THE FUNCTIONAL SIGNIFICANCE OF THE HYPORHEIC ZONE IN STREAMS AND RIVERS

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ABSTRACT

The hyporheic zone is an active ecotone between the surface stream and groundwater. Exchanges of water, nutrients, and organic matter occur in response to variations in discharge and bed topography and porosity. Upwelling subsurface water supplies stream organisms with nutrients while downwelling stream water provides dissolved oxygen and organic matter to microbes and invertebrates in the hyporheic zone. Dynamic gradients exist at all scales and vary temporally. At the microscale, gradients in redox potential control chemical and microbially mediated nutrient transformations occurring on particle surfaces. At the stream-reach scale, hydrological exchange and water residence time are reflected in gradients in hyporheic faunal composition, uptake of dissolved organic carbon, and nitrification. The hyporheic corridor concept describes gradients at the catchment scale, extending to alluvial aquifers kilometers from the main channel. Across all scales, the functional significance of the hyporheic zone relates to its activity and connection with the surface stream.

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INTRODUCTION

Traditionally, most ecological research on groundwater and rivers has treated groundwater and rivers as distinct entities and has focused on within-system issues (16). One reason for this distinction reflects historical perspectives in disciplinary focus: Most groundwater studies are by hydrologists, whereas ecologists have been more interested in rivers (145). Another reason may lie in the marked differences between these two environments. Rivers typically have currents generating turbulence, short water residence time, variable discharge and physicochemical conditions, unidirectional transport of nutrients, sediments and biota, and a dynamic channel morphology, and they are well lit. In contrast, alluvial groundwater environments are more stable, have longer water residence times, exhibit laminar flow, are permanently dark, and change little in sediment bed structure (16, 20, 57, 110, 158).

Recently, attention has turned to the ecology of the *interface* between these two environments because we now recognize the connections via exchange of water, nutrients, other materials, and biota between the surface stream and alluvial groundwater. This intervening zone is the hyporheic zone (HZ) (104). Although a rich lexicon of definitions now exists (see reviews in 16, 57), the most functional emphasizes the dynamic ecotone model, where exchange of river and groundwater occurs (54, 149). Key aspects of this definition include the difficulty of defining the boundaries of this zone because they vary in time and space (12, 155, 157, 158), the shared features of the surface stream and underlying groundwater (often existing as gradients at a range of scales), and the importance of the permeability of this ecotone to the functions that occur within (54, 147, 149).

Therefore, in general terms, the hyporheic zone can be defined as a spatially fluctuating ecotone between the surface stream and the deep groundwater where important ecological processes and their requirements and products are influenced at a number of scales by water movement, permeability, substrate particle size, resident biota, and the physiochemical features of the overlying stream and adjacent aquifers.

This review focuses on the functional significance of the HZ as an ecotone viewed at several scales. Scale provides a useful framework for organizing the wealth of information we have on the HZ and assessing the hierarchy of processes (e.g. 52, 82). Where we have more information and ability to predict processes at certain scales (such as the reach scale), this review examines our ability to extrapolate among scales. We describe regulatory factors at each scale and specify potential impediments to extrapolating across scales or stream ecosystems. Rather than exhaustively review the literature on the HZ (see 16, 53, 77, 109, 157), we critique the current status of research on the functional significance of the HZ, addressing the following questions:

1. What hydrological, chemical, and biological processes occur in the HZ, and how are they interrelated at a range of scales?

2. How do these processes and their interactions influence ecological processes occurring in the surface stream?

3. What features determine the functional significance of the HZ to stream and river ecosystems?

4. What are the promising future research directions in this field, and how do they relate to river management?

We identify relevant temporal and spatial scales of these issues, emphasizing the roles of natural disturbance (e.g. floods) and human activities (e.g. catchment land use, flow regulation) on the functional significance of the HZ in streams and rivers. The relationship of the HZ to compartments other than the surface stream (Figure 1) is reviewed fully elsewhere (16, 53, 102). We contend that the significance of the HZ to the surface stream relates to its activity (e.g. nutrient transformations, respiration rates) and connection (e.g. via hydrological exchange). Both of these features are influenced by sediment characteristics and hydrology at a range of scales.

