
Hydrogeology and groundwater ecology: Does each inform the other?

W. F. Humphreys

Abstract The known, perceived and potential relationships between hydrogeology and groundwater ecology are explored, along with the spatial and temporal scale of these relations, the limit of knowledge and areas in need of research. Issues concerned with the subterranean part of the water cycle are considered from the perspective of the biology of those invertebrate animals that live, of necessity, in groundwater and the microbiological milieu essential for their survival. Groundwater ecosystems are placed in a hydrogeological context including the groundwater evolution along a flowpath, the significance of the biodiversity and of the ecosystem services potentially provided. This is considered against a background of three major components essential to the functioning of groundwater ecosystems, each of which can be affected by activities over which hydrogeologists often have control, and each, in turn, may have implications for groundwater management; these are, a place to live, oxygen and food (energy). New techniques and increasing awareness amongst hydrogeologists of the diversity and broad distribution of groundwater ecosystems offer new opportunities to develop cross disciplinary work between hydrogeologists and groundwater ecologists, already demonstrated to be a field for collaboration with broad benefits.

Keywords Biologic conditions · Ecology · Microbial processes · Salt-water/fresh-water relations · Biogeochemical dynamics

Introduction

The relationship between ecology and hydrology is well recognised (Nachtnebel and Kovar 1991) and much explored, even termed ‘ecohydrology’ (Hayashi and Roseberry 2002). Yet, despite the recognition that groundwater and surface water form a continuum (Winter et al. 1998; Arthington et al. 1992; Boulton 2005), and that groundwa-

ter ecosystems may be expected to provide significant environmental services (Boulton et al. 2008), there has been sparse consideration of the effect of surface input or withdrawals on groundwater ecosystems, not yet an ‘ecohydrogeology’. This is partly because those concerned with both aquifers and surface waters are largely unaware of the ecological complexity, biodiversity and local endemism that are contained in groundwater ecosystems. While it is recognised that surface ecosystems have a call on both surface waters (Naiman et al. 2002) and groundwater resources (Hatton and Evans 1998), there is sparse recognition that groundwater ecosystems have such needs or even what environmental flows mean in the context of groundwater ecosystems (Humphreys 2006a).

This paper explores the issues concerned with the subterranean part of the water cycle from the perspective of the biology of invertebrate animals that live of necessity in groundwater, the obligate inhabitants, as well as their microbiological milieu. It extends to groundwater some of the issues discussed elsewhere in respect of hyporheic systems (Hancock et al. 2005). Biodiversity conservation effort is increasingly focused on subterranean life generally and groundwater species are increasingly recognised as being under threat of extinction. For example, groundwater species have been scheduled under wildlife laws in the USA (US Fish and Wildlife Service 2002) and Australia (Department of the Environment, Water, Heritage and the Arts 2008). In Western Australia, numerous species and communities are similarly scheduled (Department of Environment and Conservation 2008) and groundwater fauna are considered together with surface fauna and flora in the environmental review process for major resource projects (EPA 2003) during which hydrogeological information and expertise are commonly sought. Groundwater ecology has emerged formally as a discipline quite recently (Gibert et al. 1994a), but has gained recognition from international organisations such as the World Bank (Vermeulen and Whitten 1999) and the Council of Europe (1992). This is most comprehensively enshrined in the European Groundwater Directive (2006) to incorporate ecological knowledge gained from the various disciplines of groundwater science into schemes for environmental planning and policies, although not as comprehensive as that proposed by Danielopol et al. (2004). However, groundwater ecology has been built on a long tradition of research on groundwater (Chilton 1894) and cave life (Racovitza 1907), especially in Europe (Chappuis 1927;

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W. F. Humphreys (✉)
Western Australian Museum,
Locked Bag 49, Welshpool DC, WA 6986, Australia
e-mail: bill.humphreys@museum.wa.gov.au

Delamare Deboutteville 1960) and North America (Packard 1871). The recent integration of groundwater sciences, including hydrogeology and groundwater biology, addresses groundwater ecology at the landscape scale (Danielopol et al. 2007) and this has occurred in parallel with the recent recognition that biological diversity of groundwater is much greater than formerly appreciated and much more widespread (Sket 1999; Culver and Sket 2000; Wilkens et al. 2000; Danielopol et al. 2000; Danielopol and Pospisil 2001). For example, a decade ago there was little knowledge of the groundwater fauna of Australia but it is now known to be very biodiverse, especially in the arid zone, already well exceeding that of the contiguous USA (Humphreys 2006a, 2008).

Groundwater ecosystems may be very persistent through geological time and the obligate groundwater dependent faunas they support are often important in unravelling deep history (Humphreys 2008). The species they contain may inform on the persistence of aquifers through major episodes of climate change such as periods of regional aridity (Leys et al. 2003), ice ages (Bjarni et al. 2007), orogenic and tectonic events at both local (Caccone et al. 1994; Boutin 1993; Boutin et al. 1997) and global scales (Schminke 1974; Cho et al. 2006; Wilson 2007, 2008), as well as the evidence of major marine incursions (Longley 1992) and the extent of Tethys (Jaume et al. 2001). In this way, aquifers may be living museums containing a sample

of the lineages that comprised the faunas from various geological periods, but they are dynamic systems comparable in complexity to surface ecosystems (Rouch 1977; Gibert et al. 1994a). Most recently it has been recognised that subterranean animals, which are overwhelmingly crustaceans (Figs. 1 and 2), can represent a significant component of regional biodiversity (Sket 1999; Culver and Sket 2000), typically in functionally truncated ecosystems (Gibert and Deharveng 2002) because, in the absence of light, there are no photosynthetic plants.

Using imported or in situ supplies of energy, subterranean fauna occur in all types of aquifers having voids of suitable size for a species' biology, variously in epikarst, classic limestone karst, pseudokarst (often sandstone, lava or laterite), fractured rock, calcretes, pisolites and widely in alluvial aquifers (Humphreys 2008) but where the size of the interstices may limit the distribution of many species (Pospisil 1994).

There is increasing focus on the potential of groundwater communities to inform on the connectivity and stability of aquifers (Bournaud and Amoros 1984; Messouli 2006; Guzic et al. 2008), water tracing (Pipan and Culver 2007a, b) and present (Finlay et al. 2006) or past connections (Buhay et al. 2006). In the Kolbental Valley, Germany, changes in the composition and density of groundwater fauna were found to be the best indicators of the effects of groundwater pumping on a surface

