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SHORT COMMUNICATION

HYDROLOGIC SPIRALLING: THE ROLE OF MULTIPLE INTERACTIVE FLOW PATHS IN STREAM ECOSYSTEMS[†,‡]

G. C. POOLE,[a,b,c]* S. J. O'DANIEL,[d,e] K. L. JONES,[a] W. W. WOESSNER,[f] E. S. BERNHARDT,[g]
A. M. HELTON,[a,b] J. A. STANFORD,[c] B. R. BOER[f] and T. J. BEECHIE[h]

[a] *Eco-metrics, Inc. 2520 Pine Lake Road, Tucker, GA 30084, USA*
[b] *Institute of Ecology, University of Georgia, Athens, GA 30602, USA*
[c] *Flathead Lake Biological Station, University of Montana, Polson, MT 59860, USA*
[d] *Confederated Tribes of the Umatilla Indian Reservation, P.O. Box 638, Pendleton, OR 97801, USA*
[e] *Institute for Computational System Science and Geography Department, University of California at Santa Barbara, Santa Barbara, CA 93106, USA*
[f] *Department of Geosciences, University of Montana, Missoula, MT 59812, USA*
[g] *Department of Biology, Duke University, Durham, NC, USA*
[h] *NOAA Fisheries, Northwest Fisheries Science Center, Seattle, WA, USA*

ABSTRACT

We develop and illustrate the concept of 'hydrologic spiralling' using a high-resolution (2×2 m grid cell) simulation of hyporheic hydrology across a 1.7 km^2 section of the sand, gravel and cobble floodplain aquifer of the upper Umatilla River of northeastern Oregon, USA. We parameterized the model using a continuous map of surface water stage derived from LIDAR remote sensing data. Model results reveal the presence of complex spatial patterns of hyporheic exchange across spatial scales. We use simulation results to describe streams as a collection of hierarchically organized, individual flow paths that spiral across ecotones within streams and knit together stream ecosystems. Such a view underscores the importance of: (1) gross hyporheic exchange rates in rivers, (2) the differing ecological roles of short and long hyporheic flow paths, and (3) the downstream movement of water and solutes outside of the stream channel (e.g. in the alluvial aquifer). Hydrologic spirals underscore important limitations of empirical measures of biotic solute uptake from streams and provide a needed hydrologic framework for emerging research foci in stream ecology such as hydrologic connectivity, spatial and temporal variation in biogeochemical cycling rates and the role of stream geomorphology as a dominant control on stream ecosystem dynamics. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: hyporheic zone; river; floodplain; groundwater; surface water; biogeochemistry; temperature; aquatic habitat

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INTRODUCTION

The channel, underlying alluvial aquifer and associated floodplain or riparian zone are highly interactive components of stream ecosystems (sensu Fisher *et al.*, 1998b; see also 'Fluvial System Structure' in Poole and Berman, 2001). Based on this composite view of streams, the hyporheic zone has been firmly established as an ecologically important characteristic of alluvial aquifers, from headwater rivulets to major rivers (Stanford and Ward, 1988; Findlay, 1995; Brunke and Gonser, 1997). The bidirectional exchange of water between the channel and alluvial aquifer (hyporheic exchange) influences habitat diversity and ecological processes in stream channels (Battin, 2000; Dent *et al.*, 2001), and creates a patchy and dynamic matrix of near-channel groundwater habitats for

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*Correspondence to: G.C. Poole, Eco-metrics, Inc. 2520 Pine Lake Road, Tucker, GA 30084, USA. E-mail: gpoole@eco-metrics.com

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microbial assemblages and macroinvertebrate communities (Ellis *et al*., 1998; Malard *et al*., 2002; Brunke *et al*., 2003).

Researchers commonly view hyporheic exchange as a vertical process. For instance, hyporheic recharge (surface water flowing into the hyporheic zone) and hyporheic discharge (re-emerging hyporheic water) are commonly described as 'downwelling' and 'upwelling', and hyporheic exchange is cited as driving vertical connectivity in fluvial landscapes (Ward, 1989; Kondolf *et al*., 2006). Yet, horizontal hyporheic flow is also important; for example, studies often describe the lateral extent of a hyporheic zone (Wroblicky *et al*., 1998) or patterns of horizontal hyporheic water movement (Woessner, 2000; Poole *et al*., 2006).

Whether considering the vertical or horizontal dimension, hyporheic flow paths are hierarchically nested (Fisher *et al*., 1998a; Gooseff *et al*., 2006). Flow paths may exist entirely within the streambed, penetrate mid-channel or point bars, flow between channels (e.g. main channels, side channels, spring channels and tributary channels on a flood plain), or span kilometres along a floodplain (Dent *et al*., 2001; Wondzell, 2006; Gooseff *et al*., 2007). These nested scales of hyporheic flow comprise a complex but integrated groundwater flow network driven by the interactions among stream discharge and channel geomorphology (Wondzell and Swanson, 1996; Kasahara and Wondzell, 2003; Cardenas *et al*., 2004; Poole *et al*., 2006; Wondzell, 2006; Zarnetske *et al*., 2007) (Table I). Various conceptual models exist for describing groundwater and surface-water interactions in streams, including bank storage, vertical connectivity (Amoros and Bornette, 2002), hyporheic corridors (Stanford and Ward, 1993) and 'gaining' or 'losing' channel reaches (referring to a channel's net water gain from or loss to the underlying aquifer; Woessner, 2000). However, none recognizes hyporheic hydrology as a population of individual flow paths with a wide range of residence times, nor addresses the ecological importance of the resulting variation in physical and biogeochemical components of stream habitats.

In this paper, we use field observations and remote sensing data to develop a high-resolution groundwater flow model of the hyporheic zone on the Umatilla River floodplain, northeastern Oregon, USA. We use the model results to illustrate the ecological importance of hydrologic flow paths at multiple spatial scales (Fisher *et al*., 2004) and to develop hydrologic spiralling as a conceptual hydrologic framework for lotic ecosystems.