The explicit recognition of scale for describing hierarchies in patterns and processes and generating hypotheses in ecology has proved valuable (1, 82). Scale issues have been central to some conceptual models in stream ecology (e.g. 52, 97, 112) and have been used as a framework from studies of individuals (e.g. 108) to entire ecosystems (e.g. 130). However, few efforts have been made to explicitly put hyporheic research into a scale context (e.g. Figure 2 in 57) and link the relationships between physical and biological processes. We have adopted this scale-based approach, and although the relationships and gradients
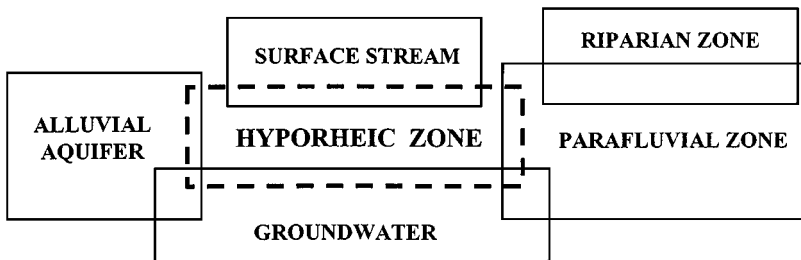

Figure 1 Simplified schematic diagram of the hydrological compartments that can interact with the hyporheic zone. Alluvial aquifers typify floodplain rivers with coarse alluvium and are often considered synonymous with groundwater. The parafluvial zone lies under the active channel, which lacks surface water, and it can interact with subsurface water of the riparian zone.
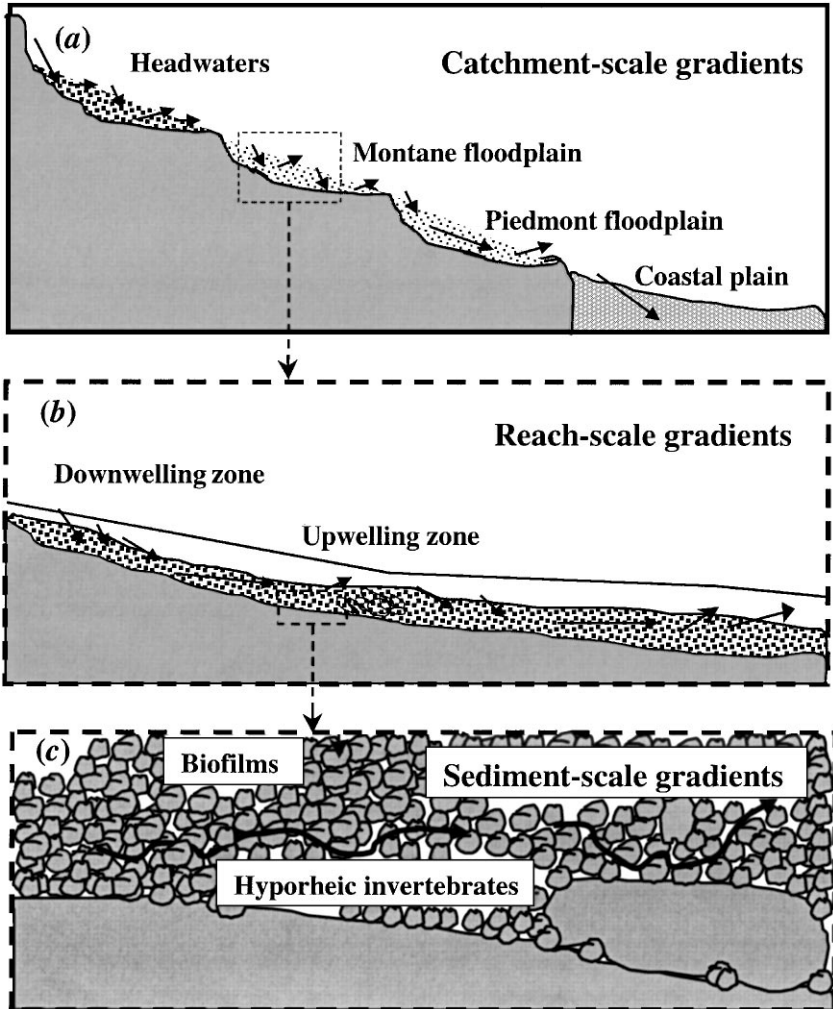
Figure 2   Lateral diagrammatic view of the hyporheic zone (HZ) at three spatial scales. At the catchment scale (*a*), the hyporheic corridor concept predicts gradients in relative size of the HZ, hydrologic retention, and sediment size (126). At the reach scale (*b*), upwelling and downwelling zones alternate, generating gradients in nutrients, dissolved gases, and subsurface fauna. At the sediment scale (*c*), microbial and chemical processes occur on particle surfaces, creating microscale gradients. *Arrows* indicate water flow paths.

occur along a continuum, we focus on three discrete spatial scales: sediment, reach, and catchment (Figure 2).

