

Nutrient Retention and the Problem of Hydrologic Disconnection in Streams and Wetlands

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ABSTRACT

Some aquatic systems have disproportionately high nutrient processing rates, and may be important to nutrient retention within river networks. However, the contribution of such biogeochemical hot spots also depends on water residence time and hydrologic connections within the system. We examined the balance of these factors in a comparative study of nitrate (NO_3^-) uptake across stream and flow-through wetland reaches of northern Wisconsin, USA. The experimental design compared NO_3^- uptake at different levels: the ecosystem level, for reaches ($n = 9$) consisting of morphologically contrasting subreaches (*SLOW*, low mean water velocity; *REF*, reference, or higher mean water velocity); the sub-ecosystem level, for subreaches consisting of morphologically contrasting zones (*TS*, transient storage zone; *MC*, main channel zone). *SLOW* subreaches had 45% lower ecosystem-level uptake rate (K , t^{-1}) on average, indicating reduced uptake efficiency in flow-through wetlands relative to streams. The four largest K values (total $n = 24$) also occurred in *REF* sub-

reaches. *TS:MC* uptake rate varied (range 0.1–6.0), but *MC* zones consistently accounted for most NO_3^- uptake by the ecosystem. In turn, *TS* influence was limited by a tradeoff between *TS* zone uptake rate and the strength of *TS–MC* hydrologic connection (α or F_{med}). Additional modeling of published hydrologic parameter sets showed that strong *MC* dominance of uptake (>75% of total uptake), at the scale of solute release methods (meters to kilometers, hours to days), is common among streams and rivers. Our results emphasize that aquatic nutrient retention is the outcome of a balance involving nutrient uptake efficiency, water residence time, and the strength of hydrologic connections between nutrient sources and sinks. This balance restricts the influence of hydrologically disconnected biota on nutrient transport, and could apply to diverse ecosystem types and sizes.

Key words: stream; wetland; river; nutrient; uptake; ecosystem; hydrologic connectivity; transient storage; nitrate; nitrogen.

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INTRODUCTION

Examinations of nutrient retention have improved our understanding of the functioning of forests (Bormann and Likens 1979; Vitousek and Reiners 1975), streams (Fisher and others 1982), and also linkages between those habitats (Valett and others 2002). More recently, growing concern about human alterations of the global N cycle (Vitousek

and others 1997) fostered abundant N research in streams, where comparative studies across sites have been emphasized (for example, Mulholland and others 2009; Webster and others 2003). Now there is much interest in understanding the role of streams relative to other habitat types, and in patterns within the broader river network. But resulting studies have exposed a lack of empirical information for habitats that can greatly influence river network nutrient transport (Powers and others 2009; Tank and others 2008).

Many works point to wetlands as important sites of nutrient cycling and organic matter settling (for example, Jansson and others 1994), and this has contributed to a common view that wetlands function as biogeochemical hot spots within river networks. Biogeochemical hot spots possess disproportionately high nutrient reaction rates (t^{-1}) relative to the surrounding matrix (McClain and others 2003). Although nutrient cycles in both natural and treatment wetlands are documented by a rich literature (for example, Kadlec and Wallace 2009; Naiman and Melillo 1984), the ecosystem-level biogeochemical role of wetlands relative to other ecosystem types has been elucidated mostly through review and meta-analysis of separate studies (for example, Fisher and Acreman 2004; Jordan and others 2011; Seitzinger and others 2006) rather than direct empirical comparison. That is problematic for river network modeling because patterns aggregated across different locations and source waters could be poor representations of patterns occurring within actual river networks.

Ultimately, the contribution of different habitats to nutrient retention within river networks depends not only on nutrient processing rate, but also on water residence time and hydrologic connections between nutrient sources and sinks. For example, previous research within lotic ecosystems has emphasized the biogeochemical role of transient storage (*TS*) or “dead” zones (Mulholland and others 1997; Valett and others 1996, 1997), which have a high water residence time relative to other components of the ecosystem. *TS* zones can be either surface features (in-channel) or subsurface features (Briggs and others 2009; Ensign and Doyle 2005; Gucker and Boechat 2004), and both can be sites of rapid nutrient uptake and transformation when occupied by organic matter deposits, microbes, and algae. Nevertheless, for *TS* zones to contribute substantially to nutrient retention within ecosystems or river networks, these habitats must process nutrients rapidly enough to outweigh limits imposed by hydrologic disconnection from main nutrient flow.

The problem of hydrologic disconnection is not unique to biogeochemical hot spots that occur in the *TS* zone of streams. Rather, physical boundaries occur internally within many ecosystems, imposing limits to resource exchanges. For example, thermal stratification within lakes prevents mixing between surface and deep waters (Wetzel 2001). At smaller scales, low water movement in the marine benthos has been shown to reduce nutrient supply to cell boundary layers of corals (Atkinson and Bilger 1992; Thomas and Atkinson 1997), and even in more turbulent streams can limit nutrient transfer to benthic surfaces containing algae and microbes (Gantzer and others 1988; Mulholland and others 1994). Likewise, entrainment of organic matter and fine sediments within the benthos of streams can clog interstitial spaces of substrata (Orr and others 2009; Schmalchli 1992). Thus, ecosystem components that have disproportionately high nutrient processing rates may not contribute substantially to total ecosystem retention unless so permitted by hydrologic connections.

Here, we compare uptake of reactive N (nitrate) at the ecosystem level (flow-through wetlands vs. streams) and sub-ecosystem level (*TS* zones vs. main channel (*MC*)/thalweg zones) using experimental solute releases in contrasting systems of northern Wisconsin. We focus on two questions: (A) Which systems have higher rates of nutrient uptake? and (B) Which systems provide the largest contribution to total nutrient retention of the reach? We propose that the contribution to nutrient retention by a nutrient sink is limited by three factors: (1) uptake efficiency within the sink; (2) residence time of the sink; and (3) rate of transfer (that is, strength of hydrologic connection) between a nutrient source and the sink. In our framework, the contribution to nutrient retention by any system is thus maximized at some optimum of those three criteria and could depend on inter-relatedness and tradeoffs among them. If present, such tradeoffs would impose constraints on nutrient processing heterogeneity within river networks, and could partly explain the observation that seemingly diverse water bodies share a similar nutrient processing rate (Essington and Carpenter 2000; Wollheim and others 2006).

METHODS

Metrics and notation are shown in Table 1. We examined uptake of nitrate (NO_3^-) across morphologically diverse streams and flow-through wetlands of rural northern Wisconsin, USA. To do so, we located reaches that contained longitudinal

Table 1. Metrics and Notation

Symbol	Units	Metric name	Origin
Q	$L^3 t^{-1}$	Discharge	Field measurement
w	L	Mean channel width	Field measurement
d	L	Mean channel depth	Calculation
u	$L t^{-1}$	Mean water velocity	Calculation
α	t^{-1}	Exchange coefficient	OTIS parameter
D	$L^2 t^{-1}$	Dispersion coefficient	OTIS parameter
A	L^2	Main channel area	OTIS parameter
A_s	L^2	Transient storage zone area	OTIS parameter
F_{mean}	Unitless	Proportion of mean water travel time owing to transient storage	Calculation
F_{med}^{200}	Unitless	Proportion of median water travel time owing to transient storage	Calculation
Dal	Unitless	Dahmkohler number	Calculation
λ	t^{-1}	Main channel decay coefficient	OTIS parameter
λ_s	t^{-1}	Transient storage zone decay coefficient	OTIS parameter
K	t^{-1}	Whole stream decay coefficient	Calculation
V_f	$L t^{-1}$	Uptake velocity	Calculation
U	$M L^{-2} t^{-1}$	Areal uptake rate	Calculation
S_w	L	Uptake length	Calculation
P	Unitless	Proportion of experimental inputs taken up	Calculation
P_s	Unitless	Proportion of experimental inputs taken up by <i>TS</i> zone	Calculation

