are filled with silt, clay and fine particulate organic matter (Ward et al., 1998), as found in the bed sediments of large rivers such as the Danube, for example. At such sites, invertebrate assemblages are impoverished and dominated by relatively few species that tolerate low oxygen conditions (Danielopol, 1976). In contrast, oxygen concentrations are high in well-sorted and coarse sediments and these are often found in mountain streams such as the Oberer Seebach, Austria, and the Flathead River, Montana, USA. In these situations diverse assemblages of interstitial metazoans develop (Ward et al., 1998).

Dissolved oxygen concentrations within sediments are not uniform. Areas close to surface running waters are usually well oxygenated but concentrations decrease during the subsurface passage of water, mainly because of sediment respiration (Findlay et al., 1993). Dissolved oxygen in interstitial habitats also displays seasonal and/or diel fluctuations. For example, the superficial bed sediments of Sycamore Creek Arizona, have low oxygen concentrations during the low summer discharge, when surface water no longer penetrates subsurface sediments but interstitial oxygen concentrations are high at other times of the year (Stanley and Boulton, 1995).

Temperature exerts the primary control on phenologies and life histories, physiology and local distribution patterns of aquatic organisms. It also sets the limit of their distributional range (Ward et al., 1998). The temperature of groundwaters is much more stable than surface waters, although the temperature of sediments in downwelling zones varies with that of the stream.

The usable pore space is strongly related to the nature of the sediment, but little is known about the most ecologically important variables i.e. the actual sizes of, and connections between, the voids (Ward et al., 1998). Pore spaces are small in fine-grained sediments, but water content is high. In well-sorted sediments, pores are large but the overall water content (i.e. porosity) is lower than in fine sediments (Bretschko and Klemens, 1986). In these sediments most water moves freely through the voids, permeability is high and animals can swim through the larger pores or cling and crawl over grain surfaces (Ward et al., 1998). Dole-Olivier et al. (2004) found that most stygobitic taxa were most abundant and/or diverse in the most permeable geological formations (the karst aquifer and coarse alluvium, both of which are also characterised by high oxygen content).

Natural stream sediments are rarely well-sorted and normally contain an array of grain sizes. Large quantities of small grains clog larger interstices, increase the resistance to water flow and reduce the habitat space for the sediment community (Ward et al., 1998). These adverse effects may be counterbalanced by the large area of biofilm associated with fine sediment grains.

6 Environmental management approaches for subterranean aquatic ecosystems

6.1 Introduction

This section addresses a range of potential environmental outcomes that the Environment Agency may wish to examine for hypogean habitats.

As required by the Water Framework Directive (WFD), rivers cannot be considered apart from their catchments; river management must be integrated with catchment management. Rivers should be viewed as four-dimensional environmental systems with longitudinal, lateral, vertical and temporal variability.

The ecologically sound management of rivers also requires acceptance of Stanford and Ward's (1993) 'hyporheic corridor' concept. Indeed, the assemblages present in groundwater and hyporheic (including its lateral component) habitats represent an integral part of the biodiversity of the whole lotic ecosystem.

6.2 Protection and enhancement of biodiversity

Current evidence (see section 4.2) suggests that England and Wales possess a restricted stygobite fauna in comparison to much of the rest of continental Europe. Moreover, several of the species that do occur have been recorded at relatively few sites, although it is quite possible that further species occur but have not yet been discovered.

One species, *Niphargus glenniei,* is a priority species in the UK Biodiversity Action Plan (UK BAP), which calls for action to be taken on monitoring new and known sites for this organism. Local authorities are required to develop strategies to protect and enhance this species and its habitat.

Although species richness of stygobites is limited – by definition they do not occur in habitats other than the hyporheos and groundwater – these habitats make a unique contribution to UK biodiversity. There are extensive assemblages of stygophile fauna occurring in both hyporheic and groundwater habitats; these may perform important functions such as modulating the activity of the hyporheic biofilm by grazing and bioturbation (see Chapter 4 for full discussion).

