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Hydrologic connectivity as a framework for understanding biogeochemical flux through watersheds and along fluvial networks

Tim Covino

Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO, USA

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ABSTRACT

Hydrologic connections can link hillslopes to channel networks, streams to lakes, subsurface to surface, land to atmosphere, terrestrial to aquatic, and upstream to downstream. These connections can develop across vertical, lateral, and longitudinal dimensions and span spatial and temporal scales. Each of these dimensions and scales are interconnected, creating a mosaic of nested hydrologic connections and associated processes. In turn, these interacting and nested processes influence the transport, cycling, and transformation of organic material and inorganic nutrients through watersheds and along fluvial networks. Although hydrologic connections span dimensions and spatiotemporal scales, relationships between connectivity and carbon and nutrient dynamics are rarely evaluated within this framework. The purpose of this paper is to provide a cross-disciplinary view of hydrologic connectivity — highlighting the various forms of hydrologic connectivity that control fluxes of organic material and nutrients — and to help stimulate integration across scales and dimensions, and collaboration among disciplines.

1. Introduction

Hydrologic connectivity is a broad term that has been used in various contexts by numerous researchers, but its meaning often differs among disciplines (Bracken et al., 2013; Michaelides and Chappell, 2009). The different meanings are due in part to the varying influence that hydrologic connectivity has on a wide variety of watershed processes of physical (Ambroise, 2004; Fryirs et al., 2007) and biological (Amoros and Bornette, 2002) importance (Table 1). Water connects hillslopes to channel networks, streams to lakes, subsurface to surface, land to atmosphere, terrestrial to aquatic, and upstream to downstream. Through these myriad hydrologic connections water is the medium that facilitates (in large part) the movement of energy, solutes, and particulate material through and across the land.

Hydrologic connectivity can be established via surface or subsurface pathways and occurs along four dimensions; these are lateral, vertical, and longitudinal spatial dimensions, and the fourth dimension is time (Ward, 1989; Ward and Stanford, 1983). While this conceptual framework is useful for organizing the way we envision hydrologic connectivity, in reality connections are not simply in one direction or another but typically span multiple dimensions. Hydrologic connections in each direction operate across temporal scales from seconds to millennia (Ward, 1989) and spatial scales from submeter to thousands of kilometers (Harvey et al., 1996). Accordingly, hydrologic connections and exchanges occur across various interacting dimensions and spatiotemporal scales (Fig. 1).

In this contribution to the Binghamton special issue on connectivity, I will discuss how various forms of hydrologic connectivity can influence biogeochemical fluxes (e.g., organic carbon, OC; nitrogen, N; and phosphorous, P) through watersheds and along channel networks. In Section 2 I introduce some of the various forms of hydrologic connectivity, including stream-hillslope, stream-groundwater, river-floodplain, longitudinal, and stream-lake connections. Then, in Section 3 I highlight some of the interactions across scales and dimensions. The purpose of this paper is to provide a cross-disciplinary view of hydrologic connectivity by gathering information from various fields and perspectives in one location. Ideally, the concept of hydrologic connectivity can offer a framework not only to understand how landscapes are connected in space and time, but also to knit together disciplinary interests across geomorphic, hydrologic, and ecologic perspectives.

2. Forms of hydrologic connectivity

2.1. Stream-hillslope connectivity

Stream-hillslope connectivity provides a fundamental linkage between terrestrial and aquatic environments (Table 1). These linkages can establish as surface overland flow or subsurface connections and are spatially and temporally variable (Dunne and Black, 1970a, 1970b; Dunne and Leopold, 1978; Hewlett, 1982; Hewlett and Hibbert, 1967). Certain hillslopes in a watershed may remain connected to the channel

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E-mail address: Tim.Covino@colostate.edu.

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Table 1
Description of five layers of hydrologic connectivity along with direction of connectivity.

Form of hydrologic connection	Selected citations
1. Hillslope • Delivers water and nutrients to the channel network; sets the initial biogeochemical template or spatiotemporal patterns of channel network nutrient loading and concentration • Direction of connectivity is toward the channel network from the hillslope	(Blume and van Meerveld, 2015; Jencso et al., 2010; Jencso et al., 2009; Kollongei and Lorentz, 2014; Ocampo et al., 2006b; Pacific et al., 2010; Stieglitz et al., 2003; von Freyberg et al., 2014)
2. Hyporheic • Attenuates downstream fluxes and increases watershed nutrient retention, particularly for limiting nutrients that have tight nutrient spirals • Direction of connectivity is bidirectional between stream and surrounding near-stream subsurface water; exchange dynamics partially controlled by channel bed morphology	(Baker et al., 1999; Boulton, 2007; Boulton et al., 1998; Dahm et al., 1998; Hall et al., 2002; Kondolf et al., 2006; Mulholland et al., 1997; Roley et al., 2012; Stanford and Ward, 1993; Stream Solute Workshop, 1990; Thomas et al., 2001)
3. Stream-groundwater • Attenuates downstream fluxes and increases watershed water and nutrient retention; increases groundwater recharge and storage; important for hydrograph attenuation and base flow maintenance; similar to hyporheic but larger spatial and temporal scale • Direction of connectivity is bidirectional and dependent on flow conditions, head gradients, valley, and channel/near-channel geomorphology	(Covino and McGlynn, 2007; Packman and Bencala, 2000; Poole et al., 2008; Ren and Packman, 2005; Stanford and Ward, 1988; Stanford and Ward, 1993; Stonedahl et al., 2010; Winter et al., 1998; Woessner, 2000)
4. Riparian/floodplain • Attenuates downstream fluxes and increases watershed nutrient retention; can substantially alter or set reach to watershed scale nutrient flux dynamics; influences groundwater recharge and helps maintain base flow; stream incision and loss of connections between the stream/river and riparian/floodplain areas can lead to strong decreases in water and nutrient retention • Direction of connectivity is bidirectional and depends on hydrologic flow conditions, watershed wetness, and channel-floodplain geomorphology; connection can be from river out to floodplain during high flow periods and reversed during lower flow conditions	(Kondolf et al., 2006; Kufel and Leśniczuk, 2014; Malard et al., 2002; Malard et al., 2000; Roley et al., 2012; Schiemer et al., 1999; Tockner et al., 1999; Ward, 1989; Ward and Stanford, 1995a; Ward and Stanford, 1995b)
5. Longitudinal • Downstream movement of water and associated material driven by advection; human intervention can increase (e.g., canals, culverts, diversions, removals of wood/log-jams, and beaver dams) or decrease (e.g., construction of dams) connectivity; land use and land and water management can have very strong impacts on longitudinal connectivity; can substantially disrupt sediment, water, and nutrient budgets • Direction of connectivity is unidirectional (downstream) for water and sediment, and bi-directional for organisms; nutrients are largely unidirectional (downstream) except for upstream migration (e.g., marine derived nutrients from anadromous fish)	(Botosaneanu, 1979; Dynesius and Nilsson, 1994; Ligon et al., 1995; Newbold et al., 1983; Newbold et al., 1981; Newbold et al., 1982; Petts, 1984; Stream Solute Workshop, 1990; Vannote et al., 1980; Wallace et al., 1977; Ward and Stanford, 1983; Ward and Stanford, 1987; Webster, 1975; Webster, 2007; Webster and Patten, 1979; Wohl and Beckman, 2014)

network throughout the year while others either never or only transiently connect during the wettest periods and largest events (Jencso et al., 2009). During large events, surface connections from hillslopes to streams (i.e., overland flow) can deliver considerable water, sediment, organic material, and inorganic nutrients to the channel network. Conversely, subsurface connections deliver little if any sediment but can be responsible for substantial water and solute delivery to the channel network. In fact, subsurface connections to the channel network can be responsible for the majority of dissolved organic carbon (DOC) and nitrate (NO_3) loading to streams at annual timescales (Creed and Band, 1998; Marxsen et al., 1997).

