Aquifers and hyporheic zones: Towards an ecological understanding of groundwater

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Abstract Ecological constraints in subsurface environments relate directly to groundwater flow, hydraulic conductivity, interstitial biogeochemistry, pore size, and hydrological linkages to adjacent aquifers and surface ecosystems. Groundwater ecology has evolved from a science describing the unique subterranean biota to its current form emphasising multidisciplinary studies that integrate hydrogeology and ecology. This multidisciplinary approach seeks to elucidate the function of groundwater ecosystems and their roles in maintaining subterranean and surface water quality. In aquifer-surface water ecotones, geochemical gradients and microbial biofilms mediate transformations of water chemistry. Subsurface fauna (stygofauna) graze biofilms, alter interstitial pore size through their movement, and physically transport material through the groundwater environment. Further, changes in their populations provide signals of declining water quality. Better integrating groundwater ecology, biogeochemistry, and hydrogeology will significantly advance our understanding of subterranean ecosystems, especially in terms of bioremediation of contaminated groundwaters, maintenance or improvement of surface water quality in groundwater-dependent ecosystems, and improved protection of groundwater habitats during the extraction of natural resources. Overall, this will lead to a better understanding of the implications of groundwater hydrology and aquifer geology to distributions of subsurface fauna and microbiota, ecological processes such as carbon cycling, and sustainable groundwater management.

Résumé Les contraintes écologiques dans les environnements de subsurface sont en relation directe avec les écoulements des eaux souterraines, la conductivité hydraulique, la biogéochimie des milieux interstitiels, la taille des pores, et les liens hydrologiques avec les aquifères et les écosystèmes adjacents. L'écologie des eaux souterraines a évolué d'une science décrivant uniquement les biotopes souterrains à des études multidisciplinaires qui intègrent l'écologie et l'hydrogéologie. L'approche multidisciplinaire cherche à élucider le fonctionnement des écosystèmes souterrains et leur rôle consistant à maintenir la qualité des eaux souterraines et de surface. Dans les écotones des eaux de la surfaces des aquifères, les gradients géochimiques et les biofilms microbiologiques contrôlent les transformations de la qualité de l'eau. La faune de subsurface (stygofauna) construisent les biofilms, altèrent la taille des pores interstitiels à travers leur mouvement, et transportent physiquement des matériaux à travers l'environnement des eaux souterraines. Par ailleurs, les changements de leur population signalent un déclin de la qualité de l'eau.
Une meilleure intégration de l'écologie des eaux souterraines, de la biogeochimie, et de l'hydrogéologie pourra faire avancer de manière efficace de notre compréhension des écosystèmes souterrains, et spécialement en terme de bioremédiation des eaux souterraines contaminées, de maintenance et d'amélioration de la qualité des eaux de surface dépendant des écosystèmes souterrains, et l'amélioration de la protection des habitats des eaux souterraines durant l'extraction des ressources naturelles. En général, cela conduira à une meilleure compréhension de l'implication de l'hydrogéologie et de la géologie des aquifères à la distribution de la faune de subsurface et aux microbiota, aux processus écologiques tels que les cycles du carbone, et la gestion durable des eaux souterraines.

Resumen Los entornos ecológicos en ambientes subsuperficiales están relacionados directamente con el flujo de agua subterránea, la conductividad hidráulica, biogeoquímica intersticial, tamaño de los poros, y vínculos hidrológicos con acuíferos adyacentes y ecosistemas superficiales. La ecología del agua subterránea ha evolucionado a partir de una ciencia que describe la biota

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subterránea única hasta alcanzar la forma actual que enfatiza estudios multidisciplinarios que integran hidrogeología y ecología. Este enfoque multidisciplinario busca clarificar la función de los ecosistemas de agua subterránea y sus roles en el mantenimiento de la calidad de agua superficial y subterránea. En ecotonos de agua superficial y de acuíferos, los gradientes geoquímicos y biopelículas microbiales median transformaciones de calidad de agua. La fauna subsuperficial (estigofauna) se alimenta de biopeliculas, altera el tamaño de los poros intersticiales mediante su movimiento, y transporta físicamente material a través del ambiente de aguas subterráneas. Además, los cambios en sus poblaciones aportan señales de decadencia de calidad de agua. La mejor integración de ecología de aguas subterráneas, biogeoquímica, e hidrogeología incrementará significativamente nuestro entendimiento de ecosistemas subterráneos, especialmente en términos de bioremediación de aguas subterráneas contaminadas, mantenimiento o mejoramiento de calidad de agua superficial en ecosistemas dependientes de agua subterránea, y protección mejorada de habitats de agua subterránea durante la extracción de recursos naturales. Sobretodo, esto conducirá a un mejor entendimiento de las implicaciones de la hidrología de aguas subterráneas y geología del acuífero, de las distribuciones de fauna subsuperficial y microbiota, procesos ecológicos tal como ciclado de carbono, y gestión sostenible de aguas subterráneas.

Keywords Stygofauna · Hyporheic zone · Aquifer ecosystems · Groundwater/surface-water interactions · Human impacts

Introduction

In the last two decades, the tight link between the research disciplines of hydrogeology and groundwater ecology has become more evident (e.g., Noltie and Wicks 2001; Danielopol et al. 2003; Kemper 2004), especially in the application of groundwater ecology to aquifer management and water quality remediation. Most ecological constraints in subsurface environments are related directly to hydrogeological features such as groundwater flow dynamics, interstitial pore size and biogeochemistry, and hydrological linkages to adjacent aquifers and surface ecosystems (Gibert 1991). This last aspect is critical because groundwaters and surface waters are interactive components of the hydrologic system and cannot be treated in isolation (Winter et al. 1999; Winter 1999). For example, the exchange of groundwater and river water in the saturated sediments of the riverbed—the hyporheic zone—epitomises this interaction with its repercussions for the water quality in both components (Brunke and Gonser 1997; Boulton 2000b; Hancock 2002). The hydrological linkage can extend even further to so-called 'groundwater dependent ecosystems' (see later) that include terrestrial vegetation and fauna that rely on groundwater only occasionally during droughts (Hatton and Evans 1998).

Inland aquifers constitute more than 97% of the world's unfrozen fresh water (Gibert et al. 1994). These aquifers often support diverse biological assemblages of taxa that interact with each other and with the solid and liquid components of the system. Therefore, if sustainable groundwater use is an aim of water management, aquifers must be considered as active ecosystems rather than just inert reservoirs of water. Although groundwater comprises the greatest proportion of globally available fresh water, our ecological knowledge of these ecosystems lags far behind that of lakes and rivers (Boulton et al. 2003). Meanwhile, demand for groundwater intensifies, and over two billion people now depend on this resource for their daily supply (Kemper 2004). Increased concerns about declining groundwater quality and recharge rates (Alley et al. 1999) have prompted urgent calls for greater understanding of how groundwater ecosystems are affected by human activities and potential remediation strategies (Kemper 2004). Of the world's ecosystems, it is aquifers that contain the highest proportion of rare taxa with restricted distributions (Gibert and Deharveng 2002), so to be effective in the protection and management of groundwater resources, the interactions of hydrogeology and ecology across a range of physiographic and climatic landscapes must be understood.

