Ecosystems
https://doi.org/10.1007/s10021-018-0236-2

ECOSYSTEMS

Sediment–Water Surface Area Along Rivers: Water Column Versus Benthic

John R. Gardner* and Martin W. Doyle

Nicholas School of the Environment, Duke University, Environmental Hall, 9 Circuit Drive, Durham, North Carolina 27708, USA

Abstract

Aquatic ecosystems have two distinct zones: the water column and benthic zone. Although the benthic zone has received considerable attention, recent studies have found the water column capable of accounting for a majority of whole ecosystem processes in rivers. The relative role of these zones inevitably varies across a size continuum of rivers, from headwaters to large transcontinental systems. A fundamental question in aquatic science is where along this size continuum do ecosystem processes potentially shift from occurring largely in the benthic zone to largely in the water column? Sediment structures the physical template of the benthic and water column zones of rivers and the contact area between water and sediment mediates ecological, geochemical, and physical processes. High concentrations of suspended sediments are hypothesized to cause a shift from benthic to water column dominance in rivers. We developed an analytical model for the contact area between surface water and all sediment particles in benthic and water column volumes. The model was implemented with empirical data along the main stem of major US rivers. The ratio of water column to benthic sediment contact area scaled as a power function of watershed area. There was more sediment–water contact area in the water column than the benthic zone in rivers equal to or greater than 5th to 9th order depending on the river basin. This suggests material processing could be occurring largely in the water column in rivers greater than 5th order. However, dams and variation in discharge caused rivers to oscillate between water column and benthic dominance over time and space.

Key words: suspended sediment; aquatic ecosystems; water column; benthic; large rivers; river continuum; surface area.

Introduction

Aquatic systems can be broadly conceptualized as having two distinct zones in the vertical dimension: the water column and the benthic zone (Wetzel 2001). These zones may have different concentrations of nutrients and organic matter, rates of ecological processes, and assemblages of organisms, but both influence whole ecosystem function. However, the relative role of these zones across the size continuum of aquatic ecosystems is not well known. Generally, in small systems—ponds, wet-

Received 30 May 2017; accepted 17 February 2018

Electronic supplementary material: The online version of this article (https://doi.org/10.1007/s10021-018-0236-2) contains supplementary material, which is available to authorized users.

Authors Contributions JRG contributed to concept development, analysis, and manuscript development. MWD contributed to concept and manuscript development.

Corresponding author; e-mail: johngardner87@gmail.com

Published online: 05 March 2018

lands, or headwater streams—the benthic zone is considered a major driver of ecosystem processes (Covich and others 1999; McKnight and others 2004; Alexander and others 2007). For example, most primary and secondary production occurs on the benthic sediment of small streams (Waters 1977; Lamberti and Steinman 1997) along with high rates of nutrient removal (Alexander and others 2007; Mulholland and others 2008). In larger systems—large lakes, large rivers, and coastal waters—the water column becomes increasingly relevant for many of the same processes (Vannote and others 1980; Caspers 1981; Wetzel 2001; Seitzinger and others 2002). Because rivers traverse this continuum of size, from ephemeral gullies to the outlets of transcontinental rivers, a fundamental question in aquatic science is where along this size continuum do ecosystem processes shift from occurring largely in benthic zone to largely in the water column?

It is critical to understand the relative role of water column and benthic processes across river size for scaling functions and processes across a river basin. Scale is among the key challenges in ecosystem ecology (Carpenter and Turner 2017; Scholes 2017) and a central theme in the study of rivers (Vannote and others 1980; Frissell and others 1986; Poole 2002; Thorp and others 2006; McCluney and others 2014). In conceptual and numerical models of river basins, material processing rates are typically scaled across river size based on a physical metric, such as wetted perimeter or water depth (Seitzinger and others 2002; Alexander and others 2009; Bertuzzo and others 2017; Helton and others 2018; Ye and others 2017). This scaling approach assumes material processing occurs exclusively in the benthic zone, while the water column is treated simply as a vector for transport. Yet, many ecosystem processes occur in the water and are increasingly recognized (Battin and others 2008; Millar and others 2015; Reisinger and others 2015). The River Continuum Concept predicted that primary production in rivers greater than 5th order would be dominated phytoplankton rather than benthic periphyton (Vannote and others 1980; Descy and Gosselain 1994). More recently, Reisinger and others (2016) found that water column denitrification accounted for a majority of the whole ecosystem denitrification in moderate sized rivers. Reisinger and others (2015) found water column nutrient uptake was occurring at significant rates from 1st- to 5th-order rivers, and ammonium uptake increased with river size. Furthermore, Marzadri and others (2017) showed that nitrous oxide was increasingly produced in the water column relative to the benthic zone as river size increased. Collectively, these studies emphasized that water column processes increase with river size.

