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The role of the hyporheic zone across stream networks[†]

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Abstract

Many hyporheic papers state that the hyporheic zone is a critical component of stream ecosystems, and many of these papers focus on the biogeochemical effects of the hyporheic zone on stream solute loads. However, efforts to show such relationships have proven elusive, prompting several questions: Are the effects of the hyporheic zone on stream ecosystems so highly variable in place and time (or among streams) that a consistent relationship should not be expected? Or, is the hyporheic zone less important in stream ecosystems than is commonly expected? These questions were examined using data from existing groundwater modelling studies of hyporheic exchange flow at five sites in a fifth-order, mountainous stream network. The size of exchange flows, relative to stream discharge ($Q_{HEF} : Q$), was large only in very small streams at low discharge (area $\approx$100 ha; Q <10 l/s). At higher flows (flow exceedance probability >0·7) and in all larger streams, $Q_{HEF} : Q$ was small. These data show that biogeochemical processes in the hyporheic zone of small streams can substantially influence the stream's solute load, but these processes become hydrologically constrained at high discharge or in larger streams and rivers. The hyporheic zone may influence stream ecosystems in many ways, however, not just through biogeochemical processes that alter stream solute loads. For example, the hyporheic zone represents a unique habitat for some organisms, with patterns and amounts of upwelling and downwelling water determining the underlying physiochemical environment of the hyporheic zone. Similarly, hyporheic exchange creates distinct patches of downwelling and upwelling. Upwelling environments are of special interest, because upwelling water has the potential to be thermally or chemically distinct from stream water. Consequently, micro-environmental patches created by hyporheic exchange flows are likely to be important to biological and ecosystem processes, even if their impact on stream solute loads is small. Published in 2011 by John Wiley & Sons, Ltd.

Key Words hyporheic exchange flows; stream discharge; stream networks; flow exceedance probability; watershed area; hyporheic potential

Introduction

There is growing recognition that the part of streams extending below, and adjacent to, the streambed can be an important component of aquatic ecosystems. This area, commonly known as the hyporheic zone, can provide unique habitats for aquatic organisms (Stanford and Ward, 1988; Baxter and Hauer, 2000), and exchange of stream water through the hyporheic zone exposes transported solutes to unique biogeochemical environments with subsequent impacts on whole stream metabolism (Grimm and Fisher, 1984) and nutrient cycling (Triska *et al.*, 1989; Mulholland *et al.*, 1997; Mulholland and DeAngelis, 2000). Despite its broadly recognized importance, quantifying the role of the hyporheic zone in streams has proven difficult. For example, attempts to examine this question in studies comparing a wide range of stream types often do not show strong correlations between measures of hyporheic exchange and nutrient cycling at the stream-reach scale (Hall *et al.*, 2002; Webster *et al.*, 2003). These results pose two questions: (i) Are the effects of the hyporheic zone on stream ecosystems so highly variable in place and time (or among streams) that a consistent relationship should not be expected? Or (ii), is the hyporheic zone less important in stream ecosystems than is commonly expected? To answer these questions, I take a physical/hydrological

Table I. Data summary for points shown in Figure 1. Abbreviations shown in the first column were used in Figure 1 to denote specific stream reaches from the 64 km^2 Lookout Creek watershed in central Oregon, USA. Slope denotes the longitudinal gradient of the valley floor; Q_{HEF} denotes the amount of hyporheic exchange flow predicted from groundwater flow models, normalized to a 100-m reach length; Ex (p) denotes the annual flow exceedance probability for a given stream under the flow conditions used to simulate hyporheic exchange flows in the groundwater flow models. Data sources are as follows: WS1 and WS3 (Kasahara and Wondzell, 2003) with additional comparison for low- and high-baseflow conditions (Wondzell, 2006); McRae Creek (Wondzell and Swanson, 1996); upper and lower Lookout Creek (Kasahara and Wondzell, 2003)