This paper explores the future of hydrogeology in the context of groundwater ecology. After defining groundwater ecology and briefly reviewing the evolution of the discipline and recent advances, the diversity of groundwater habitats is introduced and the ecological constraints imposed by their hydrogeology upon the specialised fauna and microbiota is examined. The functional attributes of this biota are used to illustrate some of the effects of human use of this resource. The paper is concluded by discussing the future of hydrogeological and ecological research to address management problems, emphasising the importance of a landscape-level approach that still acknowledges the specific features of various groundwater and groundwater-dependent ecosystems.

Groundwater ecology and its evolution as a discipline

Groundwater ecology is the study of the interactions between groundwater organisms and their external environment, be it the immediate aquifer or a connected terrestrial system (Danielopol 1994). The earliest printed reference to the dependence of life on groundwater can be traced back to 1541, with a description of the blind fish *Sinocyclocheilus hyalinus* in the Alu Limestone caves in Yunnan, China (Romero 2001). Danielopol and Marmonier (1992) review the extensive contributions by early European groundwater researchers working in the mid-1900s, but global recognition of groundwater ecology as a specific discipline did not occur until the 1990s, heralded by an international groundwater ecology symposium in 1992 (Stanford and Simons 1992) and the publication of the first textbook dedicated to the field (Gibert et al.

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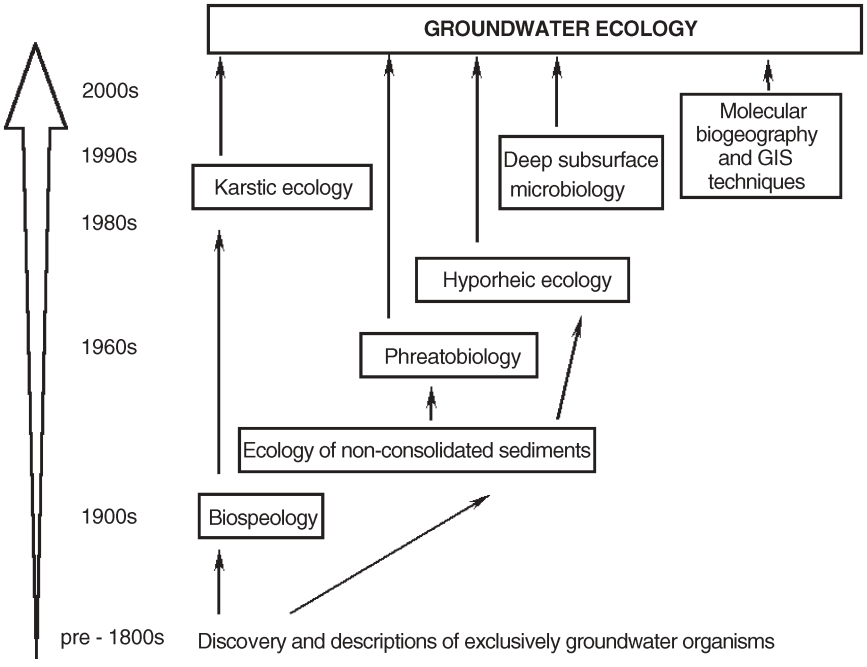

Fig. 1 The evolution of research perspectives in the development of groundwater ecology. See text for specific dates and concepts that delineated groundwater ecology in the 1990s. Updated from Gibert et al. (1994)

1994). Fig. 1 illustrates the evolution of the current discipline of groundwater ecology that now incorporates:

1. "biospeology" (or "biospeleology"), proposed by Racovitza (1907);
2. studies of the ecology of non-consolidated sediments begun in Austria by H. Spandl in the 1920s;
3. "phreatobiology," introduced by Motas (1958);
4. "hyporheic ecology" as a term coined by Orghidan (1959), but a field that primarily developed when stream and groundwater ecology merged in the 1970s from work by D. L. Danielopol, D.D. Williams and H.B.N. Hynes;
5. the synthesis by Rouch (1986) that spawned karstic ecology;
6. the development of deep subsurface microbiology in the late 1980s; and
7. the application of molecular techniques (e.g., Barton et al. 2004) and geographical information systems (GIS) for biogeographical studies.

As early as 1926, there was evidence that active microorganisms lived in groundwater, when geologist E.S. Bastin deduced the presence of anaerobic sulphate-reducing bacteria in water associated with the Sunset-Midway oilfield in California, U.S.A. (Chapelle 2001). In 1962, the fundamental link between groundwater quality and microbial activity was described (Gurevich 1962), and in the ensuing years, the role that microorganisms play in determining water chemistry became well-established (Kölbel-Boelke et al. 1988). This led to one of the major applications of groundwater ecology—the cleaning of polluted groundwater by bioremediation (Piotrowski 1989; Wenderoth et al. 2003).

Since the mid-1800s, scientists have known that subterranean waters house a diverse array of invertebrate (Botosaneau 1986), and to a lesser extent vertebrate species (Romero 2001). Groundwater animals are collectively known as *stygofauna*, after the Styx River that delineates the underworld in Greek mythology. High diversities of groundwater fauna have been described from various parts of the world (Danielopol el al. 2000; Boulton et al. 2003), revealing extreme endemicity and apparently restricted distributions of many species (Marmonier et al. 1993). For example, boreholes in the deserts of Western Australia have the world's most diverse known communities of subterranean diving beetles (Leys et al. 2003). However, many species are restricted to individual calcretes (here used to refer to the wholly or partly saturated voids in rocks formed from sand or gravel by cemented calcite). These beetle communities appeared to have evolved in isolation from other communities less than 100 km away (Leys et al. 2003).