The load of suspended materials, such as sediment, increases with river size (Meybeck and others 2003) and is hypothesized to stimulate water column material processing (Millar and others 2015; Reisinger and others 2015; Marzadri and others 2017). Sediment is a workbench for reactivity and structures the physical environment of both the water column and benthic zone. Sediment particles provide habitat for organisms and materials (Mendoza-Lera and others 2017), while water delivers additional nutrients, organic matter, organisms, and other materials that can adsorb, desorb, and aggregate with sediment or are transformed by sediment-associated microbes (Horowitz and Elrick 1987; Zimmermann-Timm 2002; Wotton 2007). The large contact area between surface water and benthic sediment has been considered a driver of ecosystem processes in headwater steams (Peterson and others 2001; Mulholland and others 2008; Gomez-Velez and others 2015), and the surface area of suspended sediments should also be a driver of water column processes. In fact, a majority of the bacterial production and enzymatic activity in the riverine water column occurs on suspended sediments (Ochs and others 2009; Liu and others 2013; Jackson and others 2014; Millar and others 2015). The studies highlighted above suggested that greater concentrations of suspended sediments may increase the role of the water column in whole ecosystem processes. However, few studies have quantified the relative importance of the water column and benthic zones for ecosystem processes as river size increases.

We incorporated broad downstream patterns in suspended sediment, sediment size, and other hydrogeomorphic characteristics into a simple analytical model that estimates the ratio of water column to benthic sediment–water contact area, referred to as the surface area ratio (R_{SA}). Henceforth, sediment–water contact area will be referred to as either benthic or suspended sediment surface area. Confronting the model with data along the main stem of major US rivers, we set out to answer three questions. What is the pattern of the ratio of water column/benthic sediment surface area along a river? Where along a river is there more water column than benthic sediment surface area? How does this vary with river discharge?

Methods

Model

Our model was based on hydrologic and geomorphic principles and estimates the sum of the surface areas of all individual sediment particles in contact with surface water in the benthic and water column zones within a bounded river reach. Conceptually, this required estimating the total number of sediment particles within a water column or benthic volume multiplied by the surface area of a sediment particle. We were primarily interested in broad patterns within and across rivers and the relative comparison between the water column and benthic zones; therefore, we applied a simple approach that is not intended to capture all interactions (for example, there are no time-varying parameters, and suspended sediment size does not vary with discharge).

The surface area of suspended sediment particles ($\mathrm{SA_s}$) was calculated as a function of sediment concentration, water volume of a reach, and sediment size assuming a spherical, uniform particle size

$$\mathrm{SA_s} = \frac{CbhL\frac{1}{\rho}}{\frac{4}{3}\pi 0.5 D_{50\mathrm{s}}^3} 4\pi 0.5 D_{50\mathrm{s}}^2 \qquad (1)$$

where C is suspended sediment concentration (kg m^{-3}), b is channel width (m), h is channel depth (m), L is channel length (m), ρ is sediment particle density (kg m^{-3}), and $D_{50\mathrm{s}}$ is the median suspended sediment diameter (m). In rivers, discharge is used to predict channel width, depth, velocity, and suspended sediment concentration as a power function generally known as rating curves (Leopold and Maddock 1953). We inserted rating curve functions for suspended sediment and channel dimensions and assumed a 1-m-long rectangular reach

$$\mathrm{SA_s} = \left(\frac{aQ^b cQ^d eQ^f \frac{1}{\rho}}{\frac{4}{3}\pi 0.5 D_{50\mathrm{s}}^3}\right) 4\pi 0.5 D_{50\mathrm{s}}^2 \qquad (2)$$

where Q is discharge (m^{-3} s^{-1}), a and b are coefficients for the width rating curve, c and d are coefficients for the depth rating curve, and e and f are coefficients for the sediment rating curve (kg m^{-3}). The rating curve expressions represent width (m), depth (m), and suspended sediment concentration (kg m^{-3}). This expression is further simplified by combining rating curve coefficients

$$\mathrm{SA_s} = \frac{3\omega Q^\lambda}{D_{50\mathrm{s}}\rho} \qquad (3)$$

where ω and λ are lumped rating curve parameters for suspended sediment concentration, width, and depth ($\omega = ace$ and $\lambda = b + d + f$).

