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Ecology and management of the hyporheic zone: stream–groundwater interactions of running waters and their floodplains

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Abstract. Over the last 25 y, stream ecosystem theory has expanded to include explicitly the vertical dimension of surface–groundwater linkages via the hyporheic zone and below alluvial floodplains. Hydrological exchange between the stream and hyporheic zone mediates transport of products from the biogeochemical activities within the sediments. *Hot-spots* of primary productivity in the surface stream often result from upwelling nutrient-rich water. Conversely, downwelling surface water supplies organic matter and dissolved O_2 to hyporheic invertebrates and microbes, enhancing hyporheic productivity. Many of the papers seminal to conceptual and empirical advances in hyporheic research have been published in *J-NABS*, reflecting stream benthologists' awareness of the relevance of processes and biota in the hyporheic zone. However, major research gaps remain. One is the need for further empirical data to test the predictions of several current conceptual frameworks that hypothesize conditions under which the hyporheic zone might be expected to contribute most to surface stream metabolism, especially in large rivers with shallow alluvial aquifers. A second is how to apply research findings about the functional significance of the hyporheic zone to river restoration and conservation. Many activities that restore or protect surface biota and habitats probably benefit hyporheic processes and fauna as well, but this prediction should be tested. Last, hyporheic exchange and the biogeochemical processes within the sediments occur across multiple hierarchical spatial scales, but we are yet to understand fully these interactions or to extrapolate successfully across scales. *J-NABS* should continue to play a significant role in publishing research on the hyporheic zone and extend the scope to include applications in river and floodplain management and restoration.

Key words: hyporheic, river restoration, hydrological exchange, alluvial aquifer, subsurface invertebrates, biogeochemical transformations, human impacts, hydrogeomorphology.

The scientific disciplines of stream ecology and benthology, aquatic biogeochemistry, hydrogeology, geomorphology, and hydrology have entwined over the last 25 y to advance our understanding of the roles played by stream–groundwater interactions in the hyporheic zone, the saturated interstices below the stream bed and adjacent banks that contain some proportion of channel water (**White 1993**[11]). The hyporheic zone can be viewed as a benthic *dynamic ecotone* (Gibert et al. 1990 [Fig. 1], **Vervier et al. 1992**) where hydrological, ecological, and biogeochemical processes interact. These interactions influence key stream ecosystem processes, such as primary productivity and nutrient cycling, in the surface stream (see **Mulholland and Webster 2010**), and the sediments harbor microbes and invertebrates (Brunke and Gonser 1997; Fig. 1) and are used by some fish for spawning

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[11] Boldface indicates paper was published in *J-NABS*

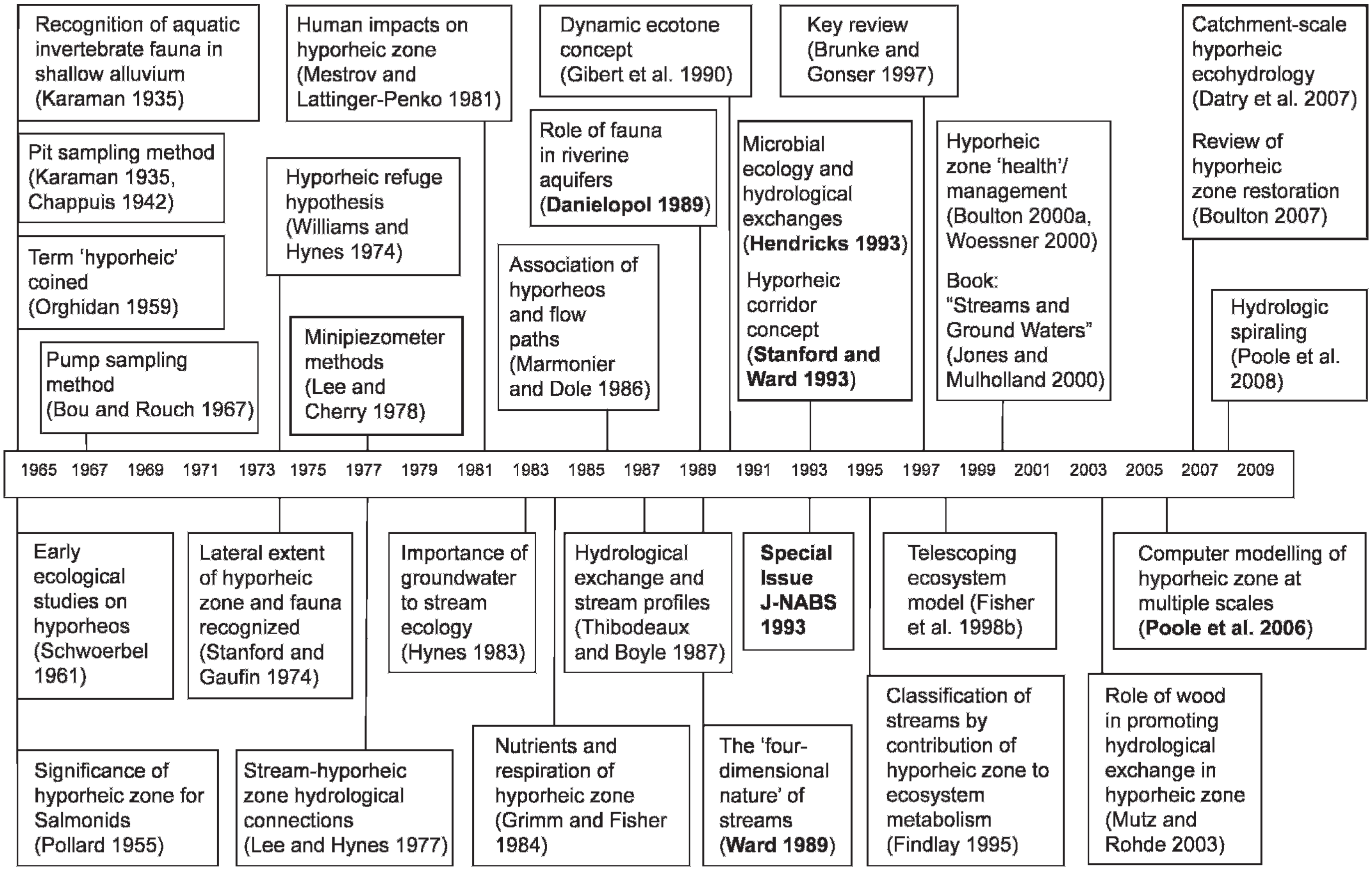

FIG. 1. A timeline of significant papers contributing to our understanding of the hyporheic zone and its functional significance. Boldface indicates papers published in *J-NABS*.