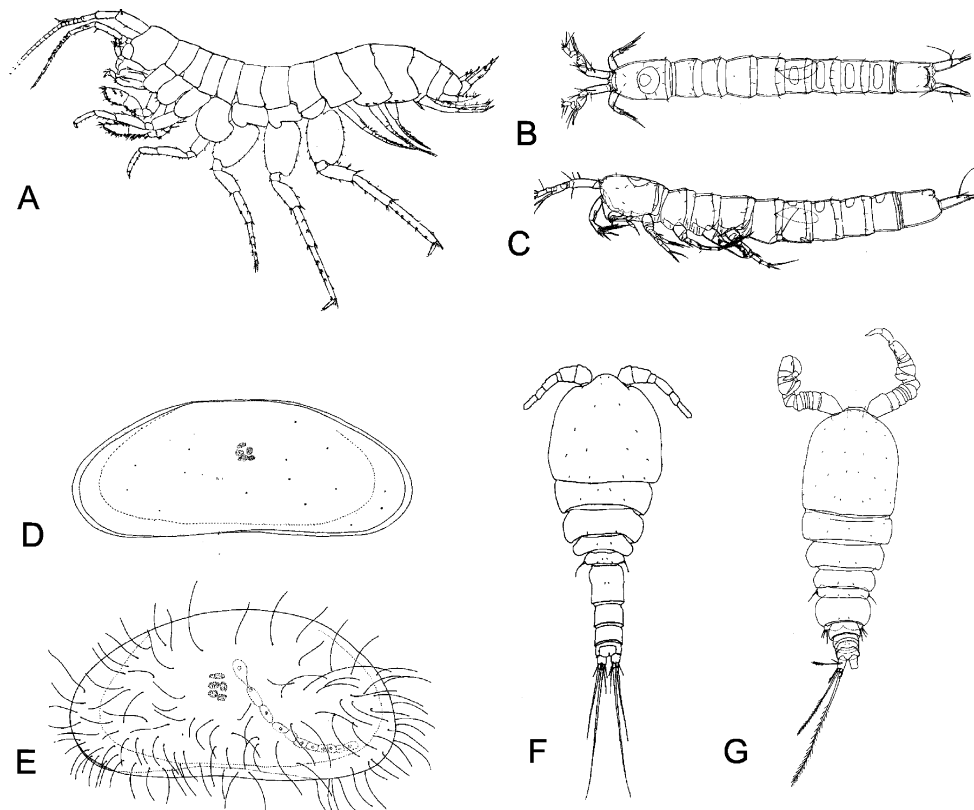


Fig. 1 Line drawings of various groundwater invertebrates. **a** *Chydaekata acuminata* Bradbury 2000 (Amphipoda, Paramelitidae); **b–c** *Parastenocaris jane* Karanovic 2006 (Copepoda, Parastenocarididae); **d** *Candonopsis (Abcandonopsis) indoles* Karanovic 2004; **e** *Candonopsis (Candonopsis) sumatrana* Karanovic 2004; **f** *Halicyclops (Rochacyclops) calm* Karanovic 2006 (Copepoda, Halicyclopiinae); **g** *Fiersicyclops (Pilbaracyclops) frustratio* Karanovic 2006 (Copepoda, Cyclopiinae). With permission

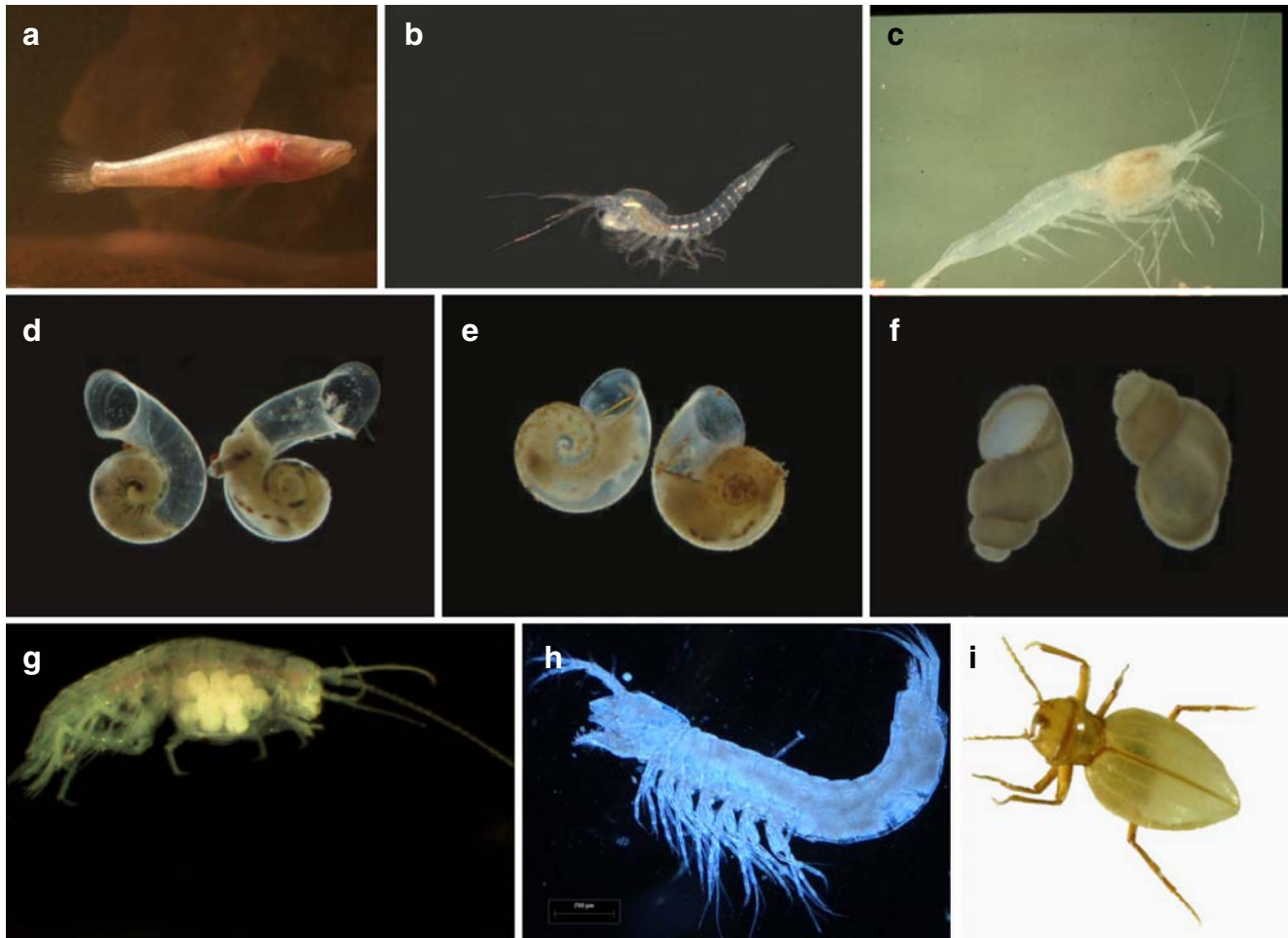


Fig. 2 Images of groundwater animals from Australia—indicative length mm—showing pale translucent bodies and absence of eyes, convergent characters in subterranean animals irrespective of taxonomic group. **a** Blind gudgeon, *Milyeringa veritas* (Eleotridae) - indicative lengths, 50 mm; **b** *Halosbaena tulki* (Thermosbaenacea), 3 mm; **c** *Stygiocaris stylifera* (Atyidae), 5 mm; **d-f** undescribed gastropods (Hydrobiidae), ca. 4 mm; **g** undescribed amphipod with eggs, 6 mm; **h** undescribed Bathynellacea, 1 mm; **i** *Nirripiarti arachnoides* (Dytiscidae), 2.3 mm. Photos: **a–b** D. Elford, Western Australia (WA) Museum; **c–f** W. Humphreys, WA Museum; **g** E. Volschenk, WA Museum; **h** P. Hancock; **i** C. Watts

groundwater dependent ecosystem. These were much more sensitive indicators than changes in hydrochemistry, or other ecological indicators in the groundwater dependent ecosystem at the surface (Hahn 2007), changes which indicated that pumped water was derived from the fractured rock aquifer bordering the valley, rather than from along the valley alluvial aquifer in which the wells were established.

These various attributes mean that groundwater can be as interesting to biologists as it is to hydrogeologists and it is contended that both disciplines have much to learn from each other. Working together will achieve better management outcomes for the sustainable utilisation, conservation, and remediation of groundwater, a resource that is often overexploited and contaminated, but on which humankind is increasingly dependent. In the context of surface waters, Dudgeon et al. (2006, p. 555) considered that the “Conservation of biodiversity is complicated by the landscape position of rivers and wetlands as ‘receivers’ of land-use effluents, and the problems posed by endemism and thus non-substitutability”, a statement of even greater

force when applied to groundwater which typically supports short-range endemic species.