Given that the stream network occupies a small fraction of the total area in many watersheds, the majority of precipitation (either rain or snow) falls on the terrestrial portions of the landscape. Accordingly, most precipitation inputs travel through and/or over the land surface before (if ever) reaching the channel network, and hydrologic connectivity facilitates the linkage between the terrestrial and aquatic environment. Consequently, streamwater typically has large proportional contributions from water that has been previously stored within the watershed (e.g., soil water, groundwater (GW)), often referred to as *old water* (Buttle, 1994). Old water is often differentiated from *new water* entering the watershed during a particular precipitation event, either rain or snowmelt, on the basis of its geochemical signature (Pinder and Jones, 1969), and these analyses have demonstrated that much of the increase in streamflow during precipitation events comes from old water sources (Buttle, 1994; Kirchner, 2003; Sklash and Farvolden, 1979; Sklash et al., 1986).

The spatial structure of hydrologic connectivity and associated flowpaths during base flow and rain or snowmelt events can have strong influence on watershed hydrologic (Ambroise, 2004) and biogeochemical (Creed and Band, 1998) response. Because of landscape heterogeneity, as water travels from contributing hillslopes to streams it will likely flow through various subsurface environments of high and low concentrations of organic material and inorganic nutrients (e.g., NO_3, PO_4). As such, the unique route a parcel of water takes from initial entry into the watershed as precipitation to arrival at the channel network has strong influence on the spatial patterns and temporal dynamics of OC (Judd and Kling, 2002; McGlynn and McDonnell, 2002; Pacific et al., 2010; Tipping et al., 1999) and nutrient (Burt et al., 2002; Hill, 1990; McHale et al., 2000; Moldan and Wright, 1998; von Freyberg et al., 2014) loading to the channel network. Because riparian areas can have high organic material and inorganic nutrient content, large contributions of DOC and NO_3 to streams can come from riparian sources, particularly in headwater systems (Fiebig et al., 1990; Hedin et al., 1998). In turn, the spatial arrangement of hillslope and riparian areas in headwater systems can have strong controls on in-stream DOC (McGlynn and McDonnell, 2003) and NO_3 (Hedin et al., 1998) concentrations and on resulting watershed exports.

The magnitude of nutrient and DOC loading to channel networks from adjacent hillslopes and riparian areas (lateral connections and sources) is partially controlled by interactions between watershed morphology and climate. As watersheds become wetter during rain and/or snowmelt events, the spatial footprint of contributing areas can expand into more locations (i.e., variable source area; Hewlett and Hibbert,

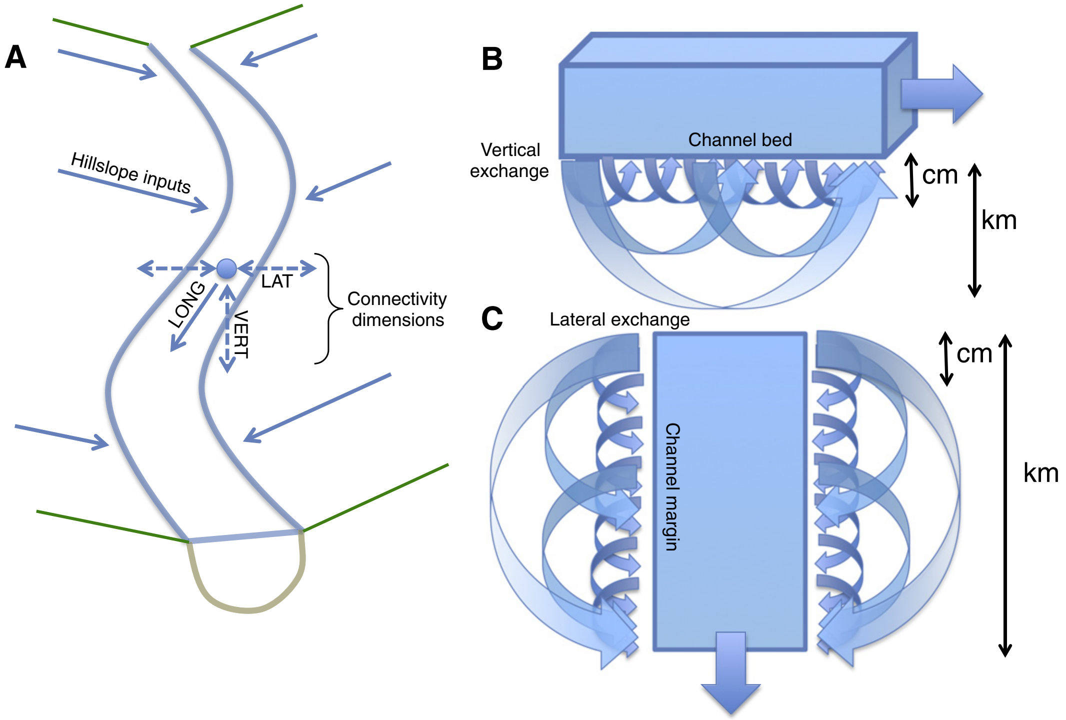


Fig. 1. (A) Conceptual diagram depicting aspects of hydrologic connectivity. Hillslope inputs to the channel network are predominantly a unidirectional connection. These inputs set the initial spatial template of organic material and nutrient concentrations across the channel network. Subsequent to loading to the channel, water interacts along three dominant spatial dimensions: lateral, vertical, and longitudinal. Connections and exchanges along the lateral and vertical dimensions are bidirectional, whereas longitudinal connections are predominantly unidirectional. (B & C) Representation of the nesting of spatial scales of interactions and hydrologic exchanges between the stream/river and surrounding landscape. (B) Vertical exchanges between channel-water and the sub-surface occur across broad spatial scales (cm–km). (C) Lateral exchanges can occur as surface (overbank, overland flow) or sub-surface connections and also span broad spatial scales.

1967) in the watershed and into near-surface soil horizons that are often organic material and/or inorganic nutrient rich (Bishop et al., 1993; Boyer et al., 1995; Creed and Band, 1998; Hornberger et al., 1994; Pacific et al., 2010). During this vertical and lateral source area expansion, contributions of organic material and inorganic nutrients from locations that only occasionally connect to the channel network can