The surface area of benthic sediment particles ($\mathrm{SA_b}$) is a function of channel width, channel depth, depth of surface water penetration into benthic sediment (hyporheic depth), porosity, and benthic sediment particle size. We assumed a spherical, uniform particle size and 1-m-long rectangular channel, leading to

$$\mathrm{SA}_b = \left(\frac{L(b+2h)(1-\phi)H}{\frac{4}{3}\pi 0.5 D_{50b}^3}\right) 4\pi 0.5 D_{50b}^2 \qquad (4)$$

where b is channel width (m), L is channel length (m), h is channel depth (m), ϕ is the porosity (dimensionless), $D_{50\mathrm{b}}$ is the median benthic sediment size (m), and H is the hyporheic depth (m). Again, we inserted rating curves for width and depth and simplified

$$\mathrm{SA}_b = \left(\frac{3H\left(aQ^b + 2cQ^d\right)(1-\phi)}{D_{50b}}\right) \qquad (5)$$

The ratio of suspended to benthic sediment surface area (R_{SA}) was found by dividing equations 3 by 5 and simplifying

$$R_{\mathrm{SA}} = \frac{D_{50b}\omega Q^\lambda}{\rho D_{50\mathrm{s}} H(aQ^b + 2cQ^d)(1-\phi)} \qquad (6)$$

This is a simple, physical expression for R_{SA} within a bounded river reach; however, our question was how R_{SA} changes along a river. Therefore, we extended this model along a river continuum by linking parameters to location along a river. Parameters with known or hypothesized general downstream trends were linked to location including Q, $D_{50\mathrm{b}}$, $D_{50\mathrm{s}}$, and H using empirical data, physical relationships, or heuristic approaches. Other parameters could not be related to location along a river due to inconsistent trends, such as hydraulic geometry and suspended sediment rating curve exponents (Asselman 2000), or due to lack of field data and presumed insignificant downstream variability, such as porosity and sediment density. These parameters were treated as either reach-specific or global parameters and are described further in the next section.

The median benthic particle size ($D_{50\mathrm{b}}$) was related to distance downstream according to the theory of downstream fining, or Sternberg's Law (Parker 1991; Pizzuto 1995) but was constrained to be no smaller than the smallest sediment size measured at a downstream location

$$D_{50b}(x) = D_o e^{-\alpha x} \tag{7}$$

where D_o is the most upstream D_{50b} (m), x is distance downstream (km), and α is a fitted parameter (m km^{-1}). We assumed the hyporheic depth (H) was proportional to the benthic sediment size and channel slope

$$H_{(x)} = \beta_D D_{50b(x)} + \beta_S S_{(x)} \tag{8}$$

where β_D and β_S are heuristic scaling parameters that link hyporheic depth to empirical data of sediment size and channel slope (S). This is not a physical relationship, and our assumptions were based on studies that showed less vertical exchange of water in larger rivers likely due to smaller sediment size (Gomez-Velez and Harvey 2014; Gomez-Velez and others 2015).

Suspended sediment size distributions and their downstream trends are not well documented (Walling and Moorehead 1989; Walling and others 2000); therefore, we linked D_{50s}–D_{50b}. We assumed that D_{50s} was three orders of magnitude smaller than D_{50b} at the upstream and downstream points and decreased linearly downstream between these points. This approach created relationships between suspended sediment size and benthic sediment size and assumed downstream suspended sediment fining consistent with empirical data (Walling and Moorehead 1989; Walling and others 2000).

Combining equations 6–8, we derived an expression for R_{SA} as a function of distance along a river

$$R_{SA(x)} = \frac{D_o e^{-\alpha x} \omega Q^{\lambda}_{(x)}}{\rho\left(\frac{D_o}{1000} - \beta_{ss} x\right)\left(\beta_D D_o e^{-\alpha x} + \beta_S S_{(x)}\right)\left(aQ^{b}_{(x)} + 2cQ^{d}_{(x)}\right)(1-\phi)} \tag{9}$$

where all parameters are as stated above and β_{ss} is the rate of the downstream change in median suspended sediment size.

As a first approximation, we assumed a uniform particle size distribution for benthic and suspended sediments equal to the median size of empirical particle size distributions. In addition to simplicity, there are limited data for most rivers on suspended sediment size distributions and how they change downstream. Suspended particle size distributions could be incorporated into our modeling framework. However, benthic particle size distributions cannot be incorporated since packing geometries must be considered. Particle packing is a complex numerical exercise itself (Jia and Williams 2001) and beyond the intent of this paper which is to document broad, basin scale trends.

Confronting the Model with Data

The model was parameterized to river reaches along the main stem of ten major US rivers. The rivers and river reaches (that is, USGS gauging stations) were selected based on specific requirements. Selected rivers required at least five river reaches that span most of the main stem length, and each reach required multiple years of continuous discharge, suspended sediment concentration, and channel dimension data. We also chose rivers across the USA to represent different physiographic regions (Figure 1). Datasets included discharge, suspended sediment concentration, channel dimensions, and benthic sediment size distributions from the US Geological Survey (USGS, http://waterdata.usgs.gov/nwis and http://cida.usgs.gov/sediment/), dam characteristics and locations from the National Inventory of Dams (NID, http://nid.usace.army.mil/cm_apex/f?p=838:12), and geospatial data for major rivers from the National Oceanic and Atmosphere Administration (NOAA, http://www.nws.noaa.gov/geodata/catalog/hydro/html/rivers.htm).

