



Imperilled subsurface waters in Australia: Biodiversity, threatening processes and conservation

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Subsurface waters in Australia span massive aquifers to small cave streams and fluctuating hyporheic zones where stream water exchanges with groundwater. Groundwater resources have been exploited heavily, especially in the arid zone, and usage is predicted to increase. Ironically, preliminary surveys of some groundwater habitats in arid northwestern Australia indicate an extraordinarily diverse subsurface fauna with apparently highly localised distributions. Elsewhere in Australia, changes to river flows, gravel extraction, and poorly managed catchment land uses have altered the extent and ecological integrity of the hyporheic zone in most gravel and sand bed rivers. In many cave streams and karst aquifers, sedimentation, pollution and changes to the water table have caused extinction or reduction of the dependent biodiversity. Most of these subsurface habitats harbour ancient groups absent from surface waters (relictual stygofauna) and are 'hotspots' of unexpected aquatic biodiversity.

Unfortunately, our knowledge of the regional extent of this biodiversity and its functional significance is fragmentary. Current threats vary according to the subsurface habitat. For example, lowering of the water table in calcrete aquifers by water abstraction may jeopardise isolated, endemic relictual faunas in Australia's arid zone whereas in many gravel bed rivers, siltation threatens the biodiversity and filtration capacity of the hyporheic zone. Groundwaters in karst, especially cave streams and their dependent fauna, are vulnerable to impacts in their surface catchments but these linkages are seldom obvious. Recognition of the intimate linkages between groundwater and many surface ecosystems has led recently to policies aimed at protecting 'Groundwater Dependent Ecosystems' in Australia. However, such protection is hampered by our scant taxonomic and ecological knowledge of these ecosystems. Successful conservation and management of groundwaters and their dependent ecosystems rely on better public understanding of their unique fauna and 'ecosystem services,' further research on subsurface processes and taxonomy, and legislative protection of rare and threatened subterranean communities and species.

Keywords: stygofauna, calcrete aquifers, hyporheic zone, caves, groundwater dependent ecosystems, aquatic invertebrates, karst, subsurface waters

Introduction

Some 97% of the world's available freshwater lies underground whereas lakes and rivers comprise less than 2% (Gibert et al., 1994). However, we know far more about the hydrology and ecology of our sur-

face water resources and they receive the majority of attention in conservation and management efforts. Largely unseen, groundwater influences the ecological processes and 'health' of many surface (epigeal) ecosystems as well as comprising a spatially immense ecosystem in its own right. For this paper, we define

groundwater as water that resides for varying periods below the ground either interstitially or free-flowing through rock fissures or in caves and karsts. This includes cave streams and pools, water giving rise to springs, and stream water that exchanges with groundwater in the saturated 'hyporheic zone' below and alongside rivers.

What the Australian continent lacks in surface water ecosystems (e.g., large rivers with high discharge, deep permanent lakes), it more than compensates with a rich array of groundwater ecosystems. Some are immense aquifers such as the Great Artesian Basin (1.7 million square kilometers, Jacobsen et al., 1983) underlying much of northeastern Australia. Others are unique. For example, the only known deep continental anchialine system in the southern hemisphere is Bundera Sinkhole, Cape Range, in northwest Western Australia. Anchialine systems are inland, mixohaline, underground waters affected by marine tides and create unique environmental conditions that have remained relatively stable for millions of years. The Bundera Sinkhole contains the only southern hemisphere representatives of the Class Remipedia and the Order Misophrioida (Humphreys, 2000) as well as many endemic species and genera of other groups with affinities to the fauna of similar caves in the North Atlantic.

Many surface water ecosystems in Australia have varying reliance on groundwater. In mesic areas, Australian rivers derive baseflow from subsurface waters and depending on bedform and porosity of the sediments, there may be considerable exchange of stream and groundwater along the course of the channel and below the banks. This region of exchange is termed the hyporheic zone (e.g., Williams and Hynes, 1974) and as well as being inhabited by specialized fauna, is functionally critical to many stream ecosystems (Brunke and Gonser, 1997; Boulton et al., 1998). Subsurface flow is also common in many Australian arid-zone rivers that may exist for long periods as series of pools connected by hyporheic flow.

Recognition of this spectrum of groundwater dependence has led to a broad classification of 'Groundwater Dependent Ecosystems' (GDEs) into four categories: river baseflow systems, aquifer and cave ecosystems, terrestrial vegetation, and wetlands (Hatton and Evans, 1998). Currently, many GDEs in Australia are threatened either directly via groundwater abstraction or indirectly through disruption of hydrological exchange (NCC NSW, 1999; Hamilton-Smith and Eberhard, 2000). In this paper, we review several GDEs representing the first two of the general types listed above. Using specific case studies that describe

the biodiversity, ecological function (where known), threats, and current policies in place to protect and conserve these ecosystems, we explore contrasts and parallels to draw some generalizations about imperilled subsurface waters in Australia, putting them into a global context.

Patterns and significance of groundwater biodiversity

As groundwater is often viewed as an 'extreme environment' where only highly adapted animals persist, biodiversity has been predicted to be relatively low (e.g., Marmonier et al., 1993). Furthermore, the absence of sunlight and hence solar-powered primary productivity truncates trophic opportunities further, and for many years, groundwaters were considered unlikely to harbour particularly diverse invertebrate assemblages. This hypothesis has been challenged (Margalef, 1993), and several recent reviews of the biodiversity of regional subterranean faunas (e.g., Stoch, 1995; Rouch and Danielopol, 1997; Danielopol et al., 2000) have forced ecologists to re-evaluate their taxonomic and geographic expectations.