(Pollard 1955 [Fig. 1], Greig et al. 2007). Explicit incorporation of vertical hydrological connectivity in conceptual models of stream ecosystems lagged behind inclusion of the more obvious longitudinal and lateral linkages (e.g., River Continuum Concept; Flood Pulse Concept). However, several perceptive authors flagged the probable importance of the hyporheic zone early (e.g., Orghidan 1959 [Fig. 1], Schwoerbel 1964, Williams and Hynes 1974 [Fig. 1]), and its inclusion is now explicit in most contemporary stream ecosystem models (e.g., Thorp et al. 2006).

Our review explores significant advances, many described in seminal *J-NABS* papers, in our understanding of benthos and processes occurring in the hyporheic zone and their significance to lotic ecosystems. We review the development of relevant hydrological, biogeochemical, and ecological themes (Fig. 1) leading up to the 1993 special issue of *J-NABS*, before examining several aspects in detail as they relate to contemporary stream benthology, hydrology, and biogeochemistry. The relevance and application of this research to current management, conservation, and restoration of rivers comprise our conclusions because human activities have impaired many of the functions of the hyporheic zone in rivers (Hancock 2002, Kasahara et al. 2009).

A Dynamic Ecotone Where Stream and Ground Water Exchange

Defining the hyporheic zone

The hyporheic zone is popularly defined as the saturated interstitial spaces below the stream bed and adjacent stream banks that contain some proportion of channel water (**White 1993**). Early attempts to delineate the hyporheic zone were based on the distribution of subsurface and surface invertebrates. For example, Schwoerbel (1961; Fig. 1) considered the hyporheic zone as a 'middle zone' between channel waters above and true ground water below. Later authors tried to refine this definition further based on the vertical and lateral distribution of interstitial invertebrates (e.g., Stanford and Gaufin 1974 [Fig. 1], Williams and Hynes 1974, Williams 1989). However, the diversity of hyporheic zone types (e.g., perched, losing, or gaining reach configurations; Malard et al.

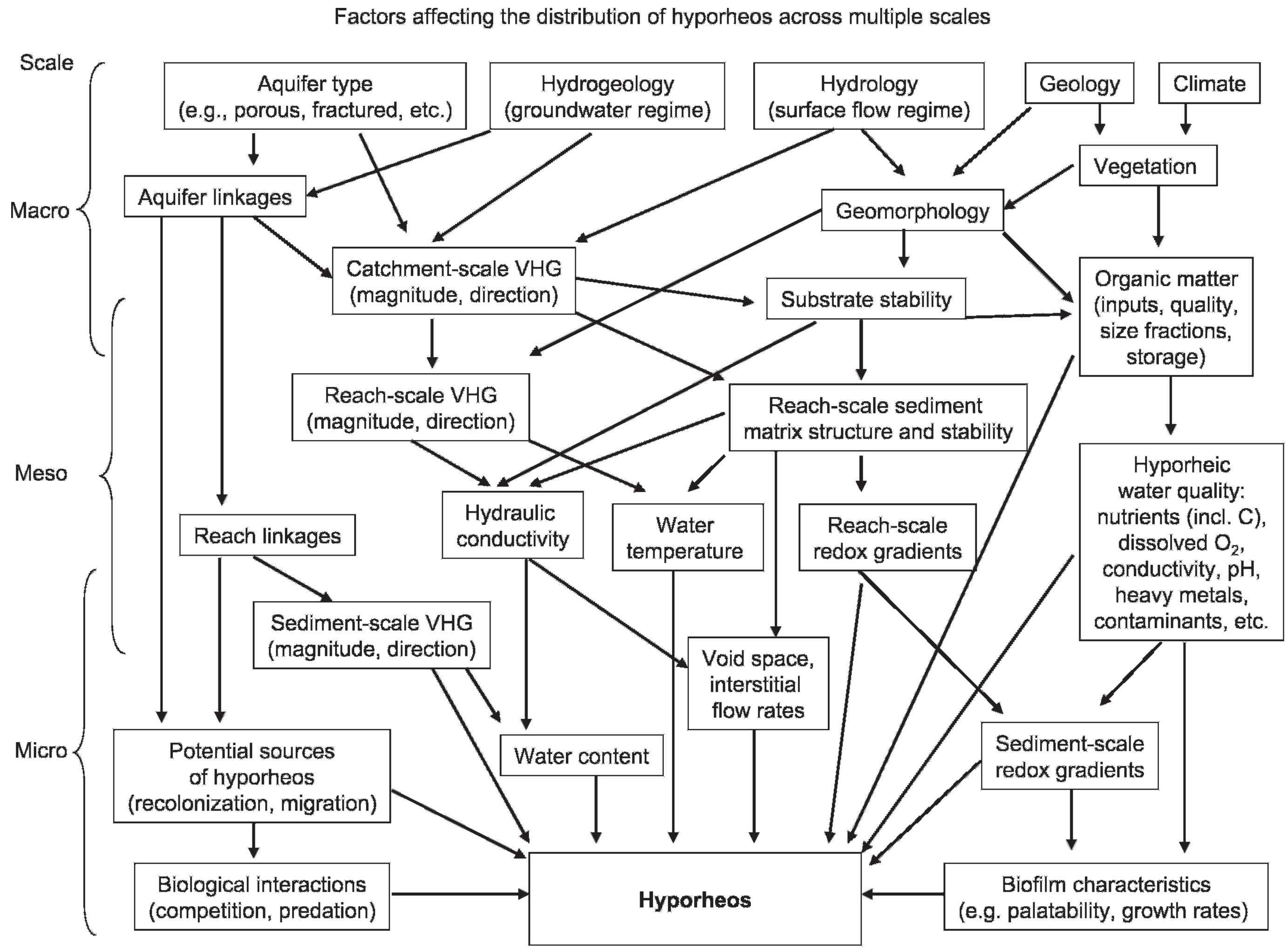

FIG. 2. Simplified diagram of the interactions among variables across 3 overlapping spatial scales (macro = landscape–catchment, meso = catchment–reach, micro = reach–sediment particle) that potentially influence the distribution and composition of the hyporheos.