SEDIMENT-SCALE PROCESSES

Particle Size, Interstitial Flow Pathways, and Microbial Activity

Fine-scale granulometric features (size, shape, and composition of sediments) derive from catchment scale geological processes and determine most physical and chemical processes in the HZ (16, 36, 89, 133). Interstitial flow patterns are a product of hydraulic gradient (direction and strength of flows, Figure 2) and streambed porosity. These flows are turbulent and irregular, creating zones of rapid, slow, and no flow (dead zones). Even where flows are brisk, dead zones exist in sheltered regions, and anaerobic processes can occur. Hence, a seemingly well-oxygenated HZ contains anoxic and hypoxic pockets associated with irregularities in sediment surfaces, small pore spaces, or local deposits of organic matter (31, 84). This heterogeneity enables biologically and chemically disparate microzones to co-occur, facilitating diverse ecological processes in a small volume. Gradients or microzones may exist because there is no hydrological exchange to break them down.

Ammonification, nitrification, and denitrification often all occur as soon as water enters the HZ (72, 73, 75, 76). These sediment-scale transformations of dissolved nitrogen (N), controlled by oxygen availability, influence the nutrient status of upwelling water with concomitant effects on surface stream processes (7, 59, 60, 141–143). Phosphorus (P) concentration in interstitial water is also affected by oxygen distribution; loss of oxygen, change in redox status, and subsequent release of P from bound iron or manganese play a role in P availability (31). Bacterial alkaline phosphatase activity has been documented in the HZ, and breakdown of organic P may be an important source of this nutrient for surface and subsurface biota (93). Less explored at the microscale is the significance of lithological and geochemical processes that can regulate availability of N and P. Sediments with high cation exchange capacity (resulting from their chemical composition and particle size) will readily sorb ammonium (139) and inorganic P (80, 131).

Key processes at this fine spatial scale include those that alter the size or amount of interstitial space or oxygen availability, including clogging of interstices by fine particles (114, 119, 162) or the translocation of fine particulate organic matter (11, 85). Distribution of particulate organic matter among sediments is particularly important in its role as a surface and substrate for microbes

and a structure that alters porosity and hydraulic conductivity (15, 16). It also acts either as a source of inorganic nutrients after mineralization or as a potential sink for ions such as phosphate through colloidal interactions. Biofilms predominate on small particles because of their large surface area (5, 81), resulting in a negative correlation between mean sediment particle size and bacterial abundances in river sediments (22). Their low porosity and influence on water velocity allow smaller sediments to trap fine organic matter, so they are generally associated with high organic matter content (84) that stimulates biofilm growth (22). Intense bacterial activity may so reduce oxygen concentrations that anaerobic processes such as denitrification predominate, fueled by labile organic matter from the surface (73) or parafluvial zones (23).

Interstitial Fauna

The interstitial spaces among sediment particles in the HZ of many streams and rivers are occupied by a diverse array of aquatic invertebrates, termed the "hyporheos" (104, 159). The hyporheos includes many types of crustaceans, segmented worms, flatworms, rotifers, water mites, and juvenile stages of aquatic insects (8, 34, 64, 109, 125, 157). Biofilms provide an important food source for the hyporheos (2, 8, 16, 158). Therefore, variables that affect the extent, composition, and food quality of the biofilms probably influence the distribution of grazing invertebrates (7, 8, 36, 56, 57, 85, 132, 133). Their feeding activities may enhance biofilm productivity (e.g. 8, 98) and break down coarse particulate detritus trapped in sediments, increasing their surface area for microbial attack. There has been little research on the dietary requirements of the hyporheos (30, 35, 158), but it seems that predatory subsurface invertebrates are particularly diverse (8, 12, 27). There is still much we need to learn about what fuels the hyporheic food web and how these energy sources vary in streams with different bed porosities, discharges, and organic matter inputs from their catchments.

Large numbers of hyporheic invertebrates may be collected [e.g. up to 10,711 in 3L (133)]. Most of these are meiofauna, less than 1 mm long when adult (64, 107). Their small size and high reproductive rate imply that they are important at the sediment scale, regulating microbial productivity and providing food for larger hyporheic invertebrates and even fish in the surface stream (107). Invertebrate activity (burrowing, formation of fecal pellets) can alter interstitial flow paths (8, 33, 34, 40), influencing the physical and chemical processes described above. The influx of fine sediments can render the HZ uninhabitable either directly by clogging the spaces or indirectly by reducing interstitial flows and flushing of nutrients, gases, and wastes (16, 99, 114). In keeping with the concept of the HZ as a dynamic ecotone, we can summarize these processes and their products as inputs and outputs whose compartments and residence

times vary temporally and spatially. The magnitude and directions of inputs and outputs become relevant at higher scales (i.e. reach and catchment), as they relate to adjacent habitats such as the surface stream (Figure 1). For example, at a local scale, fine silt may enter trout spawning gravels due to sediment runoff from a cleared catchment upstream, reducing the interstitial flow of water and hence the supply of dissolved oxygen and other requirements of developing fish eggs (25, 96). Until the next flushing flow (58), these impaired spawning gravels reduce trout recruitment and fish densities in the overlying streams. Thus, an input of silt at the local scale of a gravel bed may have ramifications at the stream scale by altering the food web.