Site	Watershed	Area (km^2)	Mean annual discharge (l/s)	Slope (m m^{-1})	K (m s^{-1})	HYP_{POT} (Slope × K; m s^{-1})	Q_{HEF} (m^3 s^{-1} per 100 m)	Q (m^3 s^{-1})	Q_{HEF}/Q (m^{-1})	Ex (p)
1-L	WS1—low baseflow	0·96	40	0·14	7×10^{-5}	1×10^{-5}	2·28	1·22	0·01869	0·90
1-H	WS1—high baseflow	0·96	40	0·14	7×10^{-5}	1×10^{-5}	2·28	4·67	0·00488	0·69
3-L	WS3—low baseflow	1·01	39	0·13	7×10^{-5}	9×10^{-6}	4·26	3·23	0·01316	0·92
3-H	WS3—high baseflow	1·01	39	0·13	7×10^{-5}	9×10^{-6}	4·26	11·46	0·00372	0·61
McR-L	McRae—low baseflow	14·00	530	0·04	5×10^{-3}	2×10^{-4}	1·27	117	0·00011	0·71
McR-H	McRae—high baseflow	14·00	530	0·04	5×10^{-3}	2×10^{-4}	1·75	590	0·00003	0·30
McR-S	McRae—storm flow	14·00	530	0·04	5×10^{-3}	2×10^{-4}	1·49	2400	0·00001	0·03
UpLO	upper Lookout—baseflow	50·00	2630	0·02	2×10^{-3}	3×10^{-5}	50·0	308	0·00069	0·86
LowLO	lower Lookout—baseflow	60·62	3190	0·01	7×10^{-4}	7×10^{-6}	1·14	873	0·00002	0·67

perspective and attempt to quantify the importance of the hyporheic zone in a mountainous stream network. From these results, I build a general conceptual model to describe the expected role of the hyporheic zone in stream networks.

An example from the Lookout Creek watershed

Lookout Creek drains a 64 km^2 mountainous watershed located in the western Cascade Mountains of Oregon, USA (44°20′N, 122°20′W). Hyporheic studies and groundwater flow simulations were conducted at five locations within the watershed. Two sites were located on the fifth-order mainstem of Lookout Creek. The lower Lookout site was located in a narrow, bedrock-confined reach whereas the upper Lookout site was located in a wide, or unconstrained alluvial reach. One site was located on McRae Creek, a fourth-order tributary to Lookout Creek. Two sites were located on first-order headwater streams, both of which drained directly to lower Lookout Creek (Table I). These study sites are all located in forested watersheds where road building and forest harvest have occurred in the past. Large wood was also removed from portions of the stream network, including much of the fifth-order stream channel. Much of the road network remains in place and in use. More detailed study site descriptions and the specifics of the model simulations are given in Wondzell (1994), Wondzell and Swanson (1996), and Kasahara and Wondzell (2003).

The relationship between hyporheic exchange flow and stream discharge at the five study sites in the Lookout Creek watershed was examined for systematic patterns related either to temporal changes in discharge at a single site or changes across a stream network under relatively uniform flow conditions. Hyporheic exchange flows at each study site were estimated from simulations using the numerical groundwater flow model, MODFLOW. Models were parameterized to measured stream boundary conditions and hydraulic conductivities measured from slug tests from relatively dense well networks covering the full model domains. Models were calibrated to simulate the head distributions measured across the well networks. In-depth study at one study site suggested groundwater flow models provide reasonable quantitative estimates of hyporheic exchange fluxes (Wondzell *et al.*, 2009a).

Results from the Lookout Creek watershed showed that $Q_{HEF} : Q$ ratios decreased as stream size increased. Because the $Q_{HEF} : Q$ ratio is sensitive to change in discharge, comparisons among streams of different sizes within a stream network may be confounded by changes in Q if the observations are made at different times and under different flow conditions. One way to control for changes in discharge is to make among-site comparisons at discharges with similar flow exceedance probabilities. Within a small watershed, or even within a hydro-climatic region, the flow exceedance probability provides some insurance that comparisons are made under similar hydrologic conditions. In this case, calibration data for model simulations at a number of sites in the Lookout Creek basin were collected around 0·70 flow exceedance probabilities, providing reasonably comparable data across a wide range of stream sizes (Table I). These data showed relatively high $Q_{HEF} : Q$ ratios in the headwater WS1 and WS3 streams and much smaller ratios in the larger McRae Creek and Lookout Creek sites.

Results from the Lookout Creek watershed also showed that $Q_{HEF} : Q$ ratios decreased with seasonal increases in discharge. For example, at McRae Creek, only small changes in hyporheic exchange flows (Q_{HEF}) were observed over a 20-fold change in stream discharge from summer low baseflow through winter high baseflow-to-peak flows during a small storm (Table I). Consequently, the $Q_{HEF}:Q$ ratio decreased approximately 15-fold as discharge increased. Hyporheic exchange was only simulated for low baseflow conditions at WS1 and WS3 (Kasahara and Wondzell, 2003). However, direct observations from the well networks at these sites showed that hyporheic exchange fluxes should have remained relatively constant over the observed range of baseflow discharges because neither the shape of the water table nor stream water elevations changed substantially. Consequently, the $Q_{HEF}:Q$ ratios would have decreased markedly with relatively modest increases in discharge (Table I).