Global, river-specific, and reach-specific parameterization was used to implement the model with data at discrete river reaches along each river. Global parameters were constant across all rivers and reaches including particle density (ρ = 2650 kg m^{-3}), porosity (ϕ = 0.4764), and hyporheic depth scaling parameters (β_D = 20 and β_S = 15). This value of porosity was chosen because it is within the median range of empirical values reported in aquatic sediments (Avnimelech and others 2001), and it is the analytically derived porosity of cubic packing which is independent of sediment size (Tucker 2009). Porosity was treated as a constant because our sensitivity analysis showed that R_{SA} was not sensitive to porosity and little empirical data exist (see supplemental materials). The value of particle density was chosen because it is the standard density for sand and was approximately the median of empirical sediment density measurements across many rivers (Buffington and Montgomery 1997). Similarly, R_{SA} was not sensitive to sediment density. The hyporheic depth scaling parameters are were chosen to provide reasonable H values across all rivers.

River-specific parameters included the most upstream benthic sediment size (D_o), the benthic sediment downstream fining exponent (α), and the

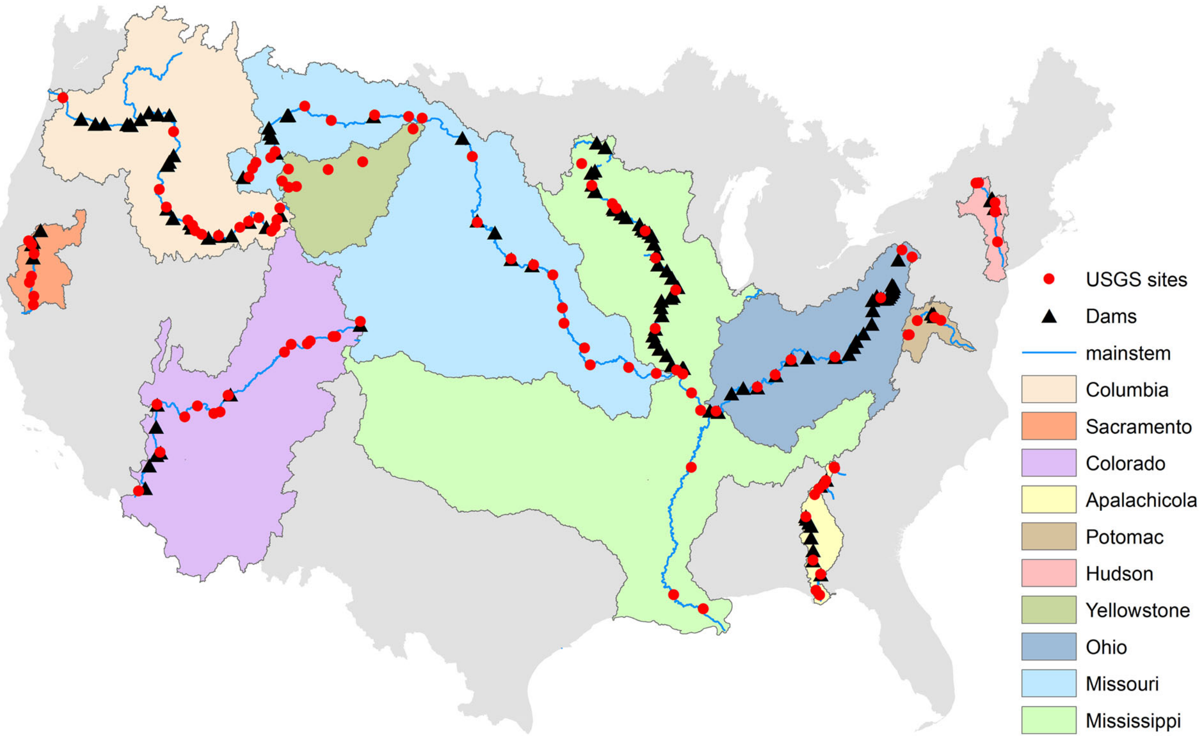

Figure 1. Map of USGS gauges where data were extracted and dams along the main stem of 10 major US river basins.

suspended sediment fining rate (β_{ss}). D_o and α were estimated by fitting equation 7 to empirical data and constraining estimates to be no smaller than the smallest downstream measurement. Field data for D_{50b} was not available in one database; therefore, we compiled values from the literature and existing datasets. For upstream locations, a literature value was typically found near the selected river reach. For more downstream sites, sediment size distribution data from USGS were used. USGS applied sieving or settling velocity methods with field-sampled sediments from which we extracted D_{50b}. See supplemental materials for a table of D_{50b}, fitted parameters, and literature citations.

