



RESEARCH ARTICLE

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Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism

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Key Points:

- Mountainous rivers frequently alternate between steep, narrow valleys and low-gradient, wide valley bottoms
- Along wide valley bottoms, beaver-mediated lateral hydrologic connectivity across the floodplain can enhance biogeochemical processing
- Determining the cumulative effects of river-floodplain disconnection is a critical next step in restoring function in altered river networks

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Abstract River networks that drain mountain landscapes alternate between narrow and wide valley segments. Within the wide segments, beaver activity can facilitate the development and maintenance of complex, multithread planform. Because the narrow segments have limited ability to retain water, carbon, and nutrients, the wide, multithread segments are likely important locations of retention. We evaluated hydrologic dynamics, nutrient flux, and aquatic ecosystem metabolism along two adjacent segments of a river network in the Rocky Mountains, Colorado: (1) a wide, multithread segment with beaver activity; and (2) an adjacent (directly upstream) narrow, single-thread segment without beaver activity. We used a mass balance approach to determine the water, carbon, and nutrient source-sink behavior of each river segment across a range of flows. While the single-thread segment was consistently a source of water, carbon, and nitrogen, the beaver impacted multithread segment exhibited variable source-sink dynamics as a function of flow. Specifically, the multithread segment was a sink for water, carbon, and nutrients during high flows, and subsequently became a source as flows decreased. Shifts in river-floodplain hydrologic connectivity across flows related to higher and more variable aquatic ecosystem metabolism rates along the multithread relative to the single-thread segment. Our data suggest that beaver activity in wide valleys can create a physically complex hydrologic environment that can enhance hydrologic and biogeochemical buffering, and promote high rates of aquatic ecosystem metabolism. Given the widespread removal of beaver, determining the cumulative effects of these changes is a critical next step in restoring function in altered river networks.

1. Introduction

River networks in mountainous catchments predominantly flow through steep, narrow valleys occasionally interspersed by low-gradient, wide valleys [Stanford and Ward, 1993]. Along these wider valley bottoms, beaver (*Castor canadensis*) activity in the form of beaver dams can create stable, multithread systems [Polvi and Wohl, 2013] with enhanced lateral hydrologic connectivity [Burchsted et al., 2010]. Here we consider lateral hydrologic connectivity as the movement of water and solutes between the river, floodplain, and riparian areas via surface [Junk et al., 1989] or subsurface [Tockner et al., 2000] flow paths. Beaver dams can hold large volumes of water in ponds [Butler and Malanson, 1995; Hood and Bayley, 2008] and expand riparian wetlands and water tables [Remillard et al., 1987; Cunningham et al., 2007], creating wet valley bottom meadows. Lateral connections across wet valley bottoms create a complex mosaic of surface (side-channels, ponds, marshes) and subsurface (hyporheic, groundwater) aquatic habitat types [Johnston and Naiman, 1990], with benefits from water quality and quantity perspectives. Although beaver activity in broad valleys of mountainous river networks can create complex physical environments that in turn buffer hydrologic and biogeochemical fluxes, we currently lack a quantitative understanding of these processes.

Lateral hydrologic connections between the river, floodplain, and riparian areas have the potential to enhance water, carbon, and nutrient retention in low-gradient, wide valley segments. These hydrologic connections are promoted by obstructions to channel flow such as logjams and beaver dams [Wohl and Beckman, 2014], which increase the magnitude, duration, and frequency of overbank flow [Westbrook et al., 2006]. Water, carbon, and nutrients that are distributed across the floodplain during high flows can subsequently be released during low flow conditions [Mertes, 1997], effectively attenuating water and solute fluxes [Hey et al., 2012]. Hydrologic connections across the floodplain can also promote high aquatic

ecosystem metabolism and biogeochemical processing by linking nutrient (e.g., nitrogen, N; phosphorous, P) and organic matter sinks and sources [Powers *et al.*, 2012]. Following resource delivery during high flows, elongated hydrologic residence times within floodplain surface and subsurface locations can enhance nutrient and organic matter processing rates and retention [Powers *et al.*, 2012]. While river-floodplain systems of wide valley segments may be important to water, carbon, and nutrient retention, they have also been disproportionately altered by human practices including mining, beaver trapping, grazing, and flow regulation [Wohl, 2001]. These landscape alterations have commonly led to hydrologic disconnection between the river and floodplain (i.e., lack of overbank flow) and presumably loss of retention capacity in altered systems. In montane regions, for instance, fluvial incision and hydrologic disconnection because of loss of beaver dams is hypothesized to be a primary cause of widespread drying of wet meadow valley bottoms [Marston, 1994].

Within mountainous river networks, the alternating valley morphology between narrow (low lateral connectivity) and wide (dynamic lateral connectivity) segments forms the so-called “beads on a string,” where the wide segments represent the beads and the narrow segments the string [Stanford *et al.*, 1996]. While these alterations provide an excellent opportunity to investigate the effects of beaver activity, valley width, and lateral hydrologic connectivity on water, carbon, and nutrient flux and aquatic ecosystem metabolism, few studies have evaluated these linkages at the river segment or greater (e.g., network) scale [but see, Bellmore and Baxter, 2014].

The primary goal of this research was to determine the relationships between: (1) lateral (river-riparian-floodplain) hydrologic connectivity; (2) water, nutrient, and carbon fluxes; and, (3) aquatic ecosystem metabolism along a low-gradient, wide valley bottom segment with beaver activity, and an adjacent (directly upstream) steeper, narrower valley segment without beaver in North Saint Vrain Creek, Rocky Mountain National Park, Colorado, USA (Figure 1). To address the overarching goals of this study, we ask the following questions:

1. How do water, nitrogen, and carbon fluxes vary between longitudinally adjacent river segments of varying valley width, beaver activity, and channel planform?

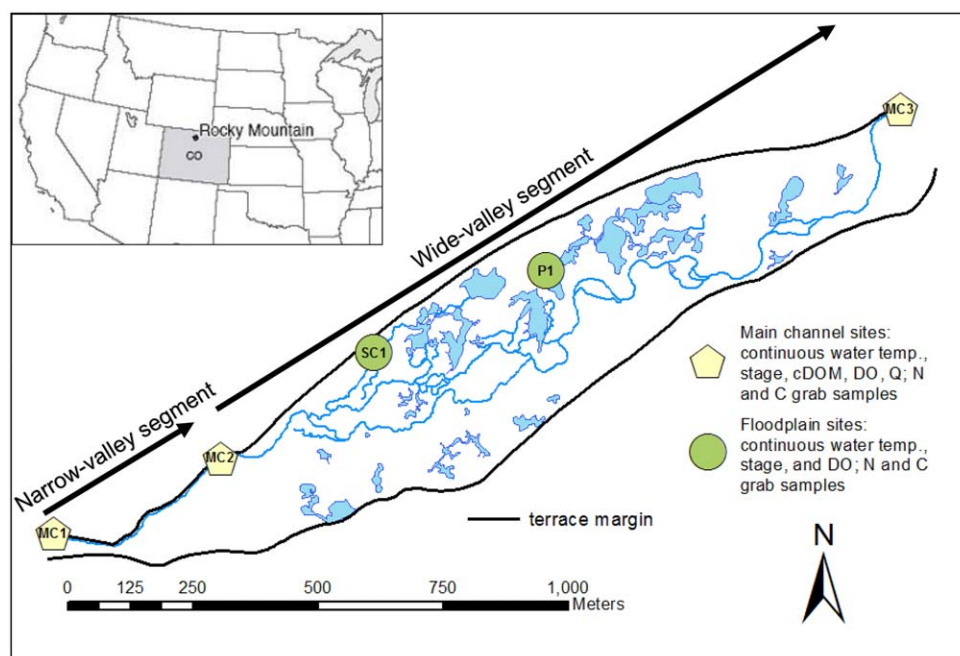


Figure 1. The single-thread segment without beaver activity (“narrow-valley”) and multithreaded segment with beaver activity (“wide-valley”) of North Saint Vrain Creek in Rocky Mountain National Park, CO with top-left insert showing location in the U.S. We present data from three main channel sites (MC1, MC2, and MC3), a side-channel (SC1), and an off-channel beaver pond (P1). MC1 and MC2 bracket the narrow-valley segment, and MC2 and MC3 bracket the wide-valley segment.

2. How does aquatic ecosystem metabolism and associated nutrient processing vary as a function of flow state and lateral hydrologic connectivity in adjacent river segments with and without beaver activity?

2. Methods

2.1. Study Site

We conducted this research in the 84 km² Wild Basin, located in the southeast corner of Rocky Mountain National Park, CO (40°13'N, 105°32'W) from May to October 2015 (Figure 1). Wild Basin contains variable forest stand ages, including several old-growth stands in which trees germinated prior to 1654 A.D. [Sibold *et al.*, 2006]. Upland vegetation consists of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*), and valley bottom vegetation consists of quaking aspen (*Populus tremuloides*), dense stands of willow (*Salix* spp.) and other woody riparian shrubs. Mean annual temperature is 5°C, with a winter average of −4°C and summer average of 14°C for the 27 years of recorded temperature data (1988–2015) (Copeland Lake snowpack telemetry, SNOTEL, #412, 2620 m elevation located within Wild Basin). Mean annual and mean summer temperature during the 2015 study period were typical relative to historic values (6°C and 15°C, respectively), while the mean winter temperature was warmer than historic values at −1°C. Annual precipitation averaged 861 mm for 30 years (1985–2015), with 52% (451 mm) in the form of snowfall. There was slightly less precipitation in 2015 than average (813 mm), although the distribution of precipitation was skewed toward winter precipitation with 64% (519 mm) in the form of snowfall (SNOTEL, #412). There is a strong elevation gradient in precipitation and snow totals, with intermittent snow typical at the Copeland Lake SNOTEL site and a persistent snowpack typical at higher elevations, extending from 29 October to 5 June in 2015 (Wild Basin SNOTEL, #1042, 2914 m).