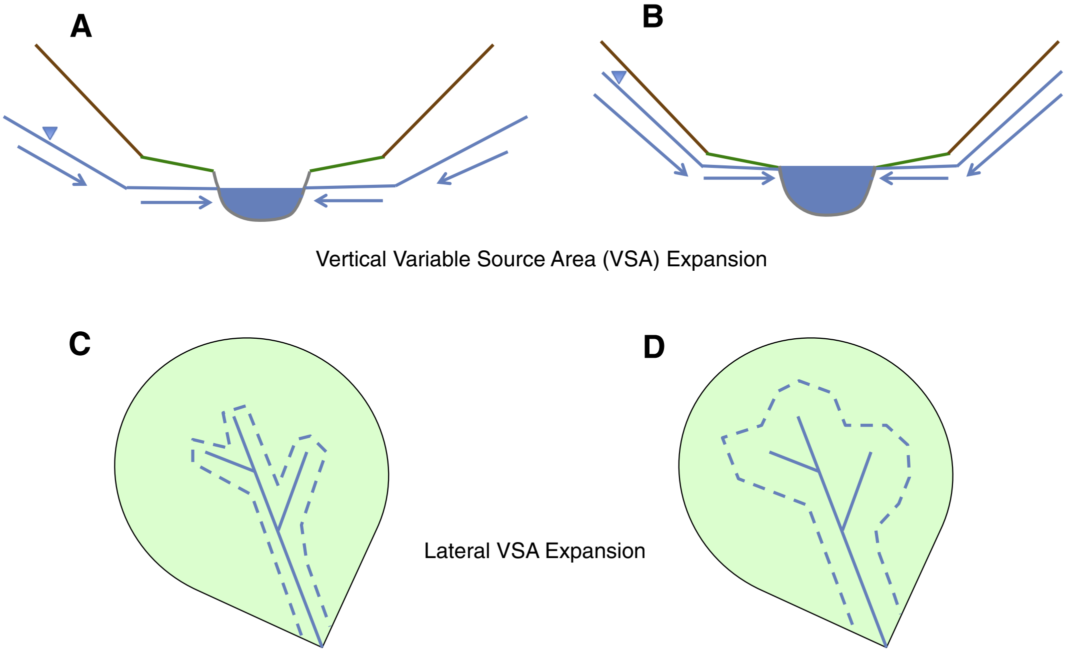


Fig. 2. (A & B) Vertical variable source area (VSA) expansion. (A) Stream-hillslope groundwater connection prior to precipitation/snowmelt event. Lateral inflows are intersecting deeper mineral soils with lower nutrient and organic carbon content leading to relatively lower nutrient and dissolved organic carbon (DOC) loading to the channel. (B) Stream-hillslope groundwater connection during and/or following precipitation/snowmelt event. Lateral inflows are intersecting shallower soils with higher nutrient and organic carbon content leading to relatively higher nutrient and DOC loading to the channel. (C & D) Lateral VSA expansion. (C) Depiction of contributing source areas during baseflow periods, and (D) the expansion of this source area as a function of precipitation/snowmelt input. VSA expansion in the vertical and lateral planes has the potential to increase nutrient and carbon loading to the channel network.

increase (Fig. 2; Bishop et al., 2004; McGlynn and McDonnell, 2003; Pacific et al., 2010; Stieglitz et al., 2003). Large amounts of dissolved nitrogen (DN) and DOC can be loaded to the channel network during rain (van Verseveld et al., 2008) and/or snowmelt events (Hornberger et al., 1994), and source area expansion has been implicated in PO_4 (Collick et al., 2015) and NO_3 (Creed and Band, 1998) export dynamics. As water levels in the watershed subside, flow paths to the channel can be restricted to deeper mineral horizons (as opposed to organic-matter-rich near-surface horizons) and can disconnect from organic material and inorganic nutrient sources, thus decreasing mass loading to the channel network (Fig. 2; Boyer et al., 1997; Hornberger et al., 1994; Pacific et al., 2010).

Because hillslope inputs have large proportional influence on the amount and chemical composition of water found in small streams and because headwater streams comprise the majority of river length in any river network (Leopold et al., 1964), considerable stream-hillslope connectivity research has occurred in headwater locations. Studies in watersheds with areas less than 100 km^2 have used intensive yet spatially distributed hillslope measures (e.g., GW levels) along with relationships between watershed morphology and the strength or duration of hillslope-riparian-stream (HRS) hydrologic connections to quantify the spatiotemporal dynamics of connectivity and to determine influences on runoff generation (Jencso and McGlynn, 2011; van Meerveld et al., 2015) and stream geochemical composition (Haynes and Mitchell, 2012; Pacific et al., 2010). In larger river systems the influence of lateral contributions to flow or stream geochemical composition can decrease and the influence of upstream (e.g., longitudinal connectivity) and autochthonous productivity can become increasingly important (Webster, 2007). This is partially an issue of volumetric mixing, where inputs to small channels comprise a much larger proportion of the total channel flow as compared to lateral inputs to larger rivers, but it is also related to shifts in physical landscape structure moving down the river continuum (Webster, 2007). As streams become larger, they generally widen; and the relative contributions from allochthonous inputs can (Webster, 2007), but may not (Meyer et al., 1997), decrease. Simultaneously, they receive increased solar input owing to decreased riparian shading, and autochthonous production can increase (Webster, 2007). However, quantifying lateral contributions or downstream transport in larger river systems remains a challenge (Meyer et al., 1997). Intensive instrumentation and/or tracer injections, while successful at smaller hillslope and stream scales, may not be appropriate or feasible in larger rivers; and geometric scaling of process understanding from small-scale studies is inadequate. Because approaches developed for smaller watershed and river sizes generally are not appropriate or practical in larger systems, new method development is needed that can address this gap. New in situ technologies (e.g., NO_3 and fluorescent-DOM, fDOM sensors) coupled with evaluation of diel signals may provide a path toward this goal (Cohen et al., 2012; Hensley and Cohen, 2016). This type of approach is attractive because it does not rely on experimental manipulation (e.g., tracer injections). Ideally, future method developments will provide approaches that are appropriate for larger watershed and river sizes and become the analogues to the tracer injection and well-network approaches commonly used in smaller streams and watersheds. These scale-appropriate methods would provide much better data input and constraints compared to the geometrically scaled information commonly used when moving from small-scale field data to larger-scale models.