Reach-specific parameters included lumped rating curve parameters (λ and ω) that represented width (a,b), depth (c,d), and suspended sediment concentration (e, f). We estimated rating curve parameters for all river reaches by fitting power functions with USGS discharge, suspended sediment, and channel dimensions data (see supplemental material for table of all fitted parameters). Discharge (Q) and hyporheic depth (H) were effectively site-specific parameters. Discharge data drove the model at each river reach, and although we used global hyporheic depth scaling parameters, H was estimated from reach-specific channel slope and D_{50b} data (Table 1).

Analysis

We introduced uncertainty into the evaluation of R_{SA} along a river using a Monte Carlo approach and varying the parameters that were not well represented physically or empirically. These parameters included the suspended sediment size and hyporheic depth along a river. After the model was parameterized for each river, we estimated R_{SA} under 1000 simulations with varied D_{50s} and H. Values of D_{50s} were randomly sampled from normal distributions at each river reach each using the model estimated D_{50s} as the mean and a standard deviation equal to 10% of the mean. Hyporheic depth at each river reach was varied by randomly sampling the scaling parameters β_D ($\mu = 20$, $\sigma = 2$) and βs ($\mu = 15$, $\sigma = 2$) from normal distributions. See the supplemental materials for detailed sensitivity analysis of R_{SA} to individual parameters in equation 6 as well as sensitivity to where R_{SA} exceeds one using equation 9.

The Monte Carlo analysis was performed across the full range of recorded discharge. Discharge was represented as flow exceedance probabilities from 0 to 1, 0 being the highest discharge on record and 1 the lowest, with 101 different discharge scenarios (that is, probability = 0.01, 0.02, 0.03…1.0). The ensemble mean R_{SA} for reach discharge condition was calculated and presented in the results. Flow

Table 1. Description of Global, River-Specific, and Reach-Specific Parameters Used in the Model Evaluation

Symbol	Units	Definition	Range from data and model evaluation
Global parameters			
φ		Porosity of bed sed	0.476401
ρ	kg m^{-3}	Density of suspended sed	2650
β_D		Hyporheic scaling factor with sed. size	Sampled from normal dist. ($\mu = 20$, $\sigma = 2$)
β_S		Hyporheic scaling factor with channel slope	Sampled from normal dist. ($\mu = 15$, $\sigma = 2$)
River-specific parameters			
α	m km^{-1}	Benthic sed. fining exponent	$-$ 0.006 to $-$ 0.014
β_{ss}	m km^{-1}	Rate of suspended sed. fining	$-10^{-7.5}$ to $-10^{-10.5}$
D_o	m	Most upstream bed sed. size	0.001 to 0.17
Reach-specific parameters			
a and b		Hydraulic geometry-width	$a = 8$ to 598 $b = 0.006$ to 0.45
c and d		Hydraulic geometry-depth	$c = 0.04$ to 16 $d = 0$ to 0.62
e and f		Suspended sediment rating curve	$e = 7 \times 10^{-10}$ to 4.5×10^{-1} $f = 0.06$ to 2.0
Q	m^3 s^{-1}	River discharge	0 to 55784
D_{50s}	m	Diameter of suspended sediment	2.5×10^{-7} to 0.00015
D_{50b}	m	Diameter of benthic sediment	0.0003 to 0.15
H	m	Hyporheic depth	0.006 to 3.1

exceedance probabilities were calculated from continuous discharge data collected over 5 years or more within each reach to normalize discharge to a common scale to compare within and across rivers.

The location along a river where R_{SA} exceeded 1 was estimated graphically under all scenarios as the distance from the river mouth as well as the watershed area of this location. The intersection of the R_{SA} curve and the horizontal line where R_{SA} equaled one was extracted using linear interpolation between the data points. Regression analysis was used to test what functions described the trends in R_{SA} along a river at median discharge. Functions that were tested included linear, power, exponential, and logarithmic. R_{SA} was transformed accordingly for each function to linearize the relationship in order to produce comparable R^2 and p values. The Network Analysis toolbox in ArcMap (ESRI, v 10.2.2) was used to find the distance along a river between all reaches and major dams. All other analyses were performed in R statistical software 3.2.2. All data are publicly available from the sources outlined above. The data we curated from these sources as well as the code are available upon request.