Wild Basin is drained by North Saint Vrain Creek, which flows east from the Continental Divide at 4046 to 1945 m at the base of the Rockies. The North Saint Vrain Creek hydrograph is dominated by seasonal snowmelt, with peak annual discharge typically in June and base flow typically from August to April. We conducted fieldwork on two river segments in North Saint Vrain Creek: (1) a nonbeaver impacted segment with a single-thread channel and limited riparian and floodplain area; and, (2) a beaver impacted segment with a multithread network with side-channels, ponds, and extensive floodplain, and riparian wetlands (Figure 1). The study segments are located above a Pleistocene terminal moraine and overlie Precambrian-age Silver Plume Granite [Braddock and Cole, 1990]. Hereafter, we refer to the nonbeaver impacted segment as “narrow-valley” and the beaver impacted segment as “wide-valley.” Along the wide-valley segment, beaver dams within side-channels and backwaters impound large volumes of water upstream. These dams are frequently breached, rebuilt, relocated, or abandoned, resulting in a physically complex template of floodplain aquatic habitats including overflow side-channels, relic side-channels, backwater ponds, and shallow open-water marshes that are often interconnected by a network of beaver-excavated canals. Floodplain aquatic habitats are fed by river water, groundwater from river infiltration, or groundwater from hillslope sources, and the relative contributions of water sources likely depend on proximity to the main channel (reviewed in Bush and Wissinger [2016]) as well as local and surrounding topography and seasonal hydrology [Bornette *et al.*, 1998]. Hydrologic connections between these habitats are highest during early summer snowmelt, and decrease as the hydrograph recedes; the water table declines, and many side-channels, ponds, and wetlands become dry.

We define two classifications of monitoring sites: (1) main channel monitoring sites; and, (2) floodplain water-body sites. We present data from three main channel monitoring sites, which we call main channel 1 (MC1), main channel 2 (MC2), and main channel 3 (MC3). The narrow-valley segment is bracketed by MC1 and MC2, and the wide-valley segment is bracketed by MC2 and MC3 (Figure 1). At main channel monitoring sites, we monitored stream stage, water temperature, dissolved oxygen, and colored dissolved organic matter (cDOM) at 15 min intervals. Colored dissolved organic matter refers to the portion of dissolved organic matter that contains chromophores that absorb UV and visible light, and fluoresce after light absorption. Additionally, we collected grab samples at MC1, MC2, and MC3 approximately once every other week to analyze for nutrients and major cations and anions.

Floodplain water-body sites include a side-channel (SC1) and an off-channel beaver pond (P1), both of which are located along the wide-valley segment (Figure 1). At SC1 and P1, we monitored stage, water

temperature, and dissolved oxygen at 15 min intervals to evaluate connectivity with the main channel and quantify aquatic ecosystem metabolism, and collected grab samples approximately once every other week to analyze for carbon, nutrients, and major anions and cations. The side-channel SC1 has relic and partially breached beaver dams, which create areas of backwater and promote hydrologic spreading. During snow-melt, SC1 is connected by surface water with the main channel and is lotic (i.e., flowing). As the hydrograph recedes, SC1 loses surface connection with the main channel and transitions from a lotic to lentic (i.e., not flowing) environment. In contrast, P1 has an active beaver lodge, is surrounded by the greatest density of dams, and has consistent water levels from high to low flows. We present aquatic ecosystem metabolism data from SC1 and P1 because they represent illustrative end-members for investigating relationships between aquatic ecosystem metabolism and variable (SC1, lotic to lentic) or more static (P1, lentic only) hydrology and hydrologic character.

2.2. Stream Discharge and Hydrologic Fluxes

At main channel and floodplain water-body sites, we recorded stream stage and temperature at 15 min intervals using capacitance rods (TruTrack Inc., Christchurch, New Zealand) with ±1 mm precision for water level and 0.1°C precision for temperature. At main channel sites, we measured discharge on a weekly basis from high to low flows using velocity-area [Dingman, 2002] or dilution gauging [Kilpatrick and Cobb, 1985] approaches. During dilution gauging, we instantaneously injected dissolved sodium chloride (NaCl) at a sufficient mixing length (50–75 m) upstream of the measurement site. We measured stream water-specific conductivity (SC) using CS547A conductivity and temperature probes (Campbell Scientific Inc., CS547A, Logan, UT) connected to CR1000 data loggers (Campbell Scientific Inc., CR1000), recording at 2 s intervals prior to the injection of NaCl to determine background SC, through the arrival of NaCl (i.e., the breakthrough curve), and after the stream returned to background conditions. We converted SC to NaCl concentrations using an empirical calibration, and calculated discharge from the breakthrough curve using equation (1):

$$Discharge = \frac{NaCl_{MA}}{\int_0^t NaCl_C(t) dt} \tag{1}$$

where $NaCl_{MA}$ is the mass of NaCl added to the stream and $NaCl_C$ is the background corrected NaCl concentration. Using weekly discharge data, we developed rating curves between stage and discharge to transform continuous stage data to a continuous discharge time series. We calculated daily and cumulative water fluxes for the narrow-valley and wide-valley river segments. The narrow-valley segment balance was

calculated as the difference between daily mean discharge measured at MC2 and MC1, and the wide-valley segment balance was calculated as the difference between daily mean discharge measured at MC3 and MC2 (Figure 1). Hydrologic fluxes for each segment were divided by segment valley length (Table 1) to standardize results for comparison.

Hydrologic fluxes at MC1, MC2, and MC3 are precise within ±13% using the root mean square propagation method [Topping, 1972] as shown in equation (2):

$$E_p = \sqrt{\sum_{i=1}^n (E_i^2 + E_2^2 + E_3^2 + \dots + E_n^2)} \tag{2}$$

where E_p is the total probable range in error (±%), n is the total number of sources of error, and E_1, E_2, E_3, E_n are potential sources of error (±%). Potential sources of error include individual velocity-area measurements, the

Table 1. Physical Characteristics for the Nonbeaver Impacted ("Narrow-Valley") and Beaver Impacted ("Wide-Valley") Segments of North Saint Vrain Creek in Wild Basin, Rocky Mountain National Park, Colorado

	Narrow-Valley Segment	Wide-Valley Segment
Catchment area at segment outlet (km ²)	82	84
Channel planform	Single-thread	Multithread
Average elevation (m)	2560	2050
Average floodplain width (m)	97	254
Valley length (m)	390	1540
Main channel length (m)	400	2100
Average main channel width (m)	9.4	8.0
Gradient (%)	2.5	0.7
Confinement	Confined ^a / Unconfined ^b	Unconfined ^a / Unconfined ^b
Morphology	Pool-riffle	Pool-riffle

^aConfinement as defined by Brierley and Fryirs [2005], in which a channel is confined if >90% of the channel length contacts a confining feature (i.e., terrace) and unconfined if <10% of the channel length contacts a confining feature.

^bConfinement as defined by the ratio of channel width to floodplain width, in which a channel is confined if the floodplain width is less than twice the channel width, and unconfined if the floodplain width is over 8 times the channel width.

Table 2. Precision in Streamflow, Dissolved Organic Carbon (DOC), and Total Dissolved Nitrogen (TDN) Measurements

	Precision	Reference
Streamflow Measurements		
Velocity-area method measuring velocity at 0.6 depth	± 8.5%	<i>Sauer and Meyer [1992]</i>
Stage-discharge relationship for a stable-channel with stable control, and 8–12 measurements per year	± 10%	<i>Slade [2004]</i>
Continuous stage using TruTrack Inc. capacitance rods	± 1%	TruTrack Inc., Auckland, New Zealand
Carbon and Nitrogen Concentrations		
Shimadzu TOC-V Combustion Analyzer (DOC)	± 0.05 mg L ⁻¹ for values < 1.0 mg L ⁻¹ ; ± 5% for values > 1.0 mg L ⁻¹	<i>Pierson et al. [2016]</i>
Shimadzu TOC-V Combustion Analyzer (TDN)	± 0.01 mg L ⁻¹ for values < 0.2 mg L ⁻¹ ; ± 5% for values > 0.2 mg L ⁻¹	<i>Pierson et al. [2016]</i>
Total Precision for Water, Carbon, and Nutrient Flux Measurements at MC1, MC2, and MC3		
	Water ± 13%	
	DOC ± 14%	
	TDN ± 14–18%	

stage-discharge relationship, and continuous stage measurements [*Harmel et al., 2006*]. For these three categories, we referenced precision values for cases that best matched the conditions of our study (Table 2).