Recent advances in groundwater ecology

The decade of the 1990s was a significant one in the field of groundwater ecology, commencing with the publication of the surface water/groundwater ecotone concept by Gibert et al. (1990). An ecotone is a transition zone between two ecosystems that displays characteristics of both. Gibert et al. (1990) argued that the hydrological interaction between surface waters and groundwaters mediated an ecotone that consisted of trends of light intensity, oxygen saturation, and amplitudes in variables such as water temperature, along with biogeochemical gradients in macronutrients such as nitrogen. This ecotone is especially evident in the hyporheic zone (see later),

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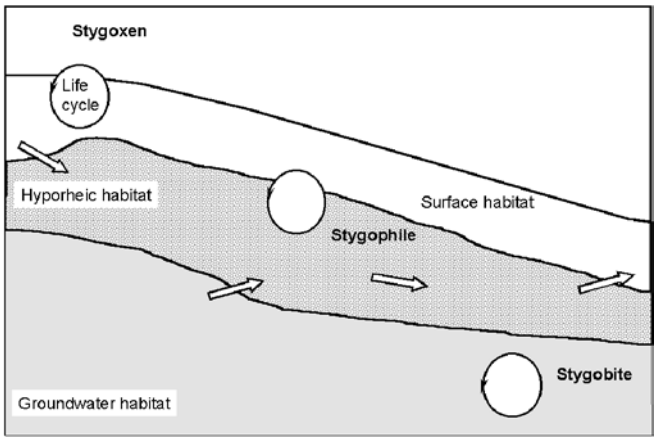

Fig. 2 A functional classification of hyporheic fauna based on their habitat affinity for groundwater. Modified from Marmonier et al. (1993)

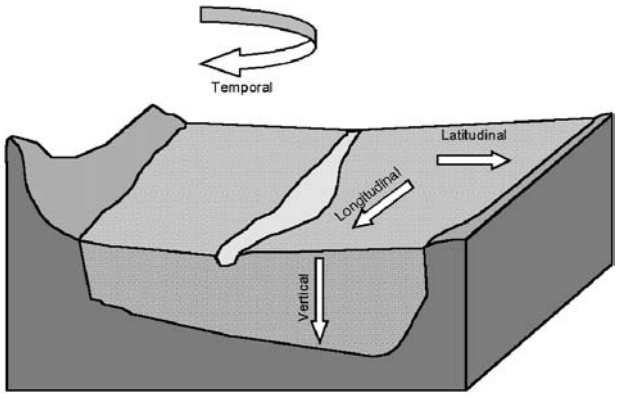

Fig. 3 The four-dimensional nature of alluvial groundwater ecosystems. Modified from Dole-Olivier et al.1994

which can act as a physical, chemical and biological filter (Vervier et al. 1992) capable of immobilising or transforming nutrients or pollutants (Bourg and Bertin 1993), preventing or reducing their transfer between groundwater and the surface (Hancock 2002).

The ecotone approach to groundwater ecology led to a functional classification of hyporheic invertebrates into three broad groups based on their affinity to the groundwater habitat (Marmonier et al. 1993). Figure 2 illustrates the different dependencies on groundwater shown by a *stygoxen* (largely confined to surface water), a *stygophile* (able to spend part of its life in the hyporheic zone but without adaptations for subterranean life), and a *stygobite* (obligated to complete its life cycle in groundwater, and with adaptations to do so). This classification has been used to illustrate the linkages between groundwater and surface water, and to reveal the impacts of human activities, such as river regulation, that alter these linkages (Claret et al. 1999).

Another significant advance in the 1990s was the synthesis of detailed reach-scale studies concerning the central role of hydrological exchange between groundwater and river water in governing the chemistry and fauna of the hyporheic zone, and even that of surface water where hyporheic upwelling occurred (e.g., the special issue of Journal of the North Americal Benthological Society, Valett et al. 1993). Related to the ecotonal paradigm above, this development brought hydrologists and groundwater ecologists together to integrate their findings and explore catchment-scale concepts such as nutrient spiralling and retention in streams with porous sediments (Jones and Mulholland 2000). Substantial technological advances in the use of tracers and groundwater modelling approaches now make it possible to collate hydrological data on pathways and residence time with ecological variables of water chemistry, faunal composition or microbial activity (Hancock 2004).

The third major development was the incorporation of specific elements of spatial scale into understanding groundwater ecosystems, especially hyporheic zones (Boulton et al. 1998). In brief, this explored the different trends that emerge when groundwater-surface water interactions are assessed at the sediment scale (sub-millimetre to metre), the reach scale (1–1,000 m), and the catchment scale (>1,000 m). While the boundaries of these scales are arbitrary, the key point is that there is potential for a hierarchical arrangement of groundwater-surface water interactions based on spatial scale, mirroring the hierarchical classification of flow systems proposed by Tóth (1963). Regional flow systems (sensu Tóth 1963) equate to the catchment scale whereas local flow systems match the reach scale described above. Flow systems depend on landscape position, but also the hydrogeology of the soil/rock material, whose permeability will govern exchange between surface and groundwater (Freeze and Cherry 1979). As the hydrology of all surface water bodies relates to their groundwater flow systems, geological characteristics of their beds, and their climatic settings (Winter 1999), these interactions must be understood and are likely to influence groundwater organisms at a variety of scales (Baxter and Hauer 2000; Boulton et al. 2002b).

To the three spatial dimensions (longitudinal, latitudinal, and vertical), Ward (1989) suggested the addition of a fourth temporal dimension in surface waters, which Dole-Olivier et al. (1994) extended to groundwater ecology. Fig. 3 shows the four dimensional nature of alluvial groundwater ecosystems. In a groundwater context, this incorporates changes that occur over long-term time scales, from changes to regional flow regimes (Herczeg et al. 2003) to short-term changes that may include seasonal fluctuations in water tables or stream channel migration resulting from floods (Wondzell and Swanson 1996). This four-dimensional view of groundwater ecosystems underpins the interstitial highway concept (Ward and Palmer 1994), proposing that species disperse over large distances along riverine valleys through many generations, evolving along the way. Although the four-dimensional view was developed in alluvial systems, it could equally apply to karstic and fractured aquifers as these can also be subject to distinct changes along all four dimensions.

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Recent developments in groundwater ecology have led to more applied research in the field of bioremediation, which takes advantage of the ability of phreatic microbes to degrade pollutants. Bioremediation has been used to treat pollution from chlorobenzenes (Van der Meer et al. 1998; Wenderoth et al. 2003), pesticides (Hoyle and Arthur 2000), and hydrocarbons (Chapelle 2001). While natural attenuation of contaminants occurs in many aquifers through biological degradation, dispersion, or dissolution, this often does not proceed at a rate that is desirable to humans. Bioremediation is a way of accelerating some of these natural processes, and for it to be successful the aquifer must contain the appropriate microorganisms and conditions favourable to degradative processes (Haack and Bekins 2000).

Currently, there are two popular bioremediation strategies: biostimulation and bioaugmentation. Biostimulation accelerates the degradative activity of indigenous bacterial communities by the addition of suitable electron donors/acceptors or nutrients (Wenderoth et al. 2003). This process relies on the existing bacterial community being able to degrade pollutants. Alternatively, bioaugmentation is when bacteria are added to aquifers to assist bioremediation. This has had more success under laboratory conditions and with soil remediation than in aquifers because the introduced bacteria are often unable to survive for long periods in the aquifer (Chapelle 2001). It should be noted that species translocations, such as occur with bioaugmentations, might have deleterious impacts on the natural ecosystem as seen in other exotic species introductions in surface ecosystems.

The culmination of these approaches and concepts from the 1990s is the current integrative discipline of groundwater ecology that incorporates the fields of hydrology, geology, biology and—more recently—sustainable management of the groundwater resource. One challenge for the future is to consider how each of these fields can help one draw generalisations about processes occurring in the broad diversity of groundwater ecosystems and to advance our understanding by using a range of methods borrowed from other disciplines. First it is necessary to appreciate the diversity of groundwater environments.