On a continental scale, Sket (1999a, 1999b) concluded that in Europe, there are approximately 2400–3000 stygobitic (groundwater) species of malacostracan crustacean compared with 12500 epigeal freshwater malacostracan species. Danielopol et al. (2000) emphasize that this aquatic stygofauna is unique compared with the fauna of surface waters even at the phylum level, and claims that stygobites account for approximately 40% of the total crustacean fauna of Europe. At a global scale, several major groups of Crustacea are found exclusively in subsurface waters (e.g., Remipedia, Thermosbaenacea, Bathynellacea, Spelaeogriphacea) and many of these groups contain endemic species that apparently have extremely limited distributions (Humphreys, 2000). However, this may reflect the low intensity of sampling of these rather inaccessible subterranean systems. Finally, it is clear that many more subsurface taxa, probably comprising a few higher taxonomic levels new to science, await discovery. For example, in the last few years, at least 10 new families and a new Class have been described from anchialine systems worldwide.

In Australia, we have little idea of our continental stores of subsurface biodiversity because of the limited scope of our sampling coverage. What little sampling has been done in Australian groundwaters in the last few years indicates that at least aquifer and

Table 1. The composition of the anchialine fauna of Cape Range (CR) and Barrow Island (BI).

Major Taxon	Species	Location
Annelida: Polychaeta: Spionidae	<i>Prionospio thalanji</i>	CR
Crustacea: Remipedia: Nectiopoda	<i>Lasionectes exleyi</i>	CR
Crustacea: Thermosbaenacea	<i>Halosbaena tulki</i>	CR, BI
Crustacea: Ostracoda: Halocyprida	<i>Danielopolina koenickeri</i>	CR
Crustacea: Copepoda: Harpacticoida	<i>Phyllopodopsyllus</i> sp. nov.	CR
Crustacea: Copepoda: Calanoida: Epacteriscidae	<i>Bunderia misophaga</i>	CR
Crustacea: Copepoda: Misophrioida: Speleophriidae	<i>Speleophria</i> sp. nov.	CR
Crustacea: Copepoda: Calanoida: Pseudocyclopiidae	<i>Stygocyclopia</i> sp. nov.	CR
Crustacea: Amphipoda: Melitidae	<i>Nedsia douglasi</i> ,	CR
Crustacea: Amphipoda: Melitidae	<i>N. fragilis</i> , <i>N. humphreysi</i> , <i>N. hurlberti</i> ,	BI
	<i>N. macrosculptilis</i> , <i>N. sculptilis</i> ,	
	<i>N. straskraba</i> , <i>N. urifimbriata</i>	
	(+3 new species)	
Crustacea: Amphipoda: Bogidiellidae	<i>Bogidomma australis</i>	BI
Crustacea: Amphipoda: Hadziidae	<i>Liagoceradocus subthalassicus</i>	BI
Crustacea: Amphipoda: Hadziidae	<i>L. branchialis</i>	CR
Crustacea: Isopoda: Cirolanidae	<i>Haptolana pholeta</i>	CR, BI
Crustacea: Syncarida: Bathynellacea	<i>Atopobathynella</i> sp. nov.	BI
Crustacea: Decapoda: Atyidae	<i>Stygiocaris lancifera</i>	CR
Crustacea: Decapoda: Atyidae	<i>S. stylifera</i>	CR, BI
Pisces: Eleotridae	<i>Milyeringa veritas</i>	CR
Pisces: Synbranchidae	<i>Ophisternon candidum</i>	CR

karst groundwater systems contain a pervasive and significant fauna that compares with some of the richest sites known anywhere in the world. For example, the anchialine systems have yielded more than 29 new species thus far, many from lineages with highly disjunct distributions (Table 1). At a continental scale, we predict that total groundwater invertebrate biodiversity will prove to be much lower than that in epigeal Australian freshwaters but certainly comparable with average groundwater biodiversity elsewhere in the world. Given the geological stability and palaeoenvironmental history of the Australian continent, the wide distribution of potential groundwater habitats, and the presence of major animal groups (particularly Crustacea) predisposed to colonization of groundwater habitats, we predict that Australia will prove to be a significant 'storehouse' of world subsurface biodiversity. This hypothesis has already been supported for some of the better-sampled karst outcrops (e.g. Cape Range—Humphreys, 2000; Tasmania—Eberhard et al., 1991; New South Wales—Thurgate et al., 2001), and for groups such as the amphipod crustaceans (Bradbury and Williams, 1997a, 1997b). There are probably numerous subterranean aquatic biodiversity 'hotspots'

(cf. Culver and Sket, 2000) characterized by high local endemism that await discovery. However, until we can document this biodiversity, such continental-scale hypotheses remain speculative.

Many subsurface habitats have persisted as relatively stable environments over long periods of time, insulated from the climatic events that profoundly affect epigeal habitats and their fauna. As such, they provide ideal refugia for surface forms able to colonise these habitats. Most stygobites (true groundwater animals) evolved from surface ancestors already pre-adapted for life in a subterranean environment (Culver et al., 1995). Animals living in these habitats frequently are small, elongate, and may have reduced eyes and pigment. Under the right conditions, populations of these animals colonise subterranean voids, become genetically isolated and undergo adaptive changes that further suit them to life underground, ultimately evolving into distinct species (Holsinger, 1988).

Subterranean faunas often include ancient lineages that have been protected underground despite major surface perturbations in climate, geomorphology and geographic position (Eberhard and Humphreys, in press). As powers of dispersal of many of these taxa are

usually limited, their present affinities and distributions reveal much about past geography and climates. This is especially true for aquatic forms such as the remiped described from the Cape Range sinkhole in 1996 (Yager and Humphreys, 1996). For example, if the dispersion of remipeds occurred by rafting on tectonic plates, as suggested for those on either side of the North Atlantic, then owing to the sequence in which the continental plates separated, the Australian remipeds are likely to have a common ancestry with those in the North Atlantic. The remiped site at Cape Range and the associated ecosystems have yielded at least seven lineages of crustaceans with affinities to the North Atlantic including copepods, amphipods, ostracods, thermosbaenaceans and isopods (Wilson and Humphreys, 2001).