hydrogeomorphic discontinuities, including stream and flow-through wetland habitat caused by culverts, natural physiography, or beaver activity. Study reaches (118–492 m in length) contained two consecutive subreaches (38–249 m in length) and the experimental configuration is shown in Figure 1. We compared NO_3^- uptake between contrasting habitats at two levels of organization: (a) the ecosystem level, for paired subreach classes within the reach (*SLOW* lower mean water velocity, u , $L t^{-1}$, confirmed following velocity measurement; *REF* reference, or higher u); (b) the sub-ecosystem level, for *MC* and *TS* zones within the subreach. *MC* zones correspond to the channel

thalweg and are the dominant flowpath for water and solute, whereas *TS* zones correspond to slack-water features including pools, eddies, and interstitial spaces of the benthos. Each study reach ($n = 9$) was visited once in summer 2009 or 2010, and one of those was visited three additional times (North Cr, $n = 4$). Land cover in the study area is predominantly temperate forest, followed by wetland and open water (lakes), whereas agricultural land is scarce and topography is low. Most sites had dissolved inorganic N (DIN) below 0.01 mg L^{-1} , soluble reactive P (SRP) below 0.01 mg L^{-1} , and dissolved organic carbon (DOC) above 5.0 mg L^{-1} (Table 2). Atomic DIN:SRP ratios were usually

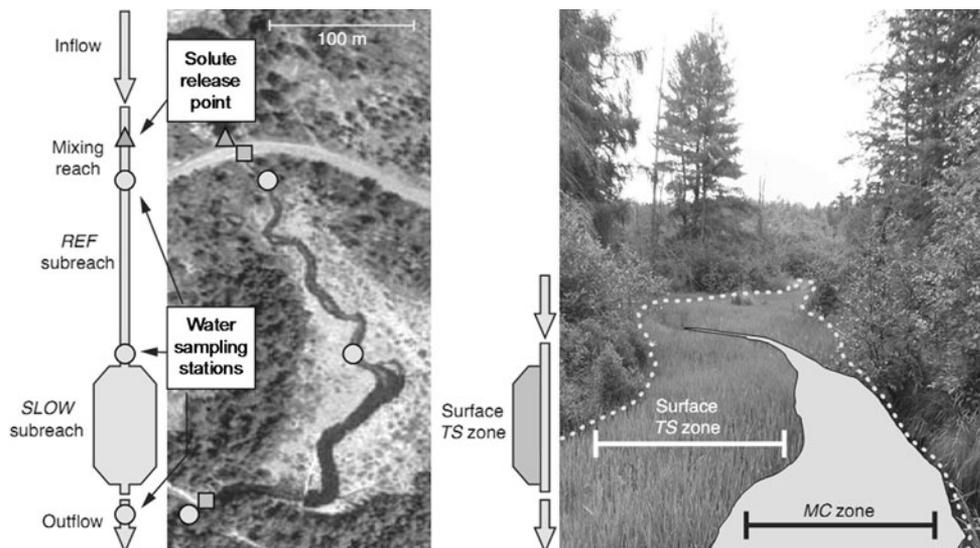


Figure 1. Experimental configuration and morphology of study reaches. Study reaches consist of paired subreaches, including *REF* and *SLOW* categories. Note that the order of *REF* and *SLOW* subreaches varied among sites (see Table 3). Subreaches consist of *MC* and surface *TS* zones. The aerial photo is the North Cr site. *Square symbols* are road culverts and *dotted line* is wetted width.

Table 2. Background Characteristics of Northern Wisconsin, USA Study Reaches ($n = 9$)

Metric category	Variable	Median	Range	1 s.d.
Chemistry	Nitrate-N* (mg L ⁻¹)	0.007	0.004–0.024	0.006
	Soluble reactive P** (mg L ⁻¹)	0.005	0.004–0.018	0.004
	Ammonium-N (mg L ⁻¹)***	0.018	0.005–0.10	0.028
	Total dissolved N (mg L ⁻¹)	0.43	0.030–0.74	0.25
	Total dissolved P (mg L ⁻¹)	0.008	0.005–0.025	0.008
	Total N (mg L ⁻¹)	0.55	0.21–1.2	0.28
	Total P (mg L ⁻¹)	0.03	0.01–0.10	0.03
	DIN:SRP (atomic ratio)	10.4	4.3–61	17.9
	Dissolved organic carbon (mg L ⁻¹)	8.4	3.2–12	3.0
Habitat, <i>REF</i> subreaches	% Substrata as fines	52	24–99	27
	% Substrata as sand	41	0.0–66	27
	% Substrata as coarse litter	0.0	0.0–21	9.0
	% Substrata as gravel + cobble	0.0	0.0–8.0	3.1
	% Coverage by emergent macrophytes	18	0.0–51	15
habitat, <i>SLOW</i> subreaches	% Coverage by submerged macrophytes	12	1.0–50	17
	% Substrata as fines	75	5.0–99	30
	% Substrata as sand	24	0.0–66	26
	% substrata as coarse litter	0.0	0.0–26	9.0
	% Substrata as gravel + cobble	0.0	0.0–11	3.7
	% Coverage by emergent macrophytes	31	0.0–86	29
	% Coverage by submerged macrophytes	3.0	1.0–17	6.1

For North Cr (visited multiple times) only observations corresponding to July 18 2009 (near midpoint of study season) are included.

*Nitrate-N < 0.01 mg L⁻¹ at all sites except LO (0.024 mg L⁻¹).

**Soluble reactive P < 0.01 mg L⁻¹ at all sites except MU (0.018 mg L⁻¹).

***Ammonium-N < 0.03 mg L⁻¹ at all sites except LO (0.10 mg L⁻¹). Three other reaches had ammonium 0.02–0.03 mg L⁻¹ (AL, MU, and N2).

less than 15, suggesting possible N limitation. Due to a consecutive arrangement, paired *REF* and *SLOW* subreaches shared common source water, and thus had similar chemistry and discharge (Q , L³ t⁻¹). The orientation of *REF/SLOW* subreaches (*first* or *second* in proximity to solute release point) varied among reaches. To control for photosynthetically active radiation (PAR), we targeted meadow sites with little or no riparian canopy (<10% canopy coverage).

Field Methods, Solute Releases, and Lab Methods

Twelve short-term, multiple rate solute releases (Demars 2008) of co-injected sodium chloride (NaCl) and sodium nitrate (NaNO₃) were conducted across paired *REF/SLOW* subreaches. Multiple rate solute releases are defined here as nutrient amendments caused by the introduction of experimental solutions at distinct constant rates, altered consecutively. The goal of this approach is to achieve multiple phases of both rapidly changing and slowly changing (near steady state) nutrient enrichment conditions in the stream over a short period (hours). Experimental solute was released

into study reaches using pneumatic pumps during sunny to mostly clear conditions near midday. Uptake estimates for paired subreaches were derived on the same day from a common solute release, using solute time series collected at three sampling stations (reach input, reach output, and boundary between subreaches). Sampling stations were positioned at well-mixed riffles, runs, culverts, or channel narrowings such that mean travel time between stations was at least 15 min, but usually about 30 min. Steady state enrichment targets at the solute release point were 10, 20, 50, and 100 µg L⁻¹ above background NO₃N concentration, each lasting 30 min. With uptake, dilution, and dispersion of solute, this ensured enrichment levels near 10 µg L⁻¹, 20, and 50 µg L⁻¹ for downstream (*second*) subreaches. Stream conditions never exceeded 120 µg L⁻¹ NO₃N. For every sampling station, there were usable NO₃⁻ values for uptake estimation (including values at least 10 µg L⁻¹ above background NO₃N at the outlet station). Recall that the order of *REF/SLOW* subreaches varied among reaches.

