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'Twixt two worlds: taxonomic and functional biodiversity at the surface water/groundwater interface

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Abstract – Between the familiar surface habitats of rivers and streams and the less well known groundwater environment lies an ecotone whose ill-defined boundaries oscillate in response to changes in surface discharge and groundwater pressure. This ecotone, termed the hyporheic zone, plays a crucial role as a dynamic chemical and physical filter between the adjacent ecosystems. It also potentially harbours a diverse fauna whose taxonomic composition in Australian waters is only now being explored. Given the dominance of this fauna by crustaceans in most parts of the world, coupled with Australia's rich hoard of syncarids and other Gondwanan relicts, it is likely that the biodiversity of the hyporheic zone of many of Australia's streams and rivers is considerable and exhibits high endemicity.

Functionally, invertebrate biodiversity in the hyporheic zone probably underpins the success and efficiency of these subsurface biological filters in gravel- and sand-bed rivers. Microbial biofilms coating the sediment particle surfaces are grazed by detritivorous hyporheic invertebrates. Hyporheic invertebrates, traditionally considered as just scientific oddities, may regulate the activity of these biofilms as they actively transform interstitial nutrients and alter flow paths and porosity. The impacts of river regulation and other human activities on the biodiversity of the hyporheic zone is unknown and little studied.

This paper reviews the published literature on the fauna of the hyporheic zone of Australia's rivers, seeking patterns in taxonomic representation in the scant data set. Drawing on overseas research, the functional significance of the biodiversity of the interstitial fauna is explored and related to a recent classification of groundwater and hyporheic invertebrates. Knowledge gaps in taxonomy of many groundwater groups and ignorance of the life histories of most hyporheic invertebrates confound present studies. There is a need for a national, standardised inventory of groundwater and hyporheic biodiversity to help focus future research efforts and use funding efficiently to expand our understanding of this little-known underworld.

INTRODUCTION

Knowledge of the biodiversity and ecological processes occurring in surface water habitats of Australia's streams and rivers has burgeoned in the last two decades (Lake, 1995; Boulton and Brock, 1999). Programs such as the national river health initiative (e.g., Kay *et al.*, 1999) have provided valuable inventories of biodiversity in Australia's rivers while annual taxonomic workshops dealing with epigean aquatic invertebrates have culminated in excellent keys to the Australian fauna (see Hawking and Smith, 1997). Such a coordinated inventory is lacking for Australia's groundwater fauna. However, there are a few regional 'hot-spots' where extensive research has been done (e.g., Humphreys and Adams, 1991; Humphreys, 2001) and numerous records of extraordinary discoveries in groundwater habitats such as caves and sinkholes (e.g., Zeidler, 1985; Poore and

Humphreys, 1992; Wilson and Ponder, 1992). These sporadic reports hint at a rich 'buried treasure' of substantial groundwater biodiversity (see elsewhere in these proceedings).

One interstitial habitat that is beginning to attract closer attention is the hyporheic zone, the saturated interstitial spaces that lie between the surface water of rivers and the true groundwater habitats below. The significance of the hyporheic zone lies in its role as a dynamic ecotone between the river and the groundwater (Gibert *et al.*, 1990) and a photic, mechanical, and biochemical filter (Vervier *et al.*, 1992). However, the boundaries of this zone are difficult to define because they vary in response to surface discharge, bed porosity, channel shape and other factors (Brunke and Gonser, 1997; Boulton *et al.*, 1998). The habitat is also notoriously difficult to sample, especially quantitatively (Palmer, 1993), so our knowledge of its biodiversity is scant. Is the

biodiversity of the hyporheic zone particularly high? Are there endemic taxa worthy of conservation? How might the biodiversity of invertebrate fauna in the hyporheic zone relate to its functional roles?

In an environment that is perpetually dark and ecosystem processes rely on extraneous sources of organic matter, we would predict a functional truncation of trophic diversity. Obligate inhabitants of the hyporheic zone, termed stygobites, stygophiles or permanent hyporheos (Gibert et al., 1994), would therefore be unlikely to include primary consumers (herbivores) whereas detritivores and predators/parasites would be predicted to predominate. Do hyporheic foodwebs support these predictions? And what are the implications of this trophic truncation for taxonomic biodiversity?

This paper commences by describing the hyporheic zone at a range of scales, and putting it into perspective with other groundwater habitats. The scant Australian literature is reviewed and shown to be wholly inadequate for hypothesis generation at this early stage. Functional approaches for classifying the hyporheic fauna based on habitat affinities are outlined, and show potential for regional and global comparisons among rivers. This paper concludes by considering some of the likely impacts of human activities on the biodiversity of the hyporheic zone, urging further systematic investigation of Australia's riverine underworld and its taxonomic and ecological significance.

The hyporheic zone: linkages at several scales

Simply put, the hyporheic zone is a region where riverine surface water and groundwater exchange. The direction of this hydrologic exchange ultimately dictates many of the physical, chemical and biological features of the hyporheic zone. Surface stream water downwells into the hyporheic zone at the heads of riffles or the leading edges of central and lateral bars (Figure 1), and may travel underground for long distances (up to several kilometres) before emerging. Such upwelling water is usually chemically altered during its travels, and capable of influencing the composition of surface communities near its outflow. For example, in some streams, upwelling water may be enriched in nutrients that otherwise limit algal growth in the surface stream so that the upwelling zones are 'hotspots' for benthic algal production (Coleman and Dahm, 1990).