A key finding of this report is that current understanding is limited to the basic biology, distribution and function of hypogean assemblages in the UK (see Chapter 7). The stygobite component of these assemblages appears to be spatially restricted (see section 6.4). *Niphargus glennei*, for example, has only been found in 24 sites in Devon and Cornwall, and research elsewhere suggests that stygobites are particularly vulnerable to anthropogenic disturbance due to their restricted distributions, poor dispersal, low reproductive rates and poor competitive ability (Danielopol et al., 2003).

In the light of this limited information, it is suggested that monitoring of hypogean assemblages is prioritised in order to track the health of these unique ecosystems. There is an active hypogean Crustacea recording scheme run by Lee Knight in association with the FBA (details can be found on the FBA website, www.fba.org.uk) and the FBA have published a useful guide to help identify hypogean fauna, which can be down-loaded from:

http://www.fba.org.uk/recorders/publications_resources/untitled/contentParagraph/00/document/CaveLife_Website.pdf

Hypogean assemblages are particularly vulnerable to low oxygen concentrations and require oligotrophic conditions for survival (Danielopol et al., 2003). These conditions would need to be maintained or restored in hyporheic habitats to enhance their biodiversity. Given their oligotrophic nature, these habitats are particularly at risk from pollution, such as from land contamination and diffuse agricultural sources. The habitats should perhaps be considered alongside other ecological receptors when assessing the risks from and impacts of human activities under relevant environmental legislation.

Groundwater and hyporheic ecosystems provide important goods and services to humans (Boulton, 2007). For example, the water filtration process in groundwater systems allows the production of high quality drinking water, a fact recognised by the Groundwater Directive 2006. The biogeochemical transformations that occur in the hyporheic zone enable cycling of nutrients and organic matter and contaminant attenuation, which also has benefits for water quality (Smith, 2005). Furthermore, the value of healthy groundwater systems can be viewed as an intergenerational capital to which precautionary protective measures should be applied (Danielopol et al., 2003).

6.3 Protecting subterranean ecosystems

During debates about whether subterranean ecosystems should be protected, it is essential to emphasise the importance of the connections between groundwater and its surrounding surface aquatic and/or terrestrial ecosystems. This connectivity occurs through the hyporheic ecotone. Good connectivity between surface and groundwater systems enables rapid replenishment of aquifers (Danielopol et al., 2000).

The subsurface habitats are among many in this connected aquatic ecosystem and should be considered for protection because of their unique assemblages and their functional role in pollution amelioration (Danielopol et al., 2003). Without protection of hypogean habitats and their assemblages, environmental restoration initiatives may ultimately fail to deliver anticipated ecological improvements. The WFD requires the Environment Agency to achieve good ecological status in surface water bodies. Given the connectivity between groundwater and surface waters, it has been argued (Danielopol et al. 2004) that a test of good ecological status should also be considered for groundwater bodies, although this is currently not part of the Directive's requirements. The protection of the subsurface habitat stems from a viewpoint that integrates the whole river catchment (Frisell and Bayles, 1996).

6.4 Management of pollution impact on subsurface aquatic ecology

The WFD expects the impact of groundwater on surface-waters to be assessed. Hyporheic assemblages are located at the interface between groundwater and surface waters and are therefore able to give an earlier warning of the ecological response of lotic ecosystems to groundwater borne pollution. Groundwater species provide the potential to biomonitor aquifers and assess their response to pollution (e.g. diffuse nitrogen pollution). Monitoring of hyporheic and groundwater assemblages would provide information on the health of these subsections of the lotic ecosystem and provide a more comprehensive assessment of a river's ecological status.

This monitoring would be particularly timely in the light of the Groundwater Directive 2006 which encourages member states to conduct research in order to provide better criteria for ensuring groundwater ecosystem quality and protection.

Designing a monitoring programme for hyporheic and groundwater assemblages raises many questions, not least the relative costs and benefits. Although sampling at the same locations used for the benthos would seem logical, hyporheic and groundwater assemblages respond to different pressures from epibenthic assemblages. Hyporheic assemblages, for instance, are strongly influenced by groundwater-surface water exchange (see section 5.3). If the aim of monitoring is to provide an 'early warning' of groundwater-borne pollution, it would seem wise to sample in upwelling zones where the influence of groundwater is at its greatest.