While the general trend of decreasing $Q_{HEF}:Q$ with increasing discharge is readily apparent from the Lookout Creek data, it is also clear that there is substantial reach to reach variation not explained by simple differences in discharge (Table I). For example, the two sites on the mainstem of Lookout Creek have roughly similar discharges, but Q_{HEF} is more than 100-fold greater at upper Lookout Creek than at lower Lookout Creek. Lower Lookout Creek flows through a bedrock-constrained reach in which hyporheic exchange is limited to a narrow gravel bar on one side of the channel with the other side of the channel pressed against exposed bedrock. In contrast, the upper Lookout Creek study site is located in one of the widest reaches found along the length of mainstem Lookout Creek and extensive hyporheic exchange occurs throughout the reach. In this case, differences in channel morphology led to a 40-fold change in the $Q_{HEF}:Q$ ratio—a change larger than that observed at McRae Creek from low baseflow to storm flow (Table I). The $Q_{HEF}:Q$ ratios at low flow were also somewhat different between the WS1 and the WS3 study sites because of differences in valley floor widths and the abundance of log jams (Wondzell, 2006).

A Generalized Conceptual Model of the Hyporheic Zone

The analyses presented above suggest that the relative size of the hyporheic zone ($Q_{HEF}:Q$ ratio) is inversely proportional to stream discharge. This relationship also appears sensitive to the underlying potential for a given stream reach to support hyporheic exchange. Thus, broad-scale, among site comparisons need to account for both factors. The discharge regime is easily characterized by simple metrics such as watershed area, annual average discharge, and flow exceedance probability. Characterising the potential of a stream reach to support hyporheic exchange is more difficult.

The potential for hyporheic exchange

The potential for hyporheic exchange will be related to both head gradients ($\Delta h/\Delta l$) and the saturated hydraulic conductivity (K) of alluvial sediment within a stream reach as described by Darcy's Law (Wondzell and Gooseff, in press). Head gradients created by changes in the longitudinal gradients along stream channels are a major factor driving hyporheic exchange in many streams. Where average longitudinal gradients are steep, steep head gradients can develop over short distances across steps, riffles and channel meanders; where gradients are low, long distances are required to create substantial head differences so that head gradients also tend to be low. Of course, in low-gradient streams the head loss along the longitudinal profile can be compressed into distinct steps but steps or riffles must then be widely spaced. Consequently, valleys with steeper longitudinal gradients can support steeper head gradients, resulting in more hyporheic exchange. Longitudinal valley gradients tend to change systematically with stream size in many mountainous stream networks such that small headwater channels tend to have steeper longitudinal gradients than do larger streams. These trends are clearly evident in the data collected from the Lookout Creek stream network (Table I).

Darcy's Law also shows that hyporheic exchange should also be linearly related to saturated hydraulic conductivity (K), with more exchange flow through coarse textured sediment with high K and less flow through fine textured sediment with low K. There is a tendency for fining of alluvial sediment with decreased longitudinal gradient, and gradient tends to decrease with watershed area, as described above. Consequently, high-gradient mountain streams would tend to have coarse streambed sediment and valley floor alluvium whereas lower gradient, lowland stream networks and mainstems of major rivers would tend to be characterized by finer sediment. Of course, these patterns are also under substantial local control. There is not a consistent pattern in K with stream size in the Lookout Creek stream network (Table I). All the study sites tend to be relatively high gradient with correspondingly high average Ks, typically in the range observed for gravels to sands (Domenico and Schwartz, 1990, Table III.2, pg. 65).