2.3. Dissolved Nutrient Concentrations and Fluxes

We collected grab samples approximately once every other week at the three main channel sites, MC1, MC2, and MC3, and floodplain sites SC1 and P1 to analyze for carbon, nutrients, and major cations and anions. Water samples were field filtered through 0.7 μm glass fiber filters (GF/F Whatman International, Ltd., Maidstone, UK) into acid-washed and stream-rinsed 125 mL high-density polyethylene bottles, placed in a dark cooler, and frozen until analysis. All samples were analyzed at the Rocky Mountain Research Station in Fort Collins [*Pierson et al., 2016*]. Phosphate (PO₄) and nitrate (NO₃) concentrations were analyzed using a Dionex ICS-3000 Ion Chromatograph, with ± 0.005 mg L⁻¹ precision for PO₄ and NO₃ concentrations below 0.1 mg L⁻¹ and ± 5% precision for values above 0.1 mg L⁻¹. Ammonium (NH₄) concentrations were analyzed using a Waters 580 Ion Chromatograph with ± 0.015 mg L⁻¹ precision for concentrations less than 0.15 mg L⁻¹ and ± 10% precision for values greater than 0.15 mg L⁻¹. Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) concentrations were analyzed using a Shimadzu TOC-V Combustion, with ± 0.01 mg L⁻¹ precision for TDN concentrations below 0.2 mg L⁻¹ and ± 5% precision for values above 0.2 mg L⁻¹, and ± 0.05 mg L⁻¹ precision for DOC concentrations below 1 mg L⁻¹ and ± 5% precision for values above 1 mg L⁻¹. Dissolved organic nitrogen (DON) concentrations were calculated as the difference between TDN and dissolved inorganic nitrogen (NH₄-N and NO₃-N).

We monitored colored dissolved organic matter (cDOM) at 15 min intervals using in situ optical cDOM fluorometers (Turner Designs Inc., Cyclops-7, San Jose, CA) shielded against light and wired to a CR1000 Campbell Scientific data logger. Each cDOM fluorometer was calibrated using Quinine Sulfate solution ($r^2 > 0.99$) prior to deployment. Dissolved organic carbon measured from weekly grab samples were strongly correlated with simultaneous cDOM values ($r^2 = 0.98$, $n = 32$, Figure 2). Using the empirically derived relationship in equation (3):

$$[DOC] = 35.20 [cDOM]^{0.98} \quad (3)$$

We transformed cDOM data to continuous DOC to calculate daily DOC fluxes at the main channel sites and daily and cumulative flux balances for the narrow-valley and wide-valley segments.

To calculate daily carbon and nitrogen fluxes along the main channel, we multiplied solute concentrations by daily mean discharge at each main channel site. For nitrogen (NO₃-N, DON, and NH₄-N) fluxes, we used grab sample data and for carbon (DOC) fluxes, we used daily mean DOC concentrations from the 15 min time series data. Narrow-valley segment balances were calculated as the difference between fluxes derived at MC2 and MC1 (Figure 1), and wide-valley segment balances were calculated as the difference between fluxes derived at MC3 and MC2 (Figure 1). Like the hydrologic flux balances, carbon and nitrogen flux balances were divided by segment valley length (Table 1) to standardize results. At MC1, MC2, and MC3, carbon

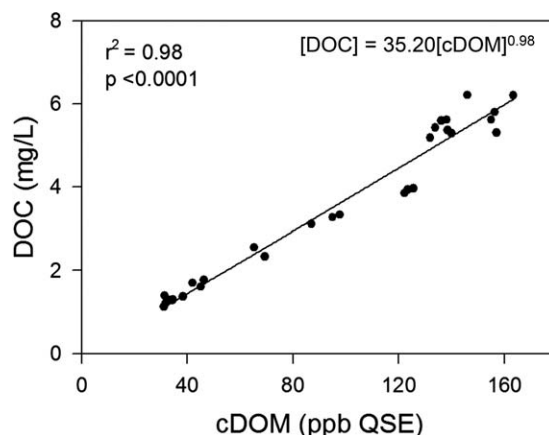


Figure 2. Relationship between dissolved organic carbon (DOC) analyzed from grab samples and simultaneous measurements of colored dissolved organic matter (cDOM) from Turner Designs Inc. Cyclops 7 sensors ($n = 32$). This relationship was used to transform continuous cDOM measurements to a continuous DOC time series at MC1, MC2, and MC3.

fluxes are precise within $\pm 14\%$, and nitrogen fluxes are precise within $\pm 14\text{--}18\%$. Precision values were calculated by propagating instrument and hydrologic flux uncertainty (Table 2) using the root-mean-square error propagation method shown in equation (2).

2.4. Estimating Aquatic Ecosystem Metabolism From Diurnal Dissolved Oxygen Curves

We calculated daily gross primary production (GPP; $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and daily ecosystem aerobic respiration (ER; $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) at main channel sites MC2 (narrow-valley outflow) and MC3 (wide-valley outflow), and floodplain sites SC1 and P1 using the open-channel, single-station diurnal dissolved oxygen (DO) change method [Odum, 1956]. The single-station diurnal DO change method integrates hyporheic, benthic, and water column metabolism over large spatial scales [Bott et al., 1978]. In the main channel, we

measured DO concentrations and water temperatures at 15 min intervals from 1 May to 28 September using Ponsel optical DO sensors (Fondriest Environmental Inc., Ponsel Digisens, Fairborn, OH). At SC1 and P1, we measured DO concentrations and water temperature at 15 min intervals from 9 June to 28 September using MiniDOT optical DO sensors (Precision Measurement Engineering Inc. MiniDOT, Vista, CA). Using the hourly rate of change in DO concentrations, we calculated GPP and ER with equation (4):

$$\Delta DO = GPP - ER + E \quad (4)$$

where E represents the net exchange of oxygen with the atmosphere between consecutive measurements. We calculated the exchange of oxygen with the atmosphere by multiplying the average DO saturation deficit or excess with the reaeration rates determined for each study reach for each time step. Reaeration rates are predominantly a function of stream velocity in lotic sites and a function of wind velocity in lentic sites. For lotic sites MC2, MC3, and SC1, we calculated hourly reaeration rates using the surface renewal model [Owens, 1974], which first calculates a mass transfer coefficient (f) by equation (5):

$$f_{(20^\circ\text{C})} = 50.8 * V^{0.67} * H^{-0.85} \quad (5)$$

where $f_{(20^\circ\text{C})}$ represents the mass transfer coefficient at 20°C (cm/h), V the velocity of stream flow (cm/s), and H the mean depth (cm). We used real-time stage data to obtain H , and developed rating curves between H , width (w), and Q to transform H to V (Q/w) to calculate hourly $f_{(20^\circ\text{C})}$. We adjusted $f_{(20^\circ\text{C})}$ to the stream water temperature following equation (6) [Elmore and West, 1961]:

$$f_{(t^\circ\text{C})} = f_{20^\circ\text{C}} * 1.024^{(t-20)} \quad (6)$$

where t represents water temperature ($^\circ\text{C}$), and divided by H to generate reaeration coefficients (k , h^{-1}) at each time step. To calculate reaeration coefficients at P1, we used empirically derived equation (7) [Boyd and Teichert-Coddington, 1992]:

$$k_{(20^\circ\text{C})} = 0.017X - 0.014 \quad (7)$$

where k is the reaeration coefficient at standard temperature (h^{-1}) and X is wind speed at 3 m height (m s^{-1}). We calculated reaeration coefficients at P1 for low wind (0.8 m s^{-1}) and high wind (4.5 m s^{-1}) scenarios. The low wind velocity was determined as an average calculated coefficient for a sheltered and stagnant pond [Boyd and Teichert-Coddington, 1992], and the high wind scenario was chosen as the highest wind velocity value for which equation (7) can be reliably applied, 4.5 m s^{-1} [Boyd and Teichert-Coddington, 1992]. We found that there was little difference in the calculated metabolism metrics for each wind speed. Because the pond was sheltered by the wind from willows, we used the low wind value for our analyses. At

Table 3. Summary (Mean \pm SD) of Temperature ($^{\circ}\text{C}$), Runoff (mm d^{-1}), and Discharge ($\text{m}^3 \text{s}^{-1}$) Data at Main Channel Sites MC1, MC2, and MC3, a Floodplain Side-Channel (SC1), and Pond (P1)^a

	MC1	MC2	MC3	SC1	P1
Temperature ($^{\circ}\text{C}$)	7.4 ± 3.4	7.7 ± 3.4	8.4 ± 3.6	9.8 ± 5.9	10.4 ± 3.7
Runoff (mm d^{-1})	2.1 ± 1.5	2.2 ± 1.8	2.4 ± 1.3		
Discharge ($\text{m}^3 \text{s}^{-1}$)	2.0 ± 1.4	2.1 ± 1.7	2.3 ± 1.3		

^aThe nonbeaver impacted segment is bracketed by MC1 and MC2, and the beaver impacted segment is bracketed by MC2 and MC3. Data are from May to October 2015.

each site, we corrected hourly rates of DO change by the hourly rates of the net exchange of oxygen with the atmosphere.

To calculate ER, we averaged the corrected hourly rates of DO change from postsunset to presunrise, and multiplied the average by 24 h in the day. We assume that during darkness, GPP is equal to 0 and any change in the rate of reaeration-corrected DO is due to ER. We calculated daily GPP by integrating the difference between the hourly rates of DO change and the average hourly nighttime rates of DO change over the photoperiod. Daily net ecosystem production (NEP) was calculated as the difference between daily GPP and the absolute value of daily ER.

3. Results

3.1. Stream Discharge, Hydrologic Fluxes, and Connectivity

Water temperature in the main channel increased slightly with downstream distance, with an average (\pm standard deviation) of $7.4 \pm 3.4^{\circ}\text{C}$ at MC1, $7.7 \pm 3.4^{\circ}\text{C}$ at MC2, and $8.4 \pm 3.6^{\circ}\text{C}$ at MC3 over the monitoring period (Table 3). Combined for all three main channel sites, the minimum recorded water temperature was 0.5°C on 10 May and the maximum recorded water temperature was 14.4°C on 15 August.