A diversity of groundwater ecosystems—broadening the definition

Traditionally, groundwater ecosystems were considered to comprise only the deep saturated sediments of the Earth, with most ecological work being done via occasional windows to this environment where springs emanate to the surface, or cave streams flow through karstic areas. Compared to surface water ecosystems, the groundwater environment was once portrayed as one where conditions are constant and physically inert, light is absent, habitats are restricted (often to fissures or interstitial pores), and the lack of available organic matter leads to simple food webs and limited productivity

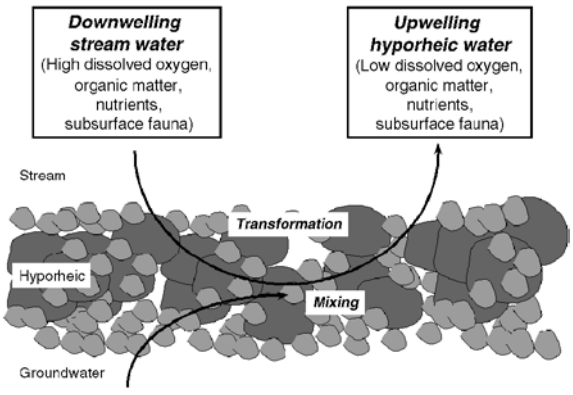

Fig. 4 The changes that occur in hyporheic water and fauna while moving from downwelling to upwelling

(Gibert et al. 1994). However, this view has changed as more data are gathered and it is now generally recognised that many groundwater ecosystems undergo substantial changes through space and time, supporting diverse processes and fluxes of material (Noltie and Wicks 2001). With growing recognition of this high inherent variability, ecological paradigms of groundwater constancy are to be replaced by concepts of disturbance and resilience similar to those applicable to surface ecosystems.

Shallow aquifers, and particularly those that form ecotones with overlying wetlands or rivers, are areas of marked fluxes of water, nutrients, and biological material. In the hyporheic zone of alluvial aquifers, river water exchanges with subsurface water at a range of scales (Boulton et al. 1998). In areas where downwelling of river water occurs, the sediments are well-oxygenated, rich in labile carbon, readily accessible to the groundwater foodweb (see later), and harbour diverse faunal assemblages, primarily stygoxenes and stygophiles (reviews in Brunke and Gonser 1997; Boulton 2000a). With increasing residence time below the riverbed, hyporheic water becomes less oxygenated, biogeochemical processes become reductive, and the hyporheic fauna becomes dominated by stygobites, as shown in Fig. 4. Upwelling hyporheic water may be rich in nutrients generating localised 'hotspots' of productivity, evidenced by prolific algal mats or active biofilms (Dent et al. 2000). For example, periphyton unable to fix nitrogen, dominated the sediments of Sycamore Creek, Arizona, U.S.A. in places where nitrate-rich water welled up from the hyporheic zone, whereas nitrogen-fixing species occurred in the downwelling areas where surface water nitrate concentrations were 3.5 times lower (Henry and Fisher 2003).

Hydrogeological processes directly control the hyporheic zone and its interactions with adjacent ecosystems, with hydrological retention strongly influenced by geology and the alluvial characteristics of the catchment (Morrice et al. 1997). Depending on the soil and rock type, particle size and shape govern the interstitial pore size and hence, the residence time of the subsurface flow paths. In some low gradient sand-bed streams draining

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granitic and sandstone catchments, hyporheic residence time is long, and biogeochemical gradients spanning orders of magnitude in chemical concentration may be established within centimetres while subsurface flow rates range from mm to cm per day (Hancock et al. 2001; Boulton et al. 2002a). Conversely, pebbles and cobbles from mixed dolerite/basalt catchments produce highly permeable hyporheic zones where subsurface flow rates can be measured in mm to cm per second, oxygen penetrates deep into the stream bed, and biogeochemical gradients extend over tens of metres (Dole-Olivier et al. 1993, Hendricks and White 1995).

There is also increasing recognition of the existence of other terrestrial and marine ecosystems partially or wholly reliant on groundwater. These groundwater dependent ecosystems (GDEs) include some communities of terrestrial vegetation, river baseflow systems, standing wetlands with subsurface linkages to the groundwater table, various terrestrial faunal communities (particularly in arid zones), and many estuarine and near-shore marine ecosystems where groundwater outwells (Clifton and Evans 2001). The degree of ecosystem dependence differs among each category, and varies seasonally and annually—some GDEs may only be reliant on groundwater during drought (Boulton 2000b). However, the common thread linking all of these ecosystems is their hydrological connection to the aquifer. Less well understood is the way these links are governed by the hydrogeology of the GDE, and this would be a productive line of research in the future, especially when trying to predict the location of GDEs in poorly-mapped regions of the globe.

Ecological constraints on life in groundwater ecosystems

Conditions in aquifers can be relatively harsh for life, with low concentrations of nutrients and carbon, limited dissolved oxygen, an absence of light, and limits on free space (Coineau 2000). However, through a series of highly specialised morphological and behavioural adaptations, stygofauna and microbes can persist in a wide variety of aquifer types, including fractured rock, calcrete, sedimentary, and anchihaline systems (Humphreys 2002). Furthermore, living beneath the ground can mean isolation from the climatic rigours of the surface, and this has allowed the fauna of some subterranean ecosystems to persist for many millions of years (Leys et al. 2003).

Stygofauna (particularly stygobites) lack pigmentation, have reduced or no eyes, and have enhanced non-optic sense organs (Coineau 2000). Many interstitial invertebrates have increased segmentation and are small-bodied to facilitate movement through the interstitial milieu (Danielopol et al. 1994). Some of these morphological traits can be seen in the examples given in Fig. 5. To survive in the low-carbon and low-oxygen aquifer environment, most stygobite species have a slow metabolism, are long-lived and slow-growing, and have few young (Gibert and Deharveng 2002; Humphreys 2002). Although many stygofauna can tolerate low concentrations of dissolved oxygen (Strayer 1994; Hakenkamp and Palmer 2000), they cannot survive severe hypoxia (dissolved oxygen <0.01 mg l^{-1} O_2) for more than 2–3 days (Malard and Hervant 1999).