Natural linkages and barriers: Effects on groundwater biodiversity

In addition to the diversity aspect, our *ecological* perspective of groundwaters also has broadened to consider the subsurface system as having a complex and interactive boundary with surface ecosystems at a range of scales (Gibert et al., 1994; Boulton et al., 1998). The upper layers in contact with aquatic, aerial or terrestrial systems are an energetically rich source-sink zone, frequently colonized by aquatic epigeal invertebrates as well as stygobites. With increasing distance from the surface, the groundwater becomes increasingly oligotrophic and lower in oxygen until only specialized microorganisms can persist in the anoxic conditions (Daniélopol et al., 2000). Along these environmental gradients, biochemical reactions occur that provide crucial 'ecosystem services' such as reduction of excessive nitrates (Duff et al., 1996), biological filtration processes that can enhance water quality (Boulton, 2000a), and organic matter retention and cycling (Kaplan and Newbold, 2000).

The strength of the linkages with epigeal systems governs environmental conditions in most groundwater ecosystems. For example, in the hyporheic zone, downwelling stream water rich in dissolved oxygen and organic matter create localized patches of oxidizing conditions in the sediments that favour particular biochemical reactions such as nitrification (Duff and Triska, 2000) and enable limited penetration of the subsurface habitat by small epigeal aquatic invertebrates ('occasional hyporheos,' Williams and Hynes, 1974). With longer residence time in the hyporheic zone (Figure 1A), dissolved oxygen concentrations decline and conditions promote reductive biochemical

reactions. Subsurface invertebrate species richness declines, and the assemblage composition becomes dominated by specialized hypogean forms with adaptations to low dissolved oxygen (Dole-Olivier and Marmonier, 1992; Boulton and Stanley, 1995). A similar gradient in aquatic species composition and water chemistry occurs in non-percolation streams (i.e., surface flow that sinks into a cave entrance) (Figure 1B). Declining light intensity restricting photosynthesis coupled with the respiration of imported organic matter reduce dissolved oxygen concentrations (Figure 1) and create conditions that favour taxa with specializations for a subsurface existence.

These gradients in environmental conditions between epigeal and hypogean habitats, also seen in anichaline systems (Humphreys, 1999a), create the microhabitat complexity that promotes coexistence of taxa with varying resource requirements, enhancing local biodiversity. Furthermore, the existence of subsurface flow paths in the hyporheic zone or through caves and aquifers enables dispersal of hypogean invertebrates via the 'interstitial highway' (Ward and Palmer, 1994). However, at an evolutionary time scale, natural disruption of such linkages (e.g., tectonic activity, changes in water tables and surface drainage patterns) may promote biodiversity by severing genetic exchange and leading to allopatric speciation. The extraordinary species richness of some invertebrate groups in calcrete aquifers in northwest Western Australia (see below) may be a result of the development of natural barriers of hypersaline water along paleo-drainage channels in the arid zone (Humphreys, 2001). However, many groups within the calcrete aquifers commonly contain sympatric congeneric species (e.g., Dytiscidae, Cyclopoida, Harpacticoida, Ostracoda), often restricted to a single calcrete aquifer, suggesting *in situ* speciation could also have occurred.

Aquifer ecosystems: Groundwater calcretes of arid northwest Australia

Groundwater calcretes often form typical karstic features with sinkholes serving as major recharge zones. These karstic calcretes have interconnected subsurface conduits, making them ideal habitat for stygobites but also especially desirable for groundwater abstraction. The Archaean rocks of the Western Shield of Australia (comprising the Pilbara and Yilgarn Cratons and associated basins) are furrowed by palaeodrainage systems that predate the separation of Australia from Antarctica. Most of these palaeodrainage systems are