Groundwater assemblages however are influenced by fracturing in the underlying aquifer (see section 5.2). It is therefore suggested that groundwater monitoring takes place in areas where fracturing is greatest, as this is where groundwater assemblages will be most extensive.

As information on the distribution of hyporheic and groundwater assemblages in England and Wales is extremely limited at present, a national survey of 'type' locations might be the best option for an initial monitoring programme. It is important to use a standardised sampling methodology to facilitate inter-site comparisons but this would almost certainly need to be different for hyporheic and groundwater assemblages as the habitats differ so widely.

6.5 Minimising the effects of abstraction on subsurface aquatic ecology

Groundwater abstraction has the potential to impact severely hyporheic assemblages as it may alter the balance of exchange between groundwater and surface water. Natural groundwater droughts may have a similar impact. A reduction in the amount of groundwater flowing into the hyporheic zone will reduce the proportion of cool, oligotrophic water in this habitat. The composition of the hyporheic assemblage will also be affected; reduced upwelling could possibly lead to a lower proportion of groundwater stygobites in the hyporheic assemblage. The impact of a change in groundwater-surface water exchange should therefore be considered during the ecological appraisal of groundwater abstraction near rivers.

The impact of abstraction on phreatic groundwater assemblages is also a concern. Our limited knowledge of the extent and distribution of these assemblages makes it difficult to predict how abstraction could affect these assemblages, but given the spatially restricted nature of their distributions and poor dispersal abilities (see Chapter 1) it is likely that these assemblages would be harmed by abstraction, particularly if the volume of available habitat is reduced.

Saline intrusion is also likely to cause some habitat loss, either due to groundwater abstraction close to the coast or mineralised waters, or due to sea level rise in southern Britain due to isostatic rebound of the land surface. The Water Resources Act 1991/Water Act 2003 requires the Environment Agency to manage water resources in a sustainable manner. In our view the effects of abstraction on both hyporheic and groundwater assemblages, and the ecological functions that they provide, should be given due consideration.

6.6 Considering the hyporheos in river rehabilitation schemes

Rehabilitation of the hyporheos is rarely considered explicitly in river restoration schemes, despite an increasing recognition of the importance of the hyporheic zone to river ecosystem function (Boulton, 2007). Schemes that do target the hyporheic zone generally seek to recover lost geomorphological units and to restore the vertical hydrological connectivity between surface waters and groundwater (Fernald et al., 2006; Kasahara and Hill, 2006). Many rehabilitation schemes designed to benefit epibenthic invertebrates will also enhance the hyporheos and the subsurface processes that they mediate (Kasahara and Hill, 2006). This is particularly true of strategies designed to facilitate fish spawning by reducing the occurrence of fine sediments in gravel and cobbles.

The reintroduction of woody debris is another common river rehabilitation strategy (Brookes et al., 2004) and may also benefit the hyporheos by promoting vertical hydrological exchange and increasing the heterogeneity of hyporheic habitats (Boulton, 2007). We suggest that future restoration schemes should think vertically as well as horizontally and consider the hyporheos as an integral part of the overall lotic ecosystem. The objectives set for restoration projects should include hyporheic processes and diversity; the benefits of these restoration activities for the hyporheos should be assessed, although this is currently seldom the case (but see Hancock and Boulton, 2005).

7 Research and monitoring gaps

7.1 Introduction

The gaps in the current knowledge of sub-surface aquatic assemblages in England and Wales are extensive. In particular, the ecological processes that occur in the hyporheos and groundwater and how they impact the overall functioning of aquatic ecosystems is poorly understood, as are the basic biologies of subterranean aquatic organisms in the UK, the distribution and abundance of assemblages and how they relate to environmental variables such as geology. Some of these gaps require research programmes to be addressed, but others could be filled by the development of appropriate monitoring strategies.