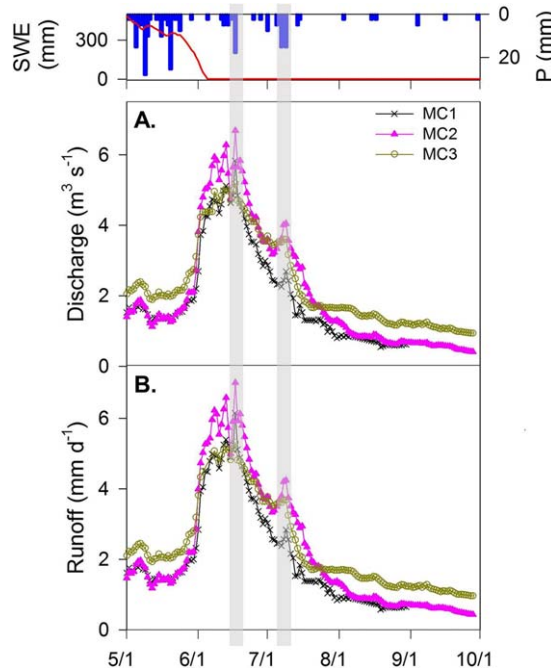


Figure 3. Precipitation (P) and snow water equivalent (SWE) with (a) volumetric daily mean discharge and (b) area-normalized daily mean runoff at main channel sites MC1, MC2, and MC3. The nonbeaver impacted segment is bracketed by MC1 and MC2, and the beaver impacted segment is bracketed by MC2 and MC3. Main channel discharge and runoff were predominantly driven by snowmelt, although both notably increased in response to the 17 June and 7–9 July storm events (shaded in gray).

Water temperature tended to be warmer and more variable in the floodplain water-bodies than the main channel, and averaged $9.8 \pm 5.9^{\circ}\text{C}$ at SC1 and $10.4 \pm 3.7^{\circ}\text{C}$ at P1 over the monitoring period (Table 3).

Main channel discharge was predominantly driven by seasonal snowmelt, with hydrographs along the channel rising abruptly following snowmelt in late May, peaking between 4 June and 22 June to $5.8 \text{ m}^3 \text{ s}^{-1}$ at MC1, $6.7 \text{ m}^3 \text{ s}^{-1}$ at MC2, and $5.2 \text{ m}^3 \text{ s}^{-1}$ at MC3, and receding to minimums of $0.3 \text{ m}^3 \text{ s}^{-1}$ at MC1, $0.4 \text{ m}^3 \text{ s}^{-1}$ at MC2, and $1.0 \text{ m}^3 \text{ s}^{-1}$ at MC3 by the end of monitoring (Figure 3). While main channel discharge was predominantly driven by snowmelt, short-term (<1 week) increases in discharge occurred during summer rainfall events (Figure 3). Discharge at MC2 (narrow-valley outflow) was consistently higher than discharge at MC1 (narrow-valley inflow), which indicated that the narrow-valley segment was a net source of water from May to October. Conversely, alternating magnitudes between discharge at MC3 (wide-valley outflow) and discharge at MC2 (wide-valley inflow) indicated that the wide-valley segment was generally a net source of water during the rising limb of the snowmelt hydrograph, a net sink during peak flows from 1 June to 23 July,

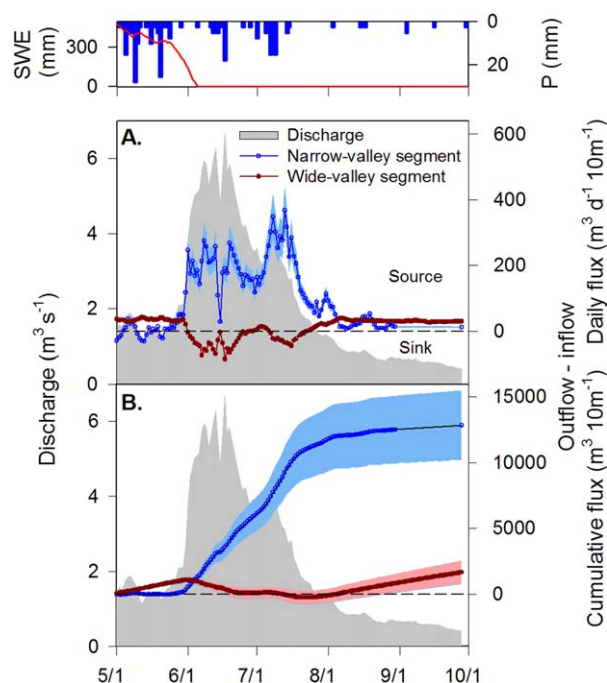


Figure 4. Precipitation (P) and snow water equivalent (SWE) and daily mean discharge (MC2) with (a) daily mean and (b) cumulative water flux balances from May to October 2015 per 10 m of valley length. Shaded values indicate uncertainty. Over the monitoring period, the nonbeaver impacted (“narrow-valley”) segment transported $1.3 \times 10^4 \text{ m}^3$ of water, whereas the beaver impacted (“wide-valley”) segment transported a net total of only $0.2 \times 10^4 \text{ m}^3$ of water for every 10 m of valley length.

and a net source again as the hydrograph receded to base flow (Figure 3). From May to October, mean (\pm standard deviation) discharge was $2.0 \pm 1.4 \text{ m}^3 \text{ s}^{-1}$ at MC1, $2.1 \pm 1.7 \text{ m}^3 \text{ s}^{-1}$ at MC2, and $2.3 \pm 1.3 \text{ m}^3 \text{ s}^{-1}$ at MC3 (Table 3).

Daily and cumulative hydrologic flux balances along the narrow-valley and wide-valley segments highlight substantial differences in hydrologic retention (Figure 4). While the narrow-valley segment was a consistent net source of water, the wide-valley segment displayed variable source-sink behavior, and was a net source of water during low flows and a net sink during higher flows (Figure 4a). From May to October, the narrow-valley segment exported a total of $1.3 \times 10^4 \text{ m}^3$ of water per 10 m of valley length, whereas the wide-valley segment exported only $0.2 \times 10^4 \text{ m}^3$ of water per 10 m of valley length (Figure 4b). This is an export of over 6 times more water from the narrow-valley segment to the wide-valley segment (Figure 4b).

Water levels along the main channel were more similar to those along the side-channel (SC1) than the pond (P1) (Figure 5). During high flows, SC1 had direct surface water connectivity with the main channel, whereas P1 had indirect surface water connectivity through smaller channels including beaver canals and side-channels. Based on abrupt changes in water levels and temperature fluctuations [e.g., Reckendorfer et al., 2006; Cabezas et al., 2011], SC1 likely had direct surface connections with the main channel from 1 June to 23 July (Figure 5). Compared to SC1, P1 stage and water temperature did not indicate strong connections or influence from main channel dynamics. Water temperatures and in particular water levels were strongly buffered at P1 relative to those at SC1, with a range of only 120 mm compared to 422 mm at SC1 (Figure 5).

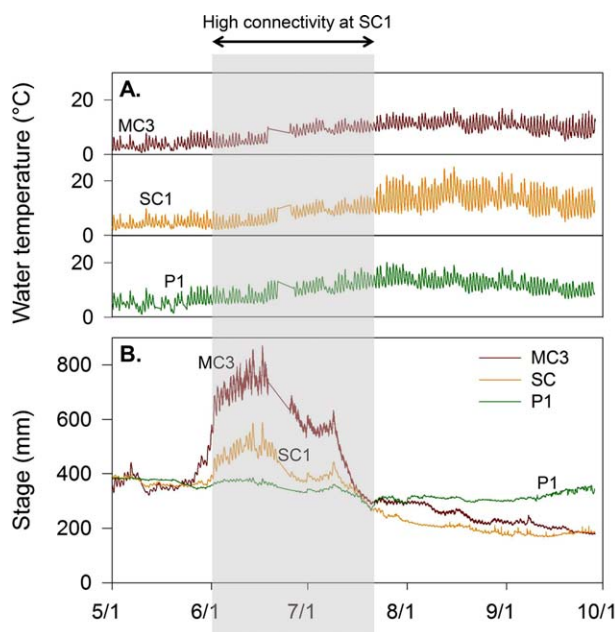


Figure 5. Water temperature and stage for the main channel (MC3), side-channel (SC1), and pond (P1) from May to October 2015. The side-channel, SC1, had strong similarities in stage with MC3 as well as abrupt changes in water temperature fluctuations, which suggest direct surface water connectivity with the main channel from 1 June to 23 July. The pond, P1, which was indirectly connected by surface water to the main channel by smaller channels including beaver canals and side-channels, had consistent stage and water temperature fluctuations from May to October.