Subterranean animals

Obligate groundwater animals are termed stygobites (var. stygobionts: Figs. 1 and 2) which commonly are white, lack eyes, and are often translucent and vermiform (worm-shaped), amongst other adaptations to subterranean life (Coineau 2000). They typically have no resting or dispersal stages, are slow-growing, long-lived and have few young (Fig. 1g), attributes that make them efficient bioaccumulators (Plénet et al. 1992), and slow to recover from reductions in their populations and difficult to study. Vertebrate stygobites (fish and salamanders) occur in karst and pseudokarst but elsewhere stygobites are invertebrates, predominantly comprising crustaceans but with a range of other phyla (including Platyhelminthes, Annelida, Nematoda, Mollusca, Arthropoda, Pisces and Cau-

data; Fig. 2) that, together with protists, Bacteria, Archaea and Fungi, are part of the ultimate groundwater dependent ecosystem (Humphreys 2006a). Groundwater fauna have three fundamental requirements, a place to live, energy (food), and oxygen or other electron acceptor (Lovley and Goodwin 1988), each of which can be affected by activities over which hydrogeologists often have control, and each of which, in turn, may have implications for groundwater management (Humphreys 2002).

A place to live

Groundwater ecosystems are dependent on subterranean water-filled voids that may vary in scale through orders of magnitude (Boulton 2001) from the spaces between particles in alluvia to massive caves and conduits in some lava tubes and karsts such as the 570 km of passages of the Mammoth Cave system in Kentucky, US (White and White 2003). Groundwater provides the essential milieu for groundwater animals, but may itself have formed the voids within a matrix required as living space by stygofauna (Humphreys 2001), for example, in cave and conduit formation in tufa and karst (Ford and Williams 2007), saltwater interface caves (Myroie and Carew 1995), and voids in lava (Perfit et al. 2003). Under some circumstances the hydrogeochemical evolution along the groundwater flowpath may cause the deposition of the matrix itself, as in groundwater (valley) calcretes (Mann and Deutscher 1978; Arakel 1986; Morgan 1993), and pisolites that, for different reasons, have temporally inverted sequences of deposition (Mann and Deutscher 1978; Heim et al. 2006).

Subterranean waters may conveniently be separated into groundwater and the hyporheic waters that occur below river channels but exchange with surface water (Jones and Mulholland 2000) and which form a broad ecotone between surface water and groundwater; this paper is concerned with the obligate groundwater animals but these may occur in both the hyporheic zone and springs. Animals are mostly restricted to the upper parts of subterranean ecosystems but in karst systems diverse stygofaunas may be found at depth, vertebrates to several hundreds of meters in artesian aquifers (Longley 1992), and invertebrates to 1 km (Essafi et al. 1998).

Groundwater ecosystems are complex, as different species are adapted to subterranean habits to different degrees and because of the wide variety of ecological niches available within groundwater ecosystems. Hence, there is a hierarchy of adaptation represented by time/distance along a flowpath or distance from the surface, as, for example, along the Rhône aquifer (Dole-Olivier et al. 1994), a hierarchy that is imposed in four dimensions: vertically through the hyporheic zone or below the groundwater surface, or river bed; laterally with distance from the river bank; longitudinally along the river basin; and through time along the flowpaths. Because groundwater flux is also related to these linear distances, there is a complex interplay between temporal and linear 'dis-

tances' along a flowpath, attributes also of interest to hydrogeologists. Groundwater flowpaths can be extremely long or very short (local, intermediate, regional; Chapelle 2001) in both spatial and temporal dimensions but, depending on the aquifer properties, a short spatial flowpath may have a long temporal flow path. These issues are well recognised in karst ecosystem studies where the rapid transit of water through open conduits (Mangin 1975) carries with it a groundwater fauna distinct from that found in the long residence time water of the karst matrix (Rouch 1977, 1986) which itself may support stable autochthonous microbial endokarst communities (Farnleitner et al. 2005).

Groundwater flow paths and responsiveness can have very long temporal scales; the Great Artesian Basin, Australia, has transit times of ~1.5 Ma (Commander 2004), while the aquifers in semi-arid Australia are in a state of net discharge (Hatton 2001) and bear witness to widespread oscillating climatic and fluctuating hydrologic conditions after the last interglacial (English et al. 2001; review in Hesse et al. 2004). Groundwater residence time is a significant factor in the hydrogeochemical evolution of groundwater, the properties of which are important to aquifer ecology that, in turn, influences the hydrogeochemical evolution (discussed in the following).

Adverse effects on a place to live

Hydrogeologists may be variously involved in actions that are overtly detrimental to stygofauna, for example removal of the matrix itself (mineral mining where open pits convert groundwater to surface water), or widespread removal of the groundwater (sustainable water abstraction, water mining or dewatering operations during civil engineering or mining projects). The effect of such activities on biodiversity will depend on whether draw-down proceeds to below the zone of voids suitable as living space, or whether a species is restricted to the area of impact (small-scale endemism: Leys et al. 2003; Lefebure et al. 2006; Cooper et al. 2007, 2008; Guzik et al. 2008), as well as the magnitude of the dewatering operations. Although the effects of such activities on subterranean ecosystems has received general interest in Western Australia (Playford 2001) and internationally, knowledge is sparse. For example, there has been almost no study of the impacts of water abstraction on aquifer ecosystems (Rouch et al. 1993; Longley 1992), and fauna may be lost rapidly following contamination (Iliffe et al. 1984). At Lyon, France, enhanced recharge increased population density and stygofauna species richness but the effects depended on the thickness of the vadose zone (Datry et al. 2005), and increased energy input may permit the successful invasion of surface forms into a previously oligotrophic environment (Notenboom et al. 1994; Malard et al. 1994). Resolution of such issues depends on access to comprehensive information on the nature and composition of the stygofauna, as well as a deep understanding of the hydrogeological environment.

Pumping is considered excessive if it results in deterioration in groundwater quality, irrespective of whether or not there is excessive drawdown (Margat 1994). Whether this is over-exploitation depends on the criteria used, but historically, these typically would not include effects on groundwater fauna. “In practice, overexploitation diagnoses are made a posteriori on the basis of observed symptoms of prolonged imbalance—continued drawdown, possible effects on boundary flows, and water quality” (Margat 1994, p. 515). Little information is available on the effect on stygofauna of changes to groundwater abstraction or to flow rates. Covertly, pumping induces low flow velocity in the groundwater, without which hypogean fauna may be sparse (Gibert et al. 1994b). However, prolonged pumping completely modifies the groundwater habitats and the faunal assemblages around the pumping well (Dole and Chessel 1986). By reducing the downstream flow volume, water abstraction will reduce the flux of oxygen and of dissolved organic carbon (DOC) at downstream stations in the aquifer, alter the redox gradients and change the vertical and lateral gradients in the flux of DO and DOC (Fig. 3). As biofilms exhibit developmental stages comparable to those seen in other complex ecosystems (Jackson et al. 2001), they may be expected similarly to be driven to different ecological stages by changed conditions, amongst which groundwater flow will be a large driver because all flow enhances biogeochemical inputs (Burnett et al. 2006).

Changed flow affects the flux of organic carbon in groundwater, a factor that has a significant influence on the physicochemical variables such as pH and redox (Eh) and, thus, on the hydrogeochemical evolution of groundwater (Pérez del Villar et al. 2004). Organic carbon (OC) is processed and consumed by groundwater animals and so their presence will accelerate the depletion of OC and DO and consequently shorten the spatial and temporal vectors of hydrogeochemical evolution (Fig. 3). The effect of changes in water quality can be illustrated with uranium series elements. Having several oxidation states, the mobility of uranium in natural environments is directly affected by changes in solution composition, redox, pH and concentration of certain complexing agents. Conversely, thorium and radium, with one oxidation state, are less affected by redox but are very sensitive to pH changes (Wanty and Schoen 1991). These properties are amongst those influential in the fractionation of heavy metals and the deposition of the groundwater calcretes in arid Australia (Morgan 1993) which are important aquifers supporting considerable biodiversity (Humphreys 2008).