A HIGH RESOLUTION MODEL OF HYPORHEIC EXCHANGE

The Minthorn study site (centred at 45.6722°N, 118.6117°W) is a 1.7 km^2 section of the Umatilla River floodplain (Figure 1). This anabranched alluvial river flows through the high desert of northeastern Oregon, USA, and ultimately into the Columbia River. The mainstem of the Umatilla River is unregulated and our study site is upstream of the significant agricultural water withdrawals that occur lower in the basin. Precipitation falls typically

Table I. Examples of scales and mechanisms of hyporheic exchange. See Dent *et al.* (2001) and Poole (2002) for more detailed classifications

Scale	Associated geomorphic features	Mechanism (source of hyporheic hydraulic gradient)
Streambed	Pool/riffle sequences	Changes in water elevation and velocity at the streambed interface occur as water flows pools and enters riffles or vice versa
Bar/Meander bend	Gravel bars, braiding, and channel sinuosity	Differences in water surface elevation between the upstream and downstream end of bars or among main and side channels create hydraulic gradients within gravel bars
Floodplain	Valley morphology	Longitudinal variation in valley width and thickness of alluvium alter the capacity of the alluvial aquifer, allowing channel water to infiltrate the aquifer where capacity increases and forcing aquifer discharge to the channel where capacity decreases; changes in valley slope tend to drive hyporheic discharge where slopes increase, and hyporheic recharge where slopes decrease

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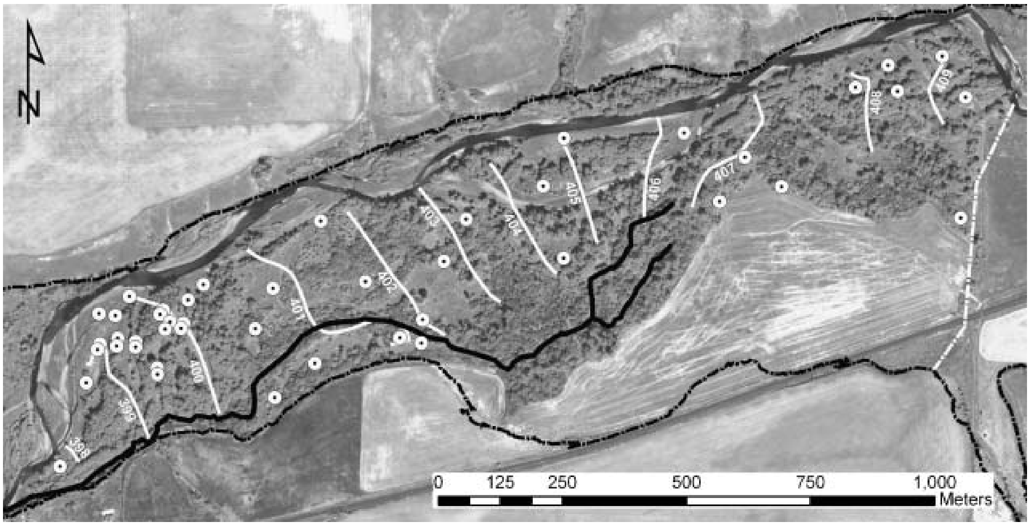

Figure 1. Aerial photograph of the Minthorn study site on the Umatilla River (Oregon, USA). Dots denote monitoring wells. Broken black lines show the northern and southern extent of the floodplain. Solid black line denotes the location of Minthorn Spring Channel. Broken white line is the arbitrary eastern site boundary. Solid white contours denote approximate water table elevations (m) interpolated from field observations in wells using the 'natural neighbour' interpolation method in ArcGIS 9.1 (ESRI, Redlands, CA)

in winter or spring, as rain on the floodplain (0.3 m year^{-1}) and as rain or snow in the surrounding Blue Mountains (0.8–1.8 m year^{-1}) (U.S. National Oceanographic and Atmospheric Administration climate data). During the period of record (1904–1989) for the USGS river gage at Pendleton (gage ID = 14021000, ~14.5 km downstream from our study site), the river discharge varied from $\sim 1\,\text{m}^3\,\text{s}^{-1}$ at baseflow to $> 50\,\text{m}^3\,\text{s}^{-1}$ during typical freshets driven by spring-time snowmelt or rain-on-snow events in the Blue Mountains. During this period, flood peaks occasionally exceeded $300\,\text{m}^3\,\text{s}^{-1}$.

On the study site, the Umatilla River flows from east to west and runs along a bedrock valley wall on the northern edge of the floodplain (Figure 1). At baseflow, the main channel commonly braids; mid-channel and lateral bars are frequent features, as are small spring channels (10 m–100 m in length) set within the bank-full scour zone. Outside of the main channel scour zone, Minthorn Spring Channel (Figure 1) emerges in an abandoned main channel trace, fed predominantly by re-emerging hyporheic water derived from the main channel (Jones *et al.*, in press-b).

We installed 48 monitoring wells (either 2.5 cm or 10.2 cm in diameter) across the study site between 1999 and 2003 (Figure 1). Each well fully penetrated the aquifer (up to 3 m in depth) and was screened along its entire length except within 0.5 m of the ground surface. A professional surveyor determined the location and elevation of the top of each well (± ~1 cm). Field technicians recorded water table elevation (± ~3 cm) and river stage (± ~1 cm) in each well and at several stream gauges during the period of 31 August–2 September 2004.

Ground penetrating radar surveys, domestic well log analyses, seismic refraction analysis and backhoe excavation revealed that the floodplain alluvium is typically 2–4 meters deep, consisting of basalt gravel, cobbles and boulders intermixed with silt, and sand lenses, and is underlain by basalt bedrock. Well water levels revealed that the summertime saturated thickness of the aquifer varies spatially, ranging from ~1 to ~3 m. Aquifer tests produced estimates of hydraulic conductivities from 300 to 700 m day^{-1} (B. Boer, unpublished data). The hyporheic zone penetrates the entire alluvial aquifer; essentially all of the alluvial aquifer water is derived from the channel (Jones *et al.*, In Press-b). As the river flows along the 40 km Umatilla Indian Reservation, summertime channel discharge decreases by about 10%; meager summertime flows in small, sparse tributaries are apparently less than channel and floodplain evapotranspiration.