Multiplying longitudinal gradient of the river valley by the saturated hydraulic conductivity measured in any stream reach provides an initial estimate of the potential to develop hyporheic exchange (HYP_{POT}). This product is roughly analogous to the Darcy Velocity, but uses reach-scale longitudinal gradient of the valley floor rather than actual estimates of ($\Delta h/\Delta l$). Expressed this way, HYP_{POT} could exceed 10^{-3} m s^{-1} in mountain streams where longitudinal gradients of alluvial reaches can equal 0·15 m m^{-1} and where K in coarse valley-floor alluvium might be similar to that of fine gravels. At the other extreme, HYP_{POT} could be as low as 10^{-15} m s^{-1}, in low-gradient streams in wetlands or tidal mud flats that can have gradients less than 10^{-4} m m^{-1} and K typical of clayey sediment. Applying the HYP_{POT} metric

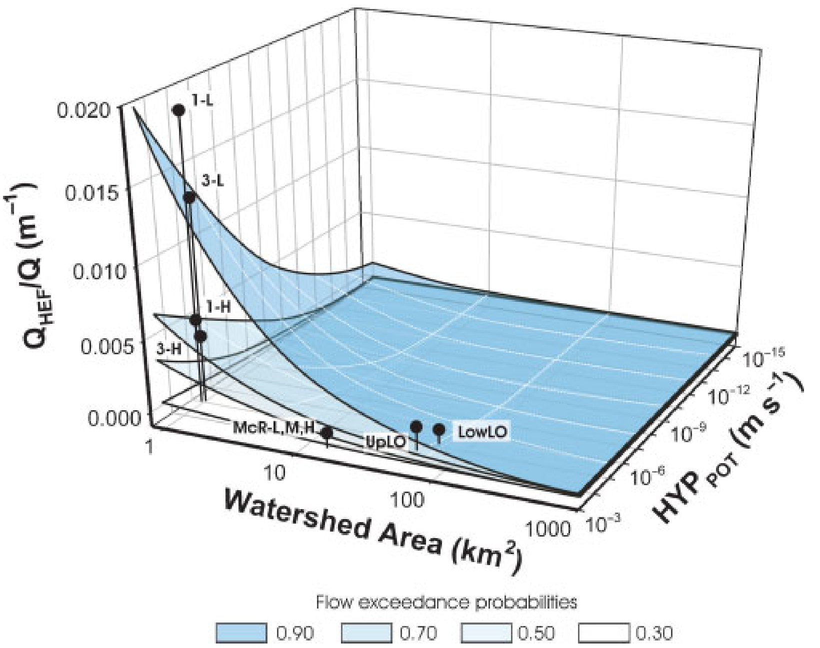

Figure 1. Conceptual depiction of the relative influence of the hyporheic zone on bulk stream water (the ratio of Q_{HEF}/Q) relative to watershed area and underlying potential of the stream network to support hyporheic exchange flow. Data points are from the Lookout Creek watershed and point labels follow Table I. The 3-D response surfaces are hypothesized relationships showing how the of Q_{HEF}/Q ratio might be expected to change with change in watershed area and the hydrogeomorphic conditions that create the potential for hyporheic exchange (HYP_{POT}). Each surface represents flow conditions characterized by the annual flow exceedance probability, from periods of very low flow (90% exceedance) to periods of moderately high flow (30% exceedance)

to the step-pool and pool-riffle stream reaches of the mountainous Lookout Creek network suggests that the potential for hyporheic exchange flow is high, which agrees well with the high $Q_{HEF} : Q$ ratios estimated for these stream reaches. Similarly, the HYP_{POT} metric is likely to work well in meandering lower-gradient streams because both valley slope and hydraulic conductivity are key variables in the equations shown by Cardenas (2009) to predict hyporheic exchange in meandering rivers.

The HYP_{POT} metric does not account for all the factors known to drive hyporheic exchange. Reach-scale changes in channel morphology can lead to large changes in Q_{HEF}, even though K and longitudinal gradients remain unchanged. For example, HYP_{POT} does not distinguish between the lower and upper Lookout Creek sites where differences in channel constraint result in more than a 10-fold difference in Q_{HEF} between these sites (Table I). The HYP_{POT} metric is not sensitive to transient exchange driven by rapid changes in stage, such as in tidally influenced rivers (Bianchin *et al.*, 2010). Perhaps more importantly, HYP_{POT} is not directly sensitive to the interactions between flow and stream bedforms that control pumping exchange (Elliott and Brooks, 1997) which is expected to be the dominant form of hyporheic exchange in many low gradient streams with relatively mobile and fine-textured bed sediment. Although pumping exchange has been widely studied, published studies do not provide quantitative estimates of the magnitude of hyporheic exchange relative to stream discharge, nor do they provide quantitative comparisons between the head gradients generated by pumping exchange and longitudinal valley gradients in streams characterized by dune-ripple channel morphology. Thus, it is currently not possible to evaluate how well HYP_{POT} would characterize the potential for pumping exchange. However, that the streambed sediment is fine textured suggests that the magnitude of hyporheic exchange is likely to be limited by relatively low K, a relationship which is clearly captured by the HYP_{POT} metric. Thus, despite some limitation, the simple HYP_{POT} metric should provide an initial rough estimate of the potential for hyporheic exchange within a given stream reach and can therefore help facilitate among-site comparisons.