At each station, samples for Cl⁻ and NO₃⁻ time series were collected in 30 mL scintillation vials using syringes and field filtration (Whatman GF/F).

For modeling purposes, solute time series were sampled over both stable and rapidly changing stages of enrichment. Specific conductivity was logged at each station using WTW meters. Prior to solute release, at least 4 $\text{Cl}^-/\text{NO}_3^-$ samples were collected at each station. After solute arrival, at least 20 $\text{Cl}^-/\text{NO}_3^-$ samples were collected at each station, with the exception of reach input stations (closest to pump) where less sampling was sufficient to accurately characterize the solute time series. High frequency Cl time series were constructed from Cl-specific conductivity relationships (Gooseff and McGlynn 2005). Discharge at each station was measured using one of the followings: dilution gaging, velocity \times area technique, mass balance technique, or culvert technique. Background ammonium-N (NH_4N), total N/P (TN/TP), total dissolved N/P (TDN/TDP), SRP, and DOC were sampled prior to each solute release. All water samples were kept on ice and in the dark following collection, then were either acidified (TN/TP, TDN/TDP) or frozen until analysis (all other analytes).

Channel surveys were conducted within 10 days following solute release. Wetted width (w) was measured using nine evenly spaced transects in each subreach. Percent of total substrata and percent coverage by macrophytes were estimated visually. Substrata classes were *finer* (silt, fine particulate organic matter), *sand*, *gravel*, *cobble*, and *coarse litter* (leaf fragments, twigs, roots). Macrophyte categories were *emergent* and *submerged*.

NO_3N (operationally, nitrate nitrogen + nitrite nitrogen) and the above N and P forms were analyzed using flow-injection analysis on an Astoria Pacific Instruments autoanalyzer (APIA). Cl was determined using a Dionex DX-500 ion chromatograph. DOC was determined using a Shimadzu carbon analyzer. Dissolved organic nutrients were estimated by difference ($\text{DON} = \text{TDN} - [\text{NO}_3\text{N} + \text{NH}_4\text{N}]$, $\text{DOP} = \text{TDP} - \text{SRP}$).

Modeling and Quantitative Analysis

Several studies have documented differences in nutrient uptake as a function of experimental enrichment concentration (Earl and others 2006, 2007; Mulholland and others 2002). We employed multiple rate solute releases (see Demars 2008) and a time series approach (see Powers and others 2009; see Runkel 2007) to produce NO_3N uptake estimates for a common range of low, unsaturated experimental NO_3N . In short, we used empirical information to restrict uptake calculations to an enrichment range at which the relationship between areal uptake rate ($\text{M L}^{-2} \text{t}^{-1}$) and nutrient

concentration is approximately linear (in accordance with first-order kinetics). This enabled an enrichment-standardized comparison of uptake between *REF* and *SLOW* subreach classes. Greater than $54 \mu\text{g L}^{-1}$ reach-centered absolute $\text{NO}_3\text{-N}$ was our exclusion criterion (empirically determined, see Appendix A in Supplementary material), as partial uptake saturation was sometimes detected near this enrichment level. The observation of under-saturated NO_3N kinetics below this enrichment level is supported by previous stream literature; O'Brien and Dodds (2010) reported a Michaelis-Menten half-saturation coefficient (K_s) of $67 \mu\text{g L}^{-1}$ for NO_3N uptake in prairie streams. Grimm and Fisher (1986) reported a threshold of $55 \mu\text{g L}^{-1}$ NO_3N for N limitation of stream periphyton growth.

NO_3N uptake was estimated from modeling of conservative (Cl) transport and nonconservative (NO_3N) transport using one-dimensional transport (advection-dispersion) with inflow and storage model (OTIS; Bencala and Walters 1983). The model has been thoroughly described in previous works (for example, Runkel 1998; Stream Solute Workshop 1990) and accounts for hydrologic gains/losses, exchange of solute between *MC* and *TS* zones, and disappearance of solute due to biotic uptake or transformation, given by:

$$\frac{\partial C}{\partial t} = -\frac{Q}{A} \frac{\partial C}{\partial x} + \frac{1}{A} \frac{\partial}{\partial x} \left(AD \frac{\partial C}{\partial x} \right) + \frac{q_L}{A} (C_L - C) + \alpha (C_s - C) - \lambda C \quad (1)$$

$$\frac{dC_s}{dt} = \alpha \frac{A}{A_s} (C - C_s) - \lambda_s C_s \quad (2)$$

where conservative transport parameters include D (dispersion coefficient, $\text{L}^2 \text{t}^{-1}$), A (C cross-sectional area, L^2), A_s (TS zone cross-sectional area, L^2), α (exchange coefficient between *MC* and *TS* zones, t^{-1}), and NO_3^- uptake parameters include λ (*MC* zone uptake rate, t^{-1}) and λ_s (*TS* zone uptake rate, t^{-1}). We used multiple steps to estimate NO_3N uptake parameters (λ and λ_s). First, we used a nonlinear least squares routine (OTIS-P) to simulate conservative transport (no uptake; $\lambda = \lambda_s = 0$) of background-corrected Cl in each subreach by fitting parameters D , A , A_s , and α . Second, we limited outlet NO_3^- observations to those not exceeding $54 \mu\text{g L}^{-1}$ reach-centered, absolute $\text{NO}_3\text{-N}$ (which always retained at least 12 values following arrival of experimental NO_3^-) and used OTIS-P to fit λ and λ_s .

Mean and median water travel time owing to *TS* (F_{mean} , F_{med}^{200}) were calculated from the following

relationships described in Runkel (2002): $F_{\text{mean}} = A_s/(A + A_s)$; $F_{\text{med}}^{200} = F_{\text{mean}} \times c$, where c is $1 - e^{-Lz}$ and $L = 200$ m. Dahmkohler numbers (DaI , unitless), which express the degree of balance between downstream transport processes and TS zone processes, were calculated as $DaI = u^{-1} \times \alpha L(1 + A/A_s)$.

The observed flux of surface water NO_3^- inputs (M_0 , M) and simulated flux of nutrient outputs (M_x , M) were used to estimate the proportion of experimental NO_3^- inputs taken up by the ecosystem [$P = 1 - M_x/M_0$], and whole stream decay coefficient [$K = (u/L) \times P$]. High model uncertainty sometimes prevented simultaneous fitting of λ and λ_s , and in those instances we assumed $\lambda = \lambda_s$ to simulate ecosystem-level uptake metrics. Uptake velocity [$v_f = K \times \text{depth}$] was calculated. u and depth were obtained from modeled and measured values [$u = Q/A$, $\text{depth} = A/w$]. The proportion of total mass uptake owing to uptake by the TS zone (P_s) was estimated [$P_s = (M_0 - \hat{M}_x)/(M_0 - M_x)$], where $\hat{M}_x(M)$ is a flux of nutrient outputs occurring in an OTIS simulation with no MC zone uptake, estimated by fixing λ to 0 and λ_s to its determined value (see Runkel 2007). Areal uptake (U , $M L^{-2} t^{-1}$) and uptake length (S_w , L) were calculated ($U = v_f \times C$, $S_w = u/K$).