2002) and the many other factors governing hyporheic invertebrate distribution (Fig. 2) confound any definition based solely on the distribution of mobile organisms (**Danielopol 1989** [Fig. 1], **White 1993**).

This problem prompted alternative or complementary definitions based on physicochemical variables. Triska et al. (1989) used tracer studies to attempt to delineate the hyporheic zone based on chemical differences between channel and ground water. They defined the 'surface zone' as the region immediately beneath the bed that is chemically indistinguishable from channel water and contains >98% channel water. Beneath the surface zone, they recognized an 'interactive zone', containing 10 to 98% channel water, the depth of which indicates the hydrologic boundary of the stream. Although the arbitrariness of these categories and their static nature would later attract criticism (**Vervier et al. 1992**), this early definition was a valuable application of hydrological criteria to help define the hyporheic zone using the very factor that drives many of the processes occurring within it.

The dynamic ecotone concept

One fruitful direction in describing the hyporheic zone has been the concept of its role as a *dynamic ecotone* (Gibert et al. 1990)—'dynamic' in that its boundaries fluctuate in response to sediment characteristics and hydrological exchange; 'ecotone' because it bounds the stream above and groundwater below. Gibert et al. (1990) highlighted the properties of elasticity, permeability, biodiversity, and connectivity of the hyporheic zone as governing its functional role in streams. Elasticity reflects the degree to which the size of the hyporheic zone fluctuates, given sediment permeability and discharge characteristics. Permeability refers to the extent to which water and materials filter across the ecotone. The hyporheic zone acts as a mechanical filter mediated by the sediments and water flows, a biochemical filter controlled by biological and chemical processes, and a photic filter. Last, the connectivity that exists between the stream and underlying ground water extends laterally below banks and flood plains, sometimes for many meters (Stanford and Ward 1988).

In a key Perspectives paper in *J-NABS*, Vervier et al. (**1992**) extended this dynamic ecotone concept and explored how permeability influenced the capacity of the hyporheic zone to act as a sink for materials in the 2 adjacent systems. For example, coarse particulate organic matter buried in the hyporheic zone during floods (e.g., Metzler and Smock 1990) is temporarily removed from the surface system. However, because of biogeochemical activities in the hyporheic zone, transformed nutrients and fine particulate organic matter are liberated into the ground water and stream water depending on the direction and magnitude of vertical hydrological exchange. Vervier et al. (**1992**) concluded that influence of the hyporheic zone on the surface stream ecosystem depended on the elasticity, permeability, biodiversity, and connectivity of this dynamic ecotone; this conclusion was to become a focus of subsequent research on the functional significance of the hyporheic zone.

Where It Began: Discovery of Hyporheic Invertebrates

Although scientists had been aware for several centuries that many deep aquifers harbored aquatic invertebrates adapted for life in a lightless world (reviews in Gibert et al. 1994, Humphreys 2006), the discovery of invertebrates in saturated sediments below and alongside streams was comparatively recent. Digging pits in gravel bars along several European rivers and sieving the seepage yielded rich hauls of invertebrates of both surface benthos (e.g., mayflies, stoneflies, chironomid midges) and interstitial groundwater fauna, such as blind water mites, isopods, and amphipods (Karaman 1935, Chappuis 1942; Fig. 1). Soon after, the use of hand pumps to extract water from up to 1 m below the stream bed (Bou and Rouch 1967; Fig. 1) demonstrated that this fauna also occurred at substantial depths below the stream in the 'hyporheische Biotop', a term coined by Orghidan (1959) that literally translates into the 'under+flow' biotope. Subsequent studies (reviewed in Brunke and Gonser 1997, Boulton 2000b) have demonstrated that the saturated sediments of many streams support a diverse invertebrate fauna, widely known as *hyporheos* (Williams and Hynes 1974). The discovery that the hyporheos could occur many hundreds of meters from the channel (Stanford and Gaufin 1974) was even more exciting and forced stream ecologists to think laterally when considering transfers of organic matter and energy in the hyporheic zone (Ward et al. 1998).

Orghidan (1959) also suggested that hyporheic sediments acted as a stable refuge for stream benthos, an idea developed further by Williams and Hynes (1974) in their 'hyporheic refuge hypothesis'. This hypothesis is tantalizing, but field and experimental evidence supporting it is equivocal (Palmer et al. 1992, Dole-Olivier et al. 1997, Olsen and Townsend 2005), and it remains an intriguing paradox worthy of further study. Colonization of the hyporheic zone by stream benthos is probably a mixture of active immigration and passive transport (Marmonier and Dole 1986 [Fig. 1], Boulton et al. 1991). Living space, dissolved O_2, and food appear to be key resources influencing the distribution of the hyporheos (Brunke and Gonser 1997, Strayer et al. 1997), with the microscale supply of energy and O_2 mediated by mesoscale factors of sediment matrix structure and direction and strength of hydrological exchange with the surface stream (Fig. 2). The food base in the hyporheic zones of the Nyack Flood Plain (Middle Flathead River, Montana) is a complex microbial biofilm (**Ellis et al. 1998**); recent determination of its composition has identified entire suites of previously undescribed microbes (Lowell et al. 2009). Biological interactions, such as competition and predation, also are likely to govern the ecology of hyporheic invertebrates, but there seem to be no published studies of these interactions, despite the prevalence of hyporheic predators in many streams (Boulton 2000b).

By the end of the 1970s, benthic stream ecology was blossoming into a vibrant discipline integrating the biogeochemical implications of the hydrological links of the 'stream and its valley' (Hynes 1975) and associated ground waters (Lee and Hynes 1977; Fig. 1). Although efforts to define the boundaries of the hyporheic zone precisely were already foundering, its ecological significance to the surface stream was becoming evident (Williams and Hynes 1974). Benthic ecologists were looking for new tools to broaden their scientific horizons and became increasingly willing to embrace the related disciplines of hydrogeology and biogeochemistry. The time was ripe for innovative paradigms and novel methods.