Gaining this knowledge will help provide a solid research platform on hyporheic and aquifer biology that could inform future decisions on sustainable catchment management, such as pollutant/nutrient management and water abstraction. The following sections describe those areas that we feel are most in need of research or monitoring programmes.

7.2 Responses of subterranean taxa to pollutants

There is some evidence to suggest that groundwater organisms are more sensitive to stressors than epigean organisms and therefore have potential as bio-indicators of pollution (Plenet, 1995). Mosslacher (2000) showed that the sensitivity of stygobitic microcrustaceans was higher than those of related epigean species and suggested that existing groundwater quality criteria are insufficient to protect the groundwater biota. However, it is unknown whether this sensitivity is widespread amongst hypogean taxa, nor whether these taxa could be used as indicators for particular pollutants. Research priorities in this area include ecotoxicological studies on the responses of hypogean taxa to pollutants.

Few studies document the effect of contaminants on hyporheic and groundwater habitats (but see Notenboom et al., 1994), however, nutrient enrichment may lead to a reduction in biological diversity in subterranean ecosystems (Elliott, 2000; Wood et al., 2002). It may also lead to an increased abundance of organisms in response to an increase in trophic resources (Wood et al., in press). Chatelliers et al. (1992) give an example of long term change in interstitial assemblages caused by human impact. Over a period of 50 years a diverse interstitial assemblage comprising more than 20 hypogean species on a floodplain of the Rhine River has declined, as a result of metal contamination, into an impoverished fauna in which strongly hypogean forms are absent.

Microbial biofilms may be a key aspect of the functional importance of the hyporheos and contamination appears to cause a shift in the composition of the microbial community (Bekins et al., 1999; Ludvigsen et al., 1999; Rooney-Varga et al., 1999). The priorities for research in this area include studies on the responses of hypogean communities (including the microbial biofilm) to contamination.

Literature detailing the impacts of diffuse pollution on groundwater/hyporheic assemblages is non-existent. The priorities for research in this area include studies to determine the impact of agricultural land use on groundwater and hyporheic assemblages.

To date very few studies have examined the possibility of using hypogean taxa to monitor pollutants (but see Hahn, 2006; Lafont et al., 1996). Research in this area should include investigations to determine the relative responses of epibenthic and hyporheic assemblages to selected pollutants. The development of monitoring methodologies for hyporheic/groundwater assemblages that could be used in river/groundwater quality surveys is also important. If adopted, we recommend that monitoring methodologies for the hyporheos and groundwaters should be standardised across the Environment Agency.

7.3 The hyporheic zone as a refuge from extreme surface conditions.

Epibenthic organisms in rivers and streams live in a variable environment where there may be high (floods) or low (droughts) flow events at unpredictable intervals. Townsend and Hildrew (1994) suggest that species may survive such disturbances by possessing traits that confer resistance to flow fluctuations (e.g. hold fast mechanisms for high flows) and/or traits that confer resilience to disturbance (e.g. the ability to use refugia). Research suggests that the hyporheic habitat is less variable than habitats on the surface of the stream bed and less vulnerable to extremes of high and low flow (Brunke and Gonser, 1997). Furthermore, it is apparent that the hyporheos of some (but not all) rivers can act as a refuge for surface dwelling taxa during such extreme events, enabling them to recolonise the surface once the disturbance has passed (Dole-Olivier et al., 1997b; Marmonier and Chatelliers, 1991; but see Palmer et al., 1992). Thus the hyporheos has the capacity to add resilience to the whole river ecosystem and contribute to its good ecological condition (and ultimately to the assessed WFD ecological status) and sustainability.

This role is likely to become even more important as extreme conditions are expected to increase as a result of climate change. It is likely that the ability of the hyporheos to act as a refuge for surface taxa is dependent on the extent of this habitat in a given river and the nature of its substratum. Additionally, this refuge may be used more by some taxa than others depending on body size, life histories, possession of resting eggs etc. Thus the epibenthic community in some rivers may be partly shaped by the presence and nature of the hyporheos and the ability of taxa to use it as a refuge. A priority for research in this area is the determination of the type of hyporheos that is used by epibenthic taxa as a refuge (i.e. just those with a porous substrate, or others as well). Studies are also needed to determine which taxa are able to use the hyporheos as a refuge and how this affects the overall epibenthic community and its functioning.