Ecological understanding of low flow conditions is rudimentary even in surface waters (Lake 2000) but pointers from surface studies do suggest that pumping effects are likely to be profound and complex depending on the intensity and duration of the abstraction, or change in flow rate as a result of changing piezometric head. Surface water withdrawal for irrigation had both direct and indirect effects some of which may be pertinent to groundwater habitats (Miller et al. 2007). Direct effects (decreased velocity, depth and wetted habitat) on fauna were proportional to the amount of water withdrawn,

whereas indirect effects (increased electrical conductivity and temperature) changed relative abundance, but not the functional feeding groups, only when withdrawal exceeded 85% ambient levels (Miller et al. 2007).

There is some familiarity with the impact of groundwater abstraction on surface groundwater dependent ecosystems (e.g. Eamus and Farrer 2006; in USA, Loftus et al. 1992; in Australia, Hatton and Evans 1998). However, although the most clearly groundwater-dependent ecosystem is that occurring in the groundwater itself (Hatton and Evans 1998; Humphreys 2006a), information is sparse on the impacts of water abstraction on the ecosystems within aquifers (Rouch et al. 1993), especially deep aquifers (Longley 1992). Groundwater levels may vary as a result of regional climatic change (Heim et al. 2006) or drainage capture (Barnett and Commander 1985) but such slow changes may not eliminate stygofauna (Humphreys 1999a). In contrast, groundwater pumping may lead to relatively rapid changes in groundwater level, as, for example, in the stygofauna rich Edwards Aquifer, Texas, USA. This community, comprising both vertebrate and invertebrate stygobites with marine and freshwater affinities, is under threat due to pumping that is withdrawing almost all the natural recharge. The adverse effects are caused by loss of spring flows, dewatering of parts of the karst, and saltwater intrusion (Longley 1992). In France, a brief high discharge pumping test on three occasions over 4 days in Baget karst (Ariège) lowered the water level by as much as 21 m below the water table. This resulted in increased microcrustacean drift (mainly harpacticoid copepods) and the karst groundwater community had not recovered after 1 year (Rouch et al. 1993). In the Kolbental Valley, Germany, changes in the composition and density of groundwater fauna, assessed using the methods in Hahn (2006), were indicators of the effects of groundwater pumping and were much more sensitive indicators than changes in hydrochemistry, or other ecological indicators in the groundwater dependent surface ecosystem (Hahn 2007).

Groundwater production typically aims not to deplete the resource excessively and may result in only local drawdown with little direct loss of habitat in the ecosystem, although the properties of the ecosystem may change profoundly. Rising groundwaters in aquifers previously drawn down produced considerable changes in groundwater chemistry in the London Basin, UK, through a range of physical and chemical processes (Mühlherr et al. 1998). Mining below the water table often requires extensive dewatering of the regolith which will reduce the volume or entirely eliminate the groundwater habitat, as, for example, the regional dewatering of the dolomite karst overlying the goldfields in Gauteng, South Africa (Buttrick 2005). Due to the special nature of groundwater biodiversity, Notenboom et al. (1994), writing of invertebrates, considered that there was a high probability of complete species extinction as a result of groundwater abstraction and this view is reinforced by the realisation, as discussed above, that many, even most groundwater species occupy very circumscribed areas—e.g.,