Integrating Stream–Groundwater Hydrology and Ecology: 1980s–1993

In 1983, Hynes published a seminal paper (Fig. 1) that urged stream ecologists to learn more about ground water because of its implications for understanding water balance and ecosystem metabolism in running waters, especially where groundwater is an important source of organic matter. He highlighted the need for stream ecologists to develop a wider appreciation of methods and paradigms in hydrogeology and promoted the textbook by Freeze and Cherry (1979) as a useful starting place. Concepts and field techniques in hydrogeology must have appeared particularly inaccessible to stream ecologists at this time. However, one early hydrogeological paper that probably played a crucial role in overcoming this hurdle was Tóth's (1963) idealized model of groundwater flow paths across the landscape. In this model, Tóth recognized 3 types of flow systems—local, intermediate, and regional—that could be superimposed hierarchically within a groundwater basin. Tóth (1963) conceptually illustrated the hierarchical connections between streams and groundwater systems, and the paper had significant consequences for later studies of stream–groundwater interactions (Hancock et al. 2005, **Poole 2010**).

Part of the problem in the uptake of hydrogeological approaches by stream ecologists apparently resulted from a mismatch of scales. Groundwater scientists tended to work at regional and catchment scales, whereas most stream ecologists in the 1980s were doing research at the stream-reach scale. The need for finer-scale methods that stream ecologists could use readily was soon filled by Lee and Cherry (1978; Fig. 1), 2 hydrogeologists who described simple, inexpensive methods to measure relevant streambed characteristics, such as vertical hydraulic gradient (VHG) and sediment hydraulic conductivities. Networks of small wells (minipiezometers) were used to measure VHG as a strong indicator of the potential direction and strength of vertical hydrological exchange at scales of 10^{-1} to 10^{2} m, and this method has been used widely (e.g., Boulton 1993, **Pepin and Hauer 2002**, **Wright et al. 2005**). Another seminal paper (Thibodeaux and Boyle 1987; Fig. 1) graphically illustrated how stream flow could affect VHG at a reach scale, prompting stream ecologists to assess hydraulic and sediment properties to understand benthic and interstitial nutrient dynamics (Grimm and Fisher 1984 [Fig. 1], **Triska et al. 1990**, **Valett et al. 1990**) and to seek associations with the distribution of the hyporheos (e.g., Marmonier and Dole 1986, Rouch 1988).

At the close of the 1980s, 2 significant *J-NABS* papers came from a special issue on global stream ecosystem theory, integrating hydrology and the ecology of the hyporheos. The 1st, Danielopol (**1989**), described long-term studies on the Danube alluvium in the Vienna Basin where aquifer water flow is largely governed by river flows. He proposed that the surficial deposits of the gravel bars along the Danube act as giant 'trickling filters' whose activity was promoted by fluctuations in water level, and he drew attention to the potential role of hyporheic invertebrates, such as the isopods *Proasellus*, in sustaining the permeability of the sediments through feeding and fecal pelletization. These suggestions led to experiments demonstrating the roles of hyporheic fauna in, for example, bioturbation (Mermillod-Blondin et al. 2000, Mermillod-Blondin and Rosenberg 2006) and N cycling (**Marshall and Hall 2004**).

The 2nd paper, Ward (**1989**), was a framework for lotic ecosystem theory that explicitly acknowledged the vertical dimension of stream ecosystems to include the hyporheic zone, elevating its significance to that of lateral and longitudinal dimensions. Ward (**1989**) added a 4th dimension, time, to account for temporal variations in the interactions across these 3 spatial dimensions and the role of disturbance in disrupting pathways along these dimensions (see **Stanley et al. 2010**). Subsequently, this framework has proven useful in ensuring that all 3 dimensions of the linkages of open ecosystems, such as streams, are fully incorporated into holistic studies of energy flow (e.g., Ward et al. 1998) and contemporary paradigms (e.g., Thorp et al. 2006).

A timely special issue

A NABS workshop in 1991 resulted in the 1993 *J-NABS* special issue "Perspectives of the Hyporheic Zone: Integrating Hydrology and Biology" (volume 12, issue 1), that was to have a major influence on hyporheic research. The issue opened with a description of the merger of 'population–community' studies of the hyporheic zone that focused on its role as habitat for invertebrates with 'process–functional' studies that viewed ecosystems from the perspective of interacting physical, chemical, and biological processes (**Valett et al. 1993**). To further set the stage, Bencala (**1993**) described a revised hydrological view of streams not as isolated 'pipes' but as multiple flow paths into and alongside the stream channel that serve as active bidirectional links. White's (**1993**) universal definition (discussed earlier) helped provide consistency in terminology, and his diagrams of cross-sectional and longitudinal models have become standard fare in papers reviewing the hyporheic zone.

Stanford and Ward (**1993**; Fig. 1) posed their 'hyporheic corridor concept', which portrays the stream as a series of dynamic convergences between surface and ground water that alternately expand and constrict because of geologic constraints along the valley. The pattern of hydrologic exchange at this whole-catchment scale is shaped by longitudinal changes in the width and depth of the alluvial sediments. Reach-scale control of surface primary and secondary production by hyporheic biogeochemical processes, which, in turn, determine surface stream nutrient concentrations at upwelling sites and influence processes in the riparian zone (see **Mulholland and Webster 2010**), was predicted. These reach-scale sequences were nested within the longitudinal continuum from headwaters to lowland rivers, which provided a catchment perspective for assessing the functional significance of the hyporheic zone to the surface stream ecosystem.

Other papers in the special issue exemplified an ecohydrological approach to understanding the functional significance of the hyporheic zone across a variety of river types (**Stanley and Boulton 1993**) and for microbial ecology (**Hendricks 1993**; Fig. 1). In a northern Michigan river, bacterial activity and production were enhanced in downwelling zones, whereas anaerobic conditions in upwelling zones promoted processes such as denitrification, ammonification, and sulfate reduction (**Hendricks 1993**). Experiments were advocated for improving our understanding of the driving variables (**Palmer 1993**), but relatively few have resulted (e.g., Boulton and Foster 1998, Sliva and Williams 2005), and scope exists for more. Apart from the practical problems of working within sediments under water, the chief difficulty seems to be successful extrapolation of conclusions drawn from experimental chambers (e.g., Mermillod-Blondin et al. 2000, **Marshall and Hall 2004**) to explain processes observed in complex hyporheic zones of rivers and streams. The special issue concluded by encouraging routine assessment of hydrological processes in future studies of the hyporheic zone (**Hakenkamp et al. 1993**), but the urgent need for technological advances in hydrology, tracer studies, and numerical modeling was already clear.