7.4 Determination of subterranean aquatic assemblages in the UK

The heterogeneity of sub-surface aquatic assemblages in space and time over a range of scales is poorly understood. The recording of the spatial distribution of hyporheic/groundwater species and assemblages in England and Wales has been an *ad hoc* process relying on the interest of disparate groups of individuals. The resultant database (see Appendix 1) appears to suggest that the distribution of groundwater stygobites is closely linked to particular geologies in England and Wales and to the glacial legacy. However, it is quite possible that hyporheic/groundwater species and assemblages occur in other aquifers and locations in England and Wales but that they have not yet been discovered. A more systematic monitoring effort of hyporheic/groundwater assemblages would improve the current understanding.

Most studies of hyporheic assemblages have been made in the headwaters of streams or in arctic, alpine or desert environments; there are relatively few studies in temperate lowland rivers.

Priorities for research in this area would include the monitoring of the hyporheic/groundwater assemblages in England and Wales in order to determine their actual distribution in relation to the major aquifers and the glacial legacy. This work could involve targeted monitoring in areas that have received little attention so far and/or systematic monitoring. Research focusing on the sub-surface aquatic assemblages of UK lowland rivers is also needed to establish their basic ecology.

7.5 The impact of land use on subterranean aquatic assemblages

Land use and land use changes have the potential to impact subterranean aquatic assemblages through the introduction of contaminants and by alterations in the hydromorphology of the aquatic environment. Subterranean habitats are at risk from the infiltration of a wide variety of potential contaminants relating to different land uses. These contaminants include fertilizers and pesticides from agriculture, hydrocarbons from vehicles and fuelling activities, pollutants from landfills, as well as liquors from industrial or domestic sources and the infiltration of pollutants from surface water (Danielopol et al., 2003).

There are few data relating to how land use in the surrounding terrestrial environment and in the riparian zone may affect groundwater and hyporheic assemblages (but see Wood et al., in press). However, Boulton et al. (1997) documented the effects of land use on hyporheic ecology in five streams and found few individuals and taxa occupied the hyporheos of streams draining pasture. The authors suggested that land clearance for pasture leads to changes in morphology through hill slumping and siltation that buries the lateral bars along the stream channel rendering it an unsuitable habitat for hyporheic fauna. Research priorities in this area include an examination of the impact of land use on groundwater and hyporheic assemblages.

7.6 Modification of the environment by subterranean aquatic assemblages

There is some evidence that hypogean organisms graze biofilms and alter their composition and activity (see Chapter 3) but how this affects microbially mediated nutrient transformations and therefore the ability of the hyporheos to attenuate nutrient inputs is unknown. There is also no information concerning the levels of control that meiofauna and macroinvertebrates exert on biofilms.

Hypogean assemblages can also act as ecosystem engineers and modify the porosity of the substratum (see section 3.2). In turn this may modulate resource availability to biofilms with resultant, as yet unknown, impacts on nutrient availability, for example. There are several important areas for research including experimentation to determine the impact of hypogean assemblages of various types (e.g. meiofauna dominated vs. macroinvertebrate dominated) on biofilms and the processes that they mediate. Further examination is also required of the effect of hypogean invertebrate bioturbation on hydraulic conductivity and chemical concentration distributions. In addition, a study of the relationships between flow and/or hydrology and microbial processes and biodiversity in the hyporheic zone would also be welcome.

7.7 Trophic dynamics of subterranean aquatic ecosystems

Groundwater/hyporheic ecosystems are largely heterotrophic but there are few data on the trophic dynamics of these ecosystems (see Section 3.1). A rare example of a stream food web that includes hyporheic taxa in England is that of Broadstone stream in the Ashdown Forest (Lancaster and Robertson, 1995; Schmid-Araya et al., 2002; Woodward et al., 2005). In another study, Edington (1977) outlined the foodweb of a cave in Wales.