To assess horizontal patterns of hyporheic flow across the floodplain, we used MODFLOW 2000 (Harbaugh *et al.*, 2000) to perform a two-dimensional, steady state simulation of this unconfined aquifer using a 2×2 m grid (model cell resolution). Hydraulic conductivity was set to 400 m day^{-1}. We assumed hydraulic conductivity was

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uniform across the site and that the basalt bedrock underlying the alluvial aquifer and forming the north and south floodplain margins (Figure 1) was impermeable to flow. A continuous map of surface water stage created from LIDAR remote sensing data (see Jones *et al.*, in press-a) was used to determine hydraulic head (water table elevation) in each grid cell that fell beneath a channel; head was held constant in these cells for the simulation. The main channel formed the western model boundary and part of the eastern model boundary. Head for the remainder of the eastern boundary was represented by interpolating the water table between the river and two strategically placed monitoring wells (Figure 1). Thus, except for half of the east model boundary, simulated hyporheic flow dynamics were driven solely by hydraulic gradients determined by the elevation and location of surface water on the floodplain.

The model produced estimates of water table elevation for each 2×2 m model cell across the floodplain ($n = 1.06$ million active model cells, which we refer to as 'floodplain locations'). By analysing simulation results in a GIS, we determined predicted locations of hyporheic discharge to the channel (i.e. active aquifer cells in the model that discharged water directly to constant head cells representing the river channel). The hyporheic flow path leading to each discharge location was determined using particle tracking software (MODPATH v4.3; Pollock, 1994), assuming a uniform porosity of 0.2. We binned flow paths by length into 40-m groupings to characterize the population of hyporheic flow paths within the alluvial aquifer.

We related hyporheic flow path distance to observed diel and seasonal patterns of groundwater temperature derived from seven data loggers (30 min recording interval); one logger in the main channel, five in hyporheic monitoring wells that intercepted groundwater flow paths originating from the main channel, and one domestic well screened in the underlying basalt bedrock aquifer. Two of the hyporheic monitoring wells were redundant; they were next to one another, shared virtually identical flow paths, and had virtually identical temperature patterns. Thus, to simplify graphical display of data, we excluded one well from this redundant pair. Each of the four remaining hyporheic monitoring wells represented a hyporheic flow path of a different length (Table II, Figure 1). Occasional instrument failure or restricted well access during periods of high water resulted in partial loss of data in two wells. We graphed the average daily water temperature for a 1-year period of record (14 July 2003–14 July 2004) for each hyporheic well, for the main channel, and for the bedrock aquifer. We also plotted the diel water temperature cycles during the days of warmest (23 July 2003) and coldest (8 February 2004) channel temperatures that occurred during periods where data were available from all four hyporheic wells.

MODEL RESULTS

Simulated water table elevations closely approximated observed water table elevations within the aquifer (Figure 2). Our model explained 99.4% of the variation in water table elevation observed across the site, suggesting that the model assumptions were reasonable and that the spatial distribution of surface water stage is the primary driver of water table elevations in the hyporheic zone.

Simulated groundwater movement is generally from east to west along the floodplain (Figure 3A), mimicking the pattern shown by interpolating field data (Figure 1). However, in contrast to simple interpolation of the sparse field data, the model's high spatial resolution revealed that local variation in river stage creates fine-scale hyporheic flow

Table II. Water temperature monitoring sites. 'Groundwater flow path length' is the estimated length of the groundwater flow path feeding the sampling site based on model results (see Model Development in main text). Locations of sampling sites shown in Figure 3

Site	Type	Groundwater flow path length (m)	Missing data
RGM	Main Channel	0	—
MB1	Hyporheic well	22	18 Oct 03–18 Nov 03
MB2	Hyporheic well	51	18 Oct 03–30 Jan 04
WMC1A	Hyporheic well	175	—
WMC22	Hyporheic well	955	—
VanPelt	Bedrock aquifer well	n/a	—

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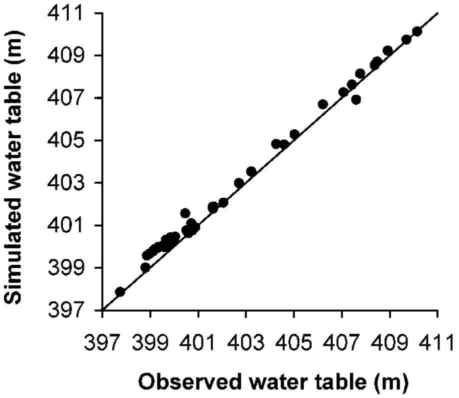

Figure 2. Simulated versus observed water table elevations in the Umatilla Floodplain alluvial aquifer. Line represents 1:1 relationship between observed and simulated values. The spatial distribution of monitoring wells is shown in Figure 1

