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Perspectives on the hyporheic zone: integrating hydrology and biology. Concluding remarks

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Abstract. Hyporheic zone research is an area of rapidly growing interest in stream ecology. Several key points have emerged as important for consideration of future research in the hyporheic zone. Hyporheic researchers need to outline explicitly the spatial scale of their own research, from single sampling locations to entire catchments, and how research at this examined scale relates to finer or larger scaled processes. Spatial and temporal scale considerations are also important when planning sampling and experimental manipulations of hyporheic processes. Stream researchers need to examine the importance of the hyporheic zone as a boundary or ecotone that potentially controls or contributes to surface water and groundwater ecosystem dynamics. Inclusion of hydrologic considerations in the research design and analysis of hyporheic processes is a promising approach that will help elevate hyporheic research from a descriptive science to a predictive one, and may help to make future cross-system comparisons possible.

Key words: hyporheic zone, stream ecology, scale, hydrology, groundwater.

The preceding papers indicate that hyporheic research can be viewed from many interesting perspectives. Researchers are clearly excited by the variety of processes occurring within the hyporheic zone and have begun to ask how these processes influence biotic assemblages, as well as catchment and stream ecosystem functioning (Valett et al. 1993). Key points in the preceding perspectives stress the necessity of including hydrologic processes in research designs and the importance of scale when interpreting results from studies that examine both hydrologic and biological patterns. The focus of this paper is to integrate some of the concepts discussed, to produce useful generalizations, and to help focus future hyporheic research.

The first point that was made repeatedly was the question of scale, including the spatial scales at which hydrology is known to influence hyporheic processes. For example, at fine scales, such as individual sampling locations, hydrologic patterns can be used to make predictions about solute gradients (Hendricks 1993, White 1993). However, since solute gradients are tightly coupled with microbial activity (Hendricks 1993), a solute distribution that is patchier than the predicted one may be an indication of biological use (Hendricks 1993). Hydrologic patterns can also be used to make predictions about fine-scale invertebrate distribution patterns (Godbout and Hynes 1982, Marmonier and Dole 1986, Marmonier and Creuzé des Châtelliers 1991, Stanley and Boulton 1993).

In contrast to individual sampling locations, a considerable increase in the amount of mixing between upwelling groundwater and downwelling surface water in the hyporheic zone is seen at the scale of individual riffles and pools (White 1993). With increased mixing of groundwater and surface water, the hyporheic zone becomes a potentially important site of solute retention, metabolism, and mineralization (Bencala 1993, Hendricks 1993, White 1993). Mixing of surface water and groundwater can directly or indirectly change invertebrate composition and abundance (Stanley and Boulton 1993) and is associated with bacterial density, activity, and production (Hendricks 1993). Thus, hydrologic patterns become an important variable generating heterogeneity in biological and physicochemical patterns in the hyporheic zone (Palmer 1993).

At a larger scale, White (1993) builds a model of expected longitudinal changes in hyporheic zone development from headwaters to downstream sections. While this conceptual model has not yet been tested, it allows predictions to be made concerning the relationship between stream order and hyporheic functioning. Further, it encourages research that will attempt to relate hyporheic zone processes between different longitudinal sections of the same stream. Since downstream increases occur in the extent of hyporheic area and the amount of hyporheic interaction with adjacent floodplain (due to increased surface water advection), predictions can be made about correlated upstream-to-downstream changes in biogeochemical processes and community structure (Stanford and Ward 1993, White 1993). In large alluvial rivers, the convergence of surface water and groundwater aquifers can be viewed as a hyporheic corridor (Stanford and Ward 1993). The hyporheic corridor concept is comparable to ecotone and boundary concepts (Wiens et al. 1985, Naiman et al. 1988) in that the hyporheic corridor may be the primary determinant of the floodplain landscape and subsurface biodiversity or production (Stanford and Ward 1993). At the scale of the entire catchment, the nature of the hyporheic zone varies from place to place depending on how local hydrology and geology influence solute transport and retention in a dynamic and bi-directional manner (Bencala 1993). Depending on the question, hyporheic researchers may need to alter the spatial scale at which they view their study area, both longitudinally and laterally.