Results

Patterns in R_{SA}

The ratio of water column to benthic sediment surface area (R_{SA}) showed great variability as a function of discharge and with distance along a river, but consistent patterns were observed across different rivers. R_{SA} varied over 12 orders of magnitude across all reaches and discharges, from 10^{-8} to 10^3 (Figures 2, 3). In 7 of 10 rivers (all but the Missouri, Colorado, and Mississippi), the variability in R_{SA} with discharge at a particular location equaled or exceeded the spatial variability in R_{SA} over the entire main stem length at median discharge (Figures 2, 3). R_{SA} at median discharge scaled as a power function of watershed area but with considerable variability across all the rivers (Figure 4).

The downstream patterns in R_{SA} were best described as a power function of watershed area and logarithmic function of distance downstream for most rivers (Figure 5). However, the Colorado, Apalachicola, and Potomac Rivers lacked significant downstream trends in R_{SA} or had low R^2 values due to spatial variability and/or too few data points to generate a significant trend. The slopes, or exponents, of the significant relationships between watershed area and R_{SA} at median discharge ranged from 0.90 to 1.99; however, the slope was 0.5 in the Apalachicola River. Spatial variability was largely expressed as sharp declines in R_{SA} (Figures 2, 3). In many cases, these sharp declines occurred directly downstream of discontinuities such as dams, particularly on the Columbia, Colorado, Missouri, and Mississippi Rivers. For the few parameterized reaches that were located directly above and below dams, the percent change in R_{SA} due to the dam increased with the size of the reservoir, or mean reservoir storage volume (Figure 6).