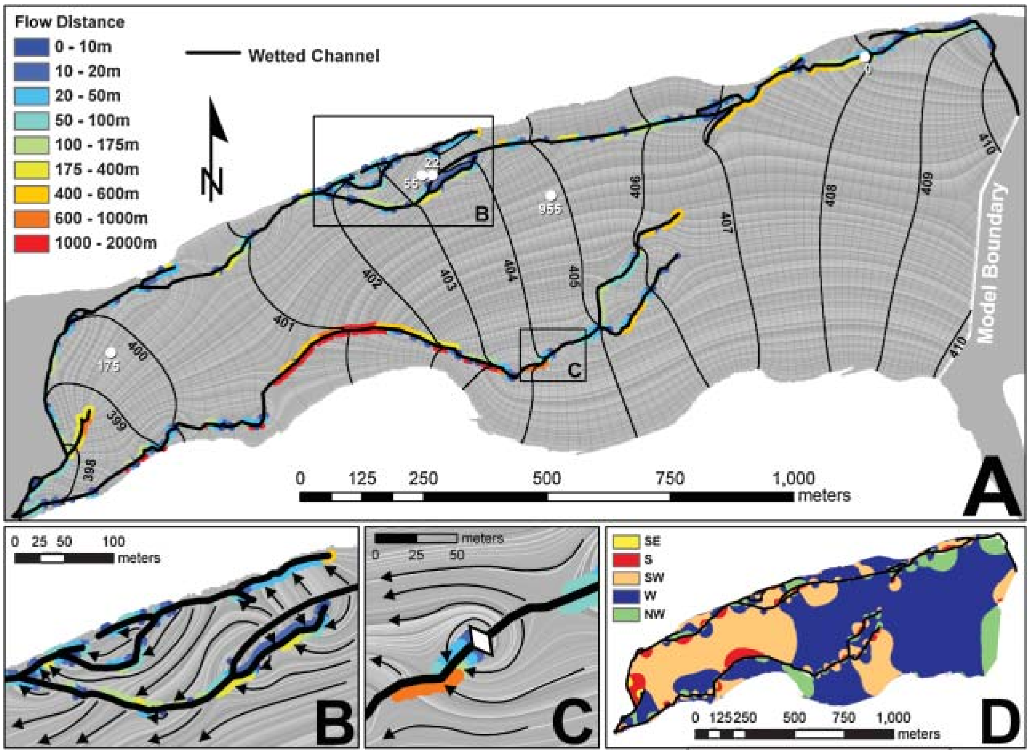

Figure 3. Model results from two-dimensional MODFLOW simulation of Minthorn study site. A: Map of simulated hyporheic flow paths. Heavy black lines show the centre of active channels during baseflow 2004, which were represented as constant head cells within the modelled aquifer. Colours along the channels denote hyporheic flow path length at each point of hyporheic discharge. Lack of colour along the channel denotes points of hyporheic recharge (i.e. hyporheic flow path length = 0). White dots show locations of hyporheic temperature loggers used to create Figure 5; white labels show length (m) of simulated flow path to each temperature sampling point (Table II). Black contours represent simulated water table elevations (m). Streamlines (background striations) indicate the shape of groundwater flow paths. Inset boxes show locations of B and C. B: Patterns of groundwater movement driven by differences in surface water elevation among the main and secondary channels. Colours and streamlines are as described in A. Arrows show direction of groundwater movement along flow paths. C: Groundwater flow patterns and enhanced hyporheic exchange associated with a sharp ‘step’ in the surface water elevation longitudinal profile; white diamond represents location of a beaver dam. Colours, streamlines and arrows are as described in B. D: Map of simulated groundwater flow direction across the alluvial aquifer, categorized into the five predominant cardinal and intercardinal directions of water movement on the floodplain

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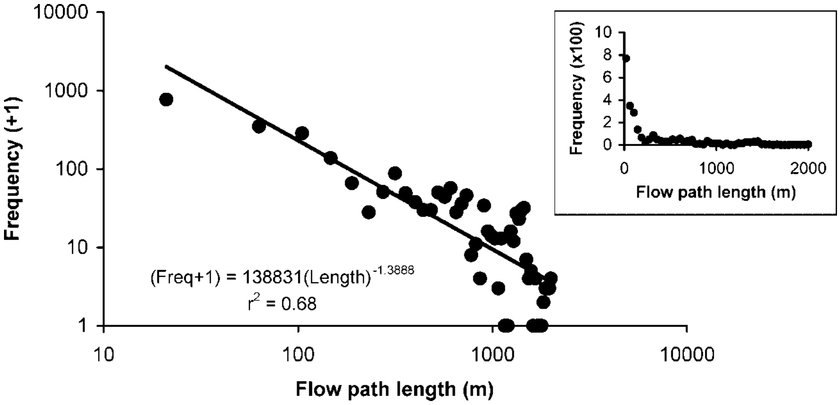

Figure 4. Frequency distribution of simulated hyporheic flow path lengths with best-fit trend line (power function). Inset graph shows the same data on linear axes

patterns nested within the general east to west trend (Figure 3B,C). The model results include patchy, interspersed patterns of hyporheic recharge (uncoloured areas along the channel, Figure 3A) and hyporheic discharge to the channel (coloured areas along the channel, Figure 3A). Long groundwater flow paths (yellows and reds) may discharge immediately adjacent to short flow paths (greens and blues), and patterns of hyporheic exchange direction and/or flow distance on one bank of the channel often differ from patterns on the opposite bank. A classification of flow direction reveals that short hyporheic flow paths (small clusters in Figure 3D) are nested within longer flow networks (larger uniform areas in Figure 3D). Short flow paths are created by sudden 'steps' in channel elevation (Figure 3C), medium flow paths are created by sinuosity and channel braiding (Figure 3B) and long flow paths (e.g. between mainstem and Minthorn Spring Channel, Figure 3A) are formed by channel avulsion over time. The frequency distribution of flow path lengths within the model (Figure 4) illustrates the predominance of short flow paths, following a power-law, similar to residence time distributions determined in other modelling (Cardenas *et al.*, 2004) and empirical (Haggerty *et al.*, 2002; Gooseff *et al.*, 2003b; Gooseff *et al.*, 2007) studies of hyporheic exchange.

In reporting and discussing our model results, we make the simplifying assumption that flow path length (flow distance) is a reasonable surrogate for residence time within the alluvial aquifer. Clearly, however, the magnitude and variety of hydraulic gradients and hydraulic conductivities within the aquifer also play an important role in controlling residence time. Nevertheless, our model provides a compelling illustration of both the complex hyporheic flow patterns and range of hyporheic flow path lengths that can exist with alluvial aquifers (Figure 3 and Figure 4). We therefore use the model results to discuss the ecological importance of hydrologic flow paths, their spatial juxtaposition and the frequency distribution of their lengths.