Undoubtedly assemblages feed on biofilms and particulate organic matter but what the paths, directions and magnitude of carbon flow through hypogean food webs is little known. Research priorities in this area include quantification of the energy flow into, through and beyond the hyporheic/groundwater food web.

7.8 Hypogean assemblage functional redundancy with the epibenthos

The functional role of organisms within the epibenthos (or surface layers) of streams is reasonably well documented, for example epibenthic foodwebs and the changes that result in these following the consideration of additional groups of organisms (Schmid-Araya et al., 2002). The response of epibenthic macroinvertebrate taxa to organic pollution is clearly understood and has been incorporated into the River InVertebrate Prediction And Classification System (RIVPACS). However, it remains unclear as to whether the hyporheos carrys out the same functions as the epibenthos. Further study is needed to understand the extent to which the hyporheos exhibits functional redundancy with the epibenthos. Research priorities in this area include the assessment of the role of hyporheic zone microbes and meiofauna on river diversity and health.

7.9 Stygobite biodiversity

Stygobites exhibit morphological convergence but this morphological similarity may disguise a larger number of cryptic species (Proudlove and Wood, 2003) (see section 4.2). In continental Europe a few studies have explored the occurrence of cryptic species using genetic techniques, but there are currently no such data available for stygobites in England and Wales and so it is not possible to state the biodiversity of these assemblages definitively. At least two species in the UK (*Niphargus fontanus* and *Proasellus cavaticus*) may harbour cryptic species (see Section 4.2). Genetic studies on stygobites in England and Wales to determine the true biodiversity of these assemblages is an important research area. Proudlove, Knight, Wood and Hanfling are currently working on these aspects in *Niphargus kochianus.*

7.10 Life history studies

Detailed life history studies allied to density measurements are necessary to calculate the secondary productivity of taxa and assemblages, but these have not been carried out for the great majority of hypogean taxa in the UK. Detailed calculations of secondary productivity are extremely rare for hyporheic assemblages and are non-existent for groundwater assemblages (see section 4.1), even though this information is vital if the contribution of the hyporheos to lotic ecosystem functioning as a whole is to be properly assessed. Research priorities in this area include life history studies of selected hypogean taxa; calculations of assemblage secondary production; and comparison with epibenthic production in targeted rivers.

7.11 Interdisciplinary research

Understanding and managing water systems requires an interdisciplinary approach to both research and management, particularly as new legislation emphasises integrated environmental management. Under the European Union Water Framework Directive (EU WFD), Europe's water bodies must be managed in an integrated and sustainable manner, taking account of stakeholder views. (Hodgson and Smith, 2007). However, a recent workshop supported by the UNESCO International Hydrological Programme concluded that more interdisciplinary research and environmental management practices are needed to understand better, predict and manage processes at the interface of environmental compartments; and that the goal of environmental regulations to improve ecological health requires a holistic approach integrating our understanding of the ecological, hydrological, biogeochemical and physical processes (Smith et al., 2007). Research priorities in this area include an increased awareness of the need to transcend traditional discipline boundaries when planning future projects.

8 Conclusions

This report itemises the obligate groundwater fauna (stygobites) currently known in England and Wales. There are few species (9) in comparison to continental Europe, however, one species (*Niphargus glenniei*) is endemic and is a UK Biodiversity Action Plan priority species. Additionally the stygophile water beetle *Hydroporus ferrugineus* is a Red Data Book notable species in the (http://www.jncc.gov.uk/page-2133).

There are relatively few records of stygobites in England and Wales, but it is quite possible that further species await discovery. Despite this limited biodiversity, these species form unique assemblages that, by definition, are not found in surface waters; they make a unique contribution to biodiversity in England and Wales. Their contribution to the functioning of groundwater ecosystems is unresolved but it is likely to be substantial, based on existing knowledge of the functioning of hyporheic and surface water ecosystems.

This analysis indicates that stygobites are most likely to be found where the bedrock geology is calcareous and where this geology occurs to the south of the limit of the Devensian glaciation. In the hyporheic zone of rivers there are substantial assemblages of stygophile species on all bedrocks, both to the north and south of the glacial limit; on suitable geologies, these may be joined by stygobites in the south, particularly in upwelling areas.