An Era of Technological Advances: 1993 to the Present

Hydrological exchanges at multiple scales in the hyporheic zone

Exchanges of water between the stream and the hyporheic zone are driven primarily by pressure differences along surface–subsurface VHGs. Broad-scale exchange arises from differences between the stream and the surrounding groundwater level, whereas small-scale hyporheic exchange is driven by the interaction of flow and channel features (Elliott and Brooks 1997; Fig. 3A). Channel features include discontinuities in slope, such as riffle–pool sequences (Harvey and Bencala 1993, Kasahara and Hill 2006), steps formed by log jams (Lautz et al. 2006), and river bends and meanders (Wroblicky et al. 1998, Kasahara and Hill 2007, Cardenas 2009). At a finer scale, they are irregularities in the stream bed, such as sediment ripples (Thibodeaux and Boyle 1987) or submerged stones or logs partly embedded in finer permeable sediments (Wallace et al. 1995), that obstruct and deflect the flow (Fig. 3B). Such irregularities produce pressure variations at the sediment–water interface that pump water into and out of the stream bed (Elliott and Brooks 1997, Cardenas et al. 2004).

The exchange of water in natural gravel-bed streams is typically complex, and turbulent stream flow induces variable inputs of stream water into near-surface regions of the bed (Fig. 3C) (**D'Angelo et al. 1993**). Saturated hydraulic conductivity of the sediments further controls the flux and depth of hyporheic exchange (Storey et al. 2003). At reach or larger scales, the geology of parent materials largely governs saturated hydraulic conductivity of alluvial sediments (Morrice et al. 1997), whereas at finer scales, nonuniform clogging (colmation) by fines can be more important (Packman and MacKay 2003; Fig. 3B).

Evolving technologies for measuring hyporheic exchange

In the last 2 decades, hyporheic exchange across a range of scales has been characterized with tracer techniques and numerical hydrological modeling. Tracer techniques entail injection of specific chemical tracers or use of background chemical concentrations as natural tracers. Since the Stream Solute Workshop (**1990**), tracer injections have become a mainstream approach to quantifying rates of hyporheic exchange and nutrient processing. Analyses of 'breakthrough curves' from stream injection of a nonreactive solute tracer provide reach-averaged estimates of the relative size of the transient storage zone and exchange rate (Bencala and Walters 1983). To estimate nutrient retention, a conservative tracer and a nutrient are co-injected into the stream and uptake lengths (the average distance traveled by a solute) are calculated by comparing plateau concentrations of the 2 tracers (Triska et al. 1989). For instance, Valett et al. (1996) co-injected a conservative (Br^-) and a biologically active tracer (NO_3^--N) into streams in 3 headwater catch-