INFLUENCES OF FLOW PATH LENGTH ON CHANNEL HABITAT DIVERSITY

Patterns of hyporheic recharge and discharge in the Umatilla River (Figure 3) demonstrate that stream reaches contain a mosaic of hyporheic exchange rates in both directions (Brunke *et al.*, 2003), underscoring the fact that gross exchange rates can be substantially greater than the net gain or loss of channel water in the reach. Moreover, the lengths of the groundwater flow paths that converge in a particular channel reach (or even within a single pool or riffle) may span several spatial scales (sensu Gooseff *et al.*, 2003a; Gooseff *et al.*, 2006). These dynamics are especially prevalent in reaches with well-developed alluvial aquifers, braided and/or sinuous channel patterns (Figure 3A,B; see also Woessner, 2000) and diverse bed topography (Kasahara and Wondzell, 2003; Gooseff *et al.*, 2006).

Hyporheic temperatures in the Umatilla River alluvial aquifer (Figure 5) illustrate the ecological importance of long versus short flow paths. Near the beginning of hyporheic flow paths (the first few meters to tens of meters), diel temperature ranges and phases diverge from that found in the main channel (Figure 5B,C), yet mean daily (24 h)

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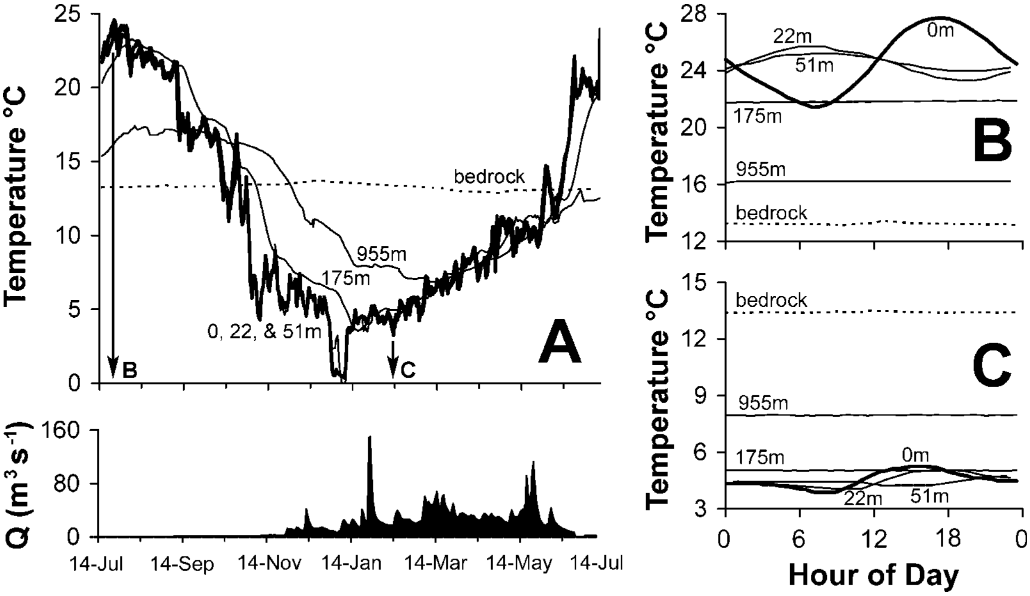

Figure 5. Water temperature patterns at five sampling sites on the Umatilla River Floodplain and in the underlying bedrock aquifer (Table II). A: Plot of daily average temperature over 1 year for the main channel ('0 m') and wells fed by hyporheic flow paths estimated to be 22, 51, 175 and 955 m in length. Temperature sampling locations are shown in Figure 3. Daily average temperature in bedrock underlying alluvial aquifer is shown for comparison. Timing of plots B and C are indicated by arrows. River hydrograph is shown for context. B: Daily temperature pattern on 23 July 2003 ($Q = 0.9\,m^3\,s^{-1}$) for each location shown in A. C: Daily temperature pattern on 8 Feb 2004 ($Q = 21.3\,m^3\,s^{-1}$) for each location shown in A

temperature remains equal to that of the channel (Figure 5A). As water proceeds along hyporheic flow paths (hundreds of meters), diel temperature variation is dampened completely (Figure 5B,C) and the daily mean temperature diverges from that of the main channel (Figure 5A). Thus, water re-emerging from short hyporheic flow paths buffers the channel's diel temperature range, while water re-emerging from long hyporheic flow paths is generally cooler than the main channel during the summer (Figure 5B) and warmer than the main channel during winter (Figure 5C) and therefore has the potential to alter the channel's daily mean temperature. Because short flow paths are numerous, they are apt to exert a cumulative effect on the diel temperature range in the main channel. Long flow paths, in contrast, tend to emerge at distinct locations along the channel (Figure 3). We surmise, then, that any associated summertime cooling or wintertime warming of surface water would be localized.

Other ecosystem processes are also influenced by hyporheic flow path length. For example, some processes like biotic nutrient assimilation can occur most rapidly at the beginning of hyporheic flow paths. Thus, flow path length may not be a substantial controlling factor. In contrast, processes such as mineralization of dissolved organic material and reductions in oxygen concentrations (sensu Findlay, 1995) occur at more uniform rates along hyporheic flow paths, suggesting longer hyporheic resident times associated with longer flow paths may be predominant drivers of these processes. Thus, whether considering temperature, biogeochemistry, or biotic responses, short and long flow paths often play variable roles in lotic ecosystems and the frequency distribution of flow path lengths can influence both habitat characteristics and associated community structure and function.

The juxtaposition and interaction of hyporheic recharge and discharge locations within a reach also have a number of important ecological consequences. For example, recharge and discharge locations have a strong influence on spawning site selection for many river-spawning fishes, especially salmon, trout and charr (Baxter and Hauer, 2000; Geist, 2000; Geist *et al.*, 2000, 2002; Coulombe-Pontbriand and Lapointe, 2004). Nutrient concentrations in stream channels may increase at sites where hyporheic water is discharged (Dent *et al.*, 2001), creating local hot spots of algae or macrophyte growth (Fisher *et al.*, 1998a). Spatial variation in interstitial oxygen concentrations associated with flow path length affects hatching success of fishes within gravels (e.g. LaCroix, 1985). Thus, habitats, water quality and biota in streams are influenced by the number and spatial arrangement of

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hyporheic recharge and discharge locations (e.g. patterns of gross exchange), as well as by variation in flow path lengths feeding locations of hyporheic discharge.