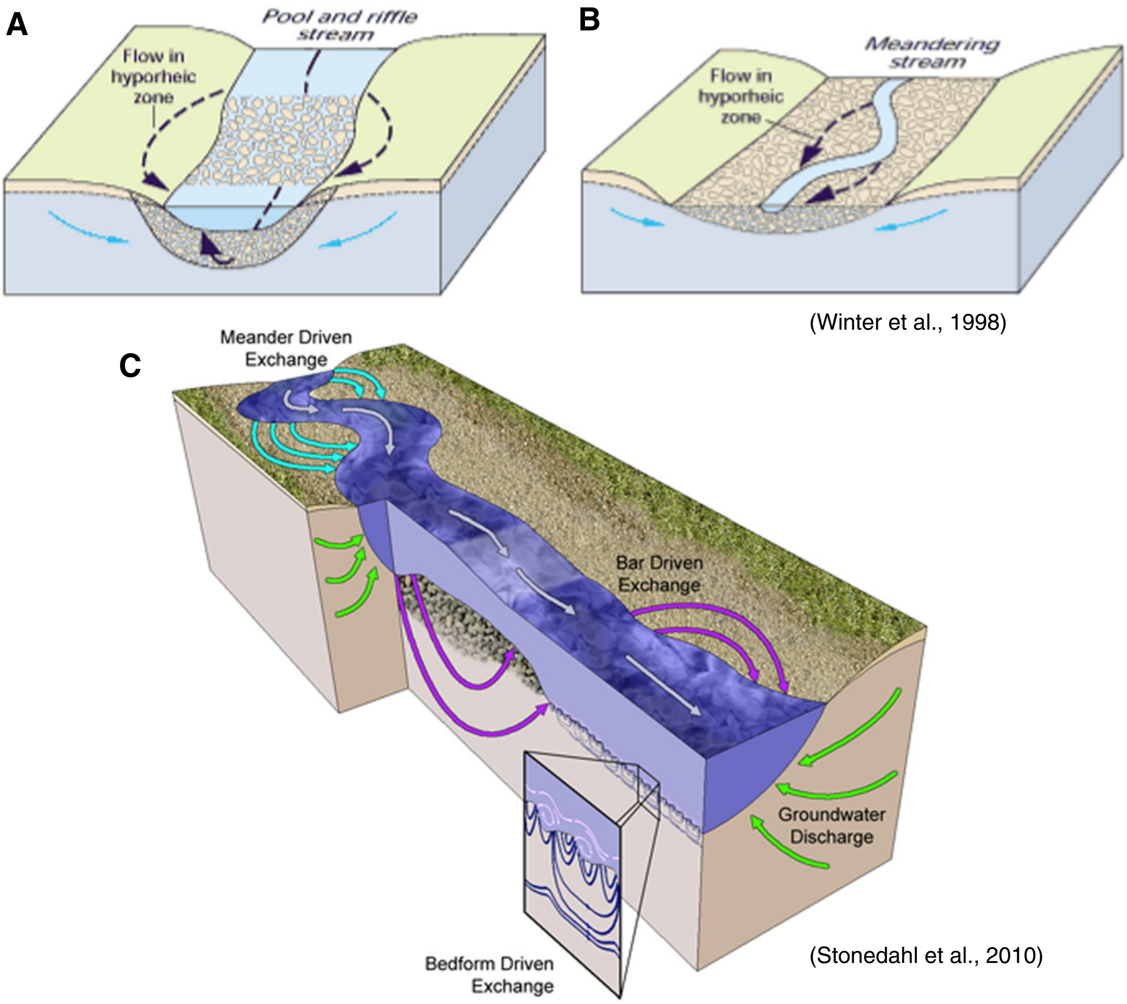
In many ways human landscape alteration has led to increased lateral connectivity between streams and the terrestrial landscapes they drain (the opposite, disconnections between rivers and floodplains are discussed in subsequent sections). Increased connections come in the form of tile drains and irrigation networks in agricultural systems (David et al., 2009; McIsaac and Hu, 2004) and impervious surfaces in urban environments (DeWalle et al., 2000; Jones et al., 2000). These rapid transport systems readily deliver water and associated material (e.g., nutrients, pollutants, road salts) to the channel network during hydrologic events (Regalado and Kelting, 2015; Yang et al., 2011). This is an area of concern for aquatic ecosystem management in part because the large amount of inorganic nutrients (e.g., nitrogen, N, and phosphate, P) humans apply to the terrestrial environment (Bouwman et al., 2013b; Filippelli, 2008; Vitousek et al., 1997) in the form of fertilizers can be readily transported to rivers, lakes, and other receiving water bodies (Baker and Johnson, 1981; Smith et al., 2015). Although debate remains regarding the strength of the relationship between hydrologic residence time and nutrient processing (discussed in the next section; Hall et al., 2002), theoretically, decreased residence time associated with increased hydrologic connectivity should lead to less nutrient processing and elevated loading to down-gradient (lateral) or down-network (longitudinal) environments. Excess nutrient loading to rivers in Midwestern portions of the United States (e.g., Mississippi River basin) has led to aquatic ecosystem degradation in inland (Lewis et al., 2011) and coastal systems (Turner and Rabalais, 2003). Concerns over elevated nutrient loading to fluvial networks and the subsequent fate of those nutrients have led to increased research attention focused on understanding nutrient loading to, and transport down, channel networks (Alexander et al., 2009; Alexander et al., 2000; Peterson et al., 2001; Wollheim et al., 2006, 2008a). While debate remains over the relative importance of hillslope (Brookshire et al., 2009) vs. in-stream (Bernhardt et al., 2003) controls over watershed nutrient budgets, clearly human alteration of the landscape has led to increased hydrologic connectivity in the lateral (e.g., tile drains, impervious surfaces) and longitudinal (e.g., channelization and disconnection from the floodplain) dimensions. Managing these considerations will require scale-appropriate methods to improve our process-based understanding and modeling capabilities, as well as greater integration across scales and dimensions.

2.2. Stream-groundwater connectivity

Connections between streams and GW have implications for hydrological and biogeochemical processes. The mixing of surface (stream) and shallow subsurface waters in porous sediments surrounding streams is often referred to as hyporheic (Orghidan, 1959) but can also be more broadly categorized as stream-GW exchange (Winter et al., 1998). These hydrologic exchanges occur across a broad range of spatial and temporal scales (Stonedahl et al., 2010), and various researchers have defined the scales of hyporheic and stream-GW exchange differently. Harvey et al. (1996) noted that smaller-scale (hyporheic) exchanges occur on spatial scales of meters and temporal scales of minutes and exist embedded within a larger network of stream-GW exchanges that occur over hundreds of meters and timescales of years. Others have expanded the spatial scale of hyporheic exchange to the floodplain extent, which can be 1000s of meters in the lateral dimension (Poole et al., 2008; Stanford and Ward, 1993). The hyporheic zone was first characterized based on physicochemical parameters and on the presence of *hyporheobionts*, biological inhabitants found neither in ground- nor surface-waters that seemed to be specific to the hyporheic zone (Orghidan, 1959). In the nearly six decades from the original characterization, studies have delineated the hyporheic zone on the basis of ecological community composition (Stanford and Ward, 1993), hydrological mixing (Triska et al., 1989), temperature (Briggs et al., 2012), tracer injections (Stream Solute Workshop, 1990), geophysical imaging (Naegeli et al., 1996; Singha and Gorelick, 2005), and combined approaches (Oxtobee and Novakowski, 2002). Although a broadly accepted delineation of the hyporheic zone or distinction between hyporheic and stream-GW exchange does not exist, these differences are largely a matter of nomenclature and convention. In fact, the overlap among these scales of exchange highlights the important point that hydrologic connections are nested and occur across numerous dimensions and spatiotemporal scales.

Spatial and temporal variability in channel characteristics such as bed topography, bed mobility, streambed pressures, and hydraulic conductivities drive hyporheic exchanges between the stream and subsurface (Harvey et al., 1996; Tonina and Buffington, 2009). This spatial and temporal variability creates a mosaic of flow paths and biogeochemical conditions surrounding the stream channel. The exchange of water between the stream and the subsurface has important influences on a variety of aquatic ecosystem processes including: solute transport (Ren and Packman, 2005), nutrient (Mulholland et al., 1997) and carbon (Wagner and Beisser, 2005) cycling, aquifer recharge (Ruehl et al., 2006), streamflow dynamics (McGlynn and Seibert, 2003), aquatic biota and biological habitat (Stanford and Ward, 1988), and water resource management (Oxtobee and Novakowski, 2002). Dominant hyporheic flow paths include downwelling and upwelling that represent vertical connections, as well as lateral exchanges that can occur at breaks in slope or along point bars and meander bends (Fig. 3, Harvey and Bencala, 1993; Poole et al., 2008; Stanford and Ward, 1993; Zarnetske et al., 2011a). Locations of downwelling and upwelling are organized by channel and valley morphology (Harvey and Bencala, 1993), and upwelling GW tends to supply nutrient-rich sources, while downwelling surface water provides oxygen-rich sources (Hedin et al., 1998; Zarnetske et al., 2011b). In regions of GW upwelling, biogeochemical processing is dominated by anaerobic processes such as denitrification; in areas of downwelling, aerobic processes are favored. This organization of biogeochemical processes occurs because dissolved oxygen (DO) concentrations tend to be the highest at the heads of hyporheic flowpaths and generally decrease along the flowpath as oxygen is consumed (Fig. 4, Malard et al., 2002; Zarnetske et al., 2011a).