Technology is becoming available to measure hydrologic interactions within the hyporheic zone. Future research needs to specifically examine the influence of hydrology on hyporheic processes at all scales. Researchers can increase the predictive power of hyporheic research with an understanding of how hydrology influences scale-associated hyporheic heterogeneity, thus elevating hyporheic research from a descriptive science to a predictive one. Further, subsequent research needs to integrate processes occurring at different scales to determine whether hyporheic systems display hierarchial patterns. Can the broad patterns observed within the hyporheic zone be predicted by summing all finer scale processes or do emergent properties related to hydrology arise (Allen and Starr 1982)?

The hyporheic zone is a fundamental component of most aquatic ecosystems and may regulate large scale catchment-level processes. Hyporheic zones can be extensive, providing vast areas for biological activity that influence nearby stream ecosystems (Stanford and Ward 1993) and support large abundances of invertebrates (see Palmer 1990 for meiofauna review, Stanford and Ward 1988, 1993). Little is known about hyporheic foodweb dynamics (Stanford and Ward 1988) or specific mechanisms of carbon production and modification with respect to groundwater–hyporheic–surface water exchange (Hendricks 1993); however, hyporheic zones have been shown to have high metabolic and chemical activity (Grimm and Fisher 1984, Hendricks 1993). The major trophic links within the hyporheic zone need to be identified along with trophic interactions between hyporheic and surface water or groundwater (Stanley and Boulton 1993, Stanford and Ward 1993). More information is needed to determine if hyporheic zone functioning is important to biotic functioning in adjacent systems (e.g., floodplains, riparian zones).

Biotic and physicochemical processes within the hyporheic zone vary not only spatially but also temporally. Seasonal variation in flow influences the amount of groundwater recharge to the hyporheic zone (Hynes 1983) and thus will influence solute transport and retention (Bencala 1993). Within a season, spates can influence aspects of hyporheic community dynamics such as abundances, vertical and lateral migration, and epigean vs. hypogean species composition (Marmonier 1991, Dole-Olivier and Marmonier 1992, Palmer et al. 1992, Stanley and Boulton 1993). This dynamic nature makes it difficult to define hyporheic zones or characterize their boundaries (Palmer 1993, White 1993). Though difficult, the attempt is especially useful with respect to the potential gains in understanding of scale-dependent issues involving biological, physical, and chemical processes.

One approach to delineating the hyporheic zone is to use microbes and invertebrates as indicator organisms for classification of hyporheic habitat, as well as for identification of different microhabitats or biotopes (Hendricks 1993, Stanford and Ward 1993, Stanley and Boulton 1993). Variation in species composition in various zones or biotopes has been associated with differences in grain size, oxygen concentration, carbon dioxide concentration, biological oxygen demand, alkalinity, suspended solids, organic material type and concentration, and other nutrients (Pennak and Ward 1986, Williams 1989, Boulton et al. 1992). Since these studies examined spatial variation in biotic and physicochemical patterns, they are potentially useful in characterizing hyporheic systems at a local scale. Other studies have already shown, however, that considerable variation in species composition occurs at larger scales, i.e., between reaches and between drainage basins (Shiozawa 1991), which must also be considered. Attempts to use biotic patterns to characterize hyporheic zones will require a greater understanding of both temporal and spatial scale issues.

Scale issues are important considerations when experiments are designed for the hyporheic zone (Palmer 1993). Researchers must consider both spatial and temporal scale when deciding on the size and duration of experiments that examine biological processes, as well as the time of year in which to conduct these experiments. As Palmer (1993) points out, these choices will influence the outcome of our experiments. Some experiments will reveal patterns specific to certain habitats and their associated hydrologic regime (riffles or runs, upwelling or downwelling zones). Others will apply to larger geographical areas (e.g., reach or drainage basin) that incorporate large scale variation in hydrologic patterns. Consideration of both spatial and temporal scale is necessary if the experimenter wants to be able to extrapolate results to an entire stream system or make catchment comparisons (Ward 1989, Poff and Ward 1990, Stream Solute Workshop 1990). Our ability to accurately predict large scale phenomena from smaller scale observations is severely limited by the small number of studies completed at scales larger than one reach (Hendricks 1993, White 1993) and by our uncertainty as to whether results from finer scales can be summed to give large scale predictions.