3.2. Dissolved Nutrient Concentrations and Fluxes

Phosphate (PO_4) concentrations measured from grab samples were all below the detection limit of 0.01 mg L^{-1} [Pierson et al., 2016]. Ammonium-N ($\text{NH}_4\text{-N}$) concentrations were low along the main channel and at SC1, with averages below

Table 4. Summary (Mean ± SD) of Dissolved Nutrient Concentrations (mg L⁻¹) at Main Channel Sites MC1, MC2 and MC3, and Floodplain Sites SC1 and P1, and of Daily Fluxes (kg d⁻¹) at MC1, MC2, and MC3^a

	Dissolved Nutrient Concentration (Mean ± SD) (mg L ⁻¹)					Daily Flux (Mean ± SD) (kg d ⁻¹)		
	MC1	MC2	MC3	SC1	P1	MC1	MC2	MC3
NH ₄ -N	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.08	0.03 ± 0.02	0.06 ± 0.08	2.16 ± 1.56	3.54 ± 3.45	3.86 ± 3.89
NO ₃ -N	0.07 ± 0.04	0.08 ± 0.04	0.07 ± 0.04	0.05 ± 0.05	0.03 ± 0.01	14.5 ± 16.3	17.7 ± 22.4	18.8 ± 20.5
DON	0.09 ± 0.04	0.10 ± 0.07	0.10 ± 0.05	0.20 ± 0.18	0.12 ± 0.05	17.1 ± 15.3	21.6 ± 23.8	21.7 ± 15.7
TDN	0.18 ± 0.06	0.19 ± 0.10	0.18 ± 0.07	0.28 ± 0.17	0.21 ± 0.08	33.5 ± 33.5	42.9 ± 49.0	44.2 ± 39.8
DOC	3.50 ± 2.05	2.95 ± 1.87	3.56 ± 1.81	4.74 ± 1.71	3.24 ± 1.81	649 ± 602	700 ± 778	725 ± 682

^aNutrient concentrations and fluxes are listed for ammonium-nitrogen (NH₄-N), nitrate-nitrogen (NO₃-N), dissolved organic nitrogen (DON), total dissolved nitrogen (TDN), and dissolved organic carbon (DOC). DOC fluxes are from 15 min time series, and nitrogen fluxes are from grab samples taken approximately every other week from May to October 2015.

0.03 mg L⁻¹, compared to P1, which averaged 0.06 mg L⁻¹ from May to October (Table 4 and Figure 6a). As the hydrograph receded, NH₄-N concentrations at P1 increased to the highest observed value by late September, 0.20 mg L⁻¹, which was 4 or more times higher than the NH₄-N concentrations measured at main channel or side-channel sites that day (Figure 6a).

At all locations, nitrate-N (NO₃-N) concentrations were strongly related to discharge dynamics and peaked on the rising limb of the seasonal snowmelt hydrograph, began decreasing prior to peak flows, and subsequently fell with the falling limb of the hydrograph (Figure 6b). NO₃-N concentrations at SC1 had the greatest range of all the sites, with a peak value of 0.14 mg L⁻¹ in early June and lows of <0.01 mg L⁻¹ from August to October (Table 4 and Figure 6b). In contrast, NO₃-N concentrations at P1 were the most stable of all sites, with a maximum value of 0.05 mg L⁻¹ in early June and lows of 0.02 mg L⁻¹ in August (Table 4 and Figure 6b). Dissolved organic nitrogen (DON) concentrations followed a similar trend as NO₃-N, with values that generally increased on the rising limb of the seasonal snowmelt hydrograph and decreased prior to peak flows (Figure 6c). However, DON concentrations increased at all sites in September. By late September, DON concentrations at SC1 were 0.60 mg L⁻¹, which was twice as high as any other location (Figure 6c).

Dissolved organic carbon (DOC) concentrations were relatively high at all locations during May as the hydrograph began to rise (Figure 6d). During this timeframe DOC concentrations increased and peaked on the rising limb of the seasonal snowmelt hydrograph, began decreasing prior to peak flows, and

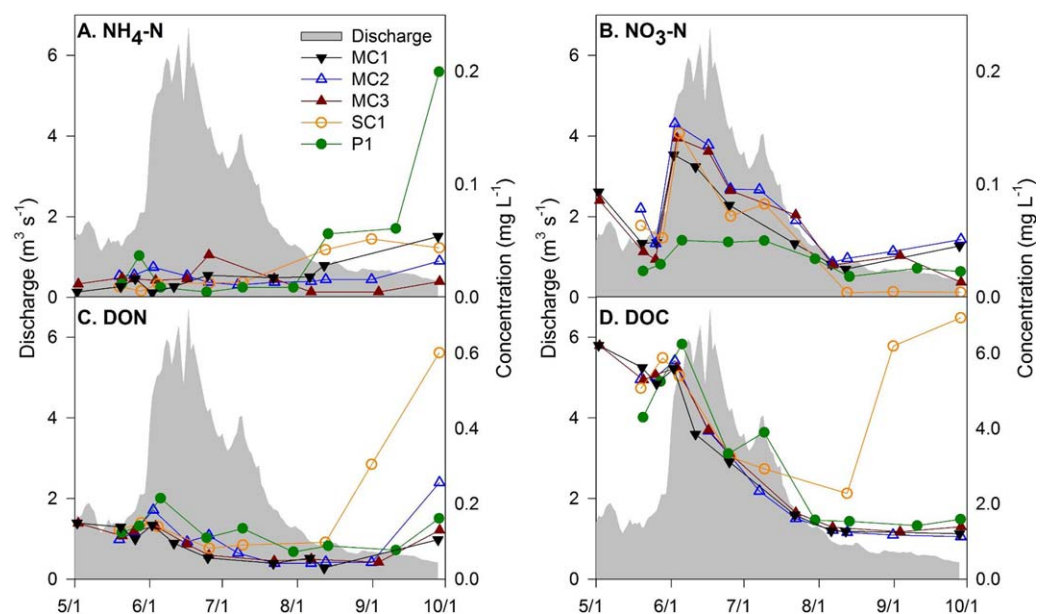


Figure 6. Daily mean discharge at MC2 and dissolved nutrient concentrations at main channel monitoring sites MC1, MC2, and MC3, a floodplain side-channel, SC1, and pond, P1.

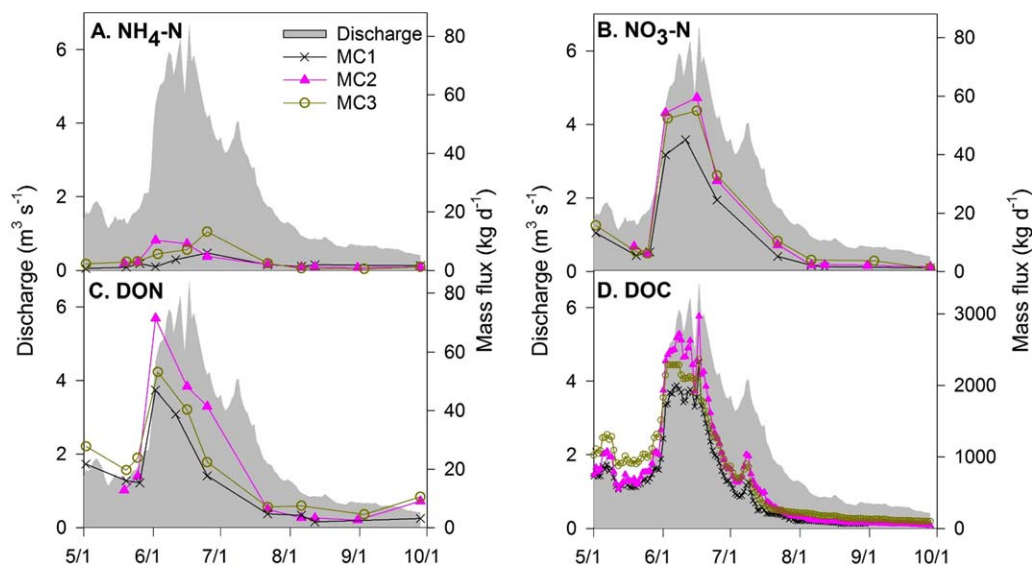


Figure 7. Daily mean discharge at MC2 and dissolved nutrient and organic carbon daily fluxes.

subsequently fell with the falling limb of the hydrograph (Figure 6d). There was one peak in DOC at P1 associated with an early July rain event, but otherwise DOC generally declined on the hydrograph falling limb until early August (Figure 6d). However, DOC concentrations rose strongly in SC1 during the August–October timeframe with a value of 6.9 mg L^{-1} on 28 September (Figure 6d).

Daily carbon and nitrogen fluxes along the main channel strongly followed the snowmelt hydrograph; fluxes were generally low in May, increased abruptly to maximum values during peak flows in June, decreased slightly prior to the hydrograph recession and stabilized at low values by late July/early August (Figure 7). Along the main channel, fluxes ranged from minimum values of $1.1 \text{ kg NO}_3\text{-N d}^{-1}$, $0.5 \text{ kg NH}_4\text{-N d}^{-1}$, $2.0 \text{ kg DON d}^{-1}$, and $40.9 \text{ kg DOC d}^{-1}$ during low flows to maximum values of $59.5 \text{ kg NO}_3\text{-N d}^{-1}$, $13.2 \text{ kg NH}_4\text{-N d}^{-1}$, $71.6 \text{ kg DON d}^{-1}$, and $2965 \text{ kg DOC d}^{-1}$ during high flows (Figure 7). From May to October, carbon and nitrogen fluxes were generally higher at MC2 (narrow-valley outflow) than MC1 (narrow-valley inflow), which indicated that the narrow-valley segment was a net source of fluvial carbon and nitrogen across flows (Figure 7). Conversely, the relative magnitudes of carbon and nitrogen fluxes alternated between MC3 (wide-valley outflow) and MC2 (wide-valley inflow), which indicated that the wide-valley segment transitioned between net source and sink behavior for fluvial carbon and nitrogen flux across flows (Figure 7).