Hydrologic connectivity provides the linkage between physical (transport) and biological (uptake and reaction rates) parameters that, combined, drive OC and nutrient processing and transport in channel networks. Patterns of hydrologic connectivity between streams, hillslopes, and the hyporheic zone are strongly related to valley and stream morphology, and interactions between hydrology and geomorphology create a hydrogeomorphic template. The mixing of nutrient-rich (subsurface) and oxygen-rich (surface) waters are directed by this hydrogeomorphic template and nutrient processing is maximized at the balance between transport/exchange and reactivity (Findlay, 1995; Gonzalez-Pinzon and Haggerty, 2013; Harvey et al., 2013). Interactions between transport and reactivity can be represented using the Dahmkohler number: $Da = \lambda / \alpha$; where Da is the Dahmkohler number, λ is the reaction rate, and α is the mass-transfer (exchange) rate between the main channel and transient storage zones. When the stream and subsurface environment are poorly connected (low α), biological processing in the hyporheic zone becomes supply limited as reactants are consumed and reaction products accumulate (Figs. 4 and 5). Conversely, at high levels of connectivity (high α), biological processing becomes reaction limited as nutrients and resources (e.g., carbon) are flushed through the system at a rate that is faster than the time necessary to optimize processing (Fig. 5). This interplay between transport



(Winter et al., 1998)

(Stonedahl et al., 2010)

Fig. 3. Conceptual depiction of various forms of hyporheic exchange (A & B, Winter et al., 1998), and nesting of hyporheic and groundwater flow paths (C, Stonedahl et al., 2010). Figures reproduced with permission of the publisher.
Reproduced from Winter, T.C., J.W. Harvey, O.L. Franke, and W.M. Alley. 1998. Ground water and surface water a single resource. USGS Circular 1139 1139, United States Geological Survey, Denver, CO and Stonedahl, S.H., J.W. Harvey, A. Worman, M. Salehin, and A.I. Packman. 2010. A multiscale model for integrating hyporheic exchange from ripples to meanders. Water Resources Research 46.

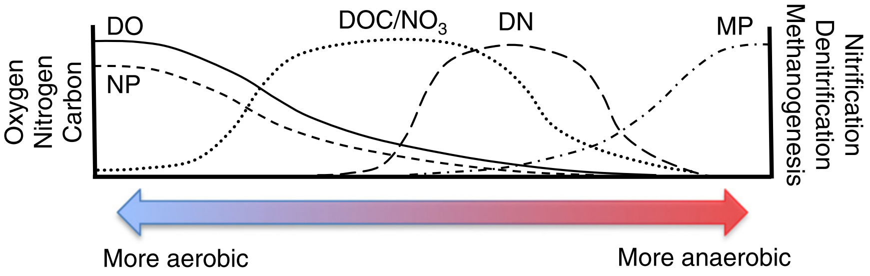


Fig. 4. Hypothetical patterns of biogeochemical resources along hyporheic flowpaths. Dissolved oxygen (DO) is highest at the heads (downwelling regions) of hyporheic flow paths. As oxygen is consumed along these flowpaths, dominant reactions shift accordingly. The mixing of well-oxygenated surface water with higher nutrient sub-surface water provides ideal conditions for biogeochemical processing in the hyporheic zone. Legend: dissolved oxygen (DO), nitrification potential (NP), dissolved organic carbon (DOC), nitrate (NO_3), denitrification (DN), methanogenesis (MP).
Adapted from Malard et al. (2002).

and reactivity partially explains why, although hypothetically expected, strong relationships between residence time and nutrient processing remain elusive (Hall et al., 2002). In fact, long residence times in transient storage zones actually necessitate a level of hydrologic disconnection from main channel flow ($\tau = 1/\alpha$; where τ is residence time), and nutrient processing in a disconnected zone will ultimately become supply limited (e.g., supply of DO from main channel). Consequently, continuously increasing uptake as a function of residence time should not be expected.

2.3. River-floodplain connectivity

Hydrologic connections across floodplains can occur via surface flow (e.g., the flood pulse concept, Junk et al., 1989) and subsurface pathways (Ward and Stanford, 1995a), and the structure of these connections influences nutrient and organic material retention (Malard et al., 2002; Tockner et al., 1999). During high flow periods, the river generally connects out to the floodplain via overbank flow; subsequently the direction of connection reverses during lower flow states with floodplain GW sustaining main-channel base flow. This bidirectional movement facilitates the exchange of substantial amounts of water, sediment, organic material, and nutrients between rivers, floodplains, and riparian wetlands. Within river-floodplain systems, a complex network of lotic (connected channels), semilotic (dead arms), and lentic (ponds) surface-water bodies can be created and maintained through episodic hydrologic connections across the floodplain (Junk et al., 1989). The spatial and temporal dynamics of hydrologic connections across the floodplain influence biogeochemical processing within each floodplain surface-water body, and intermittent connections are necessary for optimal OC and nutrient retention (Malard et al., 2000).

Depending on hydrologic conditions, river-floodplain systems can act as sources or sinks for organic material and nutrients. These conditions fall into three main categories: disconnection (phase I), seepage inflow (phase II), and upstream surface connection (phase III; Tockner et al., 1999). During phase I, the so-called *biotic interaction phase*, there is a lack of hydrologic connectivity across the floodplain and biological processing dominates organic material and nutrient retention/flux dynamics (Tockner et al., 1999). During phase II, the so-called *primary production phase*, there is *massive* nutrient contribution from the river to floodplain, and this resource supply combined with relatively high residence times contributes to high algal productivity. Lastly, during phase III, there is high hydrologic connectivity across the river-floodplain system, and physical transport processes dominate. Particulates and soluble organic matter in the floodplain are mobilized by the rising water table and flushed from the floodplain during this *transport phase* (Tockner et al., 1999). This conceptual model of river-floodplain dynamics highlights temporal shifts in physical vs. biological controls, and the importance of floodplain hydrologic connectivity, in shaping OC and nutrient retention. Hydrologic connectivity between the river and floodplain combined with flow variability (Poff et al., 1997) is critical if river-floodplain systems are to provide the ecosystem services (e.g., water filtration, hydrologic buffering) society often desires. Too often, however, upstream flow regulation (i.e., dams) coupled with lateral confinement (i.e., levees) does not allow for the episodic connections necessary to maintain river-floodplain dynamism and associated benefits.

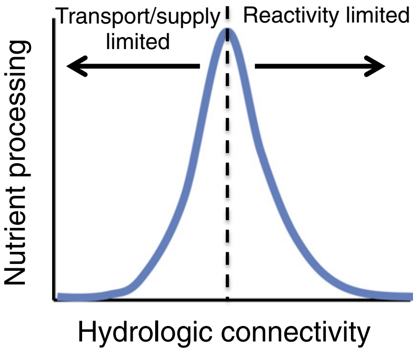


Fig. 5. Conceptual relationship between hydrologic connectivity, resource supply, biological reactivity, and resultant nutrient processing. In this hypothetical representation, nutrient processing is maximized as an optimization between supply (transport) and reactivity.

Despite the recognized benefits of river-floodplain connectivity, these connections have been severed in many landscapes, and rivers and floodplains often become disconnected as a consequence of a number of scenarios (Kondolf et al., 2006). For instance, many systems require high flow events with overbank flooding to transport sediment, maintain high GW levels, and sustain floodplain surface-water bodies (Junk et al., 1989). However, flow regulation (i.e., upstream dams, reservoirs, and diversions) has made flows of this magnitude increasingly unlikely in many locations. In addition to a general lack of flow variability, many large rivers have become constrained by a series of levees intended to protect nearby cities from potential flooding (Kondolf et al., 2006). Minimized flow variability and channelization combine to create a positive feedback, and the likelihood of the river reconnecting to the floodplain becomes increasingly improbable. The disconnection from floodplains is not unique to large rivers. Historic land-use and the prevalence of mill dams along the eastern seaboard of the U.S. has altered these historically branching stream networks with expansive riparian wetlands to the single-threaded channel form familiar today (Walter and Merritts, 2008). In many small streams of the Rocky Mountains U.S., land and water management has led to stream incision and disconnection from valley floodplains (Wohl and Beckman, 2014). Disconnecting rivers and floodplains can lead to a loss of retention capacity and can have strong implications for the down-network transport of water, sediment, organic material, and nutrients (Alexander et al., 2009; Powers et al., 2012; Wohl and Beckman, 2014; Wollheim et al., 2008b).