Future Research at the Sediment Scale

Research is needed to determine the extent to which relationships observed at the sediment scale can be extrapolated to the reach scale (10–100 m). For instance, many small-scale studies (e.g. 45, 68, 92) show that microbial processes, including respiration and growth, are tightly related to sediment organic content. The relationship between hyporheic respiration and organic matter (OM) matches that found in surface sediments (45), which implies that information derived from surface sediments can help explain factors controlling microbial processes in the HZ. Although we can predict hyporheic bacterial production in a reach because we know the distribution of sediments with various OM contents, to understand the functional significance of the HZ in that reach, we must also know the magnitude of the hydrologic exchange between hyporheic and surface habitats because this exchange provides the actual link (e.g., 7, 43, 60, 76, 142, 143, 145, 151, 154). How well do reach-scale hydrological models approximate sediment-scale water movements? This question poses a major research challenge (see also 158).

Most workers acknowledge the importance of sediment-scale processes [e.g. redox-sensitive chemical gradients (31, 101, 138, 139)], but technological and sampling limitations still hamper advances at this scale. These limitations also apply to sampling fauna at fine scales. There is a wide range of collecting methods, such as freeze-coring (13, 86, 87), pumping interstitial water (6, 9, 10, 12, 39, 153), digging pits in exposed sediments (21, 134), hand-coring (107), standpipe coring (159), and hyporheic pots (42, 94), but comparative research is needed to reveal the differences in efficiency of extraction and selectivity of these methods as well as the choice of appropriate mesh size under different conditions (63, 64, 158). Some pumping methods, for example, may sample interstitial water from regions distant from the end of the sampling tube; this method precludes replicate sampling (9, 27) and is selective (49). Until reliable, quantitative data can be collected, ecological studies such as complete food web analyses are probably impossible (30, 57).

REACH-SCALE PROCESSES

Flow Paths and Hydrologic Retention

Our best perception of the functional significance of the HZ may be at the reach scale because this has been the scale at which most workers have explored the connection of the surface stream with the HZ. The most obvious linkage is via hydrological exchange in upwelling and downwelling regions that form in response to reach-scale geomorphological features such as discontinuities in slope and depth of riffle-pool sequences, the shape of the channel and its bars, the roughness and permeability of the streambed, and obstacles (e.g. macrophytes, boulders) that extend into the channel and alter surface flow paths (16, 118, 154, 158). Commonly, decreasing stream depth at the end of a pool forces surface water down into the sediments (downwelling), displacing interstitial water that may travel for some distance before upwelling into the surface stream (Figure 2*b*). Tracer experiments (e.g. 60, 67, 72, 76, 140, 160) indicate that flow paths are usually more complex than this and can respond to other factors such as flooding and riparian transpiration. Geomorphological features such as depth to bedrock are also relevant, especially in rivers with shallow HZ; for some of these, the ecological role of the HZ may be less important to the total stream ecosystem (9, 43).

Horizontal flows entering and leaving stream banks (56) and gravel bars (72, 91, 150, 160, 161) are functionally equivalent to downwelling and upwelling through the streambed (76). Together, these flow paths contribute to hydrologic retention (*sensu* 100), a delay in transport that occurs when water enters flow paths moving more slowly than the surface stream. Hydrologic retention is strongly influenced by granulometric features. For example, among three catchments in New Mexico differing in geologic composition, retention was least in fine-grained sedimentary sandstone and highest in the bed of poorly sorted cobbles and boulders of a granitic catchment (100). Similarly, storage zone residence times increased with increasing particle size, indicating not only that more water was exchanged between the stream and aquifer, but also that water remained in the subsurface longer before it returned to the stream (100).

Within any reach, there is a maze of flow paths of different lengths, directions, and velocities. Because streams and aquifers exchange water horizontally and vertically, flow dynamics are inherently three dimensional. However, most hydrologic studies have used single-dimensional models (review in 135), and only recently have two-dimensional models been used (67, 160, 161, 163). Preliminary results from two-dimensional models have been encouraging. For example, a hydrological model for a lowland stream-floodplain system showed that although the magnitude of fluxes changed with season and water table

conditions, the general shape of the flow net connecting the stream, HZ, and floodplain remained constant, suggesting geomorphic control over the direction of exchange (160). Three-dimensional models will contribute more explicit information but require geophysical data that are difficult to obtain. Nevertheless, this information is crucial for our knowledge of the significance of the HZ to the surface stream and adjacent habitats.