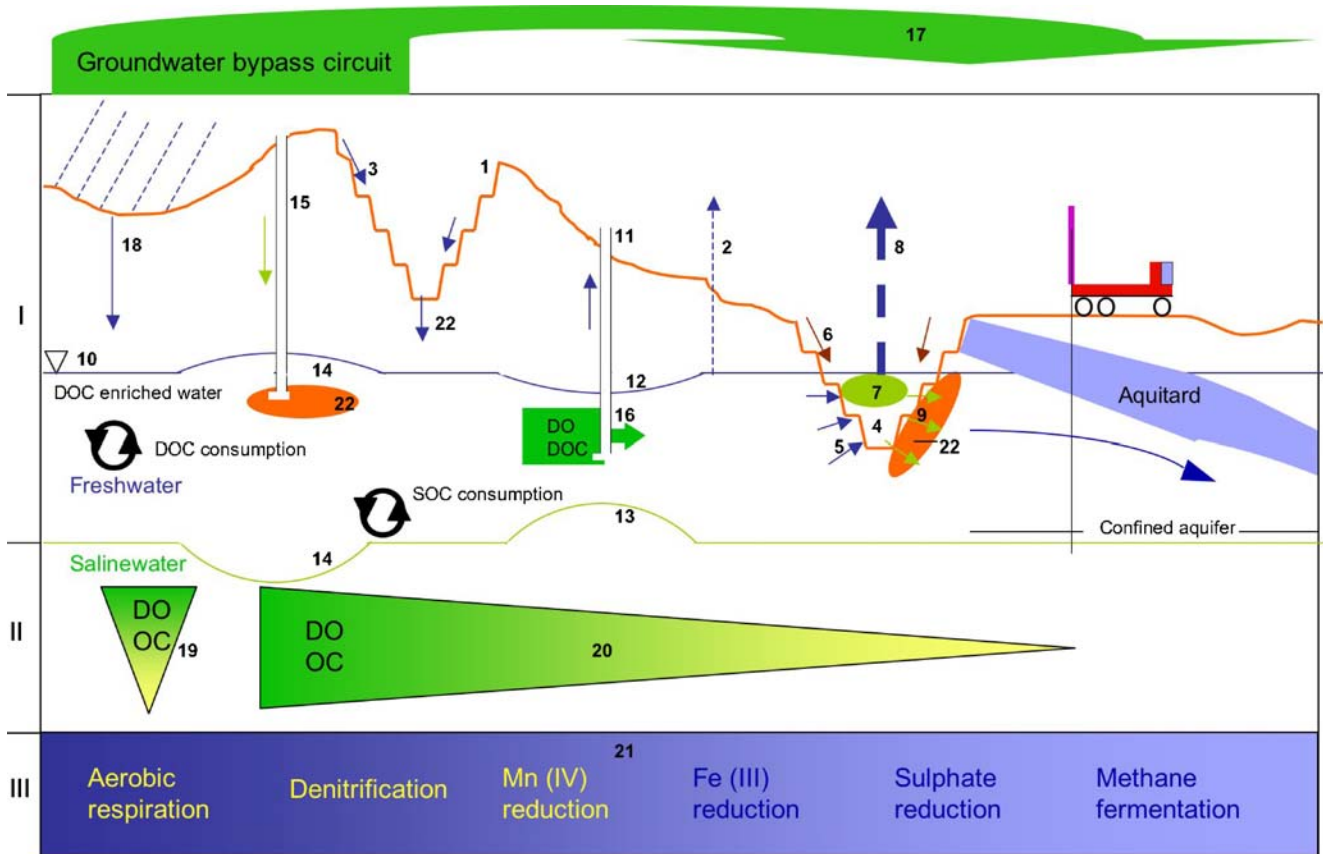


Fig. 3 Schematic diagram depicting (I) some anthropogenic impacts on the biogeochemical evolution of salinity stratified groundwater (GW) along its natural flowpath; (II) changes in dissolved oxygen (DO), and particulate (POC) and dissolved organic carbon (DOC) content, subsets of organic carbon (OC), and organic matter deposited in sediments (SOC), with depth and along the GW flowpath; (III) changes in metabolic pathways along redox (Eh) gradients—which can be very complex (Chapelle 2001)—at spatial scales (10^{-2} – 10^2 m) between boundary layers and along flow paths in confined aquifers. Note that the horizontal axes of panels I, II, and III are unrelated. Ground level (I): changes to the ground surface impact GW in many ways. Distance between ground surface and water table (2) affects evaporation influencing GW evolution especially in arid areas (Arakel 1986); 10 m is typical depth of GW calcretes (Jacobson and Arakel 1986) and to avoid salination from irrigation (FAO 1967, cited in McCrea and Balakumar 2004). Changed surface morphology affects rate, quantity and quality of recharge (3). Excavation below the water table removes matrix within which GW ecology occurs (4), forms surface water from the GW (4); may act as a lens to GW flow (5) through the void, as in GW flow through lakes (Nield et al. 1994); is a focus for contamination (use as watering point for stock/wildlife concentrates animal waste into the water (6; personal data) and eutrophic conditions (7) that favour invasion of GW by surface species (Notenboom et al. 1994; Malard 1995); increases evaporation (8) and salinity of downstream GW flow (9). Groundwater surface (10): Change in GW level effects evaporation by altering the distance to the ground surface (cf. 2), may rise GW above surface forming surface water but, in contrast to 2, without reducing the available GW habitat. Lowering GW surface may reduce GW evaporation and volume of aquifer and may fragment area of occupancy of GW organisms or fall below the level where aquifer matrix is suitable for GW animals and so lose any contribution to water quality dynamics. Water abstraction (11) dimples GW surface with drawdown cones (12) and, in salinity stratified aquifers, the upconing of the saltwater interface (13) will be amplified by the Ghyben-Herzberg effect (Chow 1964), the expression being reversed (14) below sites of artificial recharge (15). Down flow of an abstraction site (11) the flux of DO and DOC is reduced (16) but, conversely, these fluxes may be increased downflow of recharge sites (15), depending on the nature of recharge water. A GW bypass circuit past a mine pit (17) introduces ‘young’ water into an aquifer that is at a later stage of hydrogeochemical evolution possibly inimical to existing GW ecology. Oxygen and organic carbon: Natural recharge (18), DO and OC entering GW are depleted by metabolism with increasing depth (19) and along the GW flowpath (20), altering redox (Eh) conditions and contributing to the biogeochemical evolution (21) of GW. Changes to the flow vector near and downstream of abstraction (11) and injection (15) wells, and occlusion of pore space by sediments mobilized by GW injection and earthmoving (22), will alter supply of reactants and dynamics of GW ecology (16, 19, 20, 21)

many inland aquatic isopods are small range endemics that are easily lost from surface or groundwater habitats through human over-exploitation of water (Wilson 2007). However, some groundwater systems can be locally resilient to point source impacts, whether by drawdown or pollution, because repopulation of the karst network can occur from refugia adjacent to the principal drainage axis (Turquin 1981). However, in the Pilbara, Western Australia, Finston et al.

(2007), using molecular methods, found groundwater tributaries of palaeodrainage systems with episodic surface flow to contain groundwater amphipod populations that have been separated for between 2.0–8.9 Ma, indicating that these tributaries cannot serve as refugia for species inhabiting the palaeodrainage system. The extent to which this is true for recent tributaries within a catchment is poorly understood.

Changes to water basic chemistry. Quite modest changes in species composition can have major implications for the functioning and, consequently, for the ecological services that an ecological community may provide. Boulton et al. (2008) discussed the fundamentals of groundwater ecosystem functioning, indicating that subtle differences in water chemistry may alter groundwater ecology. One example is the importance, not of gross water chemistry, but of ionic balance to some stygofaunal species. Diverse stygofaunas occur over a wide range of groundwater salinities in Australia (Humphreys 2006a), largely in groundwater calcrete aquifers that evolve partly by evaporation. While salinity per se is also not a prime determinant of the distribution of many species in either marine estuaries (Wolff 1973) or salt lakes (Williams et al. 1990), the ionic ratio can be the determining factor in species distribution in brackish water even when salinity is comparable (Pora 1969). This is related to the relative amounts of Ca^{2+} , Mg^{2+} , SO_4^{2-} and HCO_3^- in solution and determines how mineral precipitation causes branch points in solute evolutionary pathways in evaporative systems (Hardie and Eugster 1970; Eugster and Jones 1979).

This focus has been applied to groundwater/salt lake research to great effect, particularly using ostracods as palaeoclimate indicators (Radke 2000; Radke et al. 2003). In the Pilbara, where there is a great diversity of groundwater Ostracoda (Karanovic 2007), which produce calcium ‘shells’, their presence was predominantly determined by pH and carbonate saturation; water with low pH, with Eh values indicating a reducing environment, or with a total nitrogen concentration in excess of 10 mg L^{-1} rarely contained Ostracoda (Reeves et al. 2007). Consequently, the transfer of groundwater of different chemical composition, often quite subtle, between aquifers, or to another part of an aquifer where the water is at a different stage of hydrogeochemical evolution, may result in changes to community structure and subsequent ecosystem services. Such inappropriate transfers can arise both by overt actions such as using water of quite different origins or the recycling of oilfield produced water through the aquifer. It may result from more subtle actions such as shortening the natural flowpath by, for example, diverting (piping) groundwater past a mine site (Fig. 3) so that it returns to the aquifer earlier in its hydrogeochemical evolution and thus potentially altering the groundwater ecosystem. This may also be an issue for more overt differences especially pertaining to temperature, DO, DOC, Eh and pH.

Saltwater intrusion into aquifers is a common issue in hydrogeology and arises principally from two causes. Firstly, excessive drawdown of the groundwater surface in salinity stratified aquifers (Fig. 3) so that, through the Ghyben-Herzberg effect, salt water up-cones into the exploited part of the aquifer (Ford and Williams 2007), even between different aquifers (Reilly 1993). Secondly, excessive pumping of near-coastal aquifers causes the coastal saltwater wedge to propagate inland, contaminating the exploitable freshwater aquifer, sometimes irredeemably. Because microbial life concentrates at physical and chemical interfaces where energy and nutrients fluctuate most dramatically

(Ash et al. 2002), groundwater estuaries and the freshwater-saltwater interface are regions of substantial biogeochemical activity (Moore 1999; Charette and Sholkovitz 2002; Testa et al. 2002; Pohlman et al. 2000). Therefore, displacement of this zone (“iron curtain”, Charette 2001) within the aquifer, either laterally or vertically, is expected to influence the hydrogeochemical evolution and the biogeochemical dynamics of the aquifer. From a stygofauna perspective, best known are anchialine systems, which are groundwater ecosystems that lack surface connections with the sea but are affected by marine tides, and exhibit marked physicochemical stratification, especially salinity (Sket 1996), and complex microbiology (Seymour et al. 2007). They contain a large number of higher crustacean taxa that only inhabit anchialine systems but comprise locally endemic species belonging to widely vicariant genera (Ilfie 2000; Jaume et al. 2001). Groundwater calcretes associated with salt lakes have similar properties and also contain rich, locally endemic stygofauna, though of very different origin (W.F. Humphreys, Western Australian Museum and University of Adelaide, unpublished data, 2006). As with wetlands (McDonald et al. 1998), the effects of salinity intrusion on subterranean estuaries (Moore 1999) can vary over a range of temporal and spatial scales even within the same system.

Hydrogeologists may also advise on other human activities with less overt effects on subterranean ecosystems. In both hyporheic systems and cave streams, the mobilisation of fine sediments, for example by dredging, quarrying or removal of vegetation, can clog sediment spaces (‘internal colmation’, Brunke and Gonser 1997) and smother surfaces (Eberhard 1995, 1999; Hamilton-Smith and Eberhard 2000). Such effects may also be expected to impact similarly on aquifer ecosystems and the resulting disruption of hydrological exchange reduces dissolved oxygen concentration (DO) and may lead to the extirpation of stygal populations (Boulton 2000a; Boulton et al. 2008). The movement and feeding activity of macrofauna in sediments (bioturbation) has profound effects on the ecological dynamics of sediments by maintaining voids and so the hydraulic conductivity (Mermillod-Blondin et al. 2005), and, in experimental microcosms, enhance ecological function in hyporheic systems (Nogaro et al. 2006), but it is unresolved whether this occurs also in deeper aquifers and it may be site dependent (Danielopol et al. 2000).