Paired t tests were used to compare differences between subreach classes ($REF/SLOW$, $first/second$) for ecosystem-level uptake (K , v_f) and hydrologic connectivity of $MC-TS$ zones (α , F_{med}^{200}). Parametric paired comparisons were used for the above, except in the case of v_f which was non-normally distributed according to the Shapiro test, and instead a Wilcoxon signed rank test was used. Statistical comparisons involving λ and λ_s could not be conducted because these parameters could not always be meaningfully estimated. Data from only one North Creek 2009 date were used in the previous analyses (NC, nearest to midpoint of study season) due to potential non-independence of values at this site. In addition to rank u , alternative subreach classification criteria were considered that also express differences in the flow characteristics of streams and wetlands. Classifying paired subreaches by rank Richardson number [$Ri = g \times \text{depth} \times u^{-0.5}$, dimensionless, where g is $9.81 \text{ m}^2 \text{ s}^{-1}$] for which a decrease indicates higher turbulence, or rank Froude number [$Fr = u \times 1/(g \times d)^{0.5}$, dimensionless] for which a decrease indicates more tranquil flow, was consistent with the classification based on rank u . Classifying paired subreaches based on rank Reynolds number [$Re = 4u \times r/\nu$, dimensionless, where r is the hydraulic radius, and ν is kinematic viscosity assumed to be $1 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$]

which decreases along the transition from lotic to lentic, was consistent with that of rank u , except for CI and LT.

Finally, we conducted a sensitivity analysis of P_s using published TS parameter sets. The published sources are listed in Appendix A (Table A in Supplementary material) and individual parameter sets are contained Appendix B (Supplementary material), and were used for simulation of P_s in Figure 5. Some literature sources reported reach-averaged discharge (Q) but no additional discharge information, and in these instances we assumed $Q_0 = Q$ and $q_L = 0$. A few studies involving small streams did not report D or L , and in those instances only, we assumed $D = 0.1 \text{ m}^2 \text{ s}^{-1}$ and $L = 200$ m. We then estimated two sets of P_s based on different assumptions ($\lambda_s:\lambda = 1.0$, with $\lambda = 1.00e^{-4} \text{ s}^{-1}$ and $\lambda_s = 1.00e^{-4} \text{ s}^{-1}$; $\lambda_s:\lambda = 5.0$, with $\lambda = 1.00e^{-4} \text{ s}^{-1}$ and $\lambda_s = 5.00e^{-4} \text{ s}^{-1}$) using simulated releases of nonconservative solute in OTIS (discussed in "Methods").

RESULTS

Hydrology and Habitat

We observed large gradients of hydraulics, hydrology, and channel form. u was substantially lower in $SLOW$ subreaches compared to REF subreaches (mean ratio 0.60; range of ratio 0.37–0.90), including two $SLOW$ values below 0.03 m s^{-1} , and six values below 0.07 m s^{-1} (Figure 2; see Table 3 for site abbreviations). Q and A ranged widely, from 19.2 to 194 L s^{-1} , and 0.32 to 4.3 m^2 , respectively. F_{mean} ranged from 0.075 to 0.54, indicating some TS zones represented a substantial proportion of total stream volume. Measures of hydrologic connectivity between TS and MC zones also ranged widely (α , $2.6e^{-5}$ to $1.3e^{-3}$; F_{med}^{200} , 0.02 to 0.38). Mean ratios of paired values ($SLOW:REF$) were 1.29 for α , and 3.37 for F_{med}^{200} , but these were highly variable and paired differences were not significantly different from zero. We found no significant differences between $first$ and $second$ subreaches for α or F_{med}^{200} . DaI ranged from 0.42 to 7.0 (with two exceptions: LO REF subreach, 9.8; ND $SLOW$ subreach, 11.9), suggesting reasonable balance between transport processes and TS zone processes, and reasonable TS parameter estimates. Substrata and aquatic vegetation varied among subreaches in relation to hydraulic gradients, and included some areas with abundant fine sediment, organic matter, and macrophytes. *Fines* dominated the substrata (median = 66%) followed by *sand* (median = 25%) which together represented greater than 70% within every subreach.

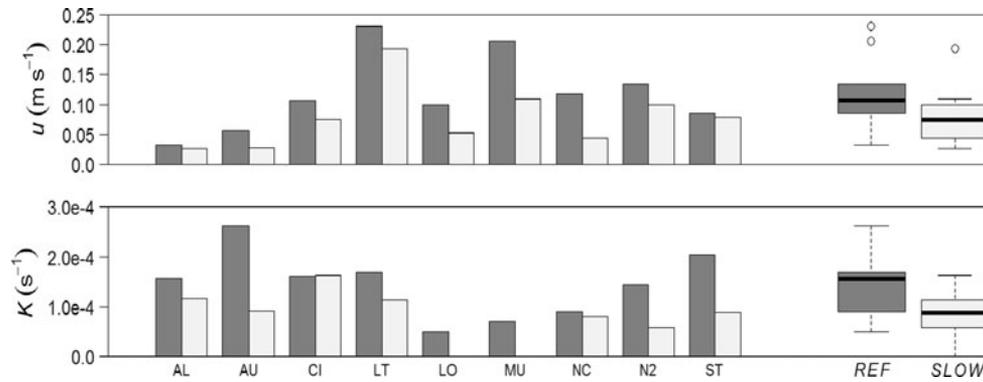


Figure 2. NO_3N uptake for paired reference (*REF*) and lower water velocity (*SLOW*) subreaches of northern Wisconsin streams and flow-through wetlands. *Dark gray REF; light gray SLOW*. The relative magnitude (rank) of mean velocity (u) was used to classify *REF* versus *SLOW* subreaches, and the mean difference in K between *REF* and *SLOW* subreaches is significant ($6.57e^{-5} \text{ s}^{-1}$ lower, or 44.7%, in *SLOW*; $P = 0.008$). Two of three additional visits to North Cr between May and August 2009 (not independent, not shown) also had lower K in the *SLOW* subreach. *Boxplot whiskers* are $1.5 \times$ interquartile range.

Ecosystem-Level Uptake

For 10 of 12 solute releases, ecosystem-level NO_3^- uptake rates (both K and v_f) were lower in *SLOW* relative to *REF* subreaches (Table 4). When limited to independent reaches shown in Figure 2, *SLOW* subreaches had 44.7% lower K on average ($n = 9$, $P = 0.008$ in paired t test). The four highest K values all occurred in *REF* subreaches (AU, ST, NA, and LT). Two cases, both in *SLOW* subreaches, had no detectable uptake (LO, MU). For North Cr, visited multiple times between May 2009 and August 2009, 3 of 4 cases had both lower K and lower v_f in the *SLOW* subreach; the exception was NB, when *REF* and *SLOW* values had overlapping confidence limits (1 s.d.). For reaches shown in Figure 2, *SLOW* subreaches had 25.3% lower v_f on average compared to *REF* subreaches ($n = 9$, not significant). In the two reaches where v_f was larger in the *SLOW* subreach (CI and LT), depth was larger and Re was lower relative to the *REF* subreach. A paired t test based on rank Re rather than rank u yielded 38.1% lower K ($P = 0.047$) and 52.5% lower v_f ($P = 0.001$) on average in the subreach with lower Re . Significant differences between paired subreaches (based on both rank u and rank Re) were upheld for K and v_f no matter which set of North Cr values (NA, NB, NC, or ND) were used. The *REF/SLOW* difference in v_f was marginally significant ($P = 0.09$, Wilcoxon signed rank test) when all North Cr values (NA, NB, NC, and ND) were used ($n = 12$). There was no statistically significant difference between *first* and *second* subreaches for K or v_f . The pattern of U between *REF/SLOW* subreaches

was consistent with that of v_f due to common background NO_3N within each study reach (recall $U = v_f \times C$). Overall, subreach NO_3^- losses (P) ranged from 0 to 43.8% of experimental inputs.