In some streams, the volume of the hyporheic zone greatly exceeds that of the surface channel (e.g., Valett et al. 1990). In rivers with large alluvial floodplains, the zone may extend laterally for several kilometres (Stanford and Ward, 1988; Stanford et al., 1994). Thus, this potentially vast
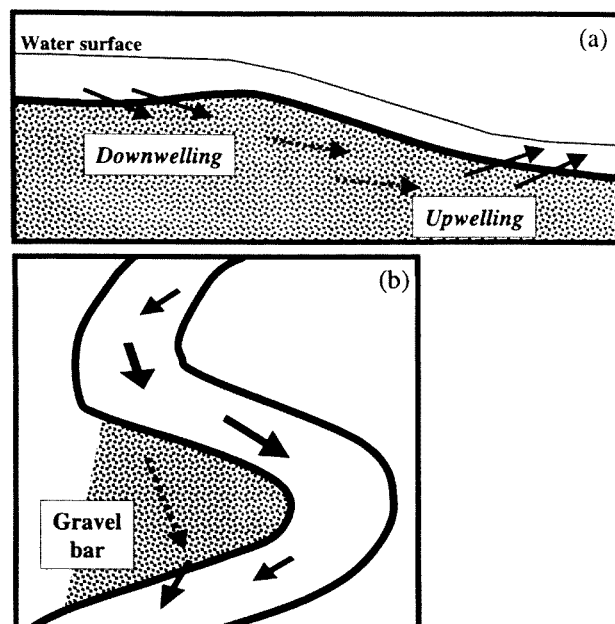
Figure 1 Interstitial pathways of water in the hyporheic zone along stream reaches from downwelling zones to upwelling zones (a) and across gravel bars (b).

zone exchanging with the surface water is capable of influencing many ecological processes in rivers and their riparian zones (Boulton, 1993; Findlay, 1995; Ward et al., 1998), and presumably their biodiversity.

The hyporheic zone can be viewed along a spectrum of temporal and spatial scales (Gibert et al., 1994). However, it is not clear the extent to which observations at one scale can be extrapolated successfully to other levels (Boulton et al., 1998). Although these scales are a continuum, it is useful to consider the hyporheic zone at three major levels: the catchment, the reach, and the sediment particle (Figure 2).

At the catchment scale, the hyporheic corridor concept (Stanford and Ward, 1993) predicts mega-scale longitudinal changes in the relative size of the hyporheic zone, its water retention, and the dominant sediment size. Expanding this to a global scale, Ward and Palmer (1994) propose an 'interstitial highway' regarded as the evolutionary pathway and long-term dispersal route for much of the subterranean fauna. They suggest that alluvial aquifers constitute a reasonably continuous hypogean habitat with linkages to many other habitats of which the hyporheic zone is only one (Figure 3). Even greater continuity along the interstitial highway may have occurred in the past because most ancient subterranean groups (e.g., syncarids) probably witnessed the breakup of Pangaea (Schminke, 1981).

In the hyporheic zone, most research has been done at the meso-scale of the reach. Here, gradients
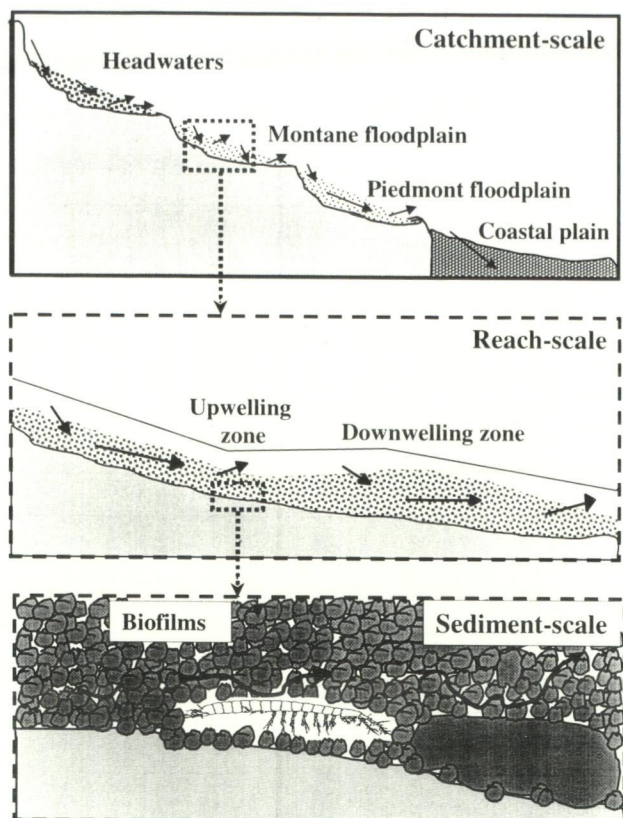
Figure 2   The hyporheic zone can be viewed at three spatial scales – catchment, reach and sediment particle. Modified from Boulton *et al.* (1998).
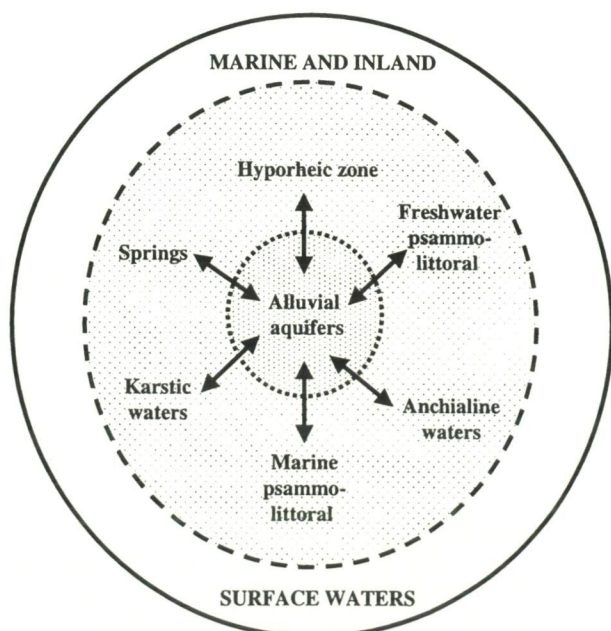

Figure 3   Alluvial aquifers act as the 'core' of the interstitial highway (central circle), with linkages to interstitial marine and freshwater habitats (middle concentric circle) that in turn link to marine and inland surface waters (outer circle). Adapted from Palmer and Ward (1994).

in nutrients, dissolved gases, other materials and subsurface invertebrates usually reflect patterns of water movement and bed permeability. In Australia, virtually all research on the fauna of the hyporheic zone has been done at the reach scale and there has never been a longitudinal study of changes in fauna along a river system (cf. Ward and Voelz, 1990).