2.4. Longitudinal connectivity

The downstream flow of water is a defining feature of lotic systems. Connections from upstream (headwater) to downstream (lowland river network) facilitate the movement of mass, energy, and organisms along channel networks. After water and associated material are loaded to the channel network via lateral connections from hillslopes, downstream advection dominates. However, there is transient storage (in-channel and subsurface) and more long-lasting retention due to exchange with deeper GW systems and considerable work has highlighted that the *stream is not a pipe* (sensu, Bencala, 2011). This comment applies to natural streams, which indeed do not operate like pipes; but man-made canals and channelized streams and rivers often do. These man-made systems serve largely as conveyance structures and represent extreme examples on the high end of the connectivity spectrum (Fig. 6). On the other extreme end of the longitudinal connectivity spectrum is the influence of man-made dams, which disconnect upstream from downstream. Dams create abrupt disruptions in the continuum of river morphology (Christiansson, 1979) and have strong impacts on river flow, sediment transport, water temperature, and the movement of organisms (Kinsolving and Bain, 1993; Poff et al., 1997; Schmidt and Wilcock, 2008; Sethi et al., 2004; Vinson, 2001). Accordingly, human alteration of hydrologic systems has strongly increased *and* decreased longitudinal hydrologic connectivity, and natural streams and rivers occupy some intermediate space on this continuum (Fig. 6).

Longitudinal hydrologic connections, from upstream to downstream, are likely the easiest to conceptualize of the three spatial dimensions, and the unidirectional flow of water has been noted as the *defining feature of streams* (Webster and Patten, 1979). As a consequence of unidirectional flow, streams and rivers supply nutrients to downstream communities and upstream migration is minimal from a nutrient budget perspective, although upstream fish migration is an exception (Webster and Patten, 1979). In this way upstream inefficiencies fuel downstream productivity. In the Midwestern region of the United States, high levels of agricultural fertilizer application has led to enhanced loading of nutrients (e.g., N) to streams and rivers draining the landscape (Dubrovsky et al., 2010). This loading occurs along lateral hydrologic connections via overland flow, GW flow, or subsurface flow through tile drains. As N concentrations in the stream network increase, the efficiency with which the aquatic ecosystem retains N decreases (Covino et al., 2012), and the system becomes *leaky* with respect to that nutrient (Dodds et al., 2002; Mulholland et al., 2002). The unfortunate result of this progression is that as the system becomes increasingly inefficient it retains a decreasing fraction of an increasing load. Ultimately, down-network communities are left with the responsibility of managing upstream inefficiencies. Because lateral and longitudinal transport are essentially inseparable, understanding OC and nutrient retention along each of these dimensions and deciphering the roles of hydrologic connectivity and concentration in determining down-network transport is important to the maintenance (or restoration) of aquatic ecosystems (Rains et al., 2015).

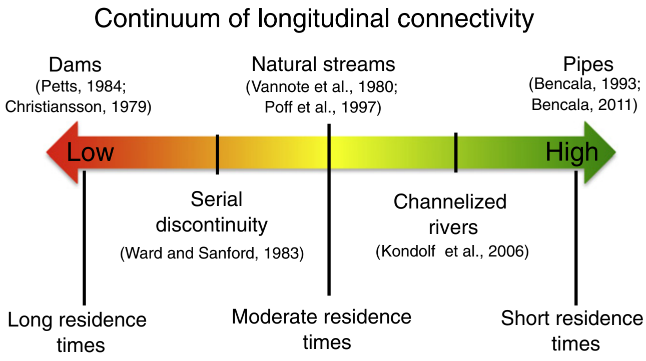


Fig. 6. Representation of the continuum of longitudinal hydrologic connectivity. Dams disconnect upstream from downstream, and occupy the low connectivity portion of the spectrum. Conversely, pipes and canals increase connections between up- and downstream locations and occupy the high connectivity portion of the spectrum. Natural streams occupy some intermediate space between these two extremes, and human alteration of hydrologic systems can push natural streams in either direction (higher or lower connectivity). The alternating sequence of lotic and lentic systems described in the serial discontinuity concept represents a movement toward lower connectivity, while channelized rivers increase longitudinal hydrologic connectivity relative to natural streams. These varying degrees of hydrologic connectivity influence hydrologic residence times, with water in pipes and canals having short residence times and water in reservoirs behind dams having much longer residence times.

Nutrient spiraling theory describes the way in which coupled physical and biological processes control nutrient transport control downstream nutrient transport (Wallace et al., 1977; Webster, 1975; Webster and Patten, 1979). This process is referred to as spiraling because nutrient cycling in fluvial systems does not occur in place; instead, nutrients travel down the network as they cycle through dissolved, particulate, and consumer compartments (Fig. 7). Prior to the development of nutrient spiraling theory, the 'downhill flow of nutrients from the hills to the sea' had been conceptualized as a *rolling motion* (Leopold, 1941). In rivers, however, because nutrients exchange between compartments while simultaneously moving downstream, their pathway can be conceptualized as an imaginary spiral (Fig. 7, Newbold et al., 1981, 1982, 1983; Webster and Patten, 1979). The average longitudinal distance required to complete one spiral is the total spiraling length (S). The total spiraling length is composed of three subcomponents: (i) the average distance traveled in dissolved form before being taken up, generally called the uptake length (S_w); (ii) the average distance traveled in the particulate form (S_p); and (iii) the distance traveled in the consumer compartment (S_c; Newbold et al., 1981, 1982). In part because S_w is generally easier to measure than S_p and S_c, the bulk of nutrient spiraling research has focused on determining S_w. Within a particular stream or river, S_w generally increases as a function of stream discharge (Peterson et al., 2001; Wollheim et al., 2001) and in-stream nutrient concentration (Earl et al., 2006; Earl et al., 2007; Mulholland et al., 2002). There are physical and biological reasons why this occurs. The first physical consideration is that as discharge increases, velocity increases, residence time decreases, and nutrients are advected farther downstream before being taken up. A second physical consideration has to do with the magnitude of interactions between nutrients in the water column and the streambed. In smaller streams it is well accepted that the majority of nutrient uptake occurs on the streambed and in the hyporheic zone (although this is debatable for larger river systems). At high stage, interactions and contact between dissolved nutrients, the channel bed, and the hyporheic zone decrease because of decreased residence time and as a function of the ratio of channel volume to bed area (Fig. 7). From a theoretical perspective, nutrient uptake should decrease as residence time shortens, but as previously noted this has not been clearly demonstrated, in part because of the multiple constraints on nutrient processing. In addition to hydrologic considerations, in-stream nutrient concentration has a strong influence on the length of nutrient spirals and S_w (Fig. 7). This is because biological uptake efficiency decreases as concentration increases and, in turn, the nutrient of concern is transported greater distances downstream within each spiral (i.e., longer uptake length, Fig. 7). While other environmental variables influence biological uptake efficiency and associated uptake lengths (e.g., temperature, light), physical transport dynamics, residence time, biological demand, and nutrient supply are generally accepted as being first order controls on downstream nutrient transport.