The analysis is based on relatively few records and stygobites may occur on different geologies and be more widespread to the north of the glacial limit. The recording of groundwater/hypogean taxa on the Environment Agency's BIOSYS system and a more systematic survey of groundwater habitats by the Environment Agency's Ecological Appraisal Teams, would enhance our understanding of these poorly understood ecosystems.

Research from continental Europe suggests that groundwater invertebrates are poor dispersers, reproduce slowly, have poor competitive ability and often exhibit restricted distributions. Thus they are very vulnerable to disturbances such as water abstraction or pollution. A key finding of this report is that there is an extremely limited understanding of the basic biology, distribution and functioning of groundwater and hyporheic assemblages in England and Wales. However, the endemic *Niphargus glenniei* appears to be restricted to Devon and Cornwall and in Ireland *Niphargus wexfordensis* has only been recorded from a single location; these species may be particularly vulnerable to disturbance. The impact of water abstraction on hyporheic/groundwater assemblages has not yet been studied in the UK, and it is concluded that further research in this area would aid in the sustainable management of this resource.

Groundwater/hyporheic assemblages could act as sentinels for the ecological health of groundwater and hyporheic systems because they exhibit a diversity of responses to the physical and chemical environment. However, their responses to environmental variables and pollution are poorly understood and it is still unknown whether their responses are different from those of epigean taxa. These uncertainties need to be resolved before monitoring programmes are devised.

When considering the protection of groundwater/hyporheic ecosystems and habitats it is vital to appreciate that they form an integral part of the whole river/hydrological catchment ecosystem. The surface, hyporheos and groundwater habitats are connected and should be considered as a continuum. An example of this connectivity is the role of the hyporheos as a refuge for surface dwelling invertebrates during disturbances.

9 Glossary

Alluvium: Sedimentary material deposited by flowing water.

Bioturbation: Disruption of sediments by feeding or burrowing organisms.

Cryptic: Species that are 'hidden' because they are morphologically very similar to others.

Dissolved Organic Carbon (DOC) Organic carbon that is dissolved in water.

Ecotone: A transition area between two adjacent ecological communities.

Endemic: A species that is restricted or peculiar to a locality or region.

Epigean: Organisms dwelling in the surface sediments of streams, rivers and lakes.

Groundwater: Water beneath the Earth's surface in contact with soil or geological strata.

Heterotrophic: An organism that requires complex organic molecules for metabolic synthesis.

Hypogean: The subsurface or subterranean environment as opposed to the surface (epigean) environment. Consists of three zones: the hyporheic (the most surficial), shallow and deep (phreatic) groundwater.

Hyporheic/hyporheic: A habitat and its biotic community occuring in the saturated interstices benteath the stream bed, and into the stream banks, that contain some proportion of channel water, or that have been altered by surface water infiltration.

Hypoxic: Environment possessing little oxygen.

Karst: Areas of limestone in which dissolution and erosion have produced fissures, underground streams and lakes.

Meiofauna: Benthic aquatic fauna that pass through a 1mm sieve but are retained on a 63µm sieve e.g. Copepoda.

Metazoan: Multicellular animals.

Oligotrophic: Water bodies that are nutrient poor.

Ovigerous: Carrying eggs.

Particulate Organic Carbon (POC): Organic carbon found in the water column or sediments that is particulate.

Pelletisation: Creation of larger units of organic matter from smaller ones, often by the production of faecal pellets.

Phreatobite: An organism that lives in deep (phreatic) groundwater.

Phenology: Periodic biological phenomena that are correlated with climatic conditions.

Polyphagous: Feeding on or utilizing many kinds of food.

Refugia: Areas where organisms can escape adverse pressures such as predation or high flow.

Stenotherm: Organism that can exist within a limited temperature range

Stygobite: Specialised subterranean organisms.

Stygophile: Found in both epigean and subterranean habitats. Not specialised to the latter but appear to actively exploit resources.

Stygoxene: May accidentally occur in subterranean habitats but have no affinities with them.

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