Uptake by *MC* and *TS* zones

NO_3^- uptake for *MC* and *TS* zones (λ and λ_s) was successfully partitioned in 12 of 22 instances with detectable NO_3^- loss. Here it is important to recognize that parameter error (1 s.d.) for λ_s was sometimes high (error:estimate > 1.0 in 6 instances). The ratio of *TS* uptake rate to *MC* uptake rate within a given subreach varied over one order of magnitude ($\lambda_s:\lambda$ from 0.1 to 6.0), including several values less than 1.0. The highest measure of *TS* uptake rate occurred in AU (*SLOW*, $\lambda_s = 3.6e^{-4} \text{ s}^{-1}$), and the highest measure of *MC* uptake rate occurred in the adjacent subreach (*REF*, $\lambda = 3.0e^{-4} \text{ s}^{-1}$). Thus, *TS* zones had a higher maximum but also a lower minimum ($\lambda_s = 1.4e^{-5} \text{ s}^{-1}$) relative to *MC* zones. The highest values of $\lambda_s:\lambda$ coincided with a weak *MC-TS* hydrologic connection (α and F_{med}^{200} , Figure 3). The ramifications of the previous pattern are demonstrated in Figure 4. In all but one model-fitted estimate, the proportion of ecosystem-level uptake (mass) attributable to *TS* zone uptake (P_s) was less than 0.30. The exception was the *SLOW* subreach of AU ($P_s = 0.44$) which had the highest reported $\lambda_s:\lambda$ value. Note that uncertainty for *TS* uptake rate was acceptable for the highest values of $\lambda_s:\lambda$, α , and F_{med}^{200} that drive the distributions in Figure 3.

Table 3. Hydrology and Geomorphology

Site name (abbreviation)	Date	Subreach class	Subreach position	Q (L s ⁻¹)	Water velocity (u, m s ⁻¹)	Width (m)	Depth (m)	F _{mean}	F _{med} ²⁰⁰	α (s ⁻¹)	Dal
Allequash Cr (AL)	Aug 27, 2009	REF	First	104	0.031	11.3	0.29	0.21	0.18	3.3E-04 ± 4E-05	3.2
			Second	112	0.026	21.6	0.20	0.48	0.38	2.0E-04 ± 2E-05	0.9
Aurora Cr (AU)	Aug 3, 2009	REF	Second	23	0.056	6.2	0.07	0.34	0.27	4.5E-04 ± 4E-05	2.1
			First	19	0.028	5.6	0.12	0.13	0.11	3.0E-04 ± 1E-04	3.1
Circle Lilly Cr (CI)	June 22, 2009	REF	Second	79	0.107	4.2	0.18	0.19	0.08	3.1E-04 ± 5E-05	2.3
			First	77	0.075	2.7	0.38	0.15	0.10	4.3E-04 ± 5E-05	4.6
			First	194	0.231	6.4	0.13	0.22	0.22	0.15	1.3E-03 ± 6E-05
Little Tamarack Cr (LT)	June 1, 2009	SLOW	Second	194	0.194	3.4	0.30	0.21	0.03	1.8E-04 ± 1E-04	1.1
			First	93	0.099	3.7	0.25	0.12	0.10	8.2E-04 ± 1E-04	9.8
Lost Cr (LO)	July 1, 2009	SLOW	Second	93	0.052	5.1	0.35	0.30	0.27	6.2E-04 ± 3E-04	3.9
			Second	176	0.206	3.6	0.23	0.26	0.13	7.4E-04 ± 3E-04	2.7
Muskellunge Cr (MU)	July 21, 2010	REF	Second	168	0.109	9.0	0.17	0.13	0.04	2.1E-04 ± 2E-05	3.1
			First	83	0.139	2.9	0.21	0.11	0.04	3.3E-04 ± 4E-05	4.6
North Cr (NA)	May 27, 2009	SLOW	Second	93	0.079	8.2	0.14	0.27	0.21	5.8E-04 ± 8E-05	6.6
			First	44	0.122	2.9	0.13	0.07	0.01	1.2E-04 ± 1E-05	2.7
North Cr (NB)	June 15, 2009	SLOW	Second	51	0.070	8.2	0.09	0.25	0.19	5.1E-04 ± 7E-05	7.0
			First	60	0.117	2.6	0.19	0.15	0.02	7.8E-05 ± 2E-05	0.9
North Cr (NC)	July 18, 2009	REF	Second	63	0.044	9.7	0.15	0.35	0.04	2.6E-05 ± 9E-07	0.4
			First	39	0.106	3.0	0.12	0.14	0.07	3.9E-04 ± 3E-05	5.5
North Cr (ND)	Aug 5, 2009	SLOW	Second	42	0.058	9.7	0.07	0.30	0.28	8.6E-04 ± 2E-04	11.9
			Second	89	0.134	4.3	0.16	0.13	0.06	4.0E-04 ± 1E-04	5.0
North Cr2 (N2)	July 1, 2010	REF	First	81	0.099	7.2	0.11	0.24	0.14	4.0E-04 ± 1E-05	1.5
			First	28	0.086	4.8	0.07	0.54	0.20	2.0E-04 ± 2E-05	0.4
Stevenson Cr (ST)	July 28, 2009	SLOW	Second	34	0.078	7.4	0.06	0.30	0.18	3.4E-04 ± 1E-05	1.8

Measures of hydrologic connectivity between MC and TS zones include F_{med}²⁰⁰ (proportion of median water travel time owing to TS) and α . F_{mean} is mean water travel time owing to TS (A_v/A + A_d). Errors are 1 SD from model fits.