Groundwater fauna is sensitive to the environmental characteristics of the water it inhabits and there is increasing evidence of the fauna’s potential as indicators (monitors) of groundwater health (Sinton 1984; Committee 1991; Malard et al. 1994; Simon and Buikema 1997; Plénet et al. 1992; Mösslacher et al. 2001; Notenboom et al. 1994) and that, rather than relying solely on hydrodynamical, physico-chemical and bacteriological data, stygofauna investigations should be incorporated into groundwater monitoring, management and protection programmes (Malard et al. 1996a; Tomlinson et al. 2007). Humphreys (2000) proposed that recovery of the groundwater ecosystem should be the criterion

for successful restoration of contaminated groundwater sites—such an ecosystem focus would permit circumstances in which contaminant recovery may be contraindicated, and others in which the status of groundwater (e.g. ionic balance, see above) is a contaminant.

Sewage polluted sites have been shown to exhibit large changes to species composition and relative abundance with respect to uncontaminated sites (Lez karst system, Hérault, France: Malard et al. 1996b. Alluvial aquifers, New Zealand: Scarsbrook and Fenwick 2003). Contamination from sewage (Sinton 1984; Malard et al. 1994; Simon and Buikema 1997), urban run-off in Montana, USA (Stanford et al. 1994), metals (Plénet et al. 1992), inorganic chemicals (Mösslacher et al. 2001), and pesticides (Notenboom et al. 1994) have been found to reduce diversity in stygofaunal communities. Organic pollution can extirpate stygofauna and lead to its replacement by epigeal fauna (Notenboom et al. 1994; Malard et al. 1994). For example, septic effluent in Banners Corner Cave stream (Virginia, USA) increased the food supply for the stygofauna but damaged the ecosystem (Simon et al. 2003) and Culver et al. (1992) recorded the loss of cave isopods and amphipods in the associated Cedars karst system as a result of organic pollution.

Drilling, whether for hydrological, geotechnical or mineral exploration or production, can impact groundwater ecosystems. The process of drilling can directly affect the properties of aquifers. For example, air percussion drilling altered the physical, chemical and biological properties of groundwater in unconsolidated sediments so severely as to compromise the sites as monitoring bores (Malard et al. 2005). A bore, whether or not cased, can act as a conduit for organic matter to the groundwater by pit-fall effect (Hancock et al. 2005) or by root growth (Humphreys 2006a). In groundwater production areas there are, typically, regulations that aim to prevent the mixing of aquifers, but this is less commonly the case regulating mineral exploration bores (=wells) when there is potential to mix waters of different quality, or to mix groundwater ecosystems of a different character. Cross contamination of microbes between aquifers at different depths is likely to be pervasive, and there is a high risk of transferring microbiota on drilling gear (Chapelle 2001) between regions, even continents, as has been well recognised in the debate over the existence of microbes deep in the earth (Amend and Teske 2004) and the impending penetration by drilling of Lake Vostok, Antarctica (Walker 1999), yet to occur.

Mining wastes may pose a major challenge both to hydrogeologists and ecologists attempting to mitigate or prevent impacts of inappropriate practices. Stygofauna may show both qualitative and quantitative changes associated with drainage from metal sulphide tailings, including those containing Pb, Zn and Cu (El Adnani et al. 2007) which can be toxic to aquatic animals, and profoundly affect their behaviour even at low concentrations (Pyle and Mirza 2007). A complex case of acid mine drainage, with profound health and environmental implications, is developing in Gauteng, South Africa, where a large karst area

was dewatered extensively to permit the development of the Rand gold mines. Some mines have been abandoned and flooding of the exposed sulphide rocks is causing uranium-rich (Winde 2006) acid mine drainage through the karst. Because there is a warren of old mine galleries penetrating the continental divide, the mine flooding is causing acid mine drainage to decant on both sides of the divide, that to the north-east draining towards the Cradle of Humankind World Heritage Area (Krige 2006), a karst area containing groundwater fauna (S. Tasaki, North West University, personal communication, 2007).

Groundwater sampling

Water quality information

Hydrogeological tomes dealing with sustainability typically do not mention groundwater ecosystems, outside the context of bioremediation (Robins 1998; Hiscock et al. 2002). Yet, hydrogeologists often advise on groundwater dependent ecosystems (GDE; Rutherford et al. 2005) and, increasingly in concert with biologists, on subterranean GDEs (Hatton and Evans 1998; Playford 2001). Development proposals may involve the implications of drawdown, groundwater flow, groundwater flow by-pass around mine sites, supplementation of local areas (cave ecosystems dependent on Gngangara Mound, Perth, Western Australia: Jasinska 1995), or to artificially charge aquifers, variously for de novo, enhanced or recharge storage, disposal of storm water or of produced water in oil fields (Humphreys 2002), other waste disposal, and acid in situ leach mining (Mudd 2004). In this section, issues are raised pertaining to some biological attributes, the implications of which are not broadly appreciated but which raise vigorous debate. Very sharp gradients in biogeochemical conditions, spanning orders of magnitude in chemical concentration (Boulton et al. 2002), may occur through the water column (Ronen et al. 1986), even at the microscale, naturally or caused by anthropogenic inputs and are suspected to occur generally (Ronen et al. 1987b). Such stratification is also seen in salinity stratified waters (Fig. 3) in both continental karstic (Watts and Humphreys 1999, 2004), and anchialine systems (Humphreys 1999b; Seymour et al. 2007), and in groundwater estuaries (Moore 1999) and this structuring is known to have significant geochemical (Moore 1999) and biological implications (Humphreys 1999b; Pohlman et al. 2000; Seymour et al. 2007).

Routine groundwater monitoring is conducted on samples taken from purged wells (3–5 well volumes of water are removed before sampling; Harter 2003). The water sample taken then represents the integral through depth of the flow rates from the aquifer to the monitoring well, rates that may vary with depth. Consequently, the resulting water quality measurements are pertinent only to the end user of the water produced. However, within the aquifer none of the water might have this characteristic and this misinformation may mask substantial differences, or even modest ones, that may be of significance to the groundwater ecosystem. Purging prevents the recording of

physicochemical structure in the water column that would inform groundwater ecology (Humphreys 2002). Obtaining groundwater quality information of utility both to hydrogeology and groundwater ecology might be incompatible and to better understand groundwater ecology it may be necessary, routinely, to undertake physicochemical profiling of undisturbed groundwater. Investigations of in situ biological and hydrochemical conditions, which are tractable in the hyporheic zone (Bou and Rouch 1967; Stocker and Williams 1972; Hahn 2002), are more difficult in deeper groundwater but have spurred novel techniques such as filtering aquifer outflows (Hahn 2005), aseptic sampling (Dunlap et al. 1977), and depth specific sampling of water and fauna (Schmidt et al. 2007b; Hahn 2007), that are the focus of increasing attention (Hahn and Matzke 2005; Schmidt et al. 2007a).