At the level of the sediment particle, micro-scale microbial and chemical processes occur on the particles' surfaces. In some cases, we suspect that microclimates exist on the particles such that aerobic and anaerobic reactions occur simultaneously and our work at the usual scale of millimetres to centimetres simply detects the collective outcome of these fine-scale reactions (Boulton *et al.*, 1998).

The functional significance of the hyporheic zone to the entire stream ecosystem at all these scales relates to its activity (e.g., nutrient transformations, metabolism) and connection (via hydrological exchange) with surface and groundwater compartments. Microbial and chemical aspects of these processes have been reviewed extensively (e.g. Jones and Holmes, 1996; Brunke and Gonser, 1997, 1999) but there has been little attention paid to the functional role of invertebrates in the hyporheic zone at the sediment, reach, and catchment scales. These influences are probably mostly indirect, subtle, and entail invertebrate activity that affects the rates of chemical and microbial processes (Boulton, 2000a). The ecological significance and rates of these influences are likely to reflect the density of subsurface invertebrates (up to 10 711 in 3L, Strayer *et al.*, 1997) as well as thermal effects on their activity and metabolism.

Biodiversity in the hyporheic zone

To my knowledge, there has been no regional assessment of biodiversity in the hyporheic zone worldwide. Studies have either focused on particular groups (e.g., microcrustacea, Rouch and Danielopol, 1997) or have dealt with the entire suite of groundwater habitats including cave and karst systems at a general level (Marmonier *et al.*, 1993, 1997). Rouch and Danielopol (1997) suggest that subterranean waters are more species-rich for some groups such as copepods and ostracods than initially thought. However, they provide a sobering caution based on intensive sampling in Austria and the French Pyrenees that long-term, quantitative survey programs are essential to obtain an accurate estimate of subsurface faunal diversity. For example, the cumulative species curve from 130 10-L Bou-Rouch pump-samples from a 75 m^2 area of the Lachein Brook, French Pyrenees rises steeply during a year's worth of sampling and shows little sign of plateau even after some 130 samples (Figure 4). The total species richness of harpacticoid
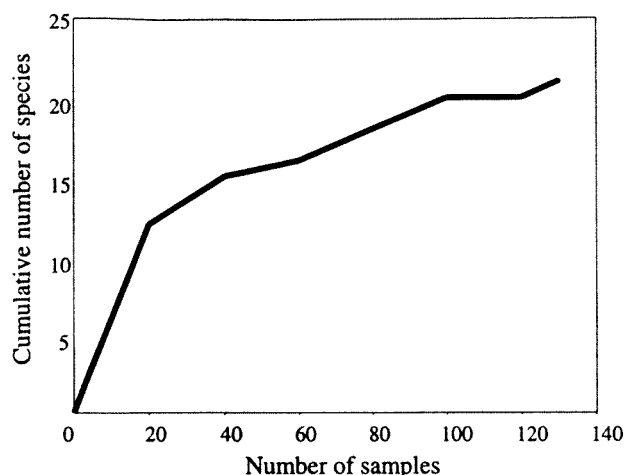
Figure 4   The cumulative number of harpacticoid
species (Cyclopoida: Copepoda: Crustacea)
plotted as a function of the number of
samples (n = 130) collected from the Lachein
Brook bimonthly from September 1985–
September 1986 (data from Rouch and
Danielopol 1997). Note that some 100 samples
are needed to collect 95% of the total species
richness at this site.

copepods (Rouch's specialist group) from this site is
21 of which 9 are stygobites (Rouch and Danielopol,
1997) although given the rise with sampling effort,
there may be more to find.

In Australia, there have been no equally intensive
studies for comparison, largely because of a lack of
taxonomic expertise in hyporheic groups. However,
in 72 6-L pump samples from the hyporheic zone of
two reaches along a subtropical NSW river (the
Never-Never River), some 20 species of water mites
in 9 families were identified by Dr Mark Harvey of
the Western Australian Museum (Boulton and
Foster, 1998). Harvey (personal communication)
considers this very diverse. Although he has used
different sampling techniques, he suggests that
surface samples can attain 15–20 species in a river,
but more commonly, there are around 10 species.
Based on Cook's (1986) Australia-wide survey of
water-mites collected from a range of habitats, only
four of some 135 sites sampled harboured 20 or
more species, and the mean number of species was
7.8 (Dr H. Proctor, Griffith University, unpublished
analyses). Walter and Proctor (1998) sampled 10
sites in south-east Queensland (a comparable region
to subtropical NSW) and reported an average of 5.7
mite species although their species-accumulation
curves imply that this is an underestimate. Of
course, comparisons of this nature are tentative as
sampling methods and intensity vary considerably
but it does indicate a 'hydracarine hot spot' in the
Never-Never River hyporheic zone.