Longitudinal Gradients

Longer hyporheic retention time promotes interaction between the biofilms on sediment particles and the nutrients and carbon entrained in subsurface flow paths (contact time *sensu* 43). Patterns in variables such as temperature (27, 156), alkalinity (131), nutrients (23, 60, 72, 141, 142, 146, 158), dissolved organic carbon (44, 46), and dissolved oxygen (7, 27, 46, 70, 91, 129, 144, 154, 158) within the HZ reflect the influx of surface water or the movement of water along a hyporheic flow path. Movement of water through porous sediments has been likened to an ion chromatograph (50), with differential separation and retention of solutes as water travels down the gradient (3). Several researchers have demonstrated hyporheic nitrification by showing the accumulation of nitrate along a flow path (72, 138). These gradients are typically coupled with oxygen depletion because of the mineralization of organic matter (23, 75), thus highlighting the role of the HZ in regenerating inorganic N, which may later become available to nutrient-limited surface biota (142, 143).

Longitudinal trends in nutrients, dissolved oxygen, and the hyporheos matched the direction and magnitude of hydrological exchange and varied in response to flooding and drying in a desert stream reach in Arizona (10, 129). Similar trends are evident in mesic rivers (128). In a regulated channel of the Rhône River, longitudinal changes in dissolved oxygen, particulate organic matter, and hyporheic fauna correlated with flow paths through a 1200 m gravel bar (91). Furthermore, these patterns varied with changes in contact time and interstitial flow rate as a result of variation in stream discharge (91; reviewed in 39), although there was also some spatial variation in response to granulometric features (36).

The Significance of the HZ to Surface Stream Biota

In streams where hydrological exchange with the HZ is active, ecological patterns that are correlated with locations of upwelling zones (Figure 2) are evident. Upwelling hyporheic water rich in nutrients can promote "hot spots" of productivity in the surface stream (7, 26, 151). For example, in some desert streams, the metabolically active HZ generates nitrate that normally limits primary production (61, 62). Upwelling water thus promotes algal activity, resulting in longitudinal gradients of nitrogen uptake in the surface stream (59) and altering

benthic algal composition (142, 144). Furthermore, after floods scour the algae, succession is more rapid at these upwelling zones (142, 143).

Aquatic macrophyte distribution may also be influenced by subsurface nutrient concentrations and water movement (48). Convection patterns below *Chara* hummocks apparently benefit the plants by drawing nutrient-rich water toward the rhizomes (69). Few studies have been made on the direct effects of vertical exchange of hyporheic water on surface invertebrates (111). Effects are probably trivial because of dilution in most rivers and the stronger influences of other variables on stream benthos such as substrate and current velocity. However, in floodplain habitats where flushing effects are low, the amount of upwelling groundwater has been found to correlate with benthic faunal composition (e.g. 18, 47) and macrophyte distribution (41).

It has been proposed that the HZ provides an important refuge for surface invertebrates from floods and droughts, predation, and deterioration in surface water quality (reviewed in 7, 8, 16, 38, 90, 106). These invertebrates range in life history strategies from those that spend most of their life in the stream and enter the HZ only briefly (occasional hyporheos, *sensu* 159) to those with a hyporheic larval stage but with subadult and adult stages that leave the HZ (amphibites; 57, 126). Individuals from virtually every insect family and most other groups found at the surface have been collected from the HZ, although few of these collections have been from depths exceeding 50 cm (8, 14).

For many small instars, the HZ is a refuge from the shear stress of strong currents and the more variable conditions that occur in the surface stream (e.g. extreme water temperatures). This more stable environment generates relatively protected and predictable conditions for eggs, pupae, and diapausing stages of invertebrates (113), and the development of fish embryos of several species (66, 99). Success of the development of salmon embryos in spawning gravels is correlated with interstitial dissolved oxygen (25, 96), and human activities leading to siltation are of concern to fisheries managers (162).

Future Research at the Reach Scale

AN APPROACH TO ASSESSING THE RELATIVE IMPORTANCE OF VARIABLES Numerous variables influence the significance of the HZ to the surface stream. Fundamentally, each variable affects the activity of the HZ, its connection with the surface stream, or both. However, the relative importance of these variables at sediment and reach scales and over time is unclear. At the reach scale, physical features such as granulometric characteristics, permeability and porosity, stream morphology (riffle/pool transitions, channel constrictions, lateral deposits), and topography (stream size, stage, slope) are relevant because they influence, among other things, hydrological exchanges. The first research challenge is to rank the controlling factors or to provide a predictive framework for

this approach. The second is to expand our hydrological models to incorporate three dimensions and to explore the extent to which sediment-scale flow paths can be extrapolated to reach-scale hydrological processes. Without reliable hydrological models, it is difficult to identify the importance of exchanges at various scales of space and time and predict changes in features of the surface stream that reflect hyporheic processes.