Comparison among streams

The expected behaviour of the hyporheic zone across a wide range of stream types and sizes can be compared using the $Q_{HEF} : Q$ ratio, stream size as measured by watershed area or average annual discharge, flow exceedance probability, and HYP_{POT} (Figure 1).

The $Q_{HEF} : Q$ ratio is large only in small streams, and even there, only at relatively low discharges. For example, in the smallest streams (WS1 & WS3) at late summer low flows (exceedance probability ∼0·9), turnover lengths of stream water through the hyporheic zone are as short as 50–75 m. That is, on average, the entire in-channel flow seeps into the hyporheic zone and is replaced by upwelling hyporheic water over distances as short as 50 m. Even at high baseflow (exceedance probability ~0·6–0·7), the turnover length of stream water is only 250 m. Thus, these streams are characterized by large $Q_{HEF}:Q$ ratios so that physical and biogeochemical processes like nutrient cycling and water temperature regimes would be strongly influenced by interactions with the hyporheic zone over large parts of the year. These small headwater streams make up more than two-thirds of the total stream network within the Lookout Creek watershed (Wondzell, 1994) and are likely to regulate solute transport from the entire watershed for large parts of the year.

Lower in the watershed, estimated turnover lengths range from 0·62 km for upper Lookout Creek (flow exceedances probability ~0·86) to 77 km for lower Lookout Creek during summer baseflow (flow exceedances probability ~0·67). The wide, unconstrained reach of upper Lookout Creek has a relatively high $Q_{HEF}:Q$ ratio and could be a hot-spot for nutrient processing in the mainstem stream. However, most of Lookout Creek is moderately to highly constrained, more similar to the lower Lookout Creek site, so that the hyporheic zone is unlikely to strongly influence the mass flux of nutrients transported through Lookout Creek in most locations.

The $Q_{HEF}:Q$ ratio decreases as stream discharge increases in wet seasons or during storms because Q_{HEF} should decrease as lateral inflows from adjacent hills begin to restrict the size of the hyporheic zone and reverse head gradients forcing flow across the floodplain toward the stream as shown by Storey *et al.* (2003). At the same time, discharge would increase markedly. At high flows (flow exceedance probabilities >0·3), the turnover lengths of stream water in WS1 and WS3 would exceed the length of these tributaries. In large streams, lower in the network, turnover lengths would be even longer so that neither stream water nor accompanying solutes would be affected by processing in the hyporheic zone. In periods of high flow, ~30% of the year, the hyporheic zone will have only a minor effect on whole watershed nutrient processing.

Not all stream types have an equal potential for hyporheic exchange. High gradient mountain streams flowing over coarse alluvium are likely to have among the highest potential for hyporheic exchange. In contrast, hyporheic exchange is likely to be much smaller in low gradient streams. Only a few studies have quantified hyporheic exchange flow in lowland streams. Storey *et al.* (2003) focused on single riffle where channel morphology is conducive to hyporheic exchange flow. Even so, the $Q_{HEF}:Q$ ratio was low at summer baseflow, giving an estimated turnover length of 21 km when stream discharge was only 100 l s^{-1}. Kasahara and Hill (2006) focused on riffles constructed for stream restoration so that head gradients and K were artificially increased. Even under these conditions, estimated turnover lengths were 8 km in a second-order tributary with summer baseflow discharge of only 9 l s^{-1}, and 1300 km in the fifth-order Silver Creek with summer baseflow discharge of 344 l s^{-1}. These studies appear to have focused only on the specific features where high rates of hyporheic exchange were expected, thus, the $Q_{HEF}:Q$ ratio is likely to be even smaller for these streams as a whole. Lacking estimates of watershed areas and the flow exceedance probabilities, these data cannot be added to Figure 1. However, these observations are consistent with the shape of the baseflow response surfaces for streams with low HYP_{POT} which show the $Q_{HEF}:Q$ ratios are small for small streams and decrease to near zero as watershed area increases.