Most overseas studies indicate that subsurface
taxonomic richness is greatest in the hyporheic zone

and least in truly phreatic groundwater habitats
(Marmonier et al., 1993, Rouch and Daniolopol,
1997). For example, comparable sets of Bou-Rouch
samples collected from hyporheic, shore (2 m from
water's edge), and phreatic habitats recorded more
than 70 taxa in the hyporheic zone samples
compared with 12–15 taxa from the other two
habitats (Pennak and Ward, 1986). The higher
biodiversity in the hyporheic zone compared with
deeper in the groundwater or laterally under the
river banks probably derives partly from inclusion
of many species that are more typically found in
surface water habitats (see later). It may also reflect
the typically higher levels of oxygen, nutrients, and
organic matter and greater rates of water circulation
(Boulton, 2000b) although locally high rates of
microbial activity may create small pockets of
anoxia inimical to invertebrates.

As we learn more about the taxonomy of the
major interstitial groups, our estimates of hyporheic
biodiversity are likely to increase substantially.
Many of these taxonomically-challenging interstitial
groups are meiofauna that seldom exceed 0.5 mm
in total body length. Such meiofauna are seldom
included in food-web studies (Ward et al., 1998) yet
may be a diverse and important food component.
For example, Schmid-Araya and Schmid (1995a)
reported 569 taxa from a 100-m stretch of the
Oberer Seebach, an Austrian gravel-bed stream.
These included 101 species of rotifers, 34 micro-
crustacean species, and 45 taxa of nematode worms.
Rotifers were the dominant prey of early instars of
stonefly nymphs and tanypod chironomid midge
larvae in the hyporheos (Schmid-Araya and
Schmid, 1995b).

Biodiversity in the hyporheic zone of Australian rivers

Unfortunately, all the published studies of the
hyporheic zone on Australian streams that I could
obtain are taxonomically incomplete. Even for the
few interstitial groups that have received taxonomic
attention beyond order, the coverage is inconsistent
(Table 1). Finally, the sampling methods differ and
it is likely that this significantly influences the
estimates of species richness from a site (Fraser and
Williams, 1997). If nothing else, Table 1 aptly
illustrates the inadequacy of our present published
data on the biodiversity of this habitat.

Marchant (1988, 1995) used a freeze-coring
technique (Table 1). This entails hammering a steel
standpipe 30 cm into the stream bed and after 24 h,
pumping it full of liquid CO_2 to freeze the
surrounding sediments to the pipe before extracting
them from the stream bed (see Marchant and
Lillywhite, 1989 for details). The primary finding
has been that most of the hyporheic fauna occurs in
the top 10 cm of the core, primarily as insects that
are more common in the surface benthos.

Table 1 Summary of taxa richness from studies of the hyporheic zone in Australian streams. A single asterisk refers to groups identified to species level, a double asterisk indicates a mixture of genus- and family-level classification, NS infers the group was not sampled (i.e. not considered a 'macroinvertebrate').

Site	Sampling method	Number of samples	Total taxa richness	Micro-crustacea	Peracarida	Syncarida Crustacea	Total	Acarina	Insecta	Others	Author(s)
Thomson R, Vic. (three sites on four occasions)	30 cm freezecore	3 x 4	38	NS?	1	0	1	2	31**	4	Marchant 1988
Acheron R, Vic. (four occasions)	30 cm freezecore	4 x 5	25	2	1	0	3	1	17**	4	Marchant 1995
Two unlogged streams, SW WA (two reaches on each)	30 cm corer	2 x 2 x 12	24	4	2	1	7	3	12	2	Trayler and Davis 1998
Two logged streams, SW WA (two reaches on each)	30 cm corer corer	2 x 2 x 12	13	3	1	0	4	2	5	2	Trayler and Davis 1998
Magela Creek, NT (3 sand tracts)	Karaman-Chappuis pits	3 x 10-25L	8	2	0	0	2	>1	2	3	Paltridge et al. 1997
Lerderderg R and Werribee R, Vic.	Karaman-Chappuis pits	5	8	NS	1*	0	1	1*	3	3	Boulton 1989
Never-Never R., NSW (2 reaches)	PVC wells	2 x 36 x 6L	61	7	2*	1*	10	20*	22**	9	Boulton and Foster 1998
Brachina Creek, SA	PVC wells	90 x 2L	31	7	1*	2*	10	>4	14**	3	Cooling and Boulton 1993

Interestingly, obligate stygobites such syncarids have not been collected by this technique and it is unclear whether this is an artifact of the sampling method and the shallow depth or, more unlikely, that syncarids do not occur in these Victorian rivers. It appears that Marchant (1988) did not include microcrustaceans in his analyses of the Thomson River (Table 1).

The work by Trayler and Davis (1998) in four streams in southwestern Australia revealed a probable impact of logging on the hyporheic fauna, resulting in a reduction in taxonomic richness. Sampling consisted of inserting a 4-cm wide corer into the sediments to 30 cm, plugging the free end with a rubber bung, and removing the core which was then frozen on dry ice for return to the laboratory (Trayler and Davis, 1998). This technique is restricted to fine sediments and gravels, and like the method used by Marchant, results are expressed as densities per volume of sediment. It is likely that pore size of the fine sediments of this study differs from the coarser river sediments of the Thomson and Acheron Rivers sampled by Marchant, further confounding direct comparisons.

In Table 1, I omitted the data from the top 1 centimetre of the samples collected by Trayler and Davis (1998) in an effort to exclude typically surface invertebrates from the comparison. Although this excluded 4–5 taxa from both sets of samples, the predominance by insects persists although it is notable that there are proportionally fewer insects in the streams whose catchments had been logged (Table 1).

Karaman-Chappuis pits are simply holes dug in the banks or river bars, and allowed to fill with subsurface water. Their name acknowledges two European scientists who used this technique early last century, and made significant contributions to our knowledge of the hyporheic fauna (see Danielopol and Marmonier, 1992). This is a simple and qualitative method, and the two examples in Table 1 were efforts to identify refuge use by aquatic invertebrates during the dry season. Compared to the other techniques, taxonomic richness is low but so is sample size. In this context, these data do little more than indicate the presence of interstitial fauna in these rivers.