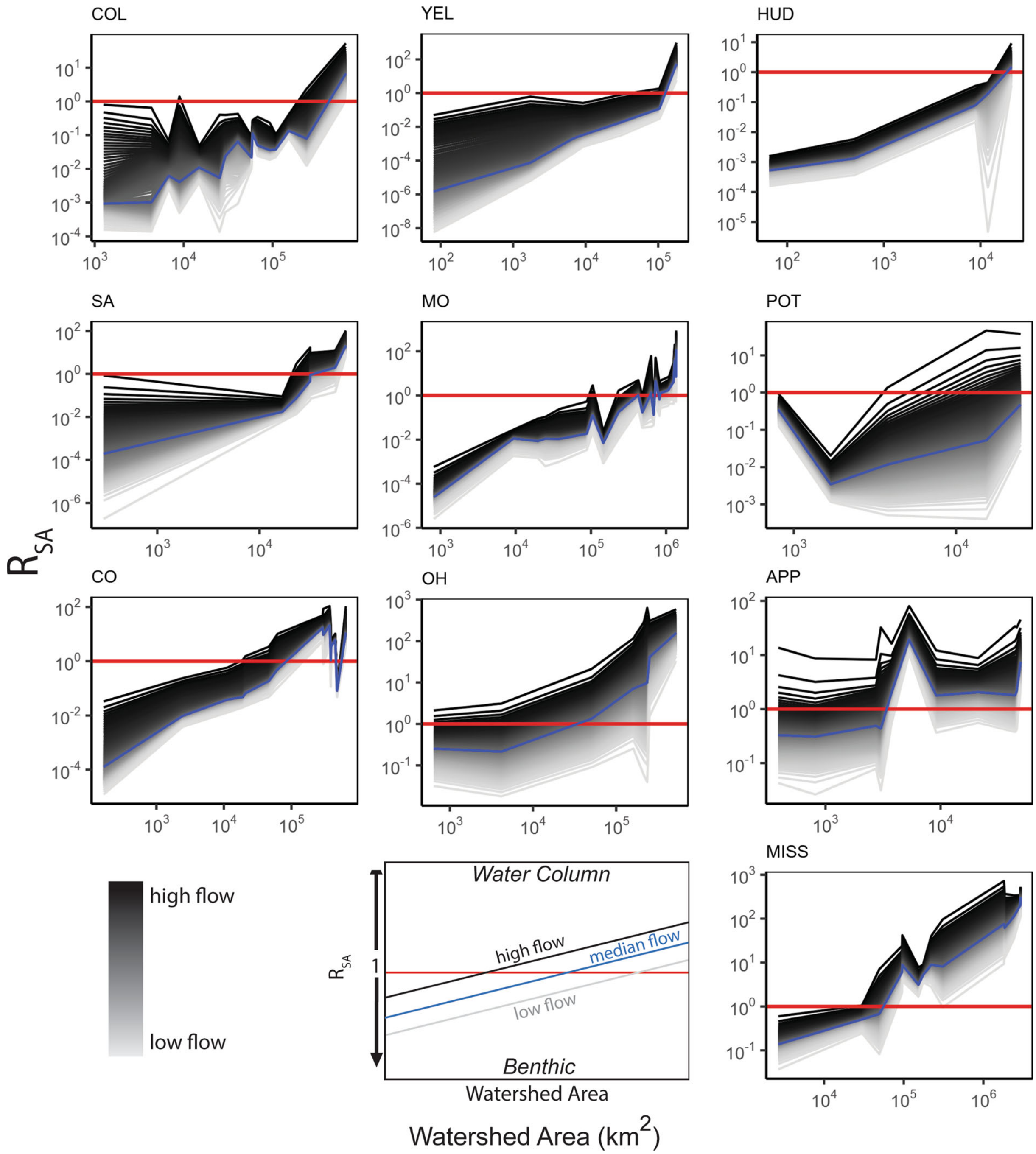

Figure 2. The ratio of suspended to benthic sediment surface area (R_{SA}) versus watershed area for all rivers. The color gradient in the *lines* represents discharge from 0 to 1 flow exceedance probability where *black* is high flow (probability = 0.0) and *light gray* is low flow (probability = 1.0). The median flow is highlighted in *blue*. Note the different scales on the axes, and all axes are logged (Color figure online).

Where Did R_{SA} Exceed 1?

There was more sediment surface area in the water column than the benthic zone (that is, R_{SA} exceeded 1) at some distance downstream in all rivers. However, R_{SA} exceeded 1 at a downstream location only under high flow in the Hudson (< 0.50 flow exceedance probability) and Potomac Rivers (< 0.23 flow exceedance probability), but under all flow conditions in the other rivers.

The percent of the river length with R_{SA} greater than 1 varied from 10% in the Hudson River, where most of the river length was benthic domi-