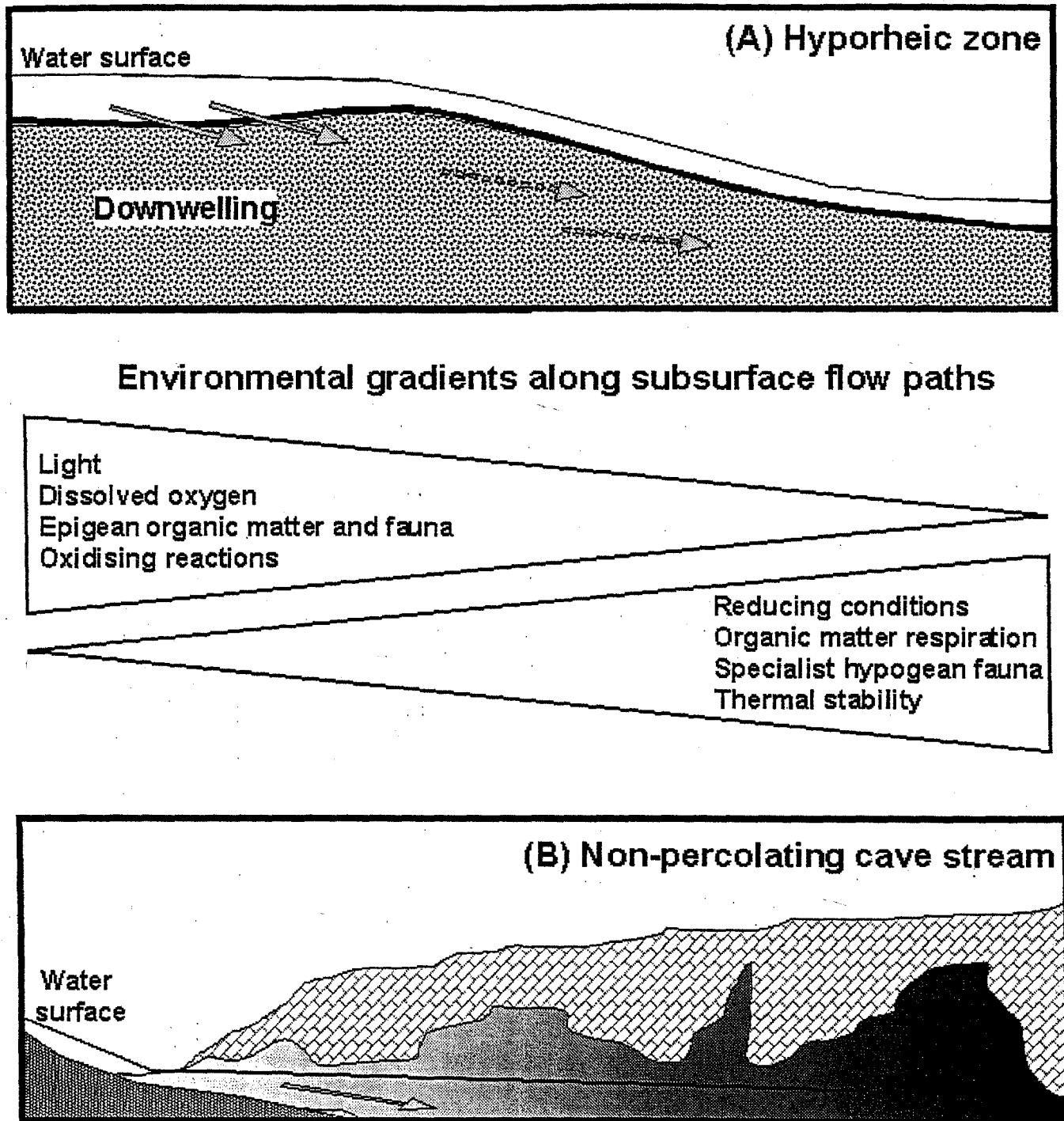


Figure 1. The parallel nature of several major trends in ecological conditions along subsurface flow gradients in hyporheic zones (A) and non-percolation cave streams (B).

inactive or are over-large for the rivers they now contain (e.g., Fortescue and Murchison Rivers, Figure 2). Calcrete deposits occur intermittently along these palaeodrainage systems, interspersed with salt lakes or playas. Rainfall recharges the groundwater and moves slowly down-gradient towards a salt lake, gradually approaching the surface where evaporation causes the deposition of carbonates (Morgan, 1993). This process

is associated with major changes in the groundwater chemistry and the water progressively changes from fresh to hypersaline. These gradients recur at intervals down the length of the palaeochannel, forming a series of isolated calcrete deposits.

The natural process of geographic isolation of these calcrete bodies appears to have led to adaptive radiation of the groundwater fauna in arid northwestern