IMPLICATIONS FOR NUTRIENT SPIRALLING STUDIES

'Nutrient spirals' are created when the downstream transport of dissolved nutrients is interrupted temporarily by benthic assimilation of nutrients from the water column and those nutrients are subsequently released back to the water column for continued downstream transport (Webster and Patten, 1979; Newbold *et al.*, 1981; Elwood *et al.*, 1983; Stream Solute Workshop, 1990). The nutrient spiralling concept has served as an organizing principle for studying and modelling nutrient and carbon transport and associated biological uptake in streams for more than a quarter century. Empirical methods for measuring solute uptake length (S_w; the average distance travelled by a molecule of solute before being taken up by biota) have been developed (e.g. nutrient enrichment and stable isotope injection experiments described by Mulholland *et al.*, 2004) and widely applied (e.g. 52 studies reviewed by Ensign and Doyle, 2006). Such techniques measure differences between a conservative (e.g. chloride) and biologically active (e.g. nutrient) tracer released experimentally into a stream channel. Any reduction in reactive tracer concentration, relative to the conservative tracer, is attributed to biotic uptake.

As a whole-system measure of nutrient dynamics in streams, uptake length is considered powerful because it is purported to provide a robust and integrative measure of 'retentive processes along the entire flow path traversed by a nutrient in dissolved form' (Valett *et al.*, 1997). But when considering a population of hyporheic flow paths, we see that empirical measures of uptake length account for biotic uptake only along hyporheic flow paths that: (1) have a hyporheic residence time less than the experiment's duration; *and* (2) are fully contained (from location of hyporheic recharge to discharge location) within the sampling reach. The effect of residence time is straightforward. If the hyporheic residence time of a flow path is longer than the experiment's duration, any tracer entering that flow path will not return to the channel during the experiment. Thus, biotic uptake along the flow path will not be incorporated into the estimated uptake length. The influence of flow path length, however, is less obvious. Consider hyporheic flow paths of length *h*, and an experimental stream reach of length *r* (Figure 6). Hyporheic flow paths can interact with the reach in one of the three ways: (1) 'inflow paths' are recharged upstream, but discharge within the reach; (2) 'outflow paths' are recharged from within the reach and discharge downstream; while (3) 'within-reach paths' are recharged and discharge within the reach. Inflow paths yield errors in measurement of uptake length because they dilute experimental tracers, thereby inflating the apparent rate of water yield from the catchment. Any tracer carried along outflow paths will appear 'lost' to the system, even though biotic uptake is occurring along the flow path. Thus, only the uptake occurring along within-reach paths (those fully contained within the reach, *r*; in Figure 6) can be incorporated into empirical estimates of uptake length, and then only if the residence time of the within-reach paths is shorter than the duration of the experiment.

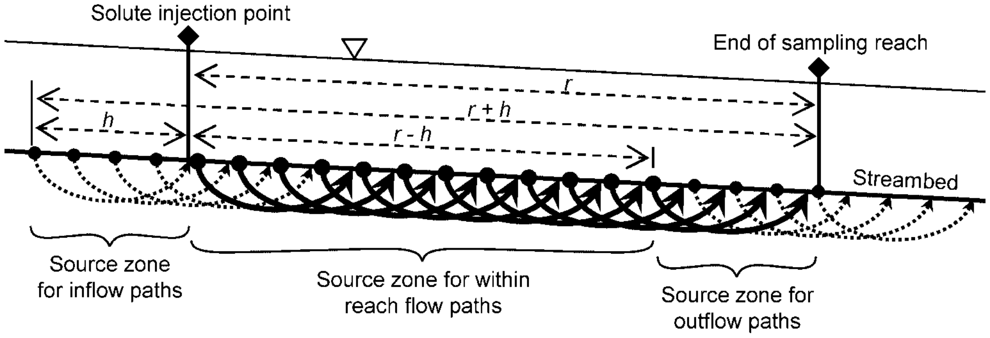

Figure 6. Longitudinal cross section of a stream system illustrating the spatial relationship between hyporheic flow path length (*h*) and sampling reach length (*r*) in determining what percentage of flow paths of length *h* will be fully contained within a sampling reach. When considering flow paths of length *h*, those represented as solid lines would be fully contained within the reach; dashed flow paths (inflow and outflow paths) will interact with the reach, but either begin upstream or emerge from the aquifer downstream of the sampling reach

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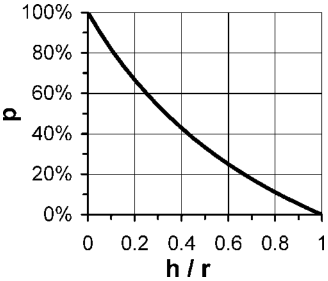

Figure 7. Likelihood (p) that a hyporheic flow path of length h will be fully contained within a sampling reach of length r

Inflow and outflow paths may be surprisingly common. The percent likelihood (p) that a flow path will be a within-reach path (rather than an inflow or outflow path) is:

$$p = 100 \bullet \frac{(r-h)}{(r+h)} \tag{1}$$

where r represents the sampling reach length and h represents the longitudinal channel distance spanned by a hyporheic flow path. As illustrated in Figure 6, the value $r+h$ represents the channel length of the source (recharge) area for all hyporheic flow paths interacting with the reach (within-reach, inflow and outflow paths), while $r-h$ represents the length of the source (recharge) area for within-reach flow paths only. (Note that Equation (1) assumes $h \leq r$. Logically, $p = 0\%$ when $h > r$.) By expressing h as a fraction of r, we find an inverse nonlinear relationship between p and h/r (Figure 7), revealing, for instance, that only those flow paths spanning $< 5\%$ of the sampling reach length have a $> 90\%$ chance of being contained within the reach and therefore incorporated into empirical estimates of uptake length.