Daily and cumulative flux balances for each segment highlight the ability of the wide-valley segment to retain carbon and nitrogen relative to the narrow-valley segment (Figure 8). From May to October, the narrow-valley segment exported 46 kg TDN and 633 kg DOC per 10 m of valley length, whereas the wide-valley segment stored 1.7 kg TDN and exported only 25 kg DOC per 10 m of valley length (Table 5 and Figures 8b, 8d). Accordingly, when standardized for segment valley length, the narrow-valley segment transported over 25 times more DOC than the wide-valley segment and was a net source, compared to a net sink, of TDN from May to October (Table 5 and Figures 8b, 8d). While the narrow-valley segment was a consistent source of DOC and TDN across all flows, the wide-valley segment exhibited variable source-sink dynamics. Specifically, the segment was a sink for water, DOC and TDN when flows exceeded $\sim 4 \text{ m}^3 \text{ s}^{-1}$ on the rising limb, and remained a sink until flows dropped to $\sim 2 \text{ m}^3 \text{ s}^{-1}$ on the falling limb of the seasonal snowmelt hydrograph (Figure 9).

3.3. Aquatic Ecosystem Metabolism

Gross primary productivity (GPP) and ecosystem respiration (ER) rates were strongly correlated with one another at each site (Figure 10). The narrow-valley outflow (MC2) generally had the lowest and most consistent metabolic processing rates of all sites, with mean (\pm standard deviation) rates of $0.09 \pm 0.14 \text{ g O}_2 \text{ m}^2 \text{ d}^{-1}$ GPP and $-0.72 \pm 0.50 \text{ g O}_2 \text{ m}^2 \text{ d}^{-1}$ ER (Table 6 and Figure 10). At MC2, GPP was relatively insensitive to

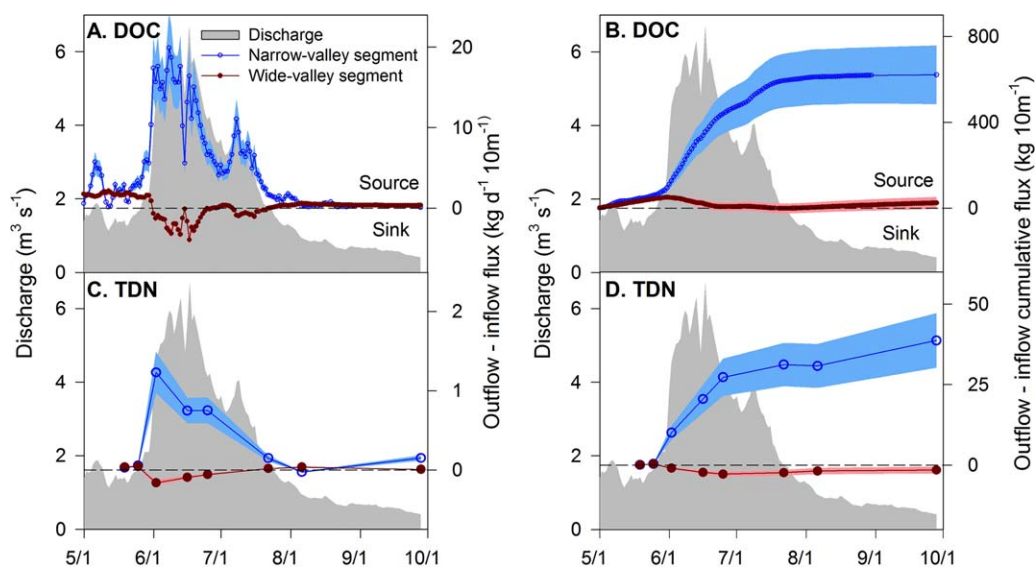


Figure 8. Daily mean discharge at MC2 along with dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) daily and cumulative flux balances for the nonbeaver impacted (“narrow-valley”) and beaver impacted (“wide-valley”) segment standardized for segment valley length. Shaded values indicate uncertainty. From May to October, the narrow-valley segment exported a net total of 46 kg TDN and 633 kg DOC per 10 m of valley length, whereas the wide-valley segment stored a net total of 1.7 kg TDN and exported a net total of 25 kg DOC per 10 m of valley length.

changes in discharge, but ER fluctuated with flow and increased during the snowmelt peak and 7–9 July storm (Figure 10). The wide-valley outflow (MC3), had higher and more variable metabolism rates than MC2, with an average GPP of $1.01 \pm 0.76 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and an average ER of $-1.77 \pm 1.10 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Table 6 and Figure 10). Metabolism rates at MC3 were lowest during the snowmelt peak and increased as the hydrograph receded to base flow, reaching a maximum of $2.88 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ GPP on 18 September and $-3.96 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ER on 21 September (Figure 10).

Within the floodplain side-channel (SC1) and pond (P1), metabolism generally increased as the hydrograph receded (Figure 10) and peaked to $2.07 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ GPP on 6 September and $-5.04 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ER on 17 August at SC1, and $1.33 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ GPP and $-1.33 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ER on 27 September at P1 (Figure 10). From May to October, SC1 generally had higher and more variable rates than P1, at $0.93 \pm 0.50 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ mean GPP and $-2.64 \pm 1.00 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ mean ER compared to $0.57 \pm 0.33 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ mean GPP and $-0.56 \pm 0.32 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ mean ER at P1 (Table 6 and Figure 10). The mean ER rate at SC1 was substantially higher than any of the other sites (Table 6 and Figure 10), and was largely attributed to the peak in ER values between -4.32 and $-5.04 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ from 14 to 20 August (Figure 10).

Table 5. Cumulative Fluxes From May to October 2015 of Ammonium-Nitrogen ($\text{NH}_4\text{-N}$), Nitrate-Nitrogen ($\text{NO}_3\text{-N}$), Dissolved Organic Nitrogen (DON), Total Dissolved Nitrogen (TDN), Dissolved Organic Carbon (DOC), and Water at Main Channel Sites MC1, MC2, and MC3, and Net Export and Retention for the Nonbeaver Impacted (“Narrow-Valley”) and Beaver Impacted (“Wide-Valley”) Segments^a

	Cumulative Flux				Segment Export (+) or Retention (-)		
	MC1 (kg)	MC2 (kg)	MC3 (kg)	Narrow-Valley (%)	Wide-Valley (%)	Narrow-Valley (kg 10 m ⁻¹)	Wide-Valley (kg 10 m ⁻¹)
$\text{NH}_4\text{-N}$	295	400	412	36	3	2.7	0.1
$\text{NO}_3\text{-N}$	1315	1953	1910	49	-2	16	-0.3
DON	1389	2434	2198	75	-10	27	-1.5
TDN	2999	4787	4520	60	-6	46	-1.7
DOC	80,966	105,672	109,446	31	4	633	25
Water	(mm)	(mm)	(mm)	(%)	(%)	(mm 10 m ⁻¹)	(mm 10 m ⁻¹)
	278	336	358	21	7	1.5	0.1
	(m ³)	(m ³)	(m ³)	(%)	(%)	(m ³ 10 m ⁻¹)	(m ³ 10 m ⁻¹)
	2.28×10^7	2.77×10^7	3.02×10^7	21	9	1.3×10^4	0.2×10^4

^aCumulative water fluxes are presented volumetrically and standardized by contributed area. Segment export and retention are presented on percent $[(\text{outflow flux} - \text{inflow flux}) / \text{inflow flux}] * 100$ and mass per 10 m of valley length $[(\text{outflow flux} - \text{inflow flux}) / 10 \text{ m of valley length}]$ bases.

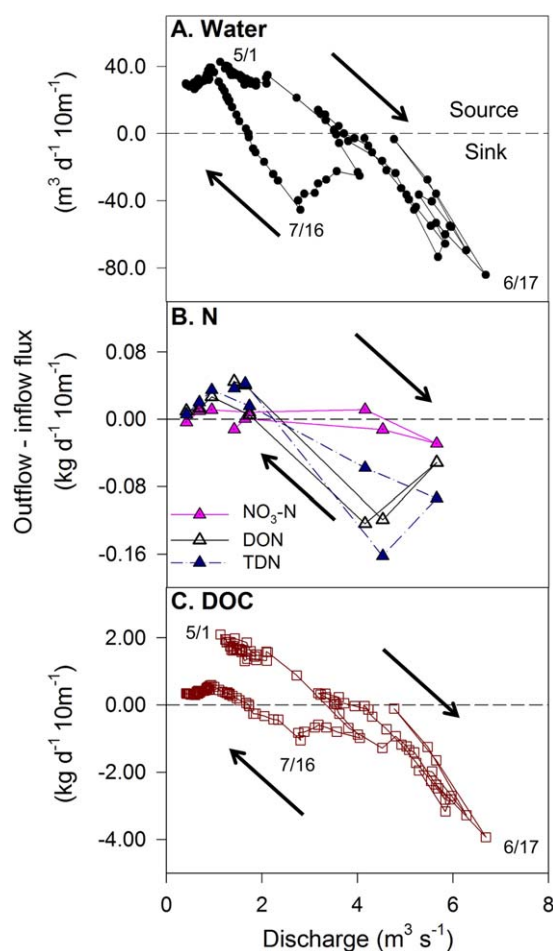


Figure 9. Source-sink dynamics for (a) water, (b) nitrate-N ($\text{NO}_3\text{-N}$), dissolved organic nitrogen (DON), and total dissolved nitrogen (TDN), and (c) dissolved organic carbon (DOC) along the beaver impacted segment as a function of discharge. The beaver impacted segment was a sink for water, TDN, and DOC when flows exceeded $\sim 4 \text{ m}^3 \text{ s}^{-1}$ on the rising limb and down to $\sim 2 \text{ m}^3 \text{ s}^{-1}$ on the falling limb of the seasonal hydrograph.