One simple starting place involves estimation of the ratio of water moving through hyporheic sediments to surface stream flow. Surface velocities can be measured or estimated using Manning's equation (58), while Darcy's Law allows estimation of subsurface velocity from hydraulic conductivity (ease with which subsurface water flows) and slope (51). Discharges in the channel and the HZ are obtained by multiplying the respective velocities by their relative cross-sectional areas (A_s = cross-sectional area of the HZ, A = cross-sectional area of the stream) to obtain a rough estimate of the proportion of water moving down the channel relative to subsurface flow. By varying factors such as slope, hydraulic conductivity, and A_s/A, we can generate values for surface/channel velocities and discharges that span natural stream conditions. For example, A_s/A can range from roughly 5 (i.e. the hyporheic cross section is five times the channel cross section) (146) to almost zero in bedrock streams (101). Similarly, although the calculations only approximate actual velocities, they match realistic surface water (0.1–2 m/s) and hyporheic velocities (0.00001–0.01 m/s). The resultant proportions of hyporheic versus channel flow vary over 4–5 orders of magnitude when plotted as a function of A_s/A with channel discharge 100–1000 times greater than hyporheic discharge except at high values of A_s/A (Figure 3).

Based on these approximations, the contribution of the HZ to the entire stream ecosystem is likely to be greatest when a relatively high proportion of the total discharge flows at intermediate velocities (allowing time for transformation processes, etc) through a relatively large HZ. This model attempts to integrate reach-scale variables such as the relative flows through given cross-sections of the HZ and the overlying surface stream with sediment-scale variables such as nutrient transformations and diffusion from the biofilms, resulting in predictions that may be extrapolated to a catchment scale.

As the proportion of surface water passing through the HZ will normally be less than 100%, the relevant question becomes, "How big a difference in biogeochemical processing is necessary for the HZ to be functionally significant?" Future research could use this model as a springboard to answer this question and to relate activity in the HZ to the degree of connection between the HZ and the surface stream. This model also allows at least first-order ranking of the controlling variables to generate testable predictions and to compare different stream reaches. Such a simple approach may suffice until more tractable hydrological models are readily available to ecologists.
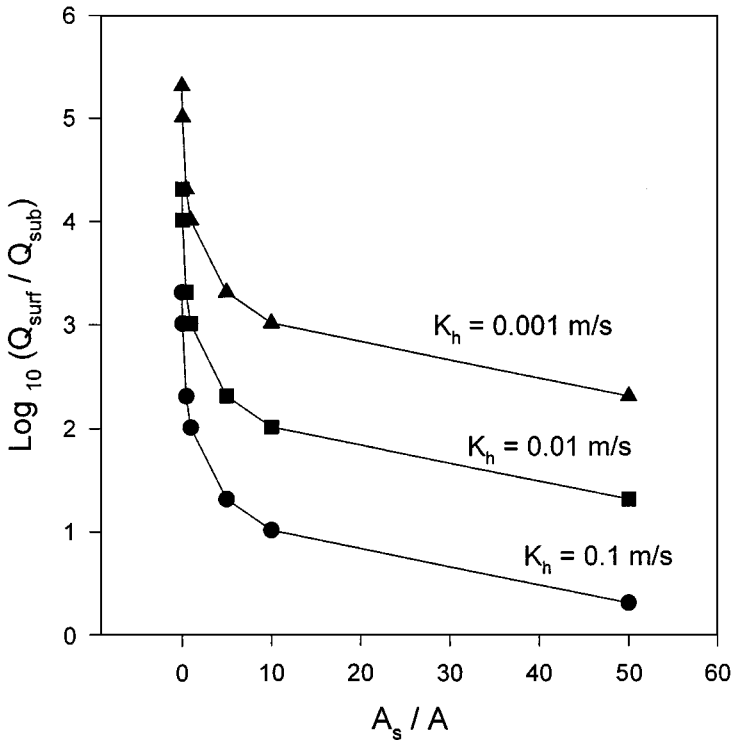
Figure 3 Log_{10}-transformed ratio of the discharge of surface (Q_{surf}) and subsurface (Q_{sub}) water derived from simple empirical models of channel and subsurface flow. K_h is hydraulic conductivity, and A_s/A is the cross-sectional area of the subsurface storage zone relative to the open channel. With this model, the hyporheic zone (HZ) is hypothesized to be most significant to stream ecosystem function when a relatively high proportion of total discharge travels at intermediate velocities through a relatively large HZ (see text).