Practically, one might assume the influence of inflow and outflow paths is minimal because short flow paths dominate hyporheic exchange (Figure 4; see also Kasahara and Wondzell, 2003) and long flow paths are rare in small streams (where uptake length is typically measured). However, several lines of evidence contradict this logic. First, modelling studies suggest that surprisingly long flow paths may exist along the interface between alluvium and bedrock in relatively small (1st–3rd order) streams (Gooseff *et al.*, 2006) or can be created by large pool-step features, for example, associated with in-channel large wood (Wondzell, 2006). Second, recent empirical evidence from tracer release studies in small streams shows that models used to estimate uptake length from tracer releases (based on the concept of 'transient storage', described below) fail to account for important longer, slower hyporheic flow paths detected with other approaches (Harvey *et al.*, 1996; Gooseff *et al.*, 2003b; Gooseff *et al.*, 2006; Wondzell, 2006).

Thus, the duration of an injection experiment and the length of the associated experimental reach represent *de facto* limitations on the fraction of hyporheic biotic retention captured by empirical estimates of uptake length (see also Harvey and Wagner, 2000). As the duration of the experiment and the length of a sampling reach decrease (or, conversely, as hyporheic flow paths increase in duration and length, e.g. in larger streams), the resulting estimate of uptake length will incorporate a smaller fraction of the true biotic uptake occurring within a stream ecosystem.

CONCEPTUALIZING THE HYDROLOGIC TEMPLATE OF LOTIC ECOSYSTEMS

Our flow path centric view of stream hydrology (see also Fisher *et al.*, 2004) contrasts with the widely applied concept of 'transient storage' (Bencala and Walters, 1983; Bencala, 1984), which describes 'the temporary retention of solutes in zones of nearly stationary water and the eventual movement of that water back to the stream channel' (Stream Solute Workshop, 1990). The transient storage paradigm divides a stream conceptually into two components, the channel and the transient storage zone. The transient storage zone represents an amalgamation of

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physical processes (surface water eddies, hyporheic storage etc.) that may impede the downstream movement of water and solutes relative to the rate expected due to advection and dispersion in the stream's channel.

Transient storage is a useful and elegant simplification of stream hydrology, especially well suited to describing longitudinal transport of stream solutes. Yet neither transient storage nor other existing hydrologic concepts (e.g. gaining and losing reaches, bank storage, vertical connectivity) address downstream water movement and solute transport outside the channel (e.g. in the hyporheic zone; *sensu* Woessner, 2000, see also Figure 3). Because they do not view streams as collections of flow paths, none of these concepts addresses all of the following: (1) the hierarchical and simultaneous nature of hyporheic recharge and discharge that controls gross hyporheic exchange rates; (2) the skewed frequency distribution of flow path lengths; and (3) the difference in ecological dynamics along short vs. long flow paths. Yet these considerations are highly relevant to emerging lotic ecosystem research questions (e.g. Table III). For instance, evaluating lotic ecosystem biogeochemistry, including so called 'hot spots and hot moments' (McClain *et al*., 2003), relies on understanding the succession of redox potential and available electron donors and acceptors along individual hydrologic flow paths (see key references, Table III). Similarly, recent studies suggest that stream geomorphology influences lotic ecosystems by controlling the convergence and divergence of individual hydrologic flow paths within stream networks or across fluvial landscapes (see key references, Table III). Thus, elucidating geomorphic controls on stream ecology may require the ability to predict how populations of hydrologic flow paths will respond to changes in stream geomorphology such as channel engineering. Such predictions would require a mechanistic, spatially explicit (Fisher *et al*., 2004) and four-dimensional (sensu Ward, 1989) view of hydrologic flow paths within streams.

Akin to the concept of material spiralling in stream corridors (Fisher *et al*., 1998b), we propose 'hydrologic spiralling' as a useful framework for envisioning multiple interactive flow paths that cross ecotones and permeate the various components of lotic ecosystems. If we consider, for instance, a stream channel and underlying hyporheic zone to be adjacent components of a lotic ecosystem separated by an ecotone (the streambed), hydrologic spirals can represent individual flow paths that link the channel to the hyporheic zone hydrologically (Figure 8). Though our modelling, data analysis, discussions and even Figure 8 have focused on the groundwater phase, such hydrologic spirals would also have a surface water phase. Specifically, the length of an individual spiral is the downstream distance a water molecule travels to complete the cycle of hyporheic recharge from the channel, flux through the alluvial aquifer, discharge back to the channel and flow in the channel to a new point of hyporheic recharge.

Although, the average hydrologic spiralling distance in a stream would equal the downstream flow distance required to exchange the entire channel discharge across an ecotone (i.e. the hydraulic uptake length; Fisher *et al*., 1998b), our vision of hydrologic spiralling emphasizes the ecological importance of the entire population of

Table III. Examples of key lotic ecosystem research foci dependent upon interactions among hydrologic flow paths within fluvial landscapes

Research focus	Tenets	Key references
Connectivity among stream ecosystem components	Streams are comprised of multiple, interactive components (channel, alluvial aquifer and floodplain/riparian zone), which are linked hydrologically, but have divergent pathways and rates of biogeochemical processing	(Ward, 1997; Ward, 1998; Fisher *et al*., 1998b; Dent *et al*., 2001; Pringle, 2003; Stanford *et al*., 2005)
Biogeochemistry of flow paths; biogeochemical 'hot spots and moments'	Relatively predictable biogeochemical transformations occur along hydrologic flow paths; yet, flow paths that converge or cross ecotones can bring together complimentary reactants to create localized and temporally variable zones of intense biogeochemical transformations with important implications for ecosystem function	(Fisher *et al*., 1998b; McClain *et al*., 2003; Fisher *et al*., 2004)
Geomorphic controls on stream ecosystem function	Variation in network topology and longitudinal variation in floodplain/aquifer structure within fluvial corridors dictate the divergence and convergence of hydrologic flow paths, mediating stream ecosystem processes	(Poole, 2002; Benda *et al*., 2004; Poole *et al*., 2006; Thorp *et al*., 2006)