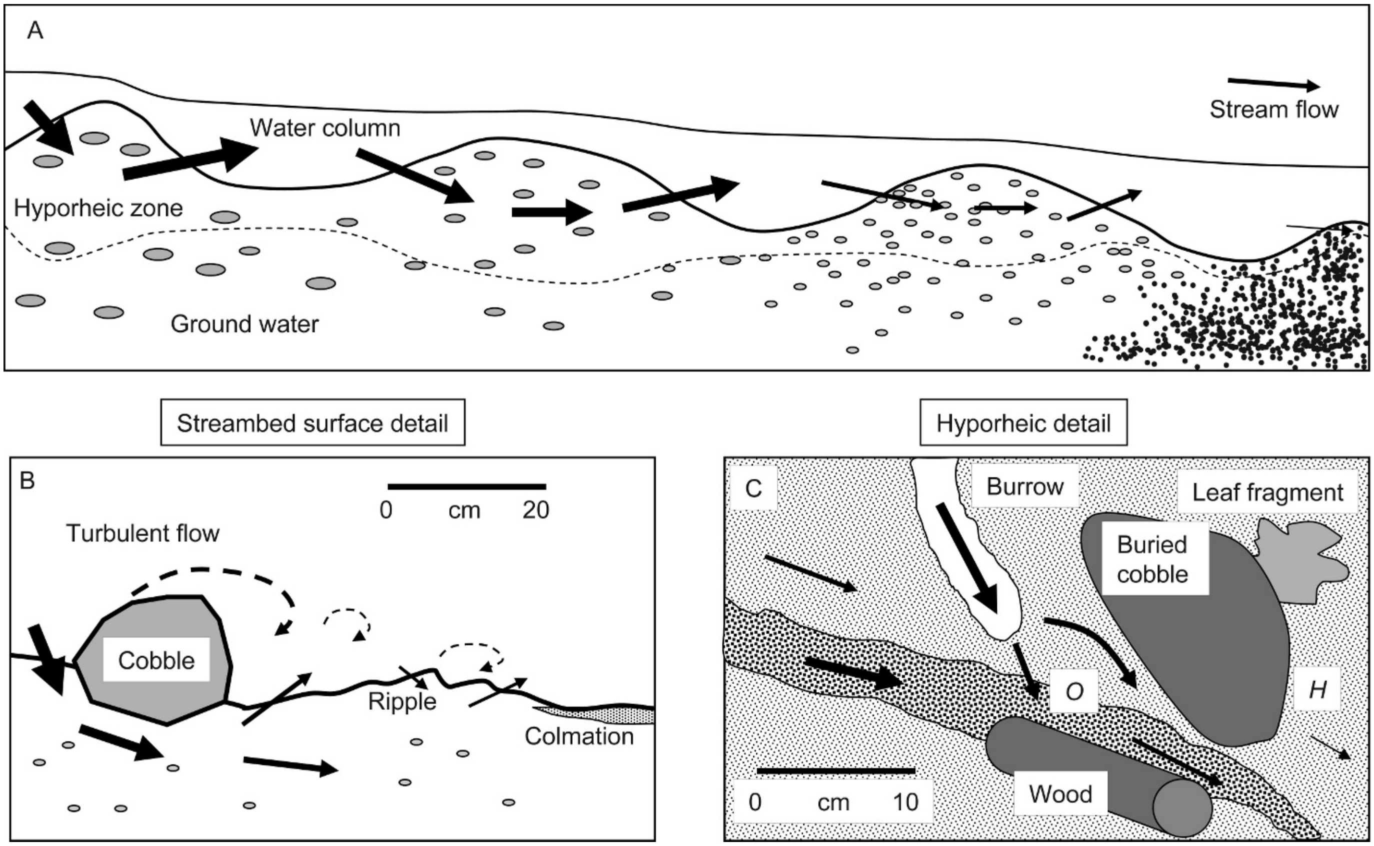

FIG. 3. The interactions of streambed topography and permeability, surface flow characteristics, distribution and size of sediments, and presence of large rocks or cobbles influence the location and extent of vertical hydraulic gradient (VHG) across a range of scales (multiple reaches) (A) and at the streambed surface (B) and within the bed (C), creating a shifting mosaic of conditions in the hyporheic zone. Arrow thickness represents magnitude of hyporheic exchange, broken line approximates groundwater table. In (C), O refers to oxygenated sediments, H refers to hypoxic regions.

ments with contrasting geology and hydraulic conductivities to study hyporheic nutrient retention. Hyporheic exchange increased, whereas NO_3^- uptake length decreased with increasing hydraulic conductivity.

Numerical hydrological modeling using hydrometric data collected from a network of wells and piezometers is another way to quantify hyporheic exchange (Harvey and Bencala 1993, Kasahara and Wondzell 2003). Wondzell and Swanson (**1996a**) used the distribution of hydraulic heads and saturated hydraulic conductivity measured from a network of wells and a groundwater flow model (MODFLOW) to quantify advective hyporheic flow and groundwater inflow in a gravel bar of a 4th-order mountain stream. The flux of hyporheic exchange quantified in this study also was used to understand N cycling within the reach (**Wondzell and Swanson 1996b**).

Transient storage models have been greatly refined in the last decade. The original form is the combination of 1-dimensional advection–dispersion equations with 1st-order mass exchanges between the main channel and a transient storage zone (e.g., Morrice et al. 1997). Subsequent modifications have included accounting for unsteady stream discharge, incorporation of multiple transient storage zones, and inclusion of diffusive solute transfers between the channel and the hyporheic zone (**Runkel et al. 1998**, Choi et al. 2000, De Smedt 2007). Poole (**2010**) has extended numerical modeling approaches to describe hyporheic exchange across multiple spatial layers in 3 dimensions over time, an elegant development that illustrates the complex nonlinear links across diverse hyporheic habitat patches (**Poole et al. 2006**; Fig. 1).

Hydrological Exchange and Stream Ecosystem Processes: the Basis of Contemporary Hyporheic Zone Research

The potential for significant contributions from the hyporheic zone to whole-stream metabolism was first demonstrated by Grimm and Fisher (1984) in an

Arizonan desert stream. In this seminal study, rates of benthic, deep sediment, and whole-stream metabolism were assessed simultaneously in open-bottom chambers, closed sediment cores, and from change in dissolved O_2 concentrations between 2 stations along the stream. The results revealed that the hyporheic zone of this highly productive desert stream contributed 40 to 50% of total ecosystem respiration, and prompted Grimm and Fisher to suggest extension of the traditional 2-layer conceptual model of stream metabolism to include the contribution of the hyporheic zone. A decade later, Findlay (1995; Fig. 1) synthesised the early literature on surface–subsurface hydrological exchange and proposed a classification of streams based on the degree to which hyporheic zones contribute to their total metabolism. This classification reflected the relationship between the proportion of total discharge passing through the hyporheic zone and the rate of hyporheic metabolic processes. The greatest potential contribution of the hyporheic zone to total metabolism was hypothesised to occur when both hyporheic discharge and hyporheic metabolic activity are high. Findlay (1995) concluded that physical factors controlling interstitial velocities and pathways predominantly determined the functional significance of hyporheic metabolism to many whole stream ecosystems.

Following Findlay's (1995) paper, numerous studies confirmed that hyporheic metabolism can equal or far exceed metabolism at the stream bed (Mulholland et al. 1997, **Naegeli and Uehlinger 1997**, Battin et al. 2003). However, Craft et al. (2002) found that microbial productivity was insufficient to support invertebrate production in the hyporheic zone of the Flathead River in Montana, USA, a result suggesting that other metabolic processes, such as methanogenesis, might be contributing energy to higher trophic levels. The organic fuel for hyporheic metabolism can be dissolved organic C (DOC) from surface stream water or ground water (Jones et al. 1995) or from infiltration and burial of particulate organic matter from the surface stream (e.g., Metzler and Smock 1990, see also **Tank et al. 2010**).

A landscape perspective—spatial mosaics and varying hydrology

Several conceptual papers have extended Findlay's (1995) original framework, mainly by elaborating spatial and temporal aspects (Fisher et al. 1998a, Kaplan and Newbold 2000, Malard et al. 2002, Stanford et al. 2005). The result has been incorporation of empirical and theoretical evidence to demonstrate how the spatial arrangement of patches of surface–subsurface exchange affects overall stream metabolism and heterogeneity in stream water variables, such as nutrient concentrations and water temperature. For example, Fisher et al. (1998a) proposed that the arrangement of sandbars and their associated hyporheic flow paths in a desert stream would govern stream-scale rates of N cycling. Earlier work had demonstrated that NO_3^--rich water upwelling at the end of hyporheic flowpaths promoted growth of green algae in the surface stream between floods (**Grimm and Fisher 1989**). As surface stream N becomes consumed, green algae are replaced by N-fixing cyanobacteria. Thus, a stream with numerous sandbars and active hyporheic zones will cycle N more rapidly than one with few sandbars and long stretches of surface stream where N is fixed rather than regenerated from the hyporheic zone.