EXPERIMENTAL APPROACHES   More experimental work is needed to explore the causal mechanisms and hypotheses generated by reach-scale descriptive surveys and to test hypotheses generated by modeling approaches such as that described above. There are methodological limitations to overcome (see 7, 63, 64, 105, 158), but we urgently need to test hypotheses about the factors that influence the rate of nutrient regeneration, that control microbial processes, and that determine patterns in composition and abundance of the hyporheos in the HZ. For example, interesting patterns in distribution of invertebrates in the HZ have often been noted, but the *causes* of this patchiness are not obvious and are usually ascribed to physical, chemical, hydrological, and sedimentary

features based on correlative data collected at rather broad scales (e.g. 9, 10, 12, 16, 27–29, 33, 34, 36, 86, 88, 89, 94, 113, 115, 128, 132, 133, 151–153, 157–159). Furthermore, these distributional patterns are modified by drying (10, 24), changes in surface water quality (74), and flooding (10, 37, 88, 90, 106), indicating a need for experiments at the reach scale that manipulate flows and hydrological exchange patterns. Although small-scale experiments (e.g. 11, 106) provide limited insights into ecological aspects such as local migration rates, they are probably at the wrong scale for assessing reach-scale responses to manipulations of hydrology or other variables.

Technologically, there is scope for innovative approaches to these larger-scale manipulations, and we may be able to design suitable experiments to take advantage of river and riparian zone restoration measures (148). Given the lack of information about the role of the HZ as a "storage area" for recolonization after natural and human-induced disturbances, there is a need to obtain more reliable data before making generalizations about population resilience and resistance at the stream-reach scale (83, 136).

CATCHMENT-SCALE PROCESSES

The Hyporheic Corridor Concept

Few studies have been conducted at this broadest scale, and theoretical models predicting how the HZ varies within a catchment are in their infancy (28, 57, 126, 155). Stanford & Ward (126) proposed the hyporheic corridor concept (HCC), which emphasizes the connections and interactions between the HZ and the catchment. Alluvial flow paths and residence time are suggested to control hyporheic biodiversity and ecosystem metabolism. The subsurface continuum formed by the "hyporheic corridor" has a lateral component connecting riparian zones, anabranches, paleochannels, and floodplain aquifers (up to 3 km from the main channel; 127) that generates a wide array of landscape features whose temporal variability relates to their degree of connection and the discharge regime in the river. Along the river continuum, vertical hydrological exchange between the HZ and the surface stream occurs at a series of points (Figure 2*a*). These points correlate with reaches with limited HZs interspersed with unconstrained alluvial reaches, like beads on a string (28). Thus, the HCC identifies catchment-scale processes whereby (*a*) production in the main channel is strongly influenced by upwelling nutrient-rich water, (*b*) riparian zone structure and dynamics reflect hyporheic flow patterns, and (*c*) the spatial and temporal variability in hydrological exchange processes and linkages promote exceptional biodiversity within the landscape.

Hyporheic development is predicted to be least in headwater streams (126, 155), peak in the intermediate reaches, and then decline in lowland rivers, where

lower alluvial hydraulic conductivities inhibit hydrologic exchange relative to lateral linkages mediated by flooding (78). While many of these predictions remain untested, in a study of solute transport in headwater streams to lowland rivers (32), A_s/A values were found to be highest for low-order streams whereas absolute storage zone size was greatest in unconstrained lowland rivers. On the other hand, studies of hyporheic flow paths in montane upland streams (100, 163) reported hyporheic flow paths much higher than predicted.

At the landscape level, variation among basins may relate to geologic control of sediment alluvial characteristics (71, 100) and patterns of runoff and catchment drainage (79). Associated with contrasting parent lithology, differing sediment hydraulic conductivity dictated the size of the HZ and the rate of exchange between the stream and the aquifer in three headwater streams (100, 146). The size of the HZ increased nearly 300-fold from a first-order stream draining sandstone and volcanic tuff compared with one originating from the cobbles and boulders of a granitic basin.

Catchment-Scale Ecological Studies of the HZ

Although biogeographic patterns of distribution and evolutionary pathways of several invertebrate groups occurring in the HZ and associated groundwater habitats are well studied (e.g. 4, 35, 132), catchment-scale studies of the ecology of invertebrates in the HZ are rare (116, 152). Broad-scale patterns do not seem as obvious as reach-scale patterns. For example, despite substantial variation in elevation (ca 2000 m) along its length, longitudinal patterns in the composition of fauna associated with the surface gravel of alluvial aquifers at nine sites along the South Platte River, Colorado, were only weakly associated with altitude (153). There was no correlation between altitude and the interstitial faunal composition deeper in the sediments, which suggested site-specific geomorphic features may be more important (152). Conversely, a survey of 14 sites across the eastern United States using comparable sampling methods indicated that correlations of faunal composition with sediment size, oxygen concentration, and organic matter were weak (133), which implied that other factors regulated these hyporheic communities.