In many rivers, sediments are too coarse for coring and Karaman-Chappuis pits cannot be used to sample submerged streambeds. Freeze-coring is expensive and laborious. As a result, techniques that entail pumping a known volume of interstitial water from a given depth (e.g., Bou-Rouch pumps) have become popular. One pumping method that I have found effective in a range of sediments involves inserting a PVC well (1.5–2 cm diameter) into the stream bed using a T-bar and a sledge-hammer, extracting the T-bar leaving the well in the bed, and pumping standardised volumes (6–10 L)

from the well using a manual bilge-pump. Abundances must be expressed per volume of interstitial water and are not comparable with results from coring techniques where sediment is removed. However, the method is rapid and cheap, and up to 50 samples per day may be collected by a pair of workers (Boulton, unpublished).

In two contrasting rivers – an arid-zone, intermittent creek in South Australia and a subtropical permanent river in NSW, relatively diverse hyporheic assemblages containing stygobite peracarid and syncarid crustaceans, interstitial microcrustaceans, and some stygobite water mites have been reported (Table 1). Unfortunately, uneven taxonomy prevents direct comparison but there is still evidence for a taxonomic dominance by insects.

What hypotheses or conclusions can be drawn from Table 1? Firstly, in contrast to true groundwater habitats where crustaceans predominate (e.g. Rouch and Daniolopol, 1997), insects are likely to be diverse, especially in downwelling zones where surface water enters the hyporheic zone. Nearly all of these insects are capable of surviving entirely in surface habitats (Claret et al., 1999a) and in fact, there are only a few obligate stygobite insects worldwide (reviewed in Boulton, 2000b). This dominance by insects has also been reported in studies of the hyporheic fauna in New Zealand (Boulton et al., 1997; Adkins and Winterbourn, 1999).

Although some hyporheic groups like the water mites may be diverse in some rivers, such taxonomic diversity is unlikely to be consistently high across the Australian continent, and it is more likely that 'species oases' sporadically occur reflecting evolutionary events or combinations of ideal habitat and dispersal pathways. For example, Horwitz (1997) demonstrates the occurrence of hot spots of localised high non-insect diversity in lentic and subterranean habitats in south-west Australia. Other taxonomic groups such as the syncarids, while seldom numerically abundant in the hyporheic zone, appear to be more widespread than expected and probably rich in species. In these groups, it is likely that there is considerable endemism and a strong fidelity to individual catchments, at least in the eastern part of Australia (Peter Serov, Centre for Natural Resources, Department of Land and Water Conservation, personal communication). We need more collections, from a wider regional spread and involving greater numbers of comparable samples to test these hypotheses in Australia. We also require a national database of groundwater and hyporheic habitats, with adequate attention to quality control and assurance in sampling and taxonomy along similar lines to the national river health program. With increasing awareness of the significance and

ubiquity of groundwater-dependent ecosystems in Australia (e.g. Hatton and Evans, 1998) and overseas (Winter et al., 1998; Danielopol et al., 1999b), perhaps such a program is plausible in the new millenium. This proposal and its potential benefits for efficient use of limited funding and scientific resources are discussed later.

Functional classifications of hyporheic invertebrates based on habitat affinity

Contemporary functional classifications of hyporheic invertebrates (the 'hyporheos') derive from categories used by European researchers studying cave ecosystems in the early 1900s (Table 2). In this classification, invertebrates were considered as stygoxenes if they spent their entire lifecycle in surface water or stygobites if they spent their entire lifecycle in groundwaters. An inter-mediate category termed stygophiles included species that spent all or part of their lifecycle in the sediments to varying degrees (Table 2). This last category was confusing to most researchers, not the least because of the general uncertainty associated with the lifecycles of most subterranean species.

In the mid-1970s, Williams and Hynes (1974) proposed a classification that was specifically designed to apply to hyporheic invertebrates. Epigean invertebrates were collectively considered as benthos whereas hyporheic invertebrates were divided into 'occasional' hyporheos if they were sometimes found in the benthos and 'permanent' hyporheos if they were obligate residents of the hyporheic zone. This classification found favour with most North American workers, and seemed reasonably workable. However, some life histories of hyporheic invertebrates are rather bizarre. One group, termed amphibites, has a life cycle that necessarily includes surface and ground waters. For example, some plecopteran stoneflies in the genera *Isocapnia*, *Paraperla* and *Kathroperla* live as nymphs in the total darkness of the deep hyporheic zone of the Flathead River, Montana before returning to the

river to emerge as terrestrial adults (Stanford and Ward, 1988; Stanford et al., 1994).

I suspect that the popularity for North American workers of the classification by Williams and Hynes reflected its publication in English in a journal readily used by this research culture. Until recently, much of the valuable pioneering work on subterranean invertebrates by European scientists was denied to monoglot English-speaking researchers but strenuous efforts by many European experts to publish in English and in widely-read journals have been extremely beneficial. The present healthy state of the discipline of groundwater ecology owes much to these efforts (Danielopol et al., 1999b).

In the mid-1990s, there was an attempt to synthesise the European and North American classifications by habitat affinity (Marmonier et al., 1993; Gibert et al., 1994, Table 2). There have been energetic moves (e.g. Claret et al., 1999a and references therein) to adopt this as a standard classification to avoid the redundancy in terminology evident in Table 2, and to emphasise the value of the functional approach. Epigean benthos are termed stygoxenes, stygophiles embrace the occasional and permanent hyporheos of Williams and Hynes (1974) as well as amphibites, and stygobites now encompass all forms that are exclusively groundwater dwellers, and have specializations for an obligate subterranean existence. Some stygobites are widely distributed in karstic and alluvial habitats [termed 'ubiquitous stygobites' by Gibert et al. (1994)] whereas others are restricted to the deep groundwater substrata of alluvial aquifers ('phreatobites').