Table 4. Measures of Nutrient Uptake

Site name (abbreviation)	Date	Subreach class	Subreach position	Background NO ₃ N (mg L ⁻¹)	Ecosystem-level uptake			Zone-level uptake				
					Uptake rate (K, s ⁻¹)	Uptake velocity (v _p , m s ⁻¹)	Uptake Length (S _{wr} , m)	P	MC uptake rate (λ, s ⁻¹)	TS uptake rate (λ _{sv} , s ⁻¹)	P _s	
Allequash Cr (AL)	Aug 27, 2009	REF	First	0.006	1.6E-04 ± 3E-05	4.6E-05	3.0E-04	200	0.32	1.7E-04 ± 5E-05	1.7E-04	-
		SLOW	Second	0.006	1.3E-04 ± 8E-06	2.6E-05	1.6E-04	198	0.27	1.4E-04 ± 4E-07	3.2E-05 ± 2E-05	0.13
Aurota Cr (AU)	Aug 3, 2009	REF	Second	0.005	2.7E-04 ± 7E-06	1.8E-05	9.6E-05	210	0.43	3.0E-04 ± 2E-07	1.8E-04 ± 8E-07	0.16
		SLOW	First	0.005	9.2E-05 ± 5E-05	1.1E-05	6.1E-05	304	0.12	6.0E-05 ± 4E-05	3.6E-04 ± 3E-04	0.44
Circle Lilly Cr (CI)	June 22, 2009	REF	Second	0.006	1.6E-04 ± 1E-04	2.8E-05	1.7E-04	664	0.22	1.6E-04 ± 6E-05	1.3E-04 ± 6E-04	0.29
		SLOW	First	0.006	1.6E-04 ± 8E-05	5.4E-05	3.5E-04	462	0.26	1.4E-04 ± 7E-05	3.3E-04 ± 3E-04	0.24
Little Tamarack Cr (LT)	June 1, 2009	REF	First	0.003	1.7E-04 ± 9E-07	2.2E-05	7.5E-05	1368	0.18	1.8E-04 ± 4E-07	1.9E-05 ± 1E-06	0.03
		SLOW	Second	0.005	1.1E-04 ± 5E-05	3.3E-05	1.6E-04	1721	0.14	1.0E-04 ± 4E-05	9.2E-05 ± 2E-04	0.15
Lost Cr (LO)	July 1, 2009	REF	First	0.024	5.1E-05 ± 3E-05	1.3E-05	3.1E-04	1933	0.07	4.7E-05 ± 4E-05	4.7E-05	-
		SLOW	Second	0.023	0.0	0.0	0.0	Infinite	0.0	0.0	0.0	-
Muskellunge Cr (MU)	July 21, 2010	REF	Second	0.006	7.1E-05 ± 7E-05	1.7E-05	1.0E-04	2913	0.07	6.6E-05 ± 4E-05	2.3E-05 ± 2E-05	0.10
		SLOW	First	0.007	0.0	0.0	0.0	Infinite	0.0	0.0	0.0	-
North Cr (NA)	May 27, 2009	REF	First	0.010	1.8E-04 ± 3E-05	3.8E-05	3.6E-04	759	0.28	1.9E-04 ± 4E-05	1.9E-04	-
		SLOW	Second	0.011	6.6E-05 ± 2E-05	9.4E-06	1.0E-04	1204	0.20	5.5E-05 ± 3E-05	5.5E-05	-
North Cr (NB)	June 15, 2009	REF	First	0.006	6.2E-05 ± 2E-05	7.9E-06	4.7E-05	1955	0.11	4.9E-05 ± 1E-05	2.5E-04 ± 1E-04	0.24
		SLOW	Second	0.008	7.5E-05 ± 2E-05	6.7E-06	5.1E-05	935	0.26	8.2E-05 ± 2E-05	1.4E-05 ± 4E-05	0.05
North Cr (NC)	July 18, 2009	REF	First	0.005	9.1E-05 ± 3E-05	1.8E-05	8.0E-05	1287	0.16	8.8E-05 ± 3E-05	8.8E-05	-
		SLOW	Second	0.007	8.0E-05 ± 9E-06	1.2E-05	8.2E-05	548	0.44	9.1E-05 ± 2E-05	9.1E-05	-
North Cr (ND)	Aug 5, 2009	REF	First	0.008	1.1E-04 ± 2E-05	1.3E-05	1.0E-04	976	0.22	1.1E-04 ± 3E-08	6.6E-05 ± 1E-04	0.07
		SLOW	Second	0.010	9.6E-05 ± 5E-06	7.1E-06	7.4E-05	606	0.40	9.0E-05 ± 8E-06	9.0E-05	-
North Cr2 (N2)	July 1, 2010	REF	Second	0.009	1.5E-04 ± 4E-05	2.3E-05	2.0E-04	924	0.23	1.4E-04 ± 5E-05	1.4E-04	-
		SLOW	First	0.008	5.9E-05 ± 6E-05	6.7E-06	5.0E-05	1674	0.06	4.9E-05 ± 7E-05	4.9E-05	-
Stevenson Cr (ST)	July 28, 2009	REF	First	0.006	2.1E-04 ± 5E-05	1.4E-05	7.8E-05	421	0.24	1.2E-04 ± 4E-05	1.7E-04 ± 2E-04	0.15
		SLOW	Second	0.005	8.9E-05 ± 9E-06	5.2E-06	2.4E-05	880	0.15	7.0E-05 ± 1E-05	7.0E-05	-

Ecosystem-level uptake was partitioned into zone-level components (MC main channel, TS transient storage); P proportion of experimental NO₃N inputs taken up by the ecosystem; P_s proportion of total uptake owing to TS zone uptake (reported if λ_s was partitioned). Errors are 1 SD from model fits.

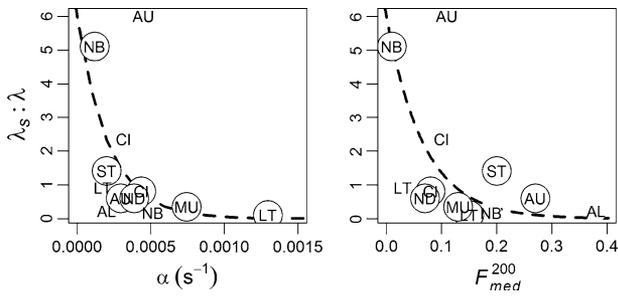


Figure 3. *TS* zone nutrient uptake rate and the strength of hydrologic connection to main nutrient flow. Two different measures of hydrologic connectivity between *TS* and *MC* zones are provided: α (exchange rate between *MC* and *TS* zones, t^{-1}), and F_{med}^{200} (proportion of median water travel time owing *TS* zone storage, unitless). $\lambda_s:\lambda$ is the rate of *TS* uptake relative to *MC* uptake for a given subreach. Uncircled low water velocity subreaches (*SLOW*). Circles reference (higher water velocity) subreaches (*REF*). Dashed lines negative exponential fits ($y \sim a * e^{-bx}$) with $a = 6.0$.

DISCUSSION

Differences in Ecosystem-Level Uptake

The contribution of different systems to nutrient retention within river networks depends on nutrient processing rate, water residence time, and hydrologic connections between nutrient sources

and sinks. Our results emphasize both the individual importance and the inter-relatedness of those factors across widely contrasting system types. Further, we provide a counter example to the idea that wetlands have disproportionately high nutrient processing rates. Rather, the four highest values of ecosystem-level uptake (K) occurred in reference (*REF*) stream systems, which also had higher uptake rates on average when compared to lower water velocity (*SLOW*) systems (Figure 2). This suggests lower uptake efficiency in flow-through wetlands relative to streams, for which there are at least three supporting lines of evidence. First, the pattern of lower uptake rates in *SLOW* subreaches was upheld in the temporal study element of North Creek for three of four visits that occurred in different months. Second, the pattern was not restricted to the metric K , as the magnitude of v_f was also lower for *SLOW* subreaches in all but two reaches (CI and LT); note that CI and LT had modest longitudinal contrasts for u , and were also the only reaches where Re was lower in the *REF* subreach. Third, the only two subreaches which had undetectable uptake were of the *SLOW* class, indicating flow-through wetland systems had not only lower uptake rates overall but also in some cases were clearly cold spots for NO_3^- uptake. Overall, our findings are consistent with the idea

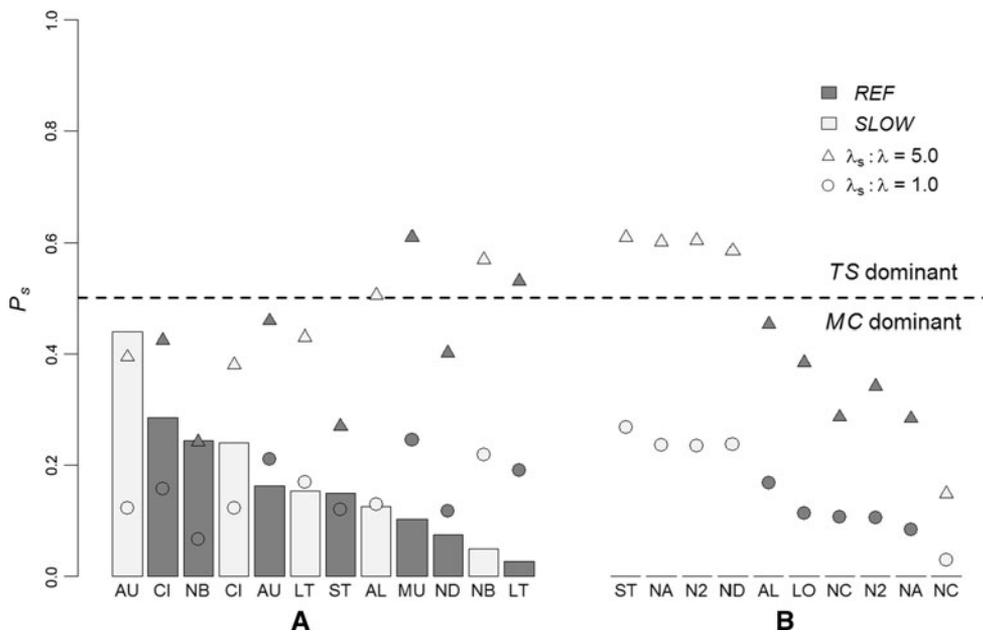


Figure 4. Contribution of *TS* zones to total NO_3N uptake for northern Wisconsin streams and flow-through wetlands. P_s proportion of ecosystem-level mass uptake owing to uptake in the *TS* zone. For subreaches in which uptake was detectable ($n = 22$), P_s values were simulated based on two alternative assumptions (circles balanced *TS* uptake rate, $\lambda_s:\lambda = 1.0$; triangles high *TS* uptake rate, $\lambda_s:\lambda = 5.0$). For group A, model-fitted P_s estimates were available from partitioned estimates of λ_s and λ (bars). For group B, model-fitted estimates were not available (ordered by circle height).

that uptake efficiency declines as water velocity slows along the transition from lotic to lentic, resulting in a tradeoff between uptake efficiency and water residence time. This tradeoff counteracts the otherwise expected pattern of increasing nutrient retention with increasing water residence time, and is likely important for wetlands and *TS* zones of streams that possess either lentic or laminar flow conditions.