The two best-known catchment-level studies of the HZ and associated groundwater environments are those of the Rhône River (France) and the Flathead River (Montana, United States). The interstitial fauna of these environments has been studied for almost two decades. Seminal work by Gibert et al (55) first drew attention to the faunal richness of the alluvial aquifers of the Rhône, and the role of hydrology and geomorphology in structuring hyporheic assemblages in space and over time is now well established (see review in 39). In 1974, many invertebrates (including stonefly nymphs) were reported from deep in the alluvial sediments of the Tobacco River, northwestern Montana (124), and this

reporting heralded the discovery of diverse (>70 taxa) invertebrate assemblages from the larger Flathead River system and further evidence for hydrological and geomorphological control of interstitial faunal composition (125; see review in 127).

Future Research and River Management at the Catchment Scale

Parallels between the conclusions from these two catchment-wide studies are striking. At a broad scale, the complexity of habitats and resultant biodiversity support predictions of the HCC. The vast areas of interfaces at a range of scales (sediment scale to riparian and aquifer ecotones) produce physicochemical gradients across which substantial fluxes and transformations of organic matter, nutrients, and other materials occur. These observations have important ramifications for river management and thus are an obvious research priority (56, 103). Both of these catchments are occupied by humans whose activities affect ecological processes occurring in the associated groundwater and hyporheic components of these rivers (e.g. cultural eutrophication, sedimentation, flow regulation; see 39, 127).

Hydrologic fluxes between various compartments and the HZ (Figure 1) mean that this zone both receives and contributes anthropogenic pollutants. Sewage discharges to surface water can significantly increase interstitial and sediment-associated nutrient concentrations, depleting hyporheic oxygen (19, 117) and fundamentally altering hyporheic biogeochemical structure and function. Similarly, chemicals in agricultural runoff can move from surface water into groundwater with little change in concentration (122, 123). If degradation occurs, it is likely to happen within the HZ rather than in deeper groundwater zones (120). Conversely, heavy metals (137), pesticides, and anthropogenic nutrients (95) can move from groundwater into surface water through the hyporheic interface. To manage these pollutants properly, we must learn more about the ecological ramifications of organic chemical, nutrient, or heavy metal loading to the HZ.

Regulation of the Rhône River, France, altered the bed geomorphology (aggradation and degradation of 4–5 m), reversing the direction of aquifer/river interaction by changing the relative elevation of the riverbed and alluvial aquifer and substantially altering the composition of the hyporheos (29). A similar uncoupling of the riparian, river, and aquifer subsystems occurred along the Rhine River and was associated with increasing geomorphic and hydrologic manipulation (17). Upstream portions of the Rhine have become entrenched, isolating the river from lateral interactions with the floodplain, drying out spring brooks, and restricting aquifer recharge to areas of the riverbed within the constraints of the hydroelectric canals.

Given the significance of hydrological connections to the role of the HZ, human activities that alter quantity and quality of sediment transport are important. These include dam construction, which reduces long-term sediment loading, and road building, farming, housing construction, suburban development, and logging, which can increase sediment loads (162). Such land uses enhance transport of fine sediment into the streambed, clogging sediments (16, 99). The impacts on fish have been studied (e.g. 121, 162), but little is known about the physical and chemical changes that are likely to occur in the HZ (114). However, negative impacts on the HZ are not always evident. Despite large amounts of fine sediment generated during construction of the Thomson Dam, Victoria, there was little silt deposition in the HZ (87). Consequences of clearing such as bank slump and removal of riparian vegetation have been postulated to influence the HZ of several small streams in New Zealand (9), although river restoration measures may prove costly.

CONCLUSIONS

The importance of bed permeability and hydrological flow patterns has been a recurring theme at a range of scales in this review and in the many attempts to synthesize and identify the key features controlling ecosystem processes in the HZ (reviewed in 7, 16, 36, 43, 57, 65, 132, 151, 157–159). At the catchment and reach scales, permeability and flow patterns determine the proportion of discharge through the HZ, which has been hypothesized to influence how biogeochemical processes in the HZ affect stream ecosystem metabolism (43).

Ultimately, the significance of the HZ to the surface stream is a function of its activity and extent of connection. Although some fine-scale measurements of hyporheic activity have been obtained (e.g. rates of respiration, nitrification), it has not yet been demonstrated that these measurements can be extrapolated to reach and catchment levels. We know the principal variables controlling hyporheic metabolic activity and the connection of the HZ to the surface stream, especially at the reach scale, but we lack a framework for assessing the relative importance of these variables across systems. Research on the HZ awaits some technological advances in hydrological modeling, reach-scale experimental procedures, and sampling methods. Although it may be argued that the HZ is important only in a limited subset of streams (i.e. relatively large HZ and A_s/A, metabolically active, substantial hydrological exchange), its role in these streams can underpin understanding of how they function, exemplified by research on desert streams and lowland gravel-bed rivers. Further, a simple budget approach undoubtedly overlooks some of the special properties and processes (e.g. nitrification and upwelling "hot spots" of productivity) that render the HZ functionally significant to the surface stream at a range of spatial scales.

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