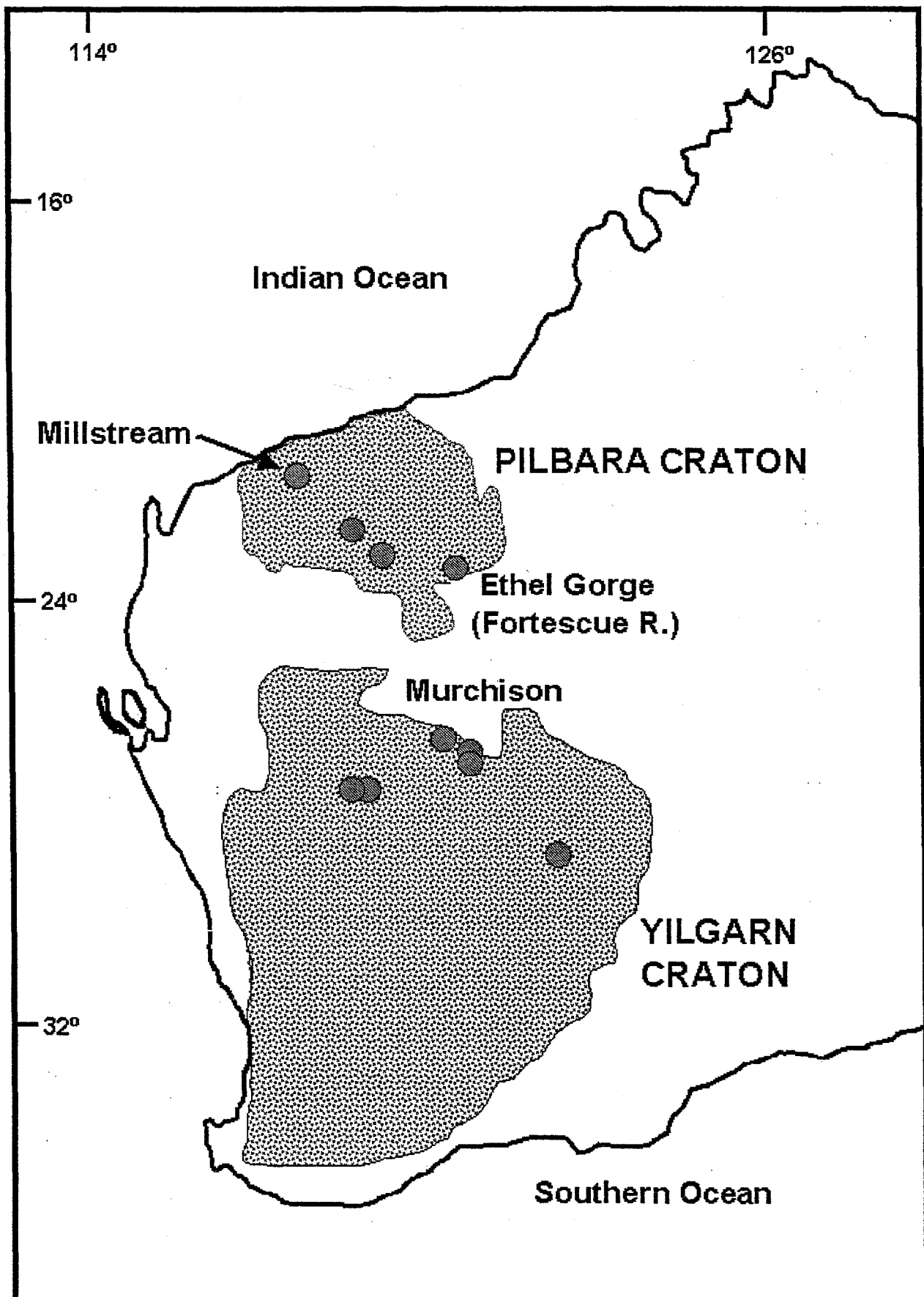


Figure 2. Two cratons (Yilgarn and Pilbara, stippled areas) in Western Australia where several 'hot spots' of stygal biodiversity have been discovered (see text for details). Shaded circles mark the main areas where calcrete aquifers and boreholes have been sampled in these two cratons.

Australia. Each major calcrete body in northwestern Australia examined so far has yielded a separate and unique complement of stygofauna, often surprisingly biodiverse (Humphreys, 1999b, 2001). For example, in the Pilbara, more species of groundwater amphipod have been described from Ethel Gorge on the Fortescue River (Figure 2) than from anywhere else in the world (14 species; Bradbury, 2000). Also in the Pilbara, rather limited sampling of groundwater has yielded seven new genera and 17 new species of candonine ostracods (I. Karanovic, Western Australian Museum, Perth, pers. comm., 2001). For comparison, South America and Africa each have only two endemic genera of candonine ostracods. Six of the genera and all of the species are known only from a single calcrete area, highlighting the localised occurrence of these biodiversity 'hot-spots.' From the Murchison region (Yilgarn Craton, Figure 2), more species of stygal diving beetles (Dytiscidae) have been described than from the rest of the world combined (Watts and Humphreys, 1999, 2000). In this area, most calcretes have two or more species of dytiscids yet none of the species is known from more than one calcrete area. Several ancient relictual groups of Crustacea have also been discovered, indicating past continental connections and climates. For example, the calcrete aquifer at Millstream (Figure 2) includes many Gondwanan relicts such as Spelaeogriffacea, a crustacean Order previously known only from caves in South Africa and Brazil (Poore and Humphreys, 1998).

In northwest Australia, the groundwater in these calcretes was used by nomadic people and more recently have been exploited for pastoral use. However, in the last decade, large scale development of mining below the water table and on-site mineral processing has led to the widespread extraction of groundwater and of calcrete limestone for construction and for neutralising acids produced by mining and mineral processing (Humphreys, 2001). Although such extraction processes within palaeovalleys may impact on the aquifer ecosystems, there is no bionomic or process information available to inform management of these stygal ecosystems. The ancient waters in the deep palaeochannel aquifers, the target of water mining, are coupled with the superficial and more responsive calcrete aquifers. As the dynamics of this coupling are unknown, the impacts of mining these deep aquifers on the stygal ecosystems and surface GDEs remain unknown; this is a research priority in this area.

In other parts of the world, changes to the water table and the direction of groundwater flow may have profound effects on populations of stygal dytiscids (Richoux and Reygrobellet, 1986). As the Australian

stygofaunal assemblages contain numerous short-range endemics yet occur in systems of potential or actual resource development, they present a real challenge for innovative environmental management (Watts and Humphreys, 2000). Resource development in the arid zone relies on water and promises tempting short-term economic benefits. It is far more difficult to attach an economic value on stygofaunal biodiversity, especially when information on potential 'ecosystem services' provided by such fauna is lacking.

Aquatic ecosystems in Australian caves and karst

Some of the earliest work on Australian groundwater fauna occurred in caves (e.g., Tenison-Woods, 1862) because of their general accessibility and potential value as a water supply. Since then, unusual and locally restricted invertebrate stygofauna have been described from Australian caves and karst (e.g., Holthuis, 1960; Knott and Lake, 1980; Ponder, 1992; Wilson and Ponder, 1992; Bradbury and Williams, 1997b). However, only two stygobitic vertebrates (fish) are known in Australia (Humphreys, 1999c). Traditionally, the subterranean fauna of Australia was perceived as being poor compared with that of the well-studied caves of Europe and North America but this perception has been overturned by recent dramatic discoveries and new insights (Eberhard and Humphreys, in press). One insight is the recognition that most caves lack surface openings and are too small for people to enter. Subterranean habitats may be classified according to the size of the voids. These range from minute cavities (<1 mm, 'microcaverns'), through cavities 1–200 mm in diameter ('mesocaverns'), up to larger caverns, tens of metres in extent ('macrocaverns') (Howarth, 1983). Of course, there is a continuum of void sizes but the preferred habitat of most stygal fauna appears to be mesocaverns where the environmental conditions tend to be more stable.

A second insight is that macrocaverns represent only a tiny fraction of the total subterranean habitat space, often interlinked as part of the 'interstitial highway' (Ward and Palmer, 1994) and no longer can caves that are large enough for humans to enter be considered as discrete 'island-like' refugia (Eberhard and Humphreys, in press). Finally, there is growing appreciation of the many ecological parallels among subterranean habitats and the substantial overlap across the previously distinct fields of biospeleology (Vandel, 1965), phreatobiology (Danieopol, 1984) and hyporheic ecology (Williams and Hynes, 1974).