Hydrologic connections within ecosystems modulate nutrient supplies to biota, and were likely important to ecosystem-level NO_3^- uptake in our study. Measures of hydrologic connectivity between *MC* and *TS* zones (α and F_{med}^{200}) ranged over one order of magnitude, whereas hydraulics (water velocity, shear stress, turbulence) also included diverse conditions ranging from laminar flow to turbulent flow. This included u down to 0.026 m s^{-1} and F_{med}^{200} up to 0.38, as well as stream conditions more consistent with those previously reported (see Appendix B in Supplementary material). The above gradients can lead to differences in local nutrient supplies to algae and microbes. For example, several studies have shown a positive effect of water motion on algal uptake of N (Gerard 1982; Parker 1981) and P (Schumacher and Whitford 1965) which promotes transport across boundary layers of cells (Borchardt 1996; Munk and Riley 1952). Also, at intermediate levels between that of the cell and the ecosystem, preferential flowpaths within surface, parafluvial, or hyporheic zones can circumvent the biota (Kadlec and Wallace 2009; Lightbody and others 2008). This phenomenon (hydrologic “short-circuiting”) was observed during pilot fluorescein (dye) releases in the *SLOW* subreach of North Cr, and is a common feature of constructed wetlands. Alternatively, the difference in K between *SLOW* and *REF* subreaches could be related to a difference in gross primary production (for example, Hall and Tank 2003). However, this seems inconsistent with our results because *SLOW* subreaches often had shallow depths and abundant benthic and epiphytic algae.

Our ability to detect a difference in nutrient uptake between *REF* and *SLOW* subreaches was facilitated not only by substantial differences in hydraulic measures but also elements of experimental design. For example, we ensured uptake estimates were associated with a low level of enrichment ($< 54 \mu\text{g L}^{-1}$, reach-centered absolute NO_3N). Lack of a statistical difference between *first/second* subreach classes for K and v_f also suggests that uptake metrics were successfully standardized to a common, low range of NO_3^- enrichment. It is nonetheless important to recognize some study

limitations when interpreting our findings. Given the timing of the research (summer baseflow conditions), the ecosystem-level difference in K between *REF* and *SLOW* subreaches may not be upheld for other times of year, changing flow states in relation to precipitation or snowmelt, or longer time scales that incorporate such dynamics. Also, in-channel solute releases do not incorporate biological activity along upwelling groundwater flowpaths which have source waters external to the surface stream. Thus, some potentially important sites and times of aquatic nutrient retention are not represented in our work. However, our results are likely representative for most of the period between cessation of snowmelt and onset of leaf-fall in northern Wisconsin streams and wetlands. Candidate NO_3^- fates for our study include (a) uptake by algae or microbes, (b) denitrification by microbes (transformation to nitrogenous gases), and (c) dissimilatory nitrate reduction to ammonium by microbes (DNRA, transformation to ammonium). Due to the short spatio-temporal scale of solute releases (meters to kilometers, hours to days) and predominance of oxygenated surface waters (*MC* as well as surface *TS* zones), NO_3^- uptake here is most likely attributable to algal or microbial uptake. Finally, we stress that even when uptake efficiency is low, the biogeochemical importance of wetlands can still be realized through high water residence time (and thus total nutrient mass), through denitrification of groundwater-N, and through remineralization of organic matter stores which provide an energy source to downstream ecosystems.

Uptake by *MC* and *TS* zones

TS zones encompass multiple habitat types that can serve different biogeochemical roles, but by most accounts, are commonly viewed as hot spots for nutrient uptake within rivers. Our results are not completely consistent with this view. In support, the highest recorded measure of uptake did occur in the *TS* zone (AU *SLOW* subreach, $3.6e^{-4} \text{ s}^{-1}$), and the ratio of *TS:MC* uptake was substantial in certain cases ($\lambda_s:\lambda > 5.0$ in two subreaches, Figure 3). For comparison, McKnight and others (2004) reported uptake estimates for an Antarctic stream, including the highest value of $\lambda_s:\lambda$ we have found in the literature at this time for NO_3^- uptake (7.8). But in contrast, our results also emphasize that *TS* zones can be cold spots for uptake relative to *MC* zones ($\lambda_s:\lambda < 1.0$ in 7 of 12 instances), leading to a higher range and coefficient of variation for *TS* zone uptake relative to *MC* zones. Some estimates of *TS* zone uptake rates