There will, of course, be exceptions to the general trends described above, with the most notable cases from large, cobble, and gravel-bedded rivers flowing through unconstrained alluvial valleys in mountainous regions. Perhaps one of the best known examples is the Nyack Floodplain on the Middle Fork Flathead River (Poole *et al.*, 2006) where hyporheic exchange has long been studied. Quantitative estimates of Q_{HEF} have not been published for this site. Synoptic discharge measurements, however, suggest a net loss of 30% of the stream discharge to the subsurface in the upper Nyack floodplain (Stanford *et al.*, 1994) suggesting that hyporheic exchange might be substantial in this large river. Similar observations have been made in other unconstrained alluvial river reaches (Laenen and Bencala, 2001; Konrad *et al.*, 2005). Unfortunately, published quantitative estimates of hyporheic exchange flows in large rivers are rare.

Mass Transport is Not All That Matters

The dominance of tracer-based approaches used to study the physical hydrology of the hyporheic zone, and associated tracer-based studies of nutrient spiraling in streams, has tended to promote a stream-centric view of the hyporheic zone with a focus on solute transport. The impression that the relative importance of the hyporheic zone to stream ecosystem processes is determined by the proportion of the stream discharge flowing through the hyporheic zone (Findlay, 1995; Jones and Holmes, 1996) likely stems from this stream-centric view point. The hyporheic zone has been recognized for its importance to stream ecosystems on many fronts, however, so that attempts to assess the relative importance of the hyporheic zone should be broader than simply questions of mass transport.

Hyporheic exchange creates unique subsurface habitats

The hyporheic zone represents a unique habitat for some organisms, with patterns and amounts of upwelling and downwelling water determining the underlying physiochemical environment of the hyporheic zone. These

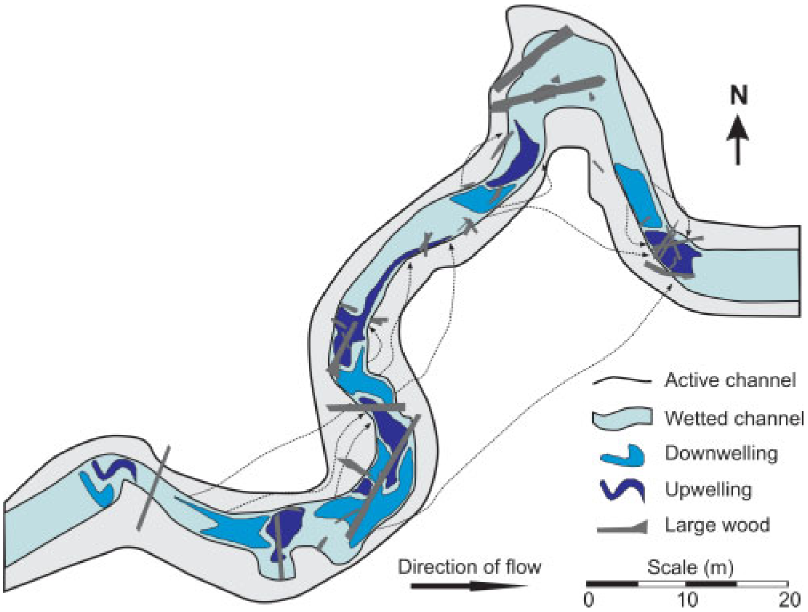

Figure 2. Plan view map of the wetted channel of Bambi Creek, Alaska (from Wondzell *et al.*, 2009b). Shaded shows zones of downwelling and upwelling located on streambed and fine-dashed arrows qualitatively depict dominant long, cross-meander flow paths derived from particle tracking in MODFLOW and MODPATH simulations

environmental differences can influence the composition, abundance, and functional attributes of microbial assemblages (Halda-Alija *et al.*, 2001; and review by Findlay and Sobczak, 2000 and references therein), meiofauna (see review by Hakencamp and Palmer, 2000 and references therein), and macroinvertebrates (Williams, 1984; Stanford and Ward, 1988). Also, exchange flows of stream water create the environmental conditions necessary for the incubation of the eggs of fish that spawn in the streambed and create the conditions supporting the early life stages of many fishes that reside in streambed gravels (Vaux, 1962; Baxter and Hauer, 2000; Malcolm *et al.*, 2005).