Food and energy sources

As groundwater ecosystems are perpetually dark, they are dependent for their energy on imported organic matter, except in the special case of chemoautotrophic energy fixation (Fisher and Likens 1973). Energy is largely derived from photosynthetically derived particulate or dissolved organic carbon (DOC) that reached the water table by downward percolation through the overlying matrix (vadose zone), or transported laterally within the groundwater flow (phreatic zone, Fisher and Likens 1973; Fig. 3). Variation in the flux of organic matter in the groundwater is a prime driver of the spatio-temporal heterogeneity in groundwater ecosystems (Datry et al. 2005). Bacteria are dependent on the fluxes in organic carbon and on the availability of labile organic compounds (see Danovaro et al. 2001) or from organic matter deposited in sediments at their formation (SOC; Krumholz 2000). The DOC in groundwater is generally low (median 0.7 mg L^{-1} DOC in 100 samples from 27 American states; Leenheer et al. 1974 cited in Malard and Hervant 1999) and is often limiting both to microbial activity—they appear to suffer nutritional stress (Anderson and Lovley 1997)—and ecosystem metabolism, as, for example, under base-flow conditions in New Mexico, USA (Baker et al. 2000). Generally, much lower levels of energy are contained in sedimentary organic carbon (SOC). Whatever the energy source, microorganisms (mostly bacteria and fungi) capture the energy (utilising either heterotrophic or chemotrophic pathways) and the resulting biofilms, which form the foundation of the subterranean ecosystem, are grazed by aquatic animals (Burns and Walker 2000; Fenwick et al. 2004). Comparable processes may be expected to support the groundwater ecosystem, *sensu lato*. Over the last 15 years, microbial communities have been found in a wide variety of situations, often deep into the Earth's surface, which are energetically dependent on non-traditional sources of energy (Krumholz 2000).

Although groundwater fauna is dependent on aerobic metabolism and typically on photosynthetically derived energy sources, there are situations where the energy to

sustain it may be derived from in situ microbial energy-releasing pathways more typically considered of geochemical importance. These include lactate and acetate fermentation, ferredoxins and the production of hydrogen and acetate in fermentation, methanogenic pathways, sulfate reduction, Fe(III) reduction and nitrate reduction (Chapelle 2001); the great diversity of microbial lineages involved is covered in the review by Griebler and Lueders (2008) published after this paper was accepted. An example of the evolution of such a system along a 170 km groundwater flowpath is provided by Lovley and Goodwin (1988). The ecosystems of the artesian Edwards Aquifer, Texas (Longley 1992) and Movile Cave, Romania (Sarbu 2000) are analogous to those associated with both hydrothermal and cold deep-sea vents (Gebruk et al. 1997). Chemoautotrophy (Kinkle and Kane 2000; Poulson and Lavoie 2000) has also been demonstrated in Frasassi Cave, Italy (Sarbu et al. 2000), and strongly implicated in anchialine systems (Pohlman et al. 2000). More recently, Por (2007) proposed a coherent hypothesis in which these various chemoautotrophic ecosystems are globally linked through geological eras in what he termed the 'Ophel'. Where microbiological processes are not precluded by high temperature, the temporal and spatial evolution of groundwater in most aquifers should strictly be described as biogeochemical rather than geochemical.

Biofilms derived from autotrophic and/or heterotrophic processes are typically the source of energy for higher organisms. Hydrogeologists, most commonly, are aware of groundwater ecosystems by reference to 'nuisance organisms', the microbiological component of groundwater ecology, often in the contexts of pipeline corrosion and fouling 'slimes' (Gerritse 1998), particularly those resulting from the range of iron bacteria associated with groundwater exploration (Tyrrel and Howsam 1997). Microbial processes are the prime determinant of groundwater quality in pristine aquifers and the principal means of restoring the quality of contaminated aquifers (Chapelle 2001). Recent studies suggest that the variability in subsurface geochemical and hydraulic conditions influence the sub-surface microbial community structure (Haack and Bekins 2000) in a manner comparable to that found in stygal communities (see Gibert et al. 1994b; Seymour et al. 2007; Boulton et al. 2008). Biofilms can be ecologically complex communities, comprising a complex and structured array of Archaea, Bacteria, protists, viruses and Fungi, which display a full array of ecological processes. For example, different swimming speeds in bacterivorous flagellates lead to niche differentiation and suggest they graze different subsets of the microbial community, differentially controlling the bacterial densities which may influence rates of biodegradation (Novarino et al. 1997). Amoebae, which are an integral part of biofilm, may consume ca. 3×10^4 biofilm cells $\text{cm}^{-2} \text{ h}^{-1}$, and ciliates may reduce the thickness of biofilm by up to 60% (Huws et al. 2005). The potential significance of Protozoa is increased because they remain effective grazers even in anaerobic environments (Kota et al. 1999).

Microbiology in groundwater largely occurs at interfaces, at surfaces rather than in the open water—but see preceding discussion on groundwater stratification—and it is in such biofilms where important biogeochemical processes are enhanced through the associated redox gradients that develop at spatial scales ranging over many orders of magnitude, from sediment particles (10^{-3} m), through water column (10^{-2} – 10^1 m), to pristine aquifers (10^2 – 10^4 m). Thus, groundwater hydrogeochemistry provides redox conditions suitable for biofilms and biofilms induce redox gradients that contribute to hydrogeochemical processes.

Changes to the porosity of aquifers may occur through mechanical, chemical or biological processes, the latter particularly through the production of biofilms. Biofilm structure, diversity and quantity are important to the functioning of ecological systems (Boulton et al. 2008) and, by changing porosity, the hydrological system. In pristine groundwater, a range of microeukaryotic organisms (protists) form a small but important component of the ecosystem as they graze on, and so help structure, the biofilm (Chapelle 2001). Because protist numbers in polluted water may increase by several orders of magnitude (Brad 2007), this may be one way by which pollution affects biofilm function. Groundwater protists, which largely comprise flagellates but include amoebae and ciliates, are hypothesised to control bacterial densities, and affect rates of biodegradation of organic compounds, as a result of niche differentiation and selective grazing (Novarino et al. 1997). The accumulation of biofilm may clog aquifers (MacDonald et al. 1999), but bacteria and archaea populations can be reduced by protist predation (Mattison et al. 2002; Kota et al. 1999) which helps to maintain hydraulic conductivity in aquifers (Sinclair et al. 1993) as a result of reduced bacterial clogging, while facilitating the recycling of scarce nutrients and thus bacterial remediation (Mattison and Harayama 2005; Rockhold et al. 2002). It is recognised that consortia of microorganisms can work to break down contaminant plumes (Haack and Bekins 2000), but the expectation has yet to be established that stygofauna may similarly interact with biofilms, and other expressions of microbial diversity, so as to promote or to restrict their joint activity and the community diversity in groundwaters (Humphreys 2000), issues developed more recently by Boulton et al. (2008).

Investigations in respect of wastewater recharge of aquifers (Gerritse 1998), owing to high organic matter content of the water, are informative for the exchange of ideas between biologists and hydrogeologists. Dissolved organic matter (DOM) affects silicate solubility (Dove and Rimstidt 1994) and DOM and CO_2 concentration affects mobilisation of carbonates (Vengosh and Keren 1996). DOM is trapped in biofilms where it may be recycled locally or exported through consumption by stygofauna (Bärlocher and Murdoch 1989), and microbial activity may be enhanced both by the feeding process (Danielopol 1989; Kinsey et al. 2007) and by nutrients excreted by hyporheic invertebrates (Boulton 2000b; Marshall and Hall 2004). Stygofauna is likely to concentrate at high DOM sources (Sinton 1984; Detry et al. 2005) where the consequent

accelerated processing of organic matter (Marshall and Hall 2004) and increased respiration will alter the redox conditions and so affect local hydrogeochemical conditions. Conversely, the increase in organic matter may permit invasion of surface species into previously oligotrophic groundwater (Malard et al. 1996a).