Humans have had strong influences on the key controls (i.e., hydrologic connectivity, transient storage, nutrient loading) over longitudinal OC and nutrient transport. These human alterations of longitudinal connectivity involve increasing (e.g., channelization) *and* decreasing (e.g., large dams) hydrologic connections and associated residence times. Increased connectivity is generally related to channel simplification or to decreasing physical complexity in stream and river networks. This includes removal of wood and beaver dams, reducing channel margin

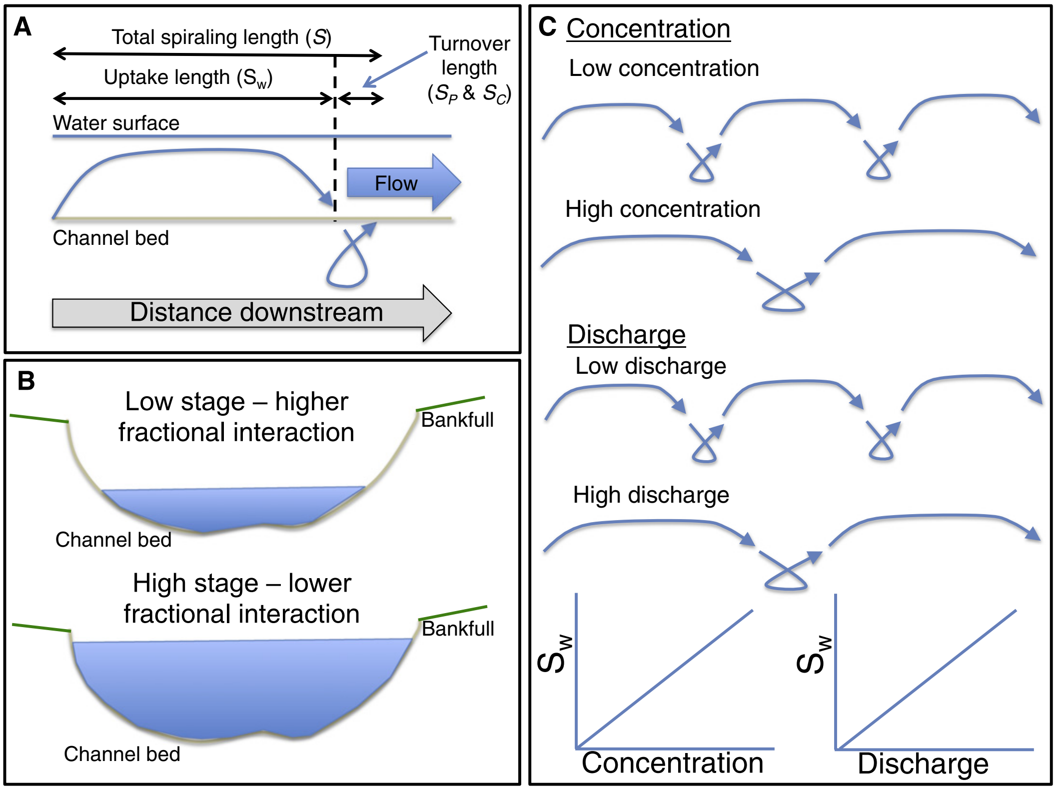


Fig. 7. (A) Description of nutrient spiraling in streams. The total spiraling length (S) is comprised of the uptake length (S_w) and the turnover length (S_p and S_c). S_w is the average length a dissolved nutrient is transported downstream before being taken up. (B) Stream/river stage has important controls on nutrient processing in channel networks. This is because the ratio of channel volume to bed area changes strongly from low to high stage conditions. Accordingly, there is higher fractional interaction between streamwater, the channel bed, and the hyporheic zone during low stage vs. high stage conditions. (C) Both flow conditions and in-stream concentrations have strong influence on downstream nutrient transport. When concentrations are low, nutrients spiral more tightly and are cycled more efficiently. Conversely, when concentrations are high, nutrients are used less efficiently and downstream loading increases as the system becomes “leaky”. Discharge has a similar result with higher downstream loading during higher flow periods. Accordingly, S_w generally increases as a function of both concentration and discharge.

irregularities, disconnecting from secondary channels and floodplains, and river channelization (Wohl and Beckman, 2014). Channel complexity generally increases the exchange of water between the main channel, surface water storage zones (e.g., pools), and subsurface storage areas (hyporheic and GW), which in turn increases transient storage and elongates solute residence times (Ensign and Doyle, 2005). The mixing of different waters (e.g., main channel and GW) in transient storage regions can create favorable biogeochemical conditions that promote high rates of nutrient processing and can enhance channel network nutrient retention (Alexander et al., 2009). However, widespread channel simplification as a consequence of land use (Walter and Merritts, 2008) has altered the transport of sediment, organic material, and nutrients. As features that create channel complexity are lost as a consequence of various land and river management practices, streams and rivers can move from their natural state toward some alternative state (Fig. 6). During this process, the natural retentive capacity of the stream can be either lost or diminished because the physical connections that enhance storage and biogeochemical processing are severed, highlighting the feedback between geomorphic form, physical transport, and biological function. Additionally, chronically high levels of nutrient loading occurring in many urban and agricultural regions exacerbate loss of natural retentive capacities in stream and river networks.

Climate change and/or increased demands on surface and GW sources can lead to increased disconnectivity along stream networks. This can happen as withdrawals or drought cause portions of the network to dry and disconnect up- from downstream. Under such circumstances, greater numbers of temporary disconnections and temporary streams would be expected. Temporary disconnection as a consequence of water diversion, reservoir storage, and GW withdrawal has fragmented habitat and led to decreased native fish biodiversity on the North American Great Plains (Falke et al., 2010). While the influence of temporary disconnections on fish populations has been documented, we currently have little information on the biogeochemical implications of the greater number of temporary streams or increased frequency of disconnection. Given that the majority of previous research on stream biogeochemical fluxes has occurred in perennial streams and the potential for greater numbers of temporary streams and frequency of disconnection in the future, research is needed on the biogeochemistry, hydrology, and geomorphology of temporary streams and intermittently disconnected networks.

2.5. Stream-lake connectivity

Lakes, reservoirs, and ponds interspersed within river networks can have strong influences on the timing, form, and magnitude of down-network organic material and nutrient export. From a physical perspective, the general trend is that transport velocities are lower, residence times are longer, and particulate material settling (sedimentation) is greater in lakes and reservoirs relative to the streams and rivers they are connected to. The biological result of these physical conditions is that biogeochemical processing is enhanced, and lakes and reservoirs can be biogeochemical *hot-spots* within fluvial networks (McClain et al., 2003). Consequently, in-network lakes and reservoirs can impose physical impediments to down-network transport, supporting high biogeochemical processing and transforming nutrient fluxes (Arp and Baker, 2007; Marcarelli and Wurtsbaugh, 2007), which highlights the importance of coupled physical and biological controls on organic material and nutrient transport. Particulate material that settles and is retained in lentic systems includes organic (particulate organic material, POM) and inorganic (sediment) fractions. The POM contains varying stoichiometric ratios of C, N, and P and other biologically important elements, depending on its original source and degree of biological processing along its flowpath. In addition to POM deposition, sediment settling in lakes and reservoirs can deposit C, N, and P that can sorb to charged surfaces (Li et al., 2013; Tanoue and Handa, 1979). This physical retention process is particularly important in relation to P (Wodka et al., 1985) because phosphate (PO_4) readily sorbs to sediment particles (Walker and Syers, 1976), but sedimentation processes can also be important in watershed C and N dynamics (Teodoru et al., 2013). Combined physical and biological processes in lakes and reservoirs can decrease annual fluxes of total N, enhance retention of total P (TP) and total suspended sediment (TSS), and decrease annual variability in TSS and TP export in forested and agricultural watersheds (Powers et al., 2014). Lentic systems have also been shown to decrease intra-annual variability in DOC export (Goodman et al., 2011) and constitute a significant component of the global carbon cycle (Tranvik et al., 2009). Recent inventories have demonstrated that lentic systems dominate the areal extent of continental waters (Downing, 2010), and their influence on nutrient dynamics is being recognized at watershed (Epstein et al., 2013; Jones, 2010), regional (Powers et al., 2014), continental (Bouwman et al., 2013a), and global (Downing, 2010; Tranvik et al., 2009) extents.