Fig. 5 Some examples of stygofauna: **a**. *Bathynella* sp. (Syncarida) length = ca. 2 mm; **b**. *Halosbaena tulki* (Thermosbaenacea) length =ca. 3 mm; **c**. *Milyeringa veritas* (Cave gudgeon) length =ca. 57 mm. Photo credits: **a**. Peter Hancock, **b–c** Douglas Elford: Western Australian Museum

Invertebrate communities varying in diversity have been collected from alluvial aquifers (15 stygobite taxa, Dumas 2002), fractured rock aquifers (8 stygobite taxa, P. Hancock unpublished data), and karstic aquifers (37 stygobite taxa, Malard et al. 1996). In all cases, hydrological, geological, and biogeochemical processes largely structure the communities. This is because it is in the milieu of the aquifer that stygofauna exist, and it is therefore the hydrogeological processes that shape the conditions in which they are able to survive. For example, hydromechanical coupling (Stephansson 2003) creates fractures in rock that potentially generate habitat for stygofaunal and microbial colonisation. In some karstic areas, hydrogen sulfide oxidises and creates voids that become habitats for entire ecological communities (Forti et al. 2002). As the hydrogeological environment governs the supply of food and nutriment to groundwater communities, it is useful to review the current understanding of groundwater foodwebs in this context.

Carbon, foodwebs, and productivity in groundwater ecosystems

Organic carbon is the basis for most life on earth, but it occurs in very low concentrations in groundwater

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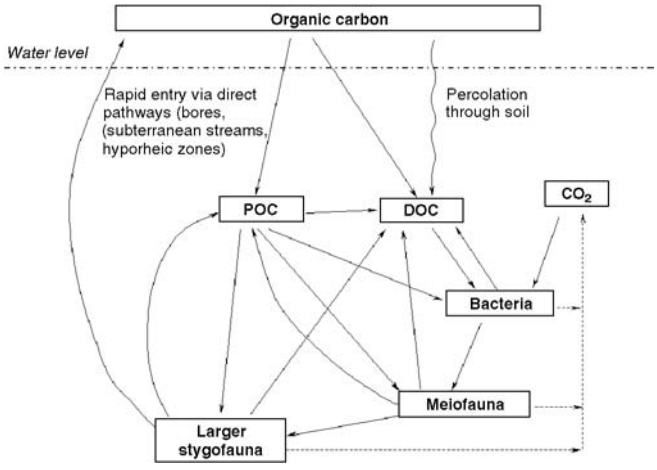

Fig. 6 Theoretical carbon-based groundwater foodweb. POC refers to particulate organic carbon. DOC refers to dissolved organic carbon. Dashed lines represent respiration

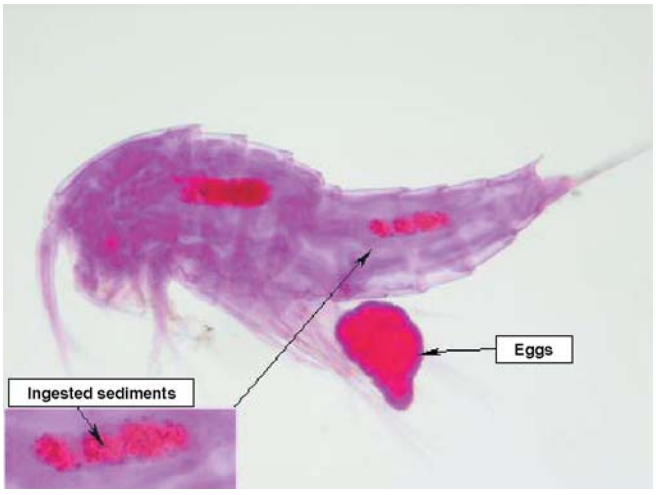

Fig. 7 A meiofaunal species of copepod crustacean (length = ca. 1 mm) with ingested sediment. Bacteria coating the sediment are digested while in the gut

(<1 mg l^{-1} in pristine aquifers, Gounot 1994). The availability of organic carbon is probably the main determinant of trophic complexity in groundwater foodwebs and ecosystems where the food web structure is already truncated by the absence of photosynthesis in the permanently-dark environment (Gibert and Deharveng 2002). This truncation means that herbivores are absent except where plant material can enter the groundwater environment such as the downwelling parts of the hyporheic zone (Claret et al. 1999). Carbon may enter the groundwater food web rapidly via conduits such as connected surface water bodies, or it can enter by slowly being leached from tree roots or soils. A typical carbon-based groundwater foodweb is illustrated in Fig. 6. Once in the sediments, carbon is either assimilated by microorganisms if it is already dissolved (Findlay and Sobczak 2000) or alternatively, bacteria and higher organisms can consume or decompose particulate organic matter. When stygofauna consume particulate organic matter directly, they assist bacterial activity by increasing the surface area available for attack, generating nutrients through excretion or death, and increasing the flux of oxygenated water through burrowing (Hakenkamp and Palmer 2000). Bacterial and faunal respiration generates carbon dioxide that can provide energy for lithotrophic bacteria, which require inorganic carbon (Chapelle 2001).

Meiofauna are minute (50–1,000 μm) interstitial invertebrates that act as conduits for carbon from microbial biofilms to larger invertebrate consumers (Hakenkamp and Palmer 2000). This predator-prey linkage between bacteria and meiofauna has been observed in hyporheic zones (Bärlocher and Murdoch 1989; Mermillod-Blondin et al. 2003), marine environments (Giere 1993), and in aquifer systems (Mauclaire et al. 2000). Stygobitic meiofauna probably ingest free-living bacteria directly, but as 99% of subsurface bacteria are attached to sediment surfaces (Lehman et al. 2001), this is only likely to account for a small proportion of the energy transfer. A more efficient mechanism is for the meiofauna to imbibe microbially-coated sediment grains as shown in Fig. 7, digest the microbes, and then excrete the grazed particles. This stimulates further bacterial growth by providing clean sediments for colonisation (Hakenkamp and Palmer 2000), but may also prevent bacterially-induced clogging in porous media (Rockhold et al. 2002).

Typically, organic carbon concentrations decline with depth and distance from the recharge area (Gounot 1994) with concomitant reductions predicted in ecosystem complexity. While this seems to hold true for stygofauna and most microorganisms, life still exists several kilometres beneath the surface (Griebler 2001). This is possible through the ability of some microbes to derive energy from other sources, such as the liberation of hydrogen from basalt in deep rock systems via chemoautotrophy (Griebler 2001). Recently there has been an increase in research of non-traditional energy sources associated with subterranean ecosystems (Sarbu 2000), especially those related to karst geomicrobiology and its interaction with redox geochemistry (Barton et al. 2004; Hutchens et al. 2004). Chemoautotrophic bacteria may derive enough energy from non-carbon sources to support ecosystems analogous to those of deep-sea hydrothermal vents (Humphreys 2002). For example, in Movile Cave, Romania, sulphide-reducing bacteria were shown to be able to support at least 18 stygofaunal species (Sarbu 2000).

Many cave stream and groundwater ecosystems principally depend on energy derived from surface detritus as dissolved organic matter (DOM) and coarse particulate organic matter (CPOM). By far, the majority of this enters in dissolved form. For example, Graening (2000) showed that 95% of the total carbon in Cave Spring Cave, Arkansas, U.S.A. entered as DOM. Using stable isotopes of carbon and nitrogen, he distinguished three trophic levels—invertebrate consumers, secondary consumers and detritivores—supported almost entirely on the dissolved carbon entering the cave. Even when CPOM is abundant, DOM can still be the dominant source of organic material

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to the cave stream food web because carbon leached off surface soils is taken up by the biofilms and travels up the stygofauna foodchain of primary and secondary consumers (Simon et al. 2003).