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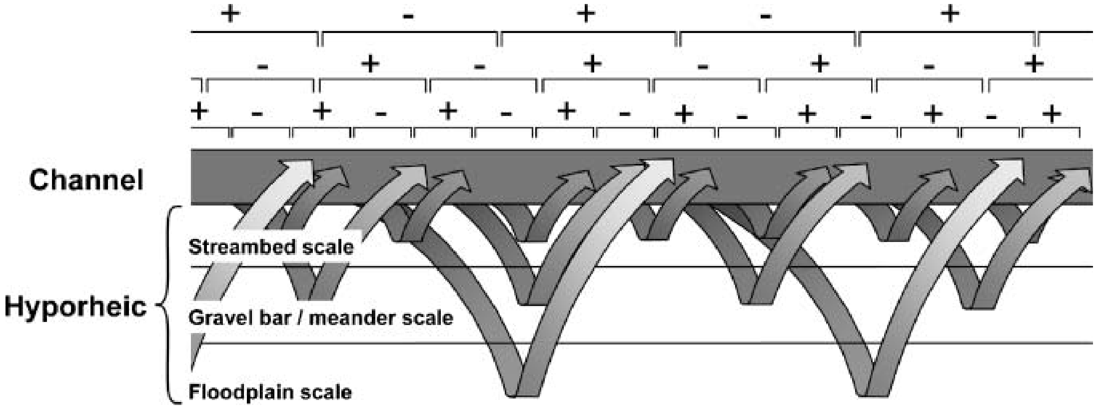

Figure 8. Longitudinal cross-section of a stream system illustrating simultaneous, nested hyporheic flow paths at multiple scales (e.g. Table I). Arrows are conceptualized hyporheic flow paths, which represent the groundwater component of hydrologic spirals. Arrow shading denotes a change in water characteristics (chemistry, temperature etc.) along the flow paths relative to channel water characteristics. Minuses and pluses represent alternating infiltration and return flow at each scale and highlight how hyporheic recharge and discharge are asynchronous across scales, yielding simultaneous bidirectional hyporheic exchange within channel reaches

hydrologic spirals rather than focusing on the mean. For instance, the overall magnitude and patterns of hyporheic exchange in a stream will determine metrics such as: (1) the frequency distribution of hydrologic spiralling distances (*sensu* Figure 4, for the groundwater phase); or (2) the length ratio between the surface and subsurface phases of hydrologic spirals. These two metrics provide useful indices of expected hydrologic dynamics, habitat variability and biological activity among streams (Battin, 2000), yet either metric (along with associated ecological influences) could vary markedly and still yield the same mean hydrologic spiralling distance. Spatial interactions among flow paths are important as well. For instance, the fact that hydrologic spirals of markedly different lengths may intermingle and return to the channel in close proximity (Figure 3) provides a mechanism to explain fine-scale variation in biogeochemistry (Valett *et al*., 1994; Dent *et al*., 2001) and channel temperature (Fernald *et al*., 2006; Arrigoni *et al*., Submitted) observed empirically near streambeds with active hyporheic exchange.

Hydrologic spiralling provides a useful framework for emerging foci of research listed in Table III. It represents the hydrology of a stream as a single integrated hydrosystem, but one comprised of multiple interactive flow paths that permeate alluvial aquifers, floodplains and stream channels, cross interceding ecotones, and therefore knit together stream ecosystems. Although our discussions have focused on hyporheic exchange, the concept is also directly applicable for characterizing other hydrodynamics, such as the formation and maintenance of perirheic mixing zones on floodplains (Mertes, 1997) as surface water spirals back and forth between the main channel and lateral surface water habitats.

Hydrologic spiralling may also provide a useful framework for developing a new generation of stream ecosystem simulation models that incorporate the influence interactive hydrologic flow paths. One approach would be to integrate lotic ecosystem dynamics (e.g. microbial metabolism and associated biogeochemical transformations) into a spatially explicit surface and subsurface hydrologic model to simulate: (a) hydrologic interaction among flow paths (e.g. Poole *et al*., 2006); and (b) the associated biotic uptake and transformations occurring along those flow paths. Such a modelling approach would build upon the long tradition of modelling spatially explicit patterns of ground- and surface-water interaction (Anderson and Woessner, 1992) and could borrow from the techniques used in terrestrial models that meld hydrology, biogeochemistry and plant growth (e.g. Parton *et al*., 1988; Running and Coughlan, 1988; Running and Gower, 1991).

CONCLUSIONS

Without question, the hydrologic template of a stream is a critical determinant of associated lotic ecosystem dynamics. Our groundwater flow model of the Umatilla River floodplain illustrates the potential complexity of

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hyporheic flow patterns in alluvial aquifers and underscores how variation in channel morphology creates multiple scales of hierarchically organized hyporheic flow paths. Based on this understanding of hyporheic hydrology, the concept of hydrologic spiralling provides a useful framework for visualizing patterns of hyporheic exchange, while highlighting the potential for downstream water movement outside the channel and clarifying the role of multiple flow path lengths in creating simultaneous hyporheic recharge and discharge within channel reaches. Viewing stream hydrology as a population of flow paths (i.e. interactive hydrologic spirals) sheds light on limitations of widely applied methods for *in situ* measures of solute retention by biota, presents a useful hydrologic framework for emerging research foci in lotic ecosystem research (Table III), and provides a clear rationale for development of spatially explicit simulation models of hydrologically mediated ecosystem dynamics in rivers and streams. We do not believe the concept of hydrologic spiralling should replace existing hydrologic conceptual models in stream ecology. Instead, we hope it will facilitate a view of stream hydrology that is flow path centric and encourage a more spatially explicit and mechanistic view of lotic ecosystem hydrology that is applicable to small streams while still capturing much of the more complex hydrology inherent in larger alluvial rivers (Figure 3).

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