Malard et al. (2002) built on the model by Fisher et al. (1998a) and sought to link the functional significance of the hyporheic zone with spatially well-defined stream structures at a landscape scale. In streams, a shifting mosaic of surface–subsurface exchange patches is produced by the heterogeneous arrangement of channel features, such as riffles and bars, and of areas of different grain sizes and sediment hydraulic conductivity. These patches vary in hyporheic discharge and flowpath length, and in turn, affect the type and intensity of metabolic processes. Such mixtures of patches of different sizes partly explain the heterogeneity of metabolic processes, which often combine the opposing processes of oxidation and reduction within a single spatial unit of a stream (even over a few millimeters).

Thus, the overall contribution to stream ecosystem processes by the hyporheic zone might be controlled by frequency and distribution of patch types. Alteration of the configuration of the patch mosaic by disturbances, such as seasonal or episodic floods (**Stanley et al. 2010)**, would contribute to temporal heterogeneity. Because hyporheic metabolism is probably limited by supply of organic C or exhaustion of terminal electron acceptors from the surface stream, metabolic activity at the reach scale should be enhanced by the occurrence of many small patches with shorter hyporheic flow paths compared to few large patches (Malard et al. 2002). This hypothesis could be tested by manipulating the size, shape, and spatial arrangement of gravel bars, especially during stream restoration projects (see later).

Hyporheic function at multiple scales

Stanford and Ward (**1993**) already had set the stage for considering hyporheic processes at multiple spatial scales with their conceptual model of how the structure of the hyporheic zone might change along a river. Integrating these multiple scales with Findlay's (1995) framework, Boulton et al. (1998) hypothesised that different variables might influence the functional significance of the hyporheic zone to streams at the sediment, reach, and catchment scales, and they sought hierarchical relationships among these controlling variables across scales. At the *sediment scale*, the main determinant of the functional significance of the hyporheic zone is grain size distribution because it governs bed permeability (Freeze and Cherry 1979) and affects the hydrological linkage with the surface stream and the supply of resources. Grain size distribution also influences organic matter accumulation, microbial abundance and activity, and interstitial dissolved O_2 concentrations (Strayer et al. 1997, Olsen and Townsend 2003), controlling potential rates of hyporheic metabolism.

At the *reach scale*, the scale at which most stream ecologists have studied the hyporheic zone, the principal driver appears to be hydrological exchange and discharge. The lengths of the hyporheic flow paths control the intensity and type of the metabolic processes, which in turn, create longitudinal gradients in the physicochemical environment along the flow paths with feedbacks to the rates and types of reach-scale metabolic processes (Boulton et al. 1998, Datry and Larned 2008). Extending this concept to the *catchment scale*, vertical and lateral components of stream and groundwater interactions and their variability are considered to be the principal variables driving the functional significance of the hyporheic zone to the surface stream (Boulton et al. 1998, Datry et al. 2008).

Variable linkages across subsystems potentially affect processing length

The Telescoping Ecosystem Model (TEM, Fisher et al. 1998b; Fig. 1), predicts how streams retain, transform, and transport matter among 4 subsystems: the surface stream, the hyporheic zone, the parafluvial zone, and the riparian zone. These 4 subsystems are cross-linked primarily by exchange of water. The hydrologic variable is 'flow path length', the distance travelled by a parcel of water in one subsystem before it enters another. 'Processing length' is defined as the average distance required to process a given amount of material, and summarizes flow path length and rates of the many processes contributing to transformation of a specific material.

Comparison of processing lengths between the hyporheic zone and surface stream illustrates their relative significance and enables comparisons of the functional significance of the hyporheic zone across a range of stream ecosystems over time. The TEM postulates that whole-ecosystem efficiency and the significance of the subsystems are functions of the disturbance regime; processing length increases when disturbances disrupt a given subsystem. Processing length then decreases during subsequent successional change and recovery. Thus, processing lengths in the subsystems 'telescope' according to the severity of different disturbances, their linkages, and their rates of recovery. An exciting future direction in hyporheic research is to assess the applicability of this model in streams with different disturbance regimes and with different degrees of hydrological linkage across subsystems. Poole et al. (2008; Fig. 1) recently modelled riverine *hydrologic spiralling* to show the substantial control of the hyporheic zone on water and solute flux, a result that emphasizes differing roles of long and short hyporheic flow paths.

Future Directions in Research on the Hyporheic Zone: Management Applications and River Restoration

Streams and Ground Waters

In 2000, *Streams and Ground Waters*, edited by Jones and Mulholland (2000; Fig. 1), synthesised the state of research on stream–ground water interactions, and thereby provided a useful benchmark against which to judge advances in the last decade. One advance in this book was the extension of Findlay's (1995) conceptual model by Kaplan and Newbold (2000) who suggested a threshold of vertical exchange at which either all bioavailable organic matter is consumed or the capacity of the hyporheic zone to metabolize organic matter is reached. Thus, either vertical hyporheic exchange or the size of the hyporheic zone might act as the primary limiting factor on the significance of the hyporheic zone to whole-system metabolism. Whether such a threshold for the metabolism of bioavailable DOC is actually achieved in nature and whether a similar threshold exists for particulate organic C remains to be seen. Given the fundamental significance of C for stream ecosystems (**Tank et al. 2010**), this future research direction is important.

Despite the last 2 decades of hydrologic and biogeochemical research in the hyporheic zone, Findlay and Sobzcak (2000) concluded that no quantitative framework yet exists that predicts where and when the hyporheic zone will play a major role in overall stream metabolism. We also still lack the ability to extrapolate metabolic data successfully from the sediment or plot scale (<1 m^2) up to reach or catchment scales; the spatial hierarchies proposed by Ward (**1989**) and Boulton et al. (1998) remain elusive. Progress is hampered by the need to combine costly metabolism studies with simultaneous measures of hydrology at appropriate scales and the consequent hydrological modelling. Meta-analysis of total stream metabolism budgets indicates that hyporheic zone contributions can range from 40 to >90% (Battin et al. 2003) and that hyporheic size, residence time, and vertical discharge interact to govern hyporheic metabolism at sediment and reach scales (Fellows et al. 2001). Further empirical data spanning time and space are needed to clarify this relationship.