One of the advantages of this functional approach has been early efforts to compare the global distribution of the six groups based on habitat-affinity to determine if there are any trends that might relate to ecological aspects of the hyporheic zone. For example, the Flathead and Rhone Rivers are both large rivers with extensive hyporheic zones

Table 2   The functional classifications based on habitat-affinity used by researchers studying interstitial invertebrates, culminating in the current 'synthetic classification' (adapted from Gibert et al. 1994; Claret et al. 1999a).

| Classification	Proponents	Surface	'Intermediate'	Groundwater
Earliest, used by Europeans for cave fauna	Thienemann, 1925, Botosaneanu, 1986	*Stygoxen* (epigean)	*Stygophile*	*Stygobite* (hypogean)
North American adaptation, used for streams	Williams and Hynes, 1974, Williams, 1984	*Benthos*	*Occasional hyporheos, permanent hyporheos*	Not applicable
Current synthetic classification, combining all interstitial classificaions	Marmonier et al., 1993, Gibert et al., 1994, Claret et al., 1999a	*Stygoxen*	*Stygophile (Occasional hyporheos, permanent hyporheos, amphibites)*	*Stygobite (ubiquitous or phreatobite)*
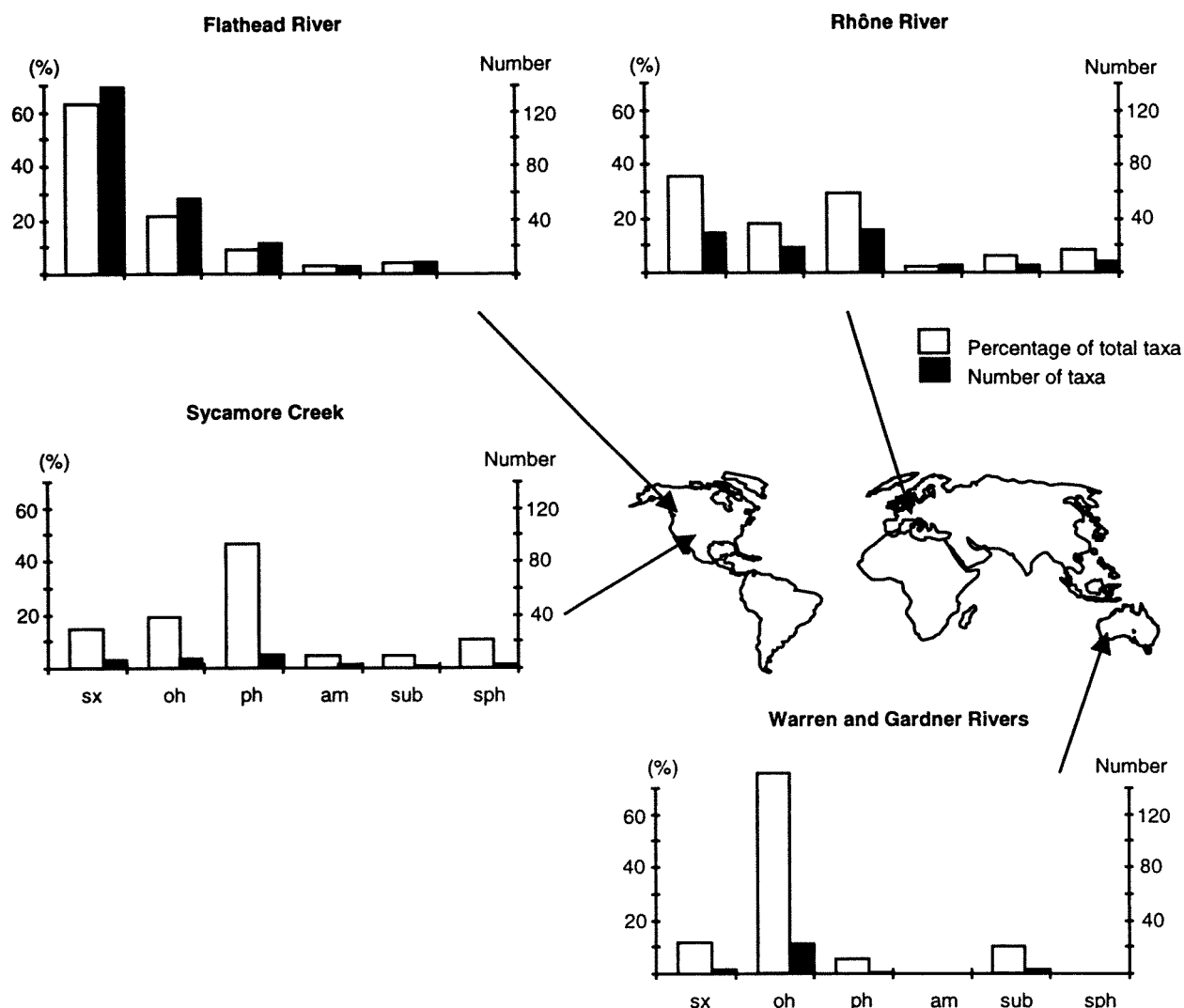
Figure 5 Global comparisons of hyporheic assemblages based on habitat affinities in two large rivers (Flathead River, Montana and Rhône River, France), a desert stream (Sycamore Creek, Arizona) and two small streams (tributaries of the Warren and Gardner Rivers, Western Australia). Although these assemblages differ taxonomically, the comparisons derive their value from functional attributes and hypothesis generation. Open bars represent the taxa as percentages, closed bars give the actual number of taxa. Stygoxenes = sx, stygophile 'occasional hyporheos' = oh, stygophile 'permanent hyporheos' = ph, stygophile amphibites = am, ubiquitous stygobites = sub, and phreatic stygobites = sph. Categories as in Claret *et al.* (1999a).

and permeable floodplains and might be expected to be functionally similar in their subsurface processes. However, they differ in proportions of stygoxenes and permanent hyporheos (Claret *et al.*, 1999a; Figure 5). In a desert stream such as Sycamore Creek, fine sediments and the variable flow regime including periodic drying may account for the relatively low proportions of stygoxenes.