Apart from near-surface and cave areas, there are few specialist predators in groundwater environments, with most animals being trophic generalists (Gibert and Deharveng 2002) that feed on smaller organisms or survive on other carbon sources. The groundwater foodweb can remain entirely within the subsurface, with stygofaunal predators forming the top trophic link, or they can be connected to the surface via habitats where hydrological exchanges occur such as in cave streams and the hyporheic zone. Stygoxen predators visiting groundwater habitats and then returning to the surface facilitate this transfer of nutrients and energy between ecosystems (Boulton 2000a).

The hydrogeology of groundwater ecosystems may control the local chemical conditions, especially where sharp redox gradients are formed. In a sulphidic cave stream, Engel et al. (2002) demonstrated nutrient cycling of autotrophically-fixed carbon by chemoorganotrophic and heterotrophic populations that occurred in an environment created by the redox stratification within a microbial mat. With distance downstream, the nutrients are cycled across redox boundaries between the microbial and abiotic components of the ecosystem, forming a nutrient spiral within a groundwater ecosystem similar to that more commonly described in surface waters. There is a need for further research to determine how hydrogeological variables influence the functioning of these complex microbiological pathways in other groundwater ecosystems. For example, how do changes in hydraulic conductivity alter retention rates in subsurface nutrients and therefore control the types of microbial populations that can be supported in different groundwater habitats?

Hydrogeological influences on groundwater ecosystems can also occur over entire catchments or groundwater recharge zones. Marked spatial and temporal changes in groundwater quality due to hydrogeochemical processes have been observed in the subsurface flow pathways in palaeovalleys of ancient river beds. In parts of the Australian arid zone, these processes result in the deposition of groundwater calcretes (Mann and Horwitz 1979) that harbour diverse stygofaunas comprising many highly-restricted endemic species (Humphreys 2001; Leys et al. 2003; Karanovic 2004). Among them is a diverse fauna of tiny crustacean Ostracoda, or 'seed shrimps' (Karanovic and Marmonier 2003). As ostracod assemblages in Australian salt lakes are strongly associated with the chemical facies of the waters they inhabit (Radke 2000), water chemistry is expected to be a primary determinant of their ecology in groundwater and work is progressing on chemical constraints to their distribution and how these are dictated by calcrete formation.

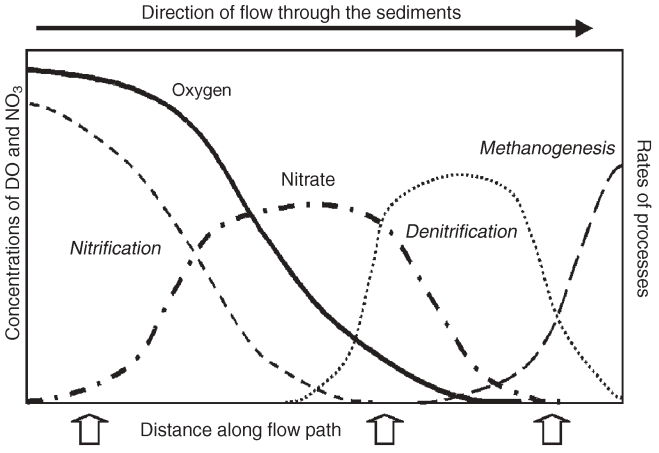

Fig. 8 Hypothetical profiles of dissolved oxygen (DO) and nitrate (NO_3) influenced by processes of nitrification, denitrification and methanogenesis (italics, thin lines) along a groundwater flow path (modified from Jones et al. 1994). Arrows indicate potential path lengths that would have very different biogeochemical processes (see text)

Groundwater—surface water interactions

As groundwater-surface water interactions have been fully reviewed by other authors (Winter 1999; Sophocleous 2002), the aim of this paper is not to repeat their material but to cover aspects that would benefit from further research by hydrogeologists. The best known region of interaction is the hyporheic zone where water is exchanged between rivers and their aquifers, travelling through a physical, chemical, and biological filter (Hancock 2002). However, little is known of the relative contributions by these elements to the transformation processes controlling water quality, and more importantly, how they are affected by changes in discharge. Sophocleous (2002) reviewed the large-scale aspects of hydrological exchange and urged the need for broader perspectives that could include multidimensional analyses and interface hydraulic characterization and spatial variability. This approach is needed, but should be couched in the context of how exchange influences biogeochemical processes in different transition zones and over different lengths of groundwater flowpaths. This is best illustrated with a specific example.

In a sand-bed desert stream (Sycamore Creek, Arizona, U.S.A.), the hyporheic microorganisms are metabolically active, especially where streamwater downwells and rates of respiration and nitrification are high (Jones et al. 1995). Water entering the hyporheic flowpaths is rich in organic matter and oxygen, promoting respiration. High rates of nitrification increase nitrate concentrations in the water (Holmes et al. 1994) and upwelling water supplies nitrate to surface mats of periphyton that rely on this nutrient. However, depending on the length of the flowpath, and the degree of mixing with upwelling groundwater the water chemistry may change further. As oxygen becomes depleted, respiration switches from aerobic to anaerobic pathways as shown in Fig. 8. Nitrate is transformed

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through denitrification, and nitrogen is respired (Duff and Triska 1990). As redox potential drops further, methanogenesis ultimately occurs in the anoxic sediments (Jones et al. 1994). Thus, at different points along a hypothetical flowpath of surface water into the hyporheic zone (Fig. 8), different chemical processes predominate and these have direct repercussions for the local microbes and stygofauna.

In agriculturally-dominated areas, where groundwater may be enriched in nutrients, these hyporheic microbial processes may be key factors in maintaining surface water quality through the prevention of eutrophication (Spruill 2000). Importantly, hydrologeological features, such as groundwater discharge, hydraulic conductivity, sediment particle size and packing, and larger scale features of channel morphology dictate the length of the flowpath and rate of water flow. Thus, there is scope for input from hydrogeologists to measure these features and relate them to ecological processes of nutrient regeneration and stygofaunal distribution in a way that allows rigorous testing of the model portrayed in Fig. 8.