3. Interactions across dimensions and scales of connectivity

On average, water originates in the hillslope regions of watersheds and is transported laterally to the channel network via surface or subsurface flow. Hydrologic connections between streams and their contributing hillslopes provide the linkage between the terrestrial and aquatic environment and deliver water, sediment, organic material, and nutrients to the fluvial network. After water and solute entry into the stream network via lateral hydrologic connectivity (generally unidirectional, toward the channel; Table 1), interactions between streams and shallow subsurface flow occurring in the hyporheic zone (bidirectional, vertical, and lateral dimensions; Table 1) have an important role in many biogeochemical processes and down-network (longitudinal) transport (Wondzell, 2011). Hyporheic exchanges are often associated with smaller spatial scales (Harvey et al., 1996), but exist within a larger network of flowpaths where water is exchanged between the stream and valley GW (Woessner, 2000). Hydrologic exchanges between the stream and subsurface environment create a mosaic of physicochemical patches, which provide habitat for a diverse array of organisms (Orghidan, 1959; Stanford and Ward, 1993), and increase system nutrient retention and transformation moving down-network (Bencala, 2011).

River-floodplain hydrologic connectivity is important from biodiversity (Amoros and Bornette, 2002) and nutrient processing (Malard et al., 2002) perspectives. Connections between rivers and floodplains are bidirectional — water can move from the river to the floodplain (high flow) or from the floodplain back to the river, and this bidirectional movement can facilitate the exchange of substantial amounts of water, sediment, organic material, and nutrients between streams/rivers, floodplains, and riparian wetlands. Overbank flooding can create a complex hydrologic network of potential water, sediment, organic material, and nutrient retention zones (Junk et al., 1989) and subsurface pathways can provide ideal conditions for hyporheic/floodplain biota (Ward and Stanford, 1995a). As a consequence of extended residence times, anoxic conditions, and ample supply of OC and nutrients, floodplains can act as *hot-spots* of biogeochemical activity and nutrient removal (Groffman et al., 2009; Naiman and Decamps, 1997; Ocampo et al., 2006a; Roley et al., 2012), but widespread river-floodplain disconnection has decreased this capacity (Kondolf et al., 2006). Unfortunately, in many urban and agricultural regions, lateral loading of nutrients to streams and rivers has increased in part because of fast delivery pathways via impervious surfaces and overland flow in urban areas and via tile drains in agricultural settings. While impervious surfaces and tile drains increase lateral connections *toward* the channel, river-floodplain disconnectivity decreases the *bidirectional* lateral connectivity that can enhance floodplain OC and nutrient retention and increases down-network longitudinal connectivity. Accordingly, nutrient retention capacities are diminished on lateral *and* longitudinal dimensions with little potential to buffer down-network loading.

These examples demonstrate the interconnections of multiple spatial dimensions of hydrologic connectivity and highlight the important point that one cannot be managed or approached in pure isolation of another. While stream-hillslope connections set the initial spatial pattern of DOC and nutrient concentrations across the channel network, hyporheic, stream-GW, and river-floodplain interactions then play a strong role in the downstream transport of those constituents. Ultimately, connections across numerous dimensions and spanning multiple spatial and temporal scales control watershed DOC and nutrient transport. The relative influence of one connection (e.g., stream hillslope) versus another (e.g., hyporheic) in controlling nutrient dynamics can shift through time. Watershed outlet signatures might be strongly dominated by hillslope contributions during wet periods when the upslope portions of the watershed are strongly connected to the channel network, while in-stream, hyporheic, and floodplain retention processes might have stronger relative impact during dry periods. Additionally, human activity has increased *and* decreased lateral and longitudinal hydrologic connections through urbanization (increased lateral, longitudinal), tile drains (increased lateral), levees (decreased lateral, increased longitudinal), channelization (decreased lateral, increased longitudinal), and dams (decreased longitudinal). Given the substantial alteration of hydrologic connections and carbon and nutrient budgets at regional to global scales, an improved understanding of the relationships between hydrologic connectivity and organic material and nutrient transport is necessary for the maintenance or restoration of aquatic ecosystems.

4. Conclusion and outlook

Multiple interacting spatial scales and dimensions of hydrologic connectivity can have strong influences on watershed and fluvial network carbon and nutrient dynamics. To develop an increased understanding of these processes, it will be necessary for field-based investigation to incorporate numerous spatial dimensions and extents, and modeling approaches to incorporate process heterogeneity and feedbacks. There is currently a lack of data at larger river and watershed scales; however, we need not only expand to larger extents but also integrate data and understanding across spatial and temporal scales. A challenge will be to link small spatial (1–10,000 m^2) and temporal (seconds to weeks) scale processes to seasonal and annual patterns observed at watershed or fluvial network extents in order to determine how processes occurring at disparate scales interconnect and feedback on one another. We cannot simply apply techniques developed in smaller stream channels to larger rivers but instead need to fundamentally rethink how to approach field-based inquiry in larger systems. Multidisciplinary efforts should include: geomorphologists, hydrologists, ecologists, engineers, social scientists, and beyond. Restoring river and watershed function in degraded landscapes will not only require cutting-edge science but also integration of societal and economic concerns. Collaborations incorporating field- and modeling-based perspectives have the potential to create new conceptual and numerical models, and generate new hypothetical constructs to test. The challenge ahead will be to develop a comprehensive view of hydrologic connectivity, incorporating interactions and feedbacks across nested scales, and drawing from multidisciplinary perspectives. To address this challenge various needs and opportunities exist, including:

- *Integrating data and understanding across the spatial dimensions of connectivity* (lateral, vertical, and longitudinal). Designing studies that incorporate these numerous components will provide an opportunity to determine how lateral, vertical, and longitudinal dimensions of connectivity link to influence watershed and network-scale patterns. Facilities and programs that help coordinate research efforts (e.g., Critical Zone Observatories, National Ecological Observatory Network) will be pivotal in this effort and should be utilized to enhance collaborative efforts. Additionally, these studies should occur across regions, climates, and land uses to ensure broad process understanding.

- *Developing new methods that are appropriate for larger systems*. Methodological advancements will provide improved process understanding across spatial and temporal scales. Paths forward include using passive, nonmanipulative approaches (e.g., diel signals) to provide data appropriate for larger-scale models as opposed to geometric scaling of small-scale data to larger spatial extents. It will be important to integrate process-based understanding developed from field studies within emerging models and, in turn, to use modeling to identify gaps in process understanding and guide field campaigns.
- *Evaluating feedbacks across temporal scales*. Similar to integration across spatial scales, increased understanding of processes and interactions across temporal scales will provide an opportunity to understand how processes occurring at short temporal scales (seconds to days/weeks) are linked to, or disconnected from, dynamics at seasonal (months to years) to geomorphic (years to millennia) time scales. This opportunity can be addressed through collaborations among scientists working at relatively short (e.g., hydrologists) and longer (e.g., geomorphologists and geologists) temporal scales and through collaborations between field- and modeling-based scientists.
- *Integrating across dimensions, scales, and disciplines*. This integrated and collaborative approach will allow scientists to address foundational questions across disciplines, such as: *How does geologic/geomorphic history influence contemporary patterns of hydrologic connectivity and associated ecosystem dynamics?*; and, *How do contemporary hydrologic connectivity and ecosystem dynamics in turn shape future landscape evolution?*

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