Based on Table 4 in Trayler and Davis (1998), I used their subsurface distribution data from the two unlogged streams to classify the fauna by habitat affinity. Taxa that only occurred in the 0–1 cm level or comprised > 100 individuals per 10 cm³ but fewer than 10 individuals per 10 cm³ in the hyporheic zone, were considered stygoxene. Ubiquitous stygobites included the blind

bathynellids and onchyiurid collembolans whereas permanent hyporheos were taxa that did not occur in the top one centimetre but were present throughout the cores down to 30 cm. Remaining taxa were considered occasional hyporheos. Compared to the other three rivers, the hyporheos of these two West Australian sites contains a high proportion of occasional hyporheos. However, without further life history data, it is impossible to assess whether amphibites were present, and these comparisons can only be considered tentative.

Presently, this approach is hampered by the preliminary nature of our data sets, our rudimentary knowledge of life history features of some of the fauna, and the varying sampling methods and taxonomic resolution (see Claret *et al.*,

1999a). However, it illustrates the potential for global and regional comparisons of taxonomically disparate assemblages of the hyporheos. This approach has also proved useful for demonstrating changes in hyporheic functional composition in response to management practices in rivers (Claret et al., 1999b).

Trophic truncations in hyporheic foodwebs

As biodiversity and ecosystem function are purported to be linked with dissipation of energy, primary and secondary production may ultimately control biodiversity at local and perhaps regional scales (e.g., Tilman, 1993; Freckman et al., 1997). If we seek a reason for the lower biodiversity in hyporheic and groundwater habitats, we need go no further than the obvious lack of primary production in these environments. In the absence of this, the trophic web of the hyporheic zone will lack herbivores, and be dependent on energy from inwelling organic matter, microbial activity in biofilms (Bärlocher and Murdoch, 1989), and in some cases, root-mats in riparian zones. As far as I know, chemoautotrophy has not been reported from the hyporheic zone and is unlikely to be a significant energy source to hyporheic foodwebs.

In fact, most hyporheic invertebrates seem to be detritivores that either 'shred' coarse particulate organic matter (> 1 mm) or graze microbial biofilms on the sediment particles (Ward et al., 1998; Boulton, 2000b). Many others are principally predators or parasites ('carnivores') ranging from large predatory syncarids (P. Serov, personal communication) to small rotifers, microturbellarian flatworms, and nematode worms (Schmid-Araya and Schmid, 1995b). It also seems that a large number of hyporheic species are probably omnivorous, feeding opportunistically (Claret et al., 1999a). Some facultative herbivores (usually stygoxenes) comprise part of the interstitial foodweb because green plant material can occur in hyporheic zone under downwelling zones but they are rare.

This 'trophic truncation' has long been known for cave faunas (Culver and Poulson, 1970) and extended to alluvial aquifers by Ward and Palmer (1994). It largely accounts for why groundwater and hyporheic faunas are not as diverse as those in epigean systems, and underpins many of the current theories about clinal changes between surface and subsurface ecosystems (e.g. Brunke and Gonser, 1999). It may also explain why the higher species richness often evident at ecotones that harbour species from both adjacent habitats is not as evident in the hyporheic zone.

There is an ironic twist to this exploration of hyporheic foodwebs and biodiversity. Within the sediments, the small-bodied, poorly studied forms are progressively more important in the interstitial foodweb as we move down from the sediment surface (Ward et al., 1998). However, we probably know most about the larger, and perhaps less ecologically-significant epigean forms. There is an urgent need to learn more about the ecology and taxonomy of the 'little things that run the world' (Wilson, 1987) and this is reflected in the increasing interest being shown in the relationship between biodiversity and ecological processes in sediment ecosystems (Freckman et al., 1997; Danielopol et al., 1999b).

Biodiversity in the hyporheic zone: knowledge gaps and threatening processes

Most of the knowledge gaps in our understanding of the taxonomic and functional biodiversity of the hyporheic zone have already been identified. One further issue, also emphasised by Marmonier et al. (1997), is that of limited and perhaps dwindling taxonomic expertise in some of the groups of groundwater animals. Some groups, particularly crustaceans, are wholly phreatic (see elsewhere, this volume, and exhibit high endemism (Botosaneanu, 1986) and a much greater biodiversity than previously thought (Danielopol et al., 1999a; Martens and Danielopol, 1999). Even for some groups with epigean representatives (e.g. Copepoda and Ostracoda), local species richness in groundwater habitats is as high as in the surface waters (Rouch and Danielopol, 1997). The inadequacy of Table 1 demonstrates how hampered we are by the limited taxonomic resolution of Australian hyporheic studies.

The second knowledge gap relates to understanding and explaining the importance of hyporheic biodiversity to river management. There have been some studies of the effects of land-use and river management on hyporheic biodiversity (Boulton et al., 1997; Trayler and Davis, 1998; Claret et al., 1999b; Marmonier et al., 1999) but most research is based on descriptive surveys rather than manipulative large-scale experiments involving studies before and after the impact. However, with our growing understanding of the functional significance of the hyporheic zone to the entire river ecosystem (Findlay, 1995; Brunke and Gonser, 1997; Boulton et al., 1998; Jones and Mulholland, 2000) coupled with efforts to present these findings in popular scientific literature (e.g. Marmonier et al., 1993) and river management conference proceedings (Boulton, 1999; Marmonier et al., 1999), this gap is closing. Recently, hypotheses about the beneficial effects of environmental flow rules in the Hunter River, New South Wales, were extended to include ecological processes and invertebrate diversity in the hyporheic zone (Boulton, Hancock and Raine, unpublished).