2014] suggest that these landscape features can be critical to enhanced network retention. For example, we observed considerable attenuation of water, DOC, and TDN fluxes across the wide-valley relative to the narrow-valley segment. Notably, most water, DOC, and nitrogen retention occurred during peak snowmelt, when export rates from the upstream narrow-valley segment were highest. In Montane river networks, lateral hydrologic connections between the river and the floodplain can drive these contrasting flux dynamics. In the steep, narrow-valley segments, increases in discharge result in increased water velocity and depth with limited lateral dissipation; conversely, in the wider valley segments, water can spread laterally across the floodplain. This lateral connectivity promotes storage of water, carbon, and nutrients at high flows, which can subsequently be released as flow recedes. Clearly, this process has implications for hydrologic buffering of flooding and droughts, but also can help maintain higher baseline aquatic ecosystem metabolism and associated biogeochemical processing, with importance from both ecological and water quality perspectives [Junk *et al.*, 1989; Tockner *et al.*, 2000]. As such, beaver-mediated hydrologic connectivity between the river, floodplain, and riparian areas has relevance for water quantity, quality, and ecosystem processes.

The high carbon and nitrogen retention rates along the wide-valley relative to the narrow-valley segment were not a function of main channel metabolism and biogeochemical processing alone. Based on stoichiometric calculations from main channel metabolism rates [see Heffernan and Cohen, 2010], assimilatory

From May to October, average net ecosystem productivity (NEP) rates were negative (net heterotrophic) at MC2, MC3, and SC1 (Table 6 and Figure 11). NEP dynamics contrasted between the narrow-valley and wide-valley river segments; for example, during peak snowmelt, narrow-valley NEP rates were the most negative and wide-valley NEP rates were the least negative relative to lower flow periods (Figure 11). NEP dynamics also contrasted between floodplain water-bodies, and were more negative and variable at SC1, with a mean of $-1.70 \pm 0.80 \text{ g O}_2 \text{ m}^2 \text{ d}^{-1}$, than at P1, with a mean of $0.01 \pm 0.09 \text{ g O}_2 \text{ m}^2 \text{ d}^{-1}$ (Table 6 and Figure 11). SC1 became increasingly net heterotrophic until 14 August, and decreased thereafter, whereas P1 NEP rates were stable through the monitoring period (Figure 11).

4. Discussion

4.1. How do Water, Nitrogen, and Carbon Fluxes Vary Between Longitudinally Adjacent River Segments of Varying Valley Width, Beaver Activity, and Channel Planform?

In North Saint Vrain Creek, a single-thread, non-beaver impacted (“narrow-valley”) segment was a net source of water, dissolved organic carbon (DOC), and total dissolved nitrogen (TDN) from May to October, whereas a multithread, beaver impacted (“wide-valley”) segment exhibited variable source-sink dynamics as a function of discharge. While low-gradient, wide-valley river segments typically occupy a small portion of montane river networks [Stanford and Ward, 1993], our data and others [e.g., Junk *et al.*, 1989; Stanford and Ward, 1993; Wohl and Beckman,

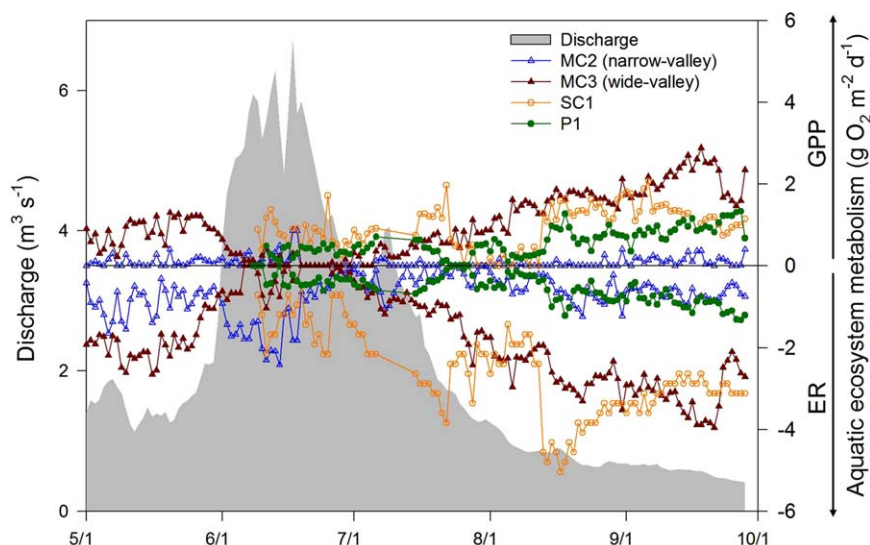


Figure 10. Daily mean discharge at MC2 along with aquatic ecosystem gross primary productivity (GPP) and ecosystem respiration (ER) at main channel sites MC2 (narrow-valley outflow) and MC3 (wide-valley outflow), the side-channel, SC1, and pond, P1.

uptake averaged $3 \text{ mg N m}^{-2} \text{ d}^{-1}$ along the narrow-valley segment and $11 \text{ mg N m}^{-2} \text{ d}^{-1}$ along the wide-valley segment. This is insufficient to account for observed retention along the wide segment and suggests that considerable retention occurred in the side-channels, ponds, marshes, and floodplain sediments of the valley bottom. Lateral hydrologic exchanges across valley bottoms can help form extensive riparian wetlands and increase the number and size of floodplain water-bodies, which can increase nitrate removal through denitrification [Hill et al., 1998] and carbon retention through uptake, sorption, and burial [McKnight et al., 1992; Wohl et al., 2012]. Using areal images, we estimate that, per valley length, the area of surface water connected to the main channel was ~ 8 times larger along the wide-valley compared to the narrow-valley segment during high flows. This estimate does not include hyporheic zones, which can be extensive in the floodplains of wide-valley bottoms [Stanford and Ward, 1988]. Given the large surface area created by floodplain water-bodies (side-channels, ponds, marshes), floodplain sediments, and hyporheic zones, it is not surprising that wide-valley segments with hydrologically connected river-floodplain systems can have high biogeochemical retention capacities. In fact, combining moderate processing rates (see above) with particularly large surface areas can result in the disproportionately high retention capacity of wide river-valley segments.

Our results also highlight the importance of beaver activity in facilitating lateral hydrologic connectivity. Currently, beaver populations in Rocky Mountain National Park are threatened as a consequence of high numbers of elk that directly compete for food and foraging materials [Peinetti et al., 2002]. In locations outside of the National Park, beaver have decreased due to human removal and harvesting. Historical beaver losses from 19 century fur trapping have resulted in a widespread shift of multithread channels with large floodplains and riparian areas to single-thread channels flowing through drier grasslands [Wolf et al., 2007; Green and Westbrook, 2009; Polvi and Wohl, 2012]. If we consider a scenario in which beaver abandon North

Table 6. Summary (Mean \pm SD) of Aquatic Ecosystem Metabolism Metrics Gross Primary Productivity (GPP), Ecosystem Respiration (ER), and Net Ecosystem Productivity (NEP) at Main Channel Sites MC2 (Narrow-Valley Outflow) and MC3 (Wide-Valley Outflow), a Side-Channel (SC1), and an Off-Channel Pond (P1)^a

	Aquatic Ecosystem Metabolism (Mean \pm SD) ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$)			
	MC2	MC3	SC1	P1
GPP	$+0.09 \pm 0.14$	$+1.01 \pm 0.76$	$+0.93 \pm 0.50$	$+0.57 \pm 0.33$
ER	-0.72 ± 0.50	-1.77 ± 1.10	-2.64 ± 1.00	-0.56 ± 0.32
NEP	-0.63 ± 0.44	-0.76 ± 0.48	-1.70 ± 0.80	$+0.01 \pm 0.09$

^aMain channel data extend from 1 May to 28 September, and side-channel and pond data extend from 9 June to 28 September 2015.

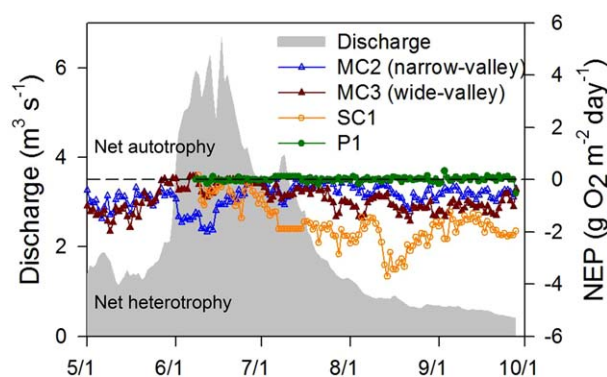


Figure 11. Daily mean discharge at MC2 with net ecosystem production (NEP) at main channel sites MC2 (narrow-valley outflow) and MC3 (wide-valley outflow), the side-channel, SC1, and pond, P1. All sites were net heterotrophic except P1, which was slightly net autotrophic.

research [Nyssen *et al.*, 2011; Majerova *et al.*, 2015; Puttock *et al.*, 2017]. Given the growing potential for drought and flooding [Dominguez *et al.*, 2012; Dennison *et al.*, 2014], and elevated nutrient loading to fluvial systems [Rabalais *et al.*, 2010], hydrologic and biogeochemical buffering is increasingly important in order to maintain high water tables during droughts, attenuate flood pulses, and store, transform, and remove carbon and nitrogen loads from river networks.

4.2. How Does Aquatic Ecosystem Metabolism and Associated Nutrient Processing Vary as a Function of Flow State and Lateral Hydrologic Connectivity in Adjacent River Segments With and Without Beaver Activity?