Despite their public profile, size and accessibility, there are relatively few detailed studies of human impacts on aquatic faunal diversity in Australian caves compared with work overseas (e.g., Gunn et al., 2000). The few studies that exist are mostly reported in the 'grey literature,' usually short-term, lack adequate pre-impact data, or suffer design limitations that prevented unequivocal conclusions (review in Hamilton-Smith and Eberhard, 2000). One of the more long-term studies has been done on the Ida Bay karst system in southern Tasmania, comprising four major horizontal stream caves—Bradley Chesterman Cave, Loons Cave, Arthurs Folly Cave and Exit Cave.

The Ida Bay karst system harbours one of the more diverse cave faunas of temperate Australia, including some 100 different invertebrate species of which 15 are obligate cave inhabitants and apparently highly endemic (review in Eberhard, 2001). During and after World War II, limestone quarries were operated in the area, and extinction of the syncarid *Anaspides tasmaniae* and most other aquatic species in Bradley Chesterman Cave by 1990 was attributed to severe sedimentation, flow regime changes, nutrient enrichment, and toxins originating from quarrying (Eberhard, 1990). In 1992, local quarrying ceased due to the deleterious effects on cave fauna and other natural heritage values, and a rehabilitation program was instigated to minimise further influx of sediments and pollutants while restoring natural catchment characteristics. Within 3 years, one species of amphipod had recolonised the cave and after 6 years, planarians, molluscs, amphipods and *A. tasmaniae* were collected from the cave (Eberhard, 1999).

Monitoring ecological impacts in caves is problematic because overall densities of many taxa are often low, taxonomic and ecological knowledge is limited, and the time scales of response and recovery are poorly known. At Ida Bay, impacts of the quarrying operations have been monitored using population densities of aquatic hydrobiid snails along with water quality monitoring. These snails were selected as biomonitors because of their sessile benthic habits, wide distribution in the cave streams, and their relatively high abundance. Initial sampling in various parts of the Ida Bay system (Little Grunt Cave, Eastern Passage of Exit Cave) demonstrated that sediments from the quarrying appeared to limit the snails' distribution by smothering areas of hard-bottom stream habitats. After quarry closure and sediment restriction, monitoring of the hydrobiids has continued but there seems little difference in snail densities between impact and control sites (Eberhard, 2001) perhaps because large quanti-

ties of sediment persist in many of the cave streams where flushing is limited. In Exit Cave, natural high flow events have removed some of the silt but snail density remains low compared to control sites. This may reflect very slow rates of recovery or persistence of the impacts of other effects of quarrying (e.g., toxins) or rehabilitation earthworks. It is also possible that snail densities in the impacted sites have always been low and highlights the importance of pre-impact data and adequate site replication.

Like the calcrete aquifers described above, much of the Ida Bay fauna remains undescribed with only limited knowledge of ecology and distribution (Eberhard, 2001). While a number of these taxa are protected under Tasmanian species legislation (Eberhard, 1999), a more practical strategy is the protection of the entire habitat. For this to succeed, linkages between hypogean and epigean environments must be maintained. Streams are crucial, serving to import food and organic matter for aquatic and terrestrial fauna within the cave. For example, large glowworm colonies in Exit Cave rely entirely on streams to import their food supply of aquatic insect larvae. Water also enters caves by percolation, seeping through tiny fissures and transporting nutrients and fauna underground. These percolation habitats are most vulnerable to trampling damage—in Loons Cave, trampling has changed the stream bed from a hard-bottom habitat to soft sediments, severely limiting hydrobiid snail distributions and altering microhabitats for other aquatic species (Eberhard, 2001).

Effective management of the Ida Bay system relies on protection of influent stream catchments and stabilisation of quarrying inputs *outside* the cave system, maintaining the linkages of percolating and non-percolating water *into* the cave, and protection of vulnerable habitats *within* the cave by educating cave-users. Fact sheets illustrating sensitive fauna and habitats and showing minimum impact caving techniques are now issued. Vulnerable habitats are protected by route marking using string-lines to confine foot traffic in sensitive areas (Eberhard, 1999) and faunal sanctuary zones have been designated. It seems clear that much of the impact on cave ecosystems is unintentional and as we understand more about cave ecology and surface-subsurface linkages, educational and management issues will be increasingly effective.

River base flow ecosystems: The special case of the hyporheic zone

The percolation processes described above for caves also generate much of the baseflow in epigean rivers,

seeping in laterally where the water table slopes towards the channel. In the saturated sediments below the channel and in the immediate vicinity of the bank, stream water exchanges with groundwater in the hyporheic zone, depending on sediment permeability, surface discharge and bedform (Figure 1A). In many sand and gravel bed rivers, the hyporheic zone acts as a physical, chemical and biological filter of surface water downwelling into the sediments (Gibert et al., 1990). As well as this filtration function, the hyporheic zone often harbours a specialised invertebrate fauna termed the hyporheos, comprising smaller forms of epigeal taxa as well as true stygobites like those found in groundwater aquifers and cave streams. In some rivers, the hyporheos appears to be quite diverse. For example, Schmid-Araya and Schmid (1995) reported 569 taxa, mostly tiny interstitial meiofauna, from the hyporheic zone of a 100-m stretch of the Oberer Seebach, an Austrian gravel-bed stream. The hyporheic zone is proposed to act as an important refuge for invertebrates during floods, droughts or other disturbances in the surface stream (Dole-Olivier et al., 1997). Interstitial invertebrates may also play key roles in maintaining the efficiency of the biological filter by grazing microbial biofilms and buried organic matter, and sustaining permeability of the sediments through their movement and burrowing activities (Boulton, 2000b).