Stygobiontic animals in Iceland have survived beneath the Pleistocene ice sheet in water kept liquid by geothermal heat (Bjarni et al. 2007), a finding that strengthens the likelihood that a rich biota may be found in the lakes beneath the Antarctic ice sheets such as Lake Vostok (Walker 1999), just as terrestrial arthropods survived continental glaciations there (Convey and Stevens 2007). Such duration is short, however, compared to the survival of stygofauna in the deep artesian Edwards Aquifer, Texas, which supports a stygofauna comprising both invertebrates and vertebrates considered to be relicts of Cretaceous marine inundation. Stygofauna occurs in water up 1 km deep in Moroccan karst (Essafi et al. 1998), in deep artesian systems in Texas (Longley 1992), and several metres below Australian deserts (Humphreys 2001) in unconfined aquifers in which they have resided for several million years (Leys et al. 2003). In contrast, in the Appalachians, USA, stygal amphipods may be recent invaders of cave streams, through generations even repeatedly invading and escaping subterranean life (Culver et al. 1995).

Dissolved oxygen

Dissolved oxygen (DO) in groundwater is one of the prime ecological factors governing the occurrence and spatio-temporal distribution of hypogean animals (Malard and Hervant 1999). DO concentration in groundwater depends on the rate of oxygen transport from the atmosphere and the rate of biological and chemical oxygen consumption within the groundwater. DO concentration generally decreases with depth in the groundwater because it tends to be rapidly consumed in the upper layers owing to incomplete degradation in the vadose zone of soil-generated labile DOC (Ronen et al. 1987a). DO is gradually consumed along the groundwater flowpath, especially in confined aquifers where the process may be dependent on sedimentary organic carbon and be consumed over 10^1 – 10^4 years, and the resulting DO gradient may vary by several orders of magnitude (Malard and Hervant 1999 (Fig. 3).

Biodiversity in groundwater is often considered severely constrained by low spatiotemporal heterogeneity and low food supply (Detry et al. 2005). However, spatial heterogeneity, exhibited at the macro (km), meso (m) and micro (cm; Ronen et al. 1987a) scales, is a reflection of both the aquifer structure and composition, the groundwater flow velocity, organic matter content, and the abundance and activity of microorganisms and stygofauna. This heterogeneity may have a temporal component owing to varying rates of recharge in response to meteorological and climatic variation, and be influenced

by stygal animals responding to lowered DO by migrating to more oxic zones (Malard and Hervant 1999). Because groundwater ecosystem processes accelerate oxidation of organic matter, they may be a prime determinant of the redox evolution that drives many hydrogeochemical processes. Under conditions of continued oxidation of organic matter without further DO input, the groundwater will evolve from aerobic conditions through a range of anaerobic conditions, progressively through zones of oxygen depletion, nitrate, manganese, iron (III) and sulphate reductions, to methanogenesis (Fig. 3, III; Fenchel and Finlay 1995). The available flux of oxygen in groundwater is much slower than in surface waters and DO concentrations of $<1 \text{ mg L}^{-1}$ are common in groundwater (Fig. 4); many groundwater organisms withstand dysoxic waters ($0.2\text{--}2.0$, $\sim 0.3\text{--}2.9 \text{ mg l}^{-1}$; Tyson and Pearson 1991) for long periods, even permanently (Humphreys 1999b). Stygal species can exploit dysoxic areas rich in DOC owing to their efficient use of food (carbon; Malard and Hervant 1999). Some stygal species, which Sket (1986) termed subthiobites, are even found beneath layers of hydrogen sulphide (Sket 1996; Pohlman et al. 1997; Humphreys 1999b; Iliffe 2000)

The respiration of plant roots immersed by rising groundwater (Bunn and Arthington 2004) or which have penetrated to aquifers down wells, typically those for mineral exploration, would be expected to deplete local and downstream DO (Humphreys 2006a), as well as provide carbon, with consequent changes to biogeochemical gradients and dynamics. Any impact on groundwater

ecosystems is unknown and primary research would be required to determine whether the guidelines governing mineral exploration drilling should be given the force of the regulations governing water bore drilling (MPR 2002).

Conclusions

Historically, the separation of hydrogeology from groundwater ecosystem dynamics is profound and the boundary has largely been traversed by biologists seeking hydrogeological information to gain understanding of groundwater ecology. In consequence, there have been notable early interdisciplinary studies that have yielded significant insights across disciplines. The greatest strides have been taken by microbiologists seeking to understand groundwater evolution and to remediate contaminated sites (e.g. Chapelle 2001). These, with few exceptions, have been done in the absence of faunal considerations, largely from ignorance of the presence of groundwater fauna (Humphreys 2006b), but partly because of the lack of techniques to investigate the often low-density populations of groundwater invertebrates in areas difficult of access. Novel methods are resolving some of the sampling difficulties and it is hoped that this paper will help to overcome one of the more serious hurdles, the general lack of knowledge amongst hydrogeologists of the presence, ubiquity and nature of groundwater ecosystems in their broader context, and of the potential for cross disciplinary research yielding broadly informative results.

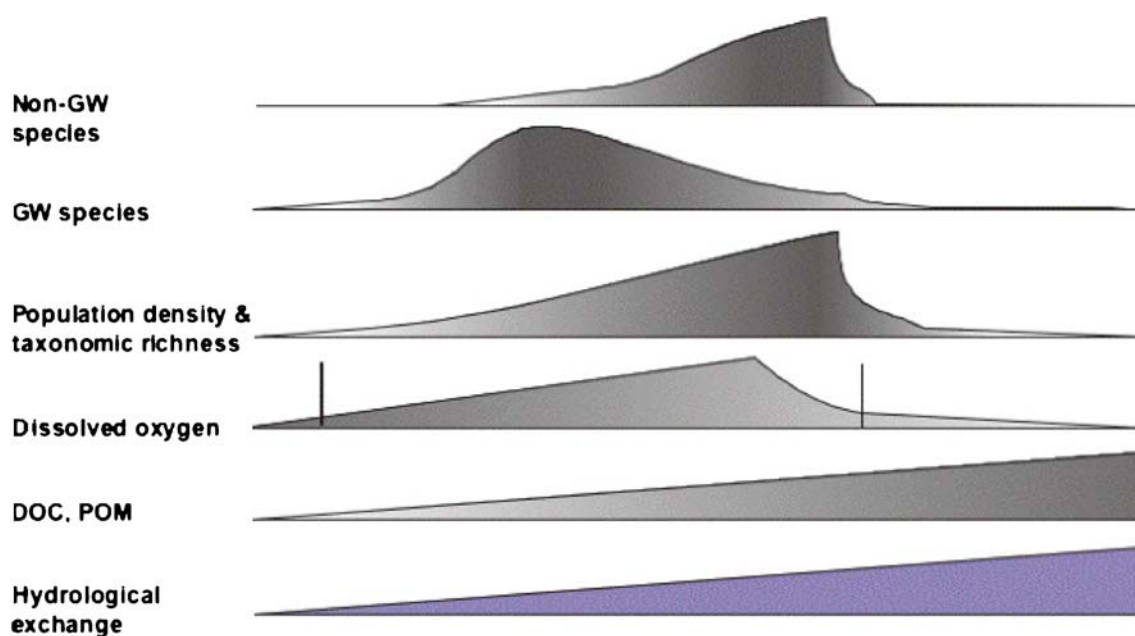


Fig. 4 Schema depicting groundwater quality and the presence of groundwater and non-groundwater species under varying levels of hydrological exchange (modified from Hahn 2007 with permission). The preferred concentration for stygobites lies between the *two vertical lines*, the height of which denotes $\text{DO}=1 \text{ mg L}^{-1}$. Dissolved oxygen increases with increasing exchange with surface water (along the *x*-axis), reaching and exceeding 1 mg L^{-1} . However, since dissolved organic carbon and particulate organic matter (DOC plus POM) may be imported laterally in groundwater flow, oxygen may subsequently decrease below 1 mg L^{-1} owing to high concentration of OM in the groundwater increasing microbial oxygen demand

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