Another pressing application of hydrogeology relates to the testing of the generality of conceptual models proposed as a framework for cross-ecosystem comparisons of groundwater-surface water interactions in standing and flowing waters. One such framework was developed to account for different ratios of subsurface meiofauna to macrofauna, and how their biological activities might affect the exchange of material between surface and groundwaters (Boulton et al. 2002b). The framework commences with predictions of changes along an axis corresponding to particle sizes ranging from fine sediments in the depositional zones of standing waters to the coarse sediments in streams where there is strong throughflow, as depicted in Fig. 9. This framework must be viewed in the context of the effects of disturbances such as spates that would cause burial, and the final model attempted to integrate disturbance frequency but remains to be tested. Not only can hydrogeologists assist with measurements and modelling of the interface characteristics at different flows (cf. Sophocleous 2002), there is scope to expand these models to catchment scales. This will allow prediction of the changes that would occur along gradients of sediment particle size and disturbance frequency along a river where groundwater-surface water interactions occur. Where disturbances are low and sediments are fine, the fauna may play a disproportionately important role in facilitating exchanges or altering the sediment matrix, and this ecological aspect could be incorporated into the hydrogeological model. it is suggested that most current hydrogeological models of groundwater systems do not explicitly include relevant ecological aspects such as stygofaunal activity or microbial processes.

The involvement of hydrogeological researchers in helping understand the ecological ramifications of groundwater-surface water interactions is not simply of academic interest. The implications of these groundwater links for the water quality and ecology of many surface water environments have been recognised by federal governments of several countries (Winter et al. 1999; Clifton and Evans 2001; Galloway et al. 2003) and as such, require legislation based on a suitable level of understanding to protect these environments and linkages (Boulton 2000b). Positive effects of managed flow releases down rivers upon the ecology of their hyporheic zone have been described (e.g., Hancock 2004) while a critical aspect of cave stream management has been the protection of their surface water recharge zones (Hamilton-Smith and Eberhard 2000). In both cases, hydrogeological features mediate the linkages but are poorly understood, compromising the application of suitable legislation.

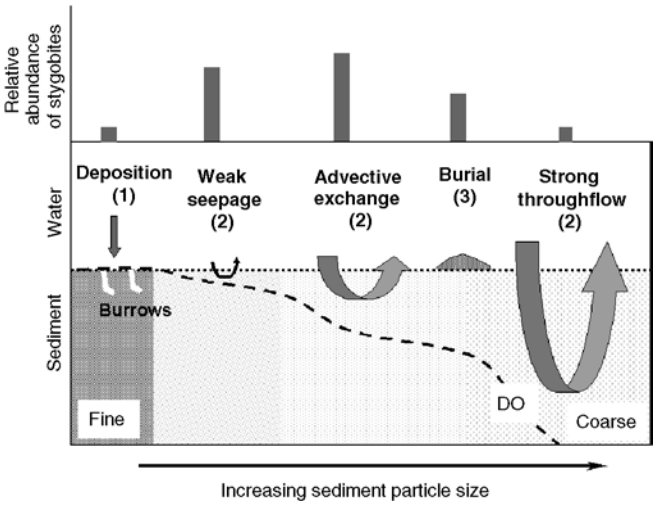

Fig. 9 Conceptual framework relating stygobites and hydrogeological parameters (grain size, hydrological exchange) between surface and subsurface habitats and how these affect organic matter pathways: 1 = deposition and settling; 2 = advective transport; 3 = burial by episodic events such as spates. The bold dashed line separates regions of lower dissolved oxygen (below) from relatively well-oxygenated sediments (above). Except for localised pockets near burrows in fine sediments, penetration of dissolved oxygen is related to ingress of downwelling water (modified from Boulton et al. 2002b)

"Groundwater estuaries" and saline waters

The seawater-groundwater interface is a site of considerable hydrogeochemical activity (Testa et al. 2002) and has been dubbed the "iron curtain," due to large amounts of precipitants (Charette 2001). Mixing between meteoric water and seawater produces brackish to saline conditions in many coastal aquifers, the depth of which may vary from a few metres in sand dunes (McLachlan et al. 1992) to many kilometres in karst (Iliffe 2000). Moore (1999) termed these "groundwater estuaries" and considered the analogy between subterranean and surface estuaries from a hydrogeochemical perspective. However, he did not draw the comparison at the microbial and faunistic level needed to integrate this concept with anchihaline ecosystems or other salinity stratified systems.

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Sometimes in these near-coastal waters, salinity stratification occurs: a point often overlooked due to the routine purging of bores prior to hydrogeochemical sampling. This information is important from an ecological point of view, as some species of groundwater fauna prefer to live in between layers of different salinities (W.F. Humphreys, unpublished data). These near-coastal groundwaters in karst and pseudokarst, where fresh or brackish water overlies seawater, may support specialised and unique ecological communities (Sket 1996) such as ancient relictual lineages spread over the former extent of the Tethys Ocean, which existed between Laurasia and Gondwana (Humphreys 1999). They occur in a complex physicochemical environment that supports microbial assemblages, including sulphur and nitrogen bacteria that yield chemolithotrophic energy to the ecosystem (Pohlman et al. 1997; Humphreys 1999). Chemolithotrophic energy sources may also be expected from the complex microbial communities found in other salinity stratified waters (Kinkle and Kane 2000). Such chemolithotrophic communities occur in stratified karstic groundwater (Holmes et al. 2001), and possibly groundwater close to salt lakes (playas), such as those in the palaeodrainage channels of the Yilgarn, Western Australia (Watts and Humphreys 2000; Humphreys 2001).

In comparison to groundwater estuaries, brackish water hyporheic zones (Williams 2003) also rely on hydrogeological processes to maintain ecological communities. In the River Aber, North Wales, U.K., hyporheic invertebrate communities changed in composition from fresh to brackish water toward the estuary, and were largely determined by sediment size, salinity and pH (Williams 2003). Fresh groundwater upwelling from the nearby aquifer was thought to be one of the dominant influences in determining salinity and pH, so in this respect hydrogeological conditions that affect the quality of the upwelling water and the hydraulic conductivity of the sediments could be critical to these communities.

Processes threatening groundwater ecosystems

From an ecological viewpoint, anthropogenic impacts on groundwater ecosystems have been categorised as either quantitative or qualitative (Danielopol et al. 2003). Quantitative impacts affect the volume or structure of the aquifer. Groundwater extraction including mine de-watering reduce the volume of saturated sediments while mining removes the sediment matrix (Hancock 2002). Impacts on water quality in the aquifer include processes such as sea-water intrusion and pollution. Not only are these types of impacts seldom readily reversible, they often occur so gradually that they are hard to detect until damage has been done.

Excessive groundwater extraction may lower the water table of an aquifer so much that it severs the links to the terrestrial ecosystems that rely on shallow groundwater to sustain them (Winter 1999). The drawdown of water dries the more porous part of the aquifer leaving the remainder unsuitable for stygofauna, as for example, in gravel aquifers and groundwater calcretes (Playford 2001). Sometimes, the drawdown results from changes in terrestrial vegetation above the recharge zone of groundwater habitats. Following the establishment of an exotic pine (*Pinus radiata*) plantation above a cave in South Australia, the water table fell by nearly a metre over five years (Grimes et al. 1995). Declines in the water table in other caves have been shown to threaten diverse aquatic communities (Jasinska et al. 1996) and alterations of surface-subsurface hydrological linkages are considered a major impact on most shallow aquifer ecosystems (Boulton et al. 2003).