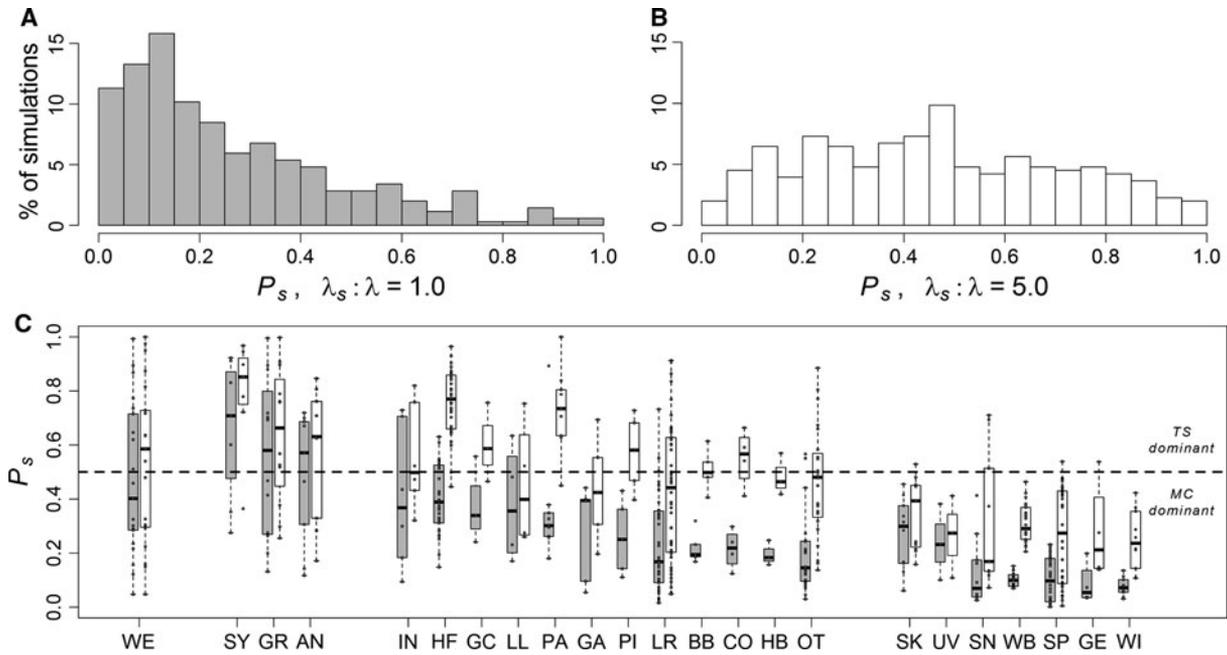


Figure 5. Simulated contribution of *TS* zones to total nutrient uptake for streams, rivers, and flow-through wetlands from published studies. *TS* parameter sets were compiled from the literature ($n = 295$, Appendices A and B in Supplementary material) to simulate P_s (proportion of ecosystem-level mass uptake owing to uptake by the *TS* zone). Two different P_s estimates are provided for each data set: **A** balanced *TS* uptake rate ($\lambda_s:\lambda = 1.0$) which corresponds to a reasonable estimate of P_s for most streams and rivers; **B** high *TS* uptake rate ($\lambda_s:\lambda = 5.0$) which corresponds to an upper bound of P_s for most streams and rivers). **C** An inter-site comparison of P_s from above. Flow-through wetland (*WE*) sites were so described by the authors, and each had mean water velocity less than 0.06 m s^{-1} . We propose three additional classes of lotic ecosystems that are grouped to the right of *WE* sites: (1) *TS dominant* (left), contribution to ecosystem-level nutrient retention (P_s) trends greater than 0.5 regardless of uptake scenario; (2) *TS sensitive* (center), P_s trends greater than 0.5 for high *TS* uptake rate only; (3) *MC dominant* (right), P_s trends less than 0.5 regardless of uptake scenario. Note that systems of the *TS dominant* class are known to have large hyporheic zones. *Boxplot whiskers* are $1.5 \times$ interquartile range for available data in each group, some of which include replication in time or space. Site codes refer to streams and rivers located in USA unless otherwise indicated: *WE* (flow-through wetland sites), *SY* (Sycamore Cr, AZ), *GR* (Green Cr, Antarctica), *AN* (streams of Andrews Experimental Forest, OR), *IN* (Indian Cr, PA), *HF* (streams of Hubbard Brook Experimental Forest, NH, excluding Hubbard Brook and Bear Brook), *GC* (Goodwin Cr, MS), *LL* (Little Lost Man Cr, CA), *PA* (Pajaro R, CA), *GA* (Gallina Cr, NM), *PI* (Pinal Cr, AZ), *BB* (Bear Brook, NH), *CO* (streams at Coweeta Hydrologic Laboratory, VA), *HB* (Hubbard Brook, NH), *SK* (St. Kevin Gulch, CO), *UV* (Uvas Cr, CA), *LR* (large rivers from Cheong and Seo 2003, including Mississippi R and Missouri R), *SN* (Snake R, CO), *WB* (West Fork Walker Branch, TN), *SP* (streams and rivers of Spain), *GE* (streams of Germany), Wisconsin (streams of southern Wisconsin). Remaining P_s values, each from sites with n less than 3 sets of *TS* parameters, are plotted together as one group (other, *OT*).

should be interpreted with caution due to high uncertainty, which could in part reflect aggregation of modeled *TS* uptake into one rather than multiple compartments (Briggs and others 2009). Here, we emphasize the surface dominance of total *TS* in our sites, which had low slopes and in general were densely occupied by macrophytes, algae, and detritus. *SLOW* subreaches contained visually apparent surface backwaters caused by lateral (fringing) vegetation, interior ponds, and occasionally, braided channels characteristic of flow-through wetlands. Meanwhile, reaches of

this study lacked coarse substrata (Table 2), and both *REF* and *SLOW* subreach classes had abundant fine sediment and organic matter deposits which can obstruct hyporheic solute exchange (*finer* >50% in 5 *REF* subreaches, and *finer* >70% in 6 *SLOW* subreaches). Also, for sites from Briggs and others (2010), the proportion of median water travel time owing to surface *TS* was more than 5-fold higher than that owing to hyporheic *TS*. We suspect the contribution of surface *TS* to total *TS* is important in many streams and rivers.

Zone-Specific Contributions to Nutrient Retention of the Ecosystem

Although the idea of biogeochemical hot spots has received much attention in recent ecological research, it is important to recognize that some hot spots do not contribute substantially to nutrient retention of whole ecosystems or river networks. For example, compared to hot spots that are hydrologically well-connected to nutrient sources, poorly connected hot spots have a diminished capacity to influence ecosystem-level nutrient retention and may not measurably alter nutrient transport. Figure 3 also shows that for *TS* zones of streams and flow-through wetlands, high *TS* uptake rate corresponded to low hydrologic connectivity to *MC* nutrient flow (by two different measures), which in our study is probably explained by a high ratio of reactive surface area to water volume in surface *TS* zones (for example, high coverage by macrophytes, algae, or detritus). In turn, the previous tradeoff should impose a strong restriction to the contribution of *TS* zones toward ecosystem-level nutrient retention (see Findlay 1995 for a similar characterization of the hyporheic zone); Figure 4 confirms this expectation. In our study, *TS* zone uptake never accounted for greater than 50% of total uptake by the ecosystem, seldom greater than 30% (1 of 12 instances), and only sometimes greater than 20% (4 of 12 instances). To date, a few other studies have provided estimates of zone-specific mass nutrient uptake. Those revealed that *TS* zones accounted for 0.01–21.7% of NO_3^- uptake in an Antarctic meltwater stream (Runkel 2007), 44–49% of NO_3^- uptake in a south Appalachian stream (Thomas and others 2003), and 52–85% of NH_4^+ uptake in tropical headwater streams (Gucker and Boechat 2004). Recognizing uncertainty for *TS* uptake, Figure 4 also shows that even under simulated conditions of high *TS* uptake rate ($\lambda_s:\lambda = 5.0$, probably not a realistic expectation for most lotic ecosystems), the majority of subreaches (14 of 22) still maintained P_s less than 0.50. In summary, across diverse streams and flow-through wetlands of northern Wisconsin, NO_3^- uptake was either weakly dominated or strongly dominated by *MC* (thalweg) mechanisms of uptake, which likely reflects biotic uptake by algal mats. Because nutrient movement is linked to water movement for both aquatic and terrestrial systems, hydrologic connections could modulate the role of biogeochemical hot spots in a broad sense.

An important question remains: How widespread is the dominance of *MC* uptake across streams and

ivers of the globe? Figure 5 attempts to answer this question, which remains a subject for future research. For *TS* parameter sets compiled from the literature (Appendices A, B in Supplementary material), we modeled two *TS* uptake scenarios: high *TS* uptake rate within the reach ($\lambda_s:\lambda = 5.0$), and uniform uptake rate within the reach ($\lambda_s:\lambda = 1.0$). Figure 5A shows that under the more plausible assumption of $\lambda_s:\lambda = 1.0$, the distribution of P_s has a high positive skew and a mean of 0.26 ($P_s > 0.3$ in only 33% of the data sets). Based on results of this article which show instances of $\lambda_s:\lambda$ less than 1.0, we suspect Figure 5A may still overestimate P_s in some cases. Figure 5B shows that even under the assumption of high *TS* uptake rate at all sites ($\lambda_s:\lambda = 5.0$), P_s has a mean of 0.43 ($P_s > 0.5$ in 36% of the data sets). Figure 5C shows that for a small number of systems, using either scenario, the proportion of ecosystem-level mass uptake owing to uptake in the *TS* zone (P_s) does commonly exceed 0.50, and occasionally exceeds 0.75. However, P_s less than 0.50 is more frequent, and many systems appear incapable of yielding P_s greater than 0.50. Overall, Figure 5 provides strong evidence that the pattern of *MC* dominance is not restricted to our sites in northern Wisconsin, USA; rather it is a widespread characteristic across system sizes, regions, and *TS* zone types. This has important ramifications for river nutrient deliveries because aquatic organisms of lotic versus lentic systems have different nutritional requirements, and decompose in a different fashion upon death.

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