The second unifying theme emerging from the preceding papers was that hyporheic researchers need to focus more on hydrologic processes in their research. Standardization of hydrologic terminology and greater explanation of techniques is needed to facilitate cross-system comparisons and ecological research in the hyporheic zone (White 1993). Among the techniques used to investigate hydrologic influences, grain size distributions and the mapping of surface water flow patterns that affect grain size are already well standardized (Buchanan 1984, Wetzel and Likens 1991). Recent advances include characterization of hyporheic upwelling and downwelling zones (Grimm and Fisher 1984, White et al. 1987, Valett et al. 1990, White 1990, Hendricks and White 1991); lateral exchange patterns between the hyporheic zone and adjacent groundwater (Triska et al. 1989, Harvey and Bencala 1993); and interstitial flow and exchange rates within the hyporheic zone (Grimm and Fisher 1984, Munn and Meyer 1988, Metzler and Smock 1990, Valett et al. 1990). New technology is needed for investigating other aspects of hydrology that may affect hyporheic processes, such as bed load transport, turbulent flow patterns, and shear stress (Davis and Barmuta 1989, Palmer 1993). Unfortunately this work has rarely been coupled with biological and ecological studies (Boulton et al. 1991, Hendricks 1993, Stanley and Boulton 1993), and very rarely has it been a routine part of experimentation (Palmer 1993).

We suggest it is necessary to determine the importance of the hyporheic zone to stream ecosystem functioning. Specifically, we need to examine how the hyporheic zone and hyporheic processes fit into existing stream paradigms (Stanford and Ward 1993, White 1993). Future research should examine the importance of the hyporheic zone as a longitudinal link between the headwaters and lower order stream sections (Vannote et al. 1980, Hendricks 1993, Stanford and Ward 1993, White 1993). The effects of subsurface storage (Triska et al. 1989) and substream flow patterns (Bencala 1993, Harvey and Bencala 1993) on hyporheic and surface water processes need to be addressed more specifically, especially with respect to nutrient spiraling theory (Elwood et al. 1983, Stream Solute Workshop 1990). Community and population dynamics are relatively unstudied in hyporheic systems and little is known about trophic relationships in the hyporheic zone (Stanley and Boulton 1993, Hendricks 1993, Stanford and Ward 1993). Understanding of hyporheic community dynamics would also add a new and interesting component to the examination of disturbance and subsequent recovery in stream systems (Fisher et al. 1982, Resh et al. 1988, Poff 1992). Considerations of patch boundary theory (Wiens et al. 1985, Naiman et al. 1988) and ecotone theory (Gibert et al. 1990, Vervier et al. 1992) are also relevant to hyporheic research. Hyporheic zones occur at the overlap of groundwater and surface water systems, and are important transition sites for nutrients and organic carbon between the two systems. As an ecotone or boundary, the hyporheic zone may modify or control the flow of material or energy between adjacent systems (Wiens et al. 1985, Naiman et al. 1988, Hendricks 1993, Stanford and Ward 1993). Little is known about the flux of material through the hyporheic zone, how this flux affects biotic processes in the hyporheic zone (Hendricks 1993, Palmer 1993), and at what spatial or temporal scales such processes are important.

Each hyporheic system is unique, but cross-system comparisons may be possible if we begin to examine the nature and extent of hyporheic differences between streams and stream orders. Specifically, we need to examine the important physical and chemical factors controlling hyporheic processes and organisms, and how hydrology affects these factors, at a variety of scales. Variation in both the **type** of hyporheic systems investigated and the **questions** being asked about these systems will require widely varying approaches. Results of hyporheic research will be increasingly comparable among different study sites if the techniques used and, more importantly, the reasoning behind their use (e.g., specific geomorphic and hydrologic constraints), are explained fully.

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