Of the two floodplain water-bodies in which we quantified aquatic ecosystem metabolism (SC1 and P1), the intermittently connected side-channel (SC1) had almost double the mean GPP and nearly 5 times the mean ER as the off-channel pond (P1). When the side-channel was connected to the main channel it was lotic in hydrologic character and ER rates were depressed, potentially because of reduced residence times and increased channel bed scour. However, as flows decreased, SC1 became increasingly lentic in hydrologic character and aquatic metabolism rates increased. This is potentially because nutrients that were delivered to the side-channel during high flows were subsequently utilized during lower flow periods as residence times became longer. During low flows, enhanced ER in the floodplain side-channel resulted in increased net heterotrophy (more negative NEP), which was counter to our initial hypothesis of net autotrophy under lentic conditions [Allan and Castillo, 2007]. Presumably, heterotrophic respiration of organic material in benthic sediments was responsible for the observed net heterotrophic response. Accordingly, biogeochemical processing in the side-channel was dependent not only on water velocities and residence times, but also on hydrologic connections with the main channel that delivered nutrients and organic material to stimulate respiration as the hydrograph receded and residence times increased.

While the side-channel had highly dynamic hydrology and associated aquatic ecosystem metabolism, water velocities in the off-channel pond were consistently at or close to 0 m s^{-1} for the duration of the monitoring period. In addition to differences in hydrologic character, metabolism rates were also much less dynamic in the pond relative to the side-channel. Pond biogeochemistry dynamics were more likely related to sediment redox conditions [Lazar *et al.*, 2015] than changes in hydrology, which were generally lacking. Stoichiometric requirements of assimilatory uptake predict that as metabolism in the pond increased from high to low flows, concentrations of inorganic N would decrease [Taylor and Townsend, 2010]. In contrast to this prediction, we observed a large and abrupt increase in pond $\text{NH}_4\text{-N}$ concentrations in late September, which indicates that the rate of N mineralization exceeded the rate of uptake and/or nitrification. Moreover, ammonium could have been generated by dissimilatory nitrate reduction [Tiedje, 1988] under anaerobic conditions in pond sediments. Indeed, previous studies have observed high $\text{NH}_4\text{-N}$ concentrations in beaver ponds and riparian wetlands [Devito *et al.*, 1989; Cirimo and Driscoll, 1993; Johnston *et al.*, 2001]. With no outlet or scouring flows, biological detritus may have continually accumulated onto an undisturbed layer of sediments as the season progressed. High biogeochemical processing combined with a lack of oxygen

Saint Vrain Creek, we would expect the wide-valley segment to transition to an environment that is more structurally and functionally analogous to the narrow-valley segment. Our findings imply that in this scenario, water, carbon, and nutrient retention and buffering capacities in the network could be substantially reduced. While loss of retention in one catchment is unlikely to affect water quantity and quality at larger spatial scales, the cumulative impacts of widespread loss of beaver meadows very likely have consequences at scales relevant to water resource, land, and ecosystem management (e.g., city, county, state levels) and is therefore considered an important avenue for future

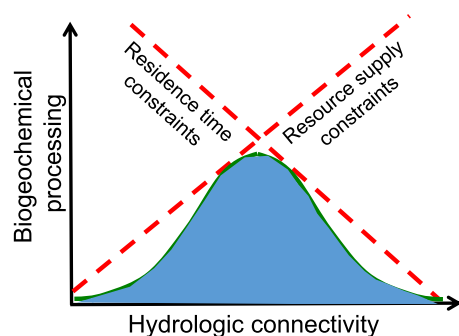


Figure 12. Conceptual diagram that demonstrates the relationships between hydrologic connectivity and biogeochemical processing. When hydrologic connectivity is low, processing rates are constrained by insufficient resource supply, and when connectivity is high, processing rates are constrained by low residence times. Biogeochemical processing is therefore optimized at intermediate levels of connectivity that provide adequate residence times and resource supplies.

to a transition from lotic to lentic conditions, as lateral connectivity decreased and SC1 lost surface water connectivity with the main channel. Additionally, there was a strong increase in DOC (6.9 mg L^{-1}) and DON (0.60 mg L^{-1}), and near-total depletion of $\text{NO}_3\text{-N}$ ($<0.005 \text{ mg L}^{-1}$) concentrations in the side-channel in August, likely because of increased biologic uptake of $\text{NO}_3\text{-N}$ and processing of particulate organic material. These relationships indicate tradeoffs between hydrologic connectivity and biogeochemical processing such that, when lateral connectivity to the main channel was high, processing rates were constrained by low residence times, but when connectivity to the main channel was absent and residence times were high, processing became constrained by insufficient resource supply (e.g., low inorganic nitrogen). Consequently, we suggest a conceptual model where ecosystem metabolism and biogeochemical processing in floodplains and beaver meadows are optimized at intermediate levels of connectivity that provide adequate residence times and resource supplies (Figure 12).

Along the main channel of North Saint Vrain Creek, metabolism rates were higher on average and more dynamic along the wide-valley than narrow-valley segment. The nonbeaver impacted narrow-valley segment was a consistent source for water, carbon, and nitrogen across flows, and demonstrated reduced biogeochemical processing and lower metabolism rates. Conversely, along the beaver impacted wide-valley segment, lateral hydrologic exchanges with the floodplain increased water, carbon, and nitrogen retention, which enhanced biogeochemical processing. Interestingly, while main channel metabolism along the wide-valley segment increased as flow decreased, aquatic ecosystem metabolism (in particular ER) along the narrow-valley segment was greatest during the highest flows. A potential explanation for this is that aquatic biogeochemical processing along the narrow-valley segment was driven by hyporheic exchange, which can be enhanced at higher discharges and flow velocities [Packman and Salehin, 2003; Ye et al., 2012]. Previous work using tracer injections has indicated that most transient storage in steep mountain streams (i.e., narrow-valley segment) results from hyporheic exchange [Wondzell, 2006]. Conversely, river-floodplain systems, as represented by the wide-valley segment, contain an interconnected network of floodplain waterbodies that can connect via surface and subsurface pathways. Hydrologic connections across the floodplain can link carbon and nutrient sinks and sources, influencing retention and biogeochemical processing. As a function of these hydrologic dynamics, the side-channel (SC1) became a biogeochemical hot spot as connection to the main channel decreased. Numerous other intermittently connected side-channels along the wide-valley segment likely responded similarly as SC1, and contributed to the enhanced metabolism rates and carbon and nutrient retention observed at the segment outlet. However, when river-floodplain systems are altered by activities such as beaver trapping, channelization, dredging, or artificial levee construction, previously intermittently connected hot spots can become permanently disconnected from the main channel. We suggest that these river-floodplain alterations can result in decreased hydrologic and biogeochemical retention capacities. In fact, loss of lateral connections across wide-valley segments may result in

renewal would induce low oxygen concentrations that suppress nitrification and enhance dissimilatory NO_3^- reduction, highlighting the importance of floodplain sediments and water-bodies in N removal processes.

Along the main channel of the wide-valley segment, seasonal trends in metabolism were more similar to the side-channel than the pond (Figure 10). During high flows, the main and side-channels were hydrologically connected and exhibited similar hydrologic and nutrient concentration dynamics. While both channels had substantial resource supplies during high flows, metabolism rates were higher along the side-channel than main channel during this time, likely as a function of water velocities. In both channels, metabolism generally increased as the hydrograph receded and water velocities decreased; however, in the side-channel, peak metabolism occurred on 6 September (GPP) and 17 August (ER), which was earlier than peak metabolism along the main channel (Figure 10). The increase in side-channel metabolism was related

hydrologic and biogeochemical functionality that is analogous to the steeper, narrower segments that already dominate the networks of mountainous catchments. Because the low-gradient wide-valley bottoms are limited in frequency and spatial extent within river networks of mountainous catchments, such features can be disproportionately important for network hydrologic and biogeochemical buffering in these landscapes.

5. Conclusions

Along two longitudinally adjacent river segments with and without beaver activity in North Saint Vrain Creek, Colorado, planform complexity and lateral hydrologic connectivity were important to the retention of water, dissolved organic carbon, and nitrogen, which in turn influenced spatiotemporal patterns in aquatic ecosystem metabolism. From May to October, the narrow, single-thread segment without beaver activity was a consistent net source of water and fluvial carbon and nutrients, while the wide, multithread segment with beaver activity exhibited variable source-sink dynamics as a function of discharge. Beaver-mediated hydrologic connections between the river, floodplain, and riparian areas promoted high carbon and nutrient retention and processing across the wide-valley segment. For example, in a side-channel with intermittent surface water connectivity with the main channel, high variability in flow and nutrient supply related to highly dynamic metabolic processing rates, particularly with respect to ecosystem respiration (ER). Compared to the side-channel, a pond that was not directly connected to the main channel via surface water had lower average and less dynamic metabolic rates. We suggest that while low flow/low connectivity periods can enhance metabolism due to increased residence times, episodic connectivity during high flows may be required to replenish resources (organic material and inorganic nutrients) and maintain high levels of ecosystem processing.

While the results here are from one catchment, the widespread disconnection of rivers and floodplains in the Rocky Mountains [Wohl, 2004; Wohl and Beckman, 2014] and beyond [Walter and Merritts, 2008] suggests that loss of hydrologic connectivity and associated biogeochemical function can have cumulative influence on catchment-scale to regional-scale water, carbon, and nutrient budgets. Beaver meadows in particular were once abundant and widespread within North America [Naiman et al., 1988; Macfarlane et al., 2015], but have become relatively rare. Determining the cumulative effects of river-floodplain disconnection is a critical next step in restoring function in altered river networks.

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