We know virtually nothing about the life histories of most Australian stygophiles and stygobites. This

ignorance hampers our use of functional attributes for global and regional comparisons (see above) and makes it difficult to predict impacts of water resource issues such as groundwater extraction and changes to surface water regimes on recruitment and survival of hyporheic invertebrates.

Most of the processes that are considered threatening to surface species (Table 12.1 in Boulton and Brock, 1999) are also likely to impact the biodiversity of hyporheic assemblages and subsurface ecological processes. Table 3 lists the primary threats that would be expected to impact on hyporheic biodiversity in Australian rivers. The effects of very few of these have been studied in Australia. Trayler and Davis (1998) found a difference in the hyporheos between two logged and two unlogged streams in south-west Australia, and advocated the inclusion of hyporheic sampling in future biomonitoring protocols in sandy streams

of this region. Also in south-western Australia, Boulton and Marmonier (unpublished data) found fewer hyporheic species in streams subject to salinization than in nearby freshwater streams. Unfortunately, without data collected prior to salinization it is difficult to know whether this difference in biodiversity may not partly reflect biogeographic patterns. These early results indicate that the 'health' of the hyporheic zone may be measured by hyporheic invertebrate biodiversity in similar ways to our assessment of river health using surface macroinvertebrate assemblage composition.

Conclusions

We have known of the existence of a diverse hyporheos for nearly 80 years. The functional significance of the hyporheic zone has only become clear in the last 20 years or so; the management implications even more recently. As we enter a new

Table 3 Human activities capable of directly or indirectly impacting biodiversity and ecological integrity of the hyporheic zone.

Threat	Predicted impacts
Reduction in water levels from groundwater extraction	Removal of saturated habitat, alteration of subsurface flows, severing links between surface and subsurface components
Extraction and diversion of surface waters	Increased frequency and extent of drying of the hyporheic zone, severing links between surface and subsurface components
Mining and substrate extraction from rivers (e.g., gravel extraction)	Physical removal of habitat, alteration of subsurface flows, sedimentation
River "beautification" in urban areas (e.g., clearing native riparian zones)	Alteration of subsurface nutrient and organic matter dynamics, alteration of subsurface flows, sedimentation
River regulation including channelization, alteration of water regime, and desnagging	Physical removal of habitat during channelization, alteration of subsurface flows (and at a fine scale by removing snags), sedimentation
Weed invasion, including exotic aquatic plants and woody rooted species	Alteration of gravel bar and riparian zone stability, potential alteration of subsurface nutrient and organic matter dynamics, potential toxicity effects
Grazing and trampling of gravel bars and riverbeds	Compaction, alteration of subsurface flows, sedimentation, input of localised nutrients
Increased erosion of riverbeds and gravel bars by water regime alteration	Physical removal of habitat, alteration of subsurface flows, scouring of interstitial biofilms, inhibition of biological filtration capacity
Siltation due to diversion of rivers, changes to water regime, overclearing, etc.	Sedimentation filling interstitial spaces, alteration of subsurface flows, severing links between surface and subsurface components
Groundwater and river salinization	Direct toxicity effects on hyporheos, indirect effects on biofilms and prey
Discharge and runoff of industrial and agricultural effluents and chemicals, stormwater runoff, heavy metals from derelict mines	Direct toxicity effects on hyporheos, indirect effects on biofilms and prey
Acidification of water from mine runoff or runoff from acid-sulfate soils	Direct toxicity effects on hyporheos, increased solubility of heavy metals, indirect effects on biofilms and prey
Thermal pollution from coldwater releases or warmed water from power stations	Altered hyporheic metabolic rates and productivity, direct physiological impacts on hyporheos and biofilms

millenium with a clearer understanding of the linkages among streams, their catchments, their airsheds and the groundwater, we have a growing appreciation of the fundamental importance of the ecotones between these ecosystem compartments, and their taxonomic and trophic biodiversity. We need to preserve this biodiversity, already threatened by many of our activities but also at risk from our ignorance of its existence. As we change the conditions on either side of the hyporheic zone, what happens 'twixt the two worlds? And if we alter the exchanges of water, nutrients, energy, and fauna across this dynamic ecotone, what will be the ultimate fate of the two worlds that depend on the maintenance of this pathway?

Australia's unique southern groundwater fauna harbours an important store of 'phylogenetic diversity' (sensu Marmonier *et al.*, 1997) in the ancient representatives of groups such as the syncarids. The ancient endemics are often so restricted in their distribution that local disappearance in many cases means their complete extinction (Rouch and Danielopol, 1997). Our present piecemeal exploration and description of subterranean habitats in Australia indicate much greater subsurface diversity than previously expected but we should adopt a more structured and coordinated approach to this inventory than presently is the case. We have the advantages of lessons learnt from the National River Health Program in terms of standardisation of sampling protocols as well as the rich experiences of the longer term programs in Austria, France, Montana and other regions where groundwater studies have progressed for over a decade. Such a collective approach is also likely to attract and more efficiently use sustained funding to provide crucial data for river and groundwater management in Australia. Groundwater and hyporheic habitat protection must occur at a large scale (e.g., drainage basins and river-aquifer systems) because of the importance of linkages between the surface and subsurface habitats. The suggested database would enable the identification and subsequent conservation of such 'key areas' (Frissell and Bayles, 1996) to preserve this buried treasure of biodiversity.

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