There have been few studies of the hyporheos of Australian streams (reviewed in Boulton, 2001), and none with the taxonomic resolution of the Oberer Seebach study. However, at least one study has indicated that there may be 'hotspots' of biodiversity of unique and obligate hyporheic taxa in some Australian rivers. Boulton and Foster (1998) collected some 20 species of water mites in 9 families from 72 6-L pump samples from the hyporheic zone of two reaches along a subtropical NSW river (the Never Never River). Further collections from one of these two sites have revealed yet more species (41 spp. from the Never Never River, Boulton and Harvey, unpublished data), implying that this may be a hyporheic hotspot of hydracarine biodiversity. Without comparable data from any other subtropical Australian rivers, this claim may be premature because the diversity of hyporheic watermites may be equally rich for many of the eastern draining rivers along the Great Divide. As in the case-study of the biodiverse calcrete aquifers, further sampling across these habitats is needed to test this hypothesis and to document the true endemism of the obligate hyporheos.

Like cave streams, most threats to hyporheic biodiversity arise from activities in the catchment that im-

pact upon the surface stream and are transmitted to subsurface habitats via alterations of hydrological linkages (Hancock, 2002). The sites on the Never Never River described by Boulton and Foster (1998) are protected because their upper reaches drain a World Heritage listed National Park. Several kilometers downstream, the valleys have been heavily logged and the river flats are currently grazed by dairy cattle or intensively cropped (potatoes, maize). Hyporheic samples from two sites in this downstream section contained few invertebrates but extremely high levels of interstitial silt (Boulton, unpublished data) implying that clogging of the sediment spaces ('internal colmation,' Brunke and Gonser, 1997) may have extinguished much of the hyporheos. Dissolved oxygen concentrations were also low in down-welling zones, implying disruption of hydrological exchange of subsurface water with that of the surface stream, and probably limiting colonization by epigeal taxa. Gravel extraction also occurs in the lower reaches of the Never Never River, and many nearby gravel-bed rivers. This poses further threats through direct removal of habitat, alteration of sediment deposition and erosion patterns, excessive siltation, bank destabilization, and local compaction where heavy machinery is used (Boulton, 2000a).

Extraction of surface and subsurface water reduces available habitat, alters flushing flows and rates of hydrological exchange between surface and subsurface water, and can change and even reverse chemical gradients and conditions in the hyporheic zone. Presently, environmental flow allocations focus on protection and maintenance of surface streams and adjacent ecosystems (Boulton and Brock, 1999); few of the current management models explicitly consider the significance of maintaining baseflow GDEs and the hyporheic zones in Australian regulated rivers. In conjunction with several projects on surface stream ecological responses, the NSW Department of Land and Water Conservation has funded a research project to explore the effects of varying flows on hyporheic processes in the Hunter River. Results so far indicate the importance of the 'parafluvial' zone along the edges of the Hunter where active exchange of river water is occurring. High densities and diversities of hyporheic invertebrates have been found in sites in the upper Hunter River (Hancock and Boulton, unpublished data) where exchange is unimpeded by fine sediments whereas the lower reaches are less speciose and colmation is more extensive. Management recommendations include exploring the effects of flushing flows for removing fine sediments from the hyporheic zone downstream and improving habitat for invertebrates as well as enhancing

the filtration capacity in the hyporheic and parafluvial zones of the Hunter.

Common themes in Australian subsurface biodiversity

The first common theme to emerge is our ignorance of the invertebrate biodiversity of our various groundwater environments. Although this is also true for most subterranean habitats overseas (Marmonier et al., 1997), it is exacerbated in Australia by the limited amount of sampling of these habitats, a paucity of taxonomic specialists in subsurface aquatic fauna, poor public understanding of the ecological value and variety of groundwater habitats, a severe underestimation of the extent of Australian GDEs made by an influential report (Hatton and Evans, 1998), and the fact that many of the groundwater areas are relatively inaccessible. The 'goods and services' roles of most groundwaters are poorly understood in Australia because aquatic research and management focus on surface environments. Groundwater comprises most of the reliable water supply of arid inland Australia but concerns about its depletion and pollution have only developed in the last few decades.

The second common theme, also evident overseas (e.g., Danielopol et al., 1997, 2000; Marmonier et al., 1997), is the high degree of endemism of Australian stygobites known to date. The true extent of endemism is yet to be revealed because of the limited sampling but for many GDEs such as the calcrete aquifers in northwestern Australia, large suites of stygobites are threatened by localized groundwater extraction and contamination. In other GDEs in temperate regions, we cannot know how much aquatic invertebrate biodiversity has been lost, especially from cave streams and sinkholes where humans have had easy access. Endemism may not be as high in the hyporheic zones of Australian rivers although this hypothesis awaits proper testing.

The third common theme, reiterated by studies worldwide (reviews in Gibert et al., 1994; Winter et al., 1998), is the intimate link between surface and subsurface aquatic ecosystems. This means that many of the threatening processes identified for surface waters also impact upon groundwaters. In river base-flow GDEs, hydrological exchange between surface and groundwaters is disrupted by excessive sedimentation, compaction, surface water abstraction and riparian zone modification (reviews in Boulton, 2000a;

Hancock, 2002). In four streams in south-western Australia, Trayler and Davis (1998) found that logging probably reduced the taxonomic richness of the hyporheic fauna. Anthropogenic salinization also appears to have led to local eradication of some hyporheic species in south-west Australian streams (Boulton and Marmonier, unpublished data). Contamination of shallow alluvial groundwater and surface water pollution directly impair interstitial activity and reduce hypogean invertebrate biodiversity (Notenboom et al., 1994; Marmonier et al., 1997). Most of Australia's subterranean biodiversity apparently occurs in shallow aquifers, rendering the subsurface aquatic fauna vulnerable to changes in water quality and quantity when groundwater recharge areas are impacted by human activities in the catchment or water tables are lowered by excessive abstraction.