Assessing the 'health' of the hyporheic zone

Another new direction that has emerged since *Streams and Ground Waters* was published is the potential for assessing the health of the hyporheic zone in a manner equivalent to that used in surface waters. Ecologists and hydrologists have long been aware of the functional significance of the hyporheic zone to stream ecosystems and the importance of vertical hydrological exchange for maintaining biological integrity, but they have been slow to communicate these findings to river managers and policy developers (Boulton 2000a, 2007, Woessner 2000; Fig. 1). Despite widespread interest in the concept of stream health (**Meyer 1997**), the notion of hyporheic health has received little attention (Boulton et al. 2008).

Many human activities affect the hyporheic zone, either through disruption of the hydrological exchange pathways or via direct contamination (Mestrov and Lattinger-Penko 1981, Hancock 2002, Kasahara et al. 2009). Even exotic surface species might impair hyporheic zone function (Bickel and Closs 2008). Effective indicators of hyporheic health must be easy to measure, readily interpretable, relevant to societal values and uses of the hyporheic zone (Boulton et al. 2008), and suitably sensitive. Boulton (2000a) proposed measures of hydrological exchange, rates of interstitial biogeochemical activity, and the biodiversity of the hyporheos as 3 potential candidates. Using processing length from the TEM (Fisher et al. 1998b) as a functional measure of hyporheic health also might be feasible. However, adoption of these potential measures of hyporheic health currently is limited by a lack of baseline data and protocols (Hahn 2006).

Hyporheic zone restoration

Typically, river restoration focuses on surface systems and their longitudinal and lateral connections, whereas the vertical dimension has been largely ignored (Ward et al. 2001, Boulton 2007). If an intact hyporheic zone underpins stream health in some streams, hyporheic restoration in reaches where the hyporheic zone is impacted by human activities is a logical direction for management applications. Instream habitat enhancement projects often modify stream channel morphology to improve habitat structure (e.g., Lester et al. 2006, Crispell and Endreny 2009). These channel modifications increase bedform roughness, heterogeneity of hydraulic conductivity, near-bed turbulence, and channel sinuosity, all of which induce hyporheic exchange flow in natural streams. For example, logs across stream channels produce a stepped longitudinal channel profile that promotes hyporheic exchange (Wallace et al. 1995). In a flume study, introduction of natural quantities of wood doubled vertical hyporheic exchange and increased the magnitude of the hyporheic zone (Mutz et al. 2007), supporting the early proposition by Mutz and Rohde (2003; Fig. 1) that restoring natural levels of instream wood could enhance hyporheic exchange in impacted streams. Assessment of hyporheic restoration trajectories could be envisaged on a 2-dimensional plot of the twin main 'drivers' of sediment structure and VHG that seek to illustrate mechanisms of response (Kasahara et al. 2009); currently, restoration ecologists lack a simple model of the hyporheic zone to use as a basis for predicting responses to manipulation of the 2 key 'drivers'.

Future research to assess the success of such restoration at a catchment scale would also shed light on large-scale processes that influence hyporheic zone function. One ambitious experiment in river ecology would be to restore 3-dimensional connectivity in a large (~50,000 km^2) dewatered, revetted, and polluted river ecosystem from headwaters to mouth. Relevant steps could be: 1) model in 3 dimensions the natural and severed connectivity for the entire system (focusing on hyporheic exchange underpinning a healthy alluvial river ecosystem), 2) evaluate potential outcomes of 3-dimensional restoration to yield a scientifically logical and economically viable restoration strategy, 3) do the restoration, and 4) quantitatively evaluate the outcome.

Conservation of the hyporheos and maintenance of hyporheic processes

As early as 1989, Danielopol was calling for protection of alluvial aquifers and their fauna, but little heed seems to have been taken of his plea (Boulton et al. 2003). Like Strayer (**2006**), we urge a more holistic view of conservation efforts in rivers to protect surface and subsurface systems and their fauna. Current inventories of the hyporheos of most streams are inadequate to identify rare or threatened species, but some assemblages of invertebrate taxa in the hyporheic zone are surprisingly diverse (Rouch and Danielopol 1997, Boulton 2000b) and should be considered in management decisions about water resource development in these areas (Boulton et al. 2003, see also **Strayer and Dudgeon 2010**). Even intermittent streams can contain a rich hyporheic biota (Datry et al. 2007 [Fig. 1], 2008). Intermittent reaches act as *temporal ecotones* between terrestrial and aquatic ecosystems and harbor a unique biota of aquatic, semiaquatic, and terrestrial taxa that contribute substantially to overall biodiversity. This biota, including the hyporheos, might be at risk from management practices that seek to increase flow permanence artificially (Datry et al. 2007), especially because the hyporheic zone can be a refuge from drying (**DiStefano et al. 2009**).

Large river floodplains and their aquifers and hyporheic zones are the most endangered landscapes on the planet (Tockner et al. 2008). Research, conservation, and management of surface and groundwater exchange processes in the context of the catchments of these large alluvial floodplain ecosystems are crucial (Stanford et al. 2005) and must be undertaken despite logistic difficulties, which are rapidly being overcome by new technologies and modelling and mapping methods (**Poole 2010**). Symposia and field-based workshops exploring application of these technologies to surface water–groundwater restoration strategies could focus on human activities, such as gravel mining and river regulation, that directly affect riverine and floodplain hyporheic zones.

Conclusions

Many papers seminal to conceptual and empirical advances in the field of hyporheic research (Fig. 1) have been published in *J-NABS*, a fact that reflects the relevance of processes and biota in the hyporheic zone to stream benthologists. Most of this work has focused on hydrological and biogeochemical processes. Studies of the association of the hyporheos with environmental variables and hyporheic exchange still are being done, but increasingly, the focus of these studies is at the catchment rather than the reach scale, taking advantage of new technologies and modeling approaches.

One major need is for more empirical studies to test the predictions of the bevy of conceptual models and frameworks that have been proposed. In particular, studies that extend over multiple sites and spatial scales and that encompass at least the full suite of hydrological extremes in a year will be valuable. Integration of hydrological and ecological variables is essential, and the recent advances in hydrological modeling and sampling technology will play key roles in this process. We also urge practical application of the research findings on the significance of the hyporheic zone to whole-stream ecosystem function, especially in river restoration and conservation. *J-NABS* is well placed to expand its scope to include more papers that integrate research and management in protecting and restoring rivers, and the social sciences of human communication and environmental education about the hyporheic zone are relevant in this context.

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