The amount of available hyporheic habitat and the environmental conditions found there is likely to be determined by the amount, spatial extent, and residence time of hyporheic exchange flows. The hyporheic zone is likely to be restricted to a shallow layer immediately adjacent to the wetted stream channel in low gradient rivers with fine-textured sediment as shown by Duff *et al.*, (1998) for the Shingobee River. Conversely, in high-gradient rivers with coarse-textured sediment, the hyporheic zone may extend more than 1000 m from the wetted channel as shown by Poole *et al.* (2008) for the Umatilla River. The physiochemical environmental patterns found within the hyporheic zone are more likely to be a function of residence time than flow-path length (Zarnetske *et al.*, 2011). While much remains unknown about the response of organisms to environmental patterns in the hyporheic zone, it is clear that the hyporheic zone is a unique and important habitat for a variety of organisms in many river systems, spanning most, if not all, of the state-space depicted in Figure 1.

Hyporheic exchange creates environmental patches on the streambed

An alternative way to evaluate the relative importance of the hyporheic zone in streams would be to focus on the streambed, rather than stream discharge. All hyporheic exchange (both upwelling and downwelling) must flow through the benthic zone, the biologically active layer composed of the streambed and the immediately underlying sediment. Benthic organisms are directly influenced by hyporheic exchange flows, and in upwelling zones, upwelling water passes through the benthic zone before it is mixed into the water column. Consequently, simple budgetary estimates of mass transport may not accurately reflect the relative importance of the hyporheic zone to stream ecosystem processes when considering the influence of the hyporheic zone on water temperature or nutrient cycling.

Hyporheic exchange flows do not occur uniformly over the streambed. Rather, different ‘patches’ on the stream bed experience different ‘upwelling’ or ‘downwelling’ environments (Figure 2; Wondzell *et al.*, 2009b). Upwelling environments are of special interest, because upwelling water has the potential to be thermally or chemically distinct from stream water. For example, Arrigoni *et al.*, (2008) showed that hyporheic exchange creates a diversity of thermal environments in the main, side, and spring channels of a large, unconstrained alluvial river during summer baseflow. Ebersole *et al.* (2003) demonstrated that hyporheic upwelling zones provided thermal refugia for cold-water fishes in streams on late summer days when discharge was low and ambient stream temperature was high. Valett *et al.* (1994) showed that hyporheic upwelling zones were enriched with nitrate, had higher algal biomass, and after floods, algal biomass recovered more quickly in upwelling zones than in downwelling zones. These results suggest that, even where the proportion of stream water exchanged through the hyporheic zone is too small to measurably change water temperatures or nutrient concentrations of the whole stream, hyporheic exchange can create environmental patches critical to structuring stream ecosystems.

Conclusions

Are the effects of the hyporheic zone so highly variable in place and time (or among streams) that a consistent relationship should not be expected? The conceptual model of the hyporheic zone presented here (Figure 1) suggests that the role of the hyporheic zone in stream ecosystems is reasonably predictable. This role does change with both location within the stream network as well as with seasonal or storm-driven changes in discharge, but these dynamics are also reasonably predictable. There can be a high degree of reach-to-reach variability created by underlying variation in channel morphology that cannot be predicted from the simple relations shown in Figure 1. However, the hydraulic and geomorphologic factors driving hyporheic exchange has seen considerable research in recent years (for example, Harvey and Bencala, 1993; Kasahara and Wondzell, 2003; Cardenas *et al*., 2004; Wondzell *et al*., 2009b) so that these controlling factors are reasonably well understood and are already being incorporated in models to estimate hyporheic exchange flows (Cardenas, 2009).

Is the hyporheic zone less important in stream ecosystems than is commonly expected? If importance is simply measured as the proportion of stream discharge exchanged through the hyporheic zone in a given stream reach, then the hyporheic zone will only play a significant role in stream ecosystem processes under limited circumstances, namely, in small streams when discharge is low. But even then it could be argued that the hyporheic zone will have a significant effect on whole network responses because small streams make up most of the stream network and most of the watershed drains into these small streams. A broader view of the hyporheic zone would include the diverse array of effects that hyporheic exchange flows can support in any given stream reach—creating unique habitats for a wide diversity of organisms either directly in the hyporheic zone or by modifying the environmental character of upwelling and downwelling patches on the streambed. Either way, the data, analyses, and conceptual model of the hyporheic zone presented here supports the expectation that the hyporheic zone is important to stream ecosystems.

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