Cave and karst groundwater ecosystems are also threatened by "external factors" such as quarrying and mining, agriculture, waste disposal, and groundwater abstraction (Gunn et al., 2000). In Australia, the impact of land clearance and agriculture is considered the most widespread and insidious threat, affecting cave microclimates, nutrient and sediment inputs, and hydrological regimes (Hamilton-Smith and Eberhard, 2000). Another widespread problem in Australia and overseas is inappropriate rubbish disposal and effluent management in karst areas that are particularly vulnerable because of their high porosity and conduit flow characteristics. Sometimes the impacts are rather indirect. In South Australia, the water level in Sheathers Cave fell by nearly a metre over 5 years following the establishment of an exotic pine (*Pinus radiata*) plantation above the cave whereas the water level in nearby Mount Burr Cave rose by about the same amount when its overlying pine plantation was destroyed by wild-fire (Grimes et al., 1995). The fall in the water table in several caves at Yancheep in Western Australia threatens a diverse community (e.g., 41 cave stream species in a 20-m reach, Jasinska et al., 1996) associated with underwater mats formed from tree roots. Most of these cave-stream animals inhabit the root mats, either grazing the living rootlets or eating root mat detritus or associated fauna (Jasinska et al., 1996). Nearly 60% of the approximately 120 karstic areas in New South Wales and Victoria, have suffered removal or major modification of their native vegetation cover, causing a loss of biodiversity associated with removal of the native vegetation, and reducing input into caves of food, such as leaves, twigs and accidental fauna (Hamilton-Smith and Eberhard, 2000).

Conclusions and synthesis

These three themes can be synthesized into a general strategy for the conservation and protection of GDEs in Australia and can build on overseas experiences. It has been suggested that it is futile to wait until all biodiversity and threatening processes have been identified before acting to protect important GDEs (Danielopol et al., 2000). Therefore, we should focus our initial efforts on protecting known 'hotspots' of biodiversity as well as areas where long-term studies of groundwater ecology have been conducted (Marmonier et al., 1997; Rouch and Danielopol, 1997) in the same way we have for surface waters (e.g., Frissell and Bayles, 1996). In Australia, we should extend this protective status to include conserving groundwaters with heavily-dependent and unique GDEs such as anchialine caves, mound springs, karstic groundwaters of northwestern Australia, cave streams, and hyporheic zones in gravel and sand-bed rivers sustained by high quality baseflow.

We advocate protection aimed at the habitat or ecosystem scale. Species recovery plans are most effective when the autecology of the threatened species is well-known. At this stage, we lack adequate knowledge of most subsurface taxa and it seems wiser to protect entire habitats and their surface recharge areas. To some degree, Australia has invoked international treaties to protect some of its GDEs. For example, caves in southwestern Tasmania, at Riversleigh in western Queensland, and Naracoorte in South Australia currently lie in World Heritage areas (Hamilton-Smith and Eberhard, 2000). Subterranean wetlands are now a category under the Ramsar Convention on Wetlands and the importance is recognised of a number of karst sites including Cape Range and several sites in the Kimberley region of Western Australia, part of the Katherine karst in the Northern Territory, caves at Chillagoe and Undara in Queensland, and a number of sites in the Naracoorte-Mount Gambier region of South Australia (Australian Nature Conservation Agency, 1996).

Such protection must be supported by public education and appreciation of the unique biodiversity of Australia's groundwaters. Currently, most conservation and management of aquatic ecosystems focus on surface habitats, sometimes to the detriment of linked groundwater systems. For example, the decision to cap surface water extraction in the Murray-Darling Basin to 1993–94 levels (Schofield et al., 2000) increased pressure on alluvial groundwater reserves in some sub-catchments. Short-term economic gains from extractive industries need to be balanced

by acknowledgement of long-term ecological issues (e.g., impacts of water abstraction in calcrete aquifers of northwestern Australia, Humphreys, 2001). Frequently, damage to fragile groundwater ecosystems may be unintentional (e.g., research diving in anchialine ecosystems, Humphreys et al., 1999; trampling in cave streams, Eberhard, 1999, 2001) and may be best addressed by targeted interpretive boards or hand-outs issued to tourists. Management must be supported by high-quality research information, presented in peer-reviewed scientific journals but also written up for a general audience in popular ecology magazines (e.g., Humphreys and Blyth, 1994), books (e.g., Eberhard and Humphreys, in press) and conference proceedings of river or cave management workshops (e.g., Boulton, 1999; Eberhard and Humphreys, 1999).

There is a considerable imbalance between the current efforts put towards protecting surface versus subsurface ecosystems. All major projects devote considerable resources in documenting vegetation and vertebrate fauna that, in the arid zone, overwhelmingly represent widespread species and rarely contain short range (project scale) endemics (e.g., for Cape Range—Baynes and Jones, 1993; Keighery and Gibson, 1993). By contrast, the subterranean fauna typically comprises short range endemics (Watts and Humphreys, 1999, 2000), often with relictual fauna of high taxonomic status (Poore and Humphreys, 1998), yet protection and documentation of this biodiversity is woefully incomplete.

Ultimately, it is not enough to simply document Australia's groundwater biodiversity. We must understand how groundwater and surface water ecosystems interact, and what roles are played by the different species in these aquatic environments. We need to know how to balance our water requirements with those of the groundwater ecosystems. In the same way that environmental flow allocations are made for river systems, groundwater environmental allocations are probably necessary for some GDEs but we are hampered by our ignorance of these water requirements. Alterations in water quality are also serious issues, especially processes of salinisation and nitrification. There is scope for some optimism. Despite the fact that since European settlement many GDEs have suffered degradation or complete loss, the last decade particularly has seen increasing recognition and protection of GDEs. This protection, sometimes indirect and not always equitable across the social and political spectrum, is reflected in environmental legislation and impact assessment policies, research directions, and public interpretation material. Fortunately, Australia still appears to have plenty

of significant subterranean 'hot spots' where it is not too late to do something about studying, conserving, and interpreting them.

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