As many stygofaunal communities have evolved to survive in stable environments (e.g., Leys et al. 2003), the rapid hydrogeological changes brought about by encroaching human activities potentially threatens their existence in many areas. Compounding this threat is the highly localised distribution of many species (Marmonier et al. 1993) and their apparent susceptibility to some pollutants (Notenboom et al. 1994). Stygofauna play key roles in aquifers including the maintenance of interstitial voids, modification of redox gradients, and the promotion of biofilm activity (Humphreys 2002; Gibert and Deharveng 2002). Therefore, their loss potentially compromises the functioning of the aquifer and its ecosystem, resulting in a decline in groundwater quality. Stygofauna communities in the hyporheic zone are particularly vulnerable to the development of both surface and groundwater resources (reviews in Boulton 2001; Hancock 2002) but seldom are considered explicitly in restoration programs.

Given the right conditions, groundwater microbes have the ability to degrade some pollutants (Haack and Bekins 2000). However, degradation may not be rapid enough to prevent the occurrence of substantial impacts to other organisms within an aquifer, or those in connected ecosystems. For example, following a break in a pipeline, liquid ammonium fertiliser entered the karstic strata of the Salem Plateau, Missouri, U.S.A., and travelled 21 km in just 12 days, killing hundreds of southern cavefish (Noltie and Wicks 2001). Contamination from sewage (Malard et al. 1994), metals (Plénet 1995), inorganic chemicals (Mösslacher 2000), and pesticides (Notenboom et al. 1994) have reduced diversity in various stygofaunal communities. Organic pollution can extirpate stygobitic fauna and lead to its replacement by stygoxens (Notenboom et al. 1994; Malard et al. 1994). For example, Culver et al. (1992) recorded the loss of cave isopods (*Caecidotea recurvata* and *Lirceus usdagalun*) and amphipods (*Crangonyx antennatus*) in the Cedars karst system, Virginia, U.S.A., as a result of organic pollution. The sensitivity of some stygofaunal species to pollution means that they can be used as biological monitors and indicators of declining water quality (Malard et al. 1996).

The intrusion of seawater into near-coastal aquifers has the potential to be a serious problem. Globally, the increased usage of near-coastal groundwater has resulted in a marked decline in the potentiometric surface and the consequent intrusion of seawater, sometimes exacerbated

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by engineering works or sea-floor dredging that breach confining layers and allow rapid infiltration (Moore 1999). Seawater intrusion changes ion exchange characteristics and has profound chemical consequences. Cycling of the potentiometric surface that results from changes in recharge and pumping rates may amplify the dispersal of seawater (and pollutants) in the aquifer, increasing the exchange between aquifer and coastal ocean (Moore 1999).

Existing groundwater sampling infrastructure and activities may also alter groundwater ecosystems, at least around the point of sampling. Monitoring wells may act as conduits for the rapid transfer of carbon from the surface into the aquifer. In some parts of Australia, large numbers of ants accumulate around the tops of monitoring wells (P. Hancock pers. obs. 2003). Although these wells are capped, ants can still enter them, fall into the aquifer, and decompose. These ants potentially provide a significant source of carbon to places where carbon would otherwise be scarce, and may encourage bacterial and stygofaunal communities to congregate around the well screen. This may affect the accuracy of water quality samples from the aquifer because bacterial activity is one of the main determinants of groundwater quality (Chapelle 2001).

Further, the aquifer surrounding existing wells may be contaminated with microbes (Griebler 2001) or invertebrates that were inadvertently introduced from other areas, or deliberately introduced during bioaugmentation. Historically, little consideration was given to the incidental transfer of bacteria and fauna from one well to another during routine groundwater sampling, and it is possible that significant inter-aquifer transfers of some species have already occurred. The impact of introduced bacteria and stygofauna is unknown. It may be that the conditions of the recently colonised aquifer is unable to sustain the new arrivals, as is currently the case with bacteria for many field-based bioaugmentation experiments (Wenderoth et al. 2003). However, as a precaution, standard sampling protocols should be modified to incorporate appropriate decontamination practices for all sampling equipment, regardless of the variable being tested.

The future of hydrogeology in the context of groundwater ecology

A strong case has been made to describe how hydrogeological variables drive the ecology of all groundwater and groundwater dependent ecosystems, either directly through aspects of matrix structure and geology or indirectly through hydrological linkages and flowpaths. Ecologists lack training in the measurement of many of these hydrogeological variables, especially in the difficult sampling environment posed by groundwater, so the first major contribution of hydrogeology is a methodological one. This would be best done in conjunction with the current process of inventory of groundwater biodiversity that is occurring in many parts of the world (e.g. the PASCALIS groundwater fauna project, Malard et al. 2001). These inventories typically assess several environmental features such as water source and local geology but would benefit from input from programs such as the karst-groundwater pollution vulnerability mapping program described by Daly et al. (2002). This program currently focuses on geological and hydrological variables but is not explicitly linked to any collection of ecological data. It is hoped that discussion of groundwater ecology in a journal about hydrogeology might stimulate this collaboration.

The educational aspect is especially critical for managers of groundwater resources. For groundwater use to be sustainable, it must be supported by relevant, high-quality research that addresses water resource needs and answers critical questions about the factors that control water quality as well as volume. This will require constant liaison among managers, hydrogeologists, and ecologists to identify and fill existing knowledge gaps. Comparatively more is known about the factors that influence groundwater volume and availability than about the processes that maintain its quality. It is likely that many biological processes (especially microbial) largely govern groundwater quality, as can be seen in the field of bioremediation. One significant contribution of hydrogeology in the future will be to understand how matrix structure, interstitial flow, and other hydrogeological aspects in different groundwater ecosystems control microbial activity. There is considerable scope for experimental manipulation of these variables, both in mesocosms in the laboratory as well as in aquifers where mining of natural resources and other activities will affect groundwater levels. Adaptive environmental management approaches (Gunderson and Holling 2001) that take advantage of monitoring hydrogeological and ecological responses to human activities potentially affecting groundwater are the obvious arena for this collaboration.

Integration of groundwater ecology, biogeochemistry, and hydrogeology promises significant advances in our understanding of subterranean aquatic systems. This is especially critical in bioremediation of contaminated groundwaters, maintenance or improvement of surface water quality in GDEs, and improved protection of groundwater habitats during extraction of natural resources. Hydrogeologists can provide information that leads to a better understanding of the effects of groundwater movement and aquifer geology on ecological processes such as carbon cycling and nutrient dynamics, subsurface faunal recruitment and persistence, and microbial activity and distribution. In turn, this understanding will enhance management of groundwater quality and quantity, support appropriate legislation for protection and sustainable use, and spawn collaborative, multi-scale research projects in the new field of ecological hydrogeology.

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