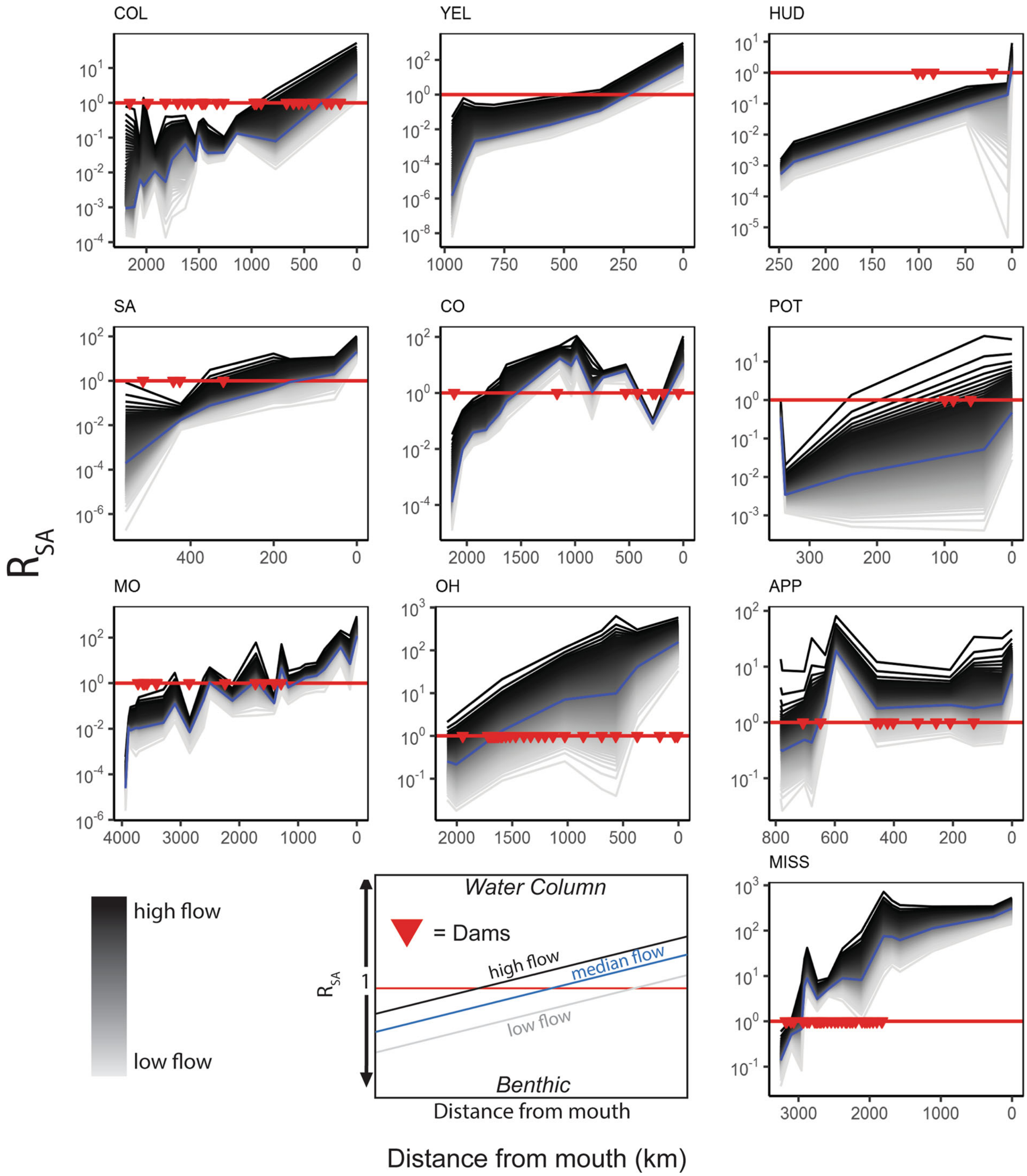

Figure 3. The ratio of suspended to benthic sediment surface area (R_{SA}) versus distance from mouth for all rivers. The color gradient in the *lines* represent discharge from 0 to 1 flow exceedance probability where *black* is high flow (probability = 0.0) and *light gray* is low flow (probability = 1.0). The median flow is highlighted in *blue*, and the location of dams is shown with *red triangles*. Note the different scales on the axes, and the *y*-axis is logged (Color figure online).

nated, to 90% in the Mississippi River, where most of the river length was water column dominated, at low flow (exceedance probability = 0.90) (Figure 7A). As flow increased, the percent of the river length with R_{SA} greater than 1 increased. At the highest flow, a majority of the main stem length was dominated by water column sediment surface area in all rivers except the Hudson (Figure 7A). At the median discharge, half of the rivers (including Apalachicola, Colorado, Mississippi, Missouri, and

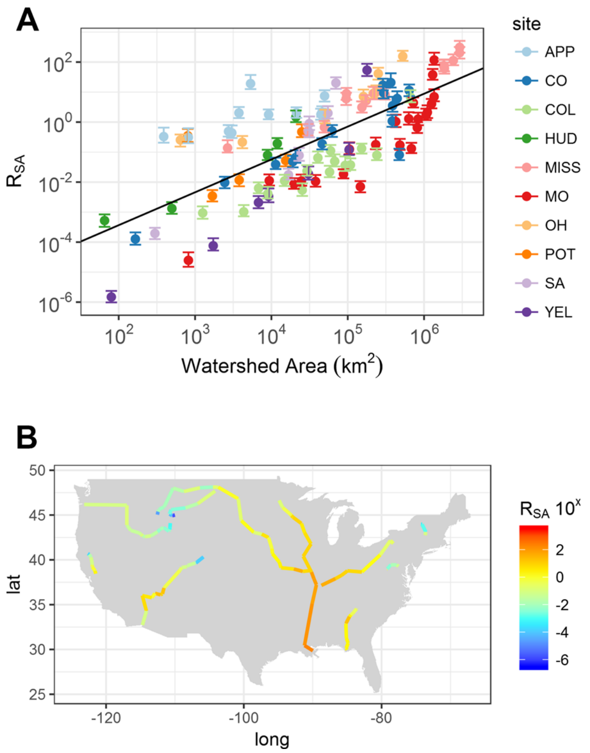

Figure 4. **A** R_{SA} at median flow (flow exceedance probability = 0.5) versus watershed area across all river basins at the locations where the model was parameterized with data. **B** Spatial visualization of R_{SA} at median flow.

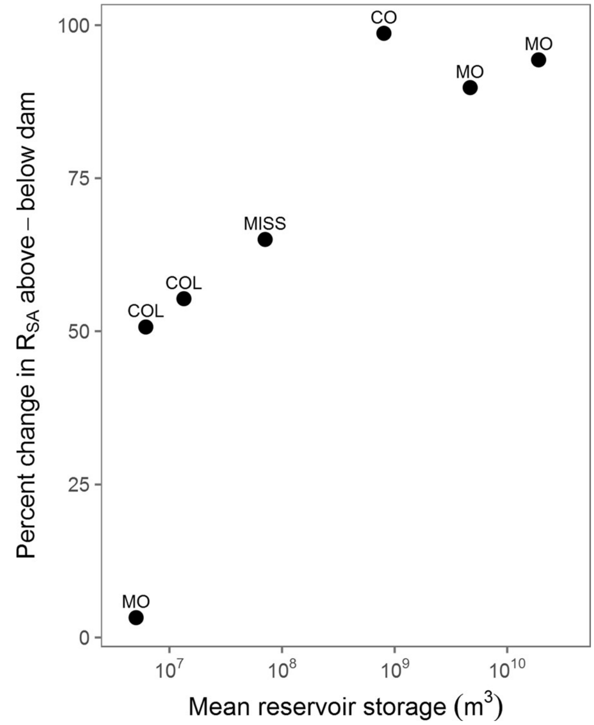

Figure 6. The percent change in R_{SA} immediately above and below major dams versus the mean reservoir water storage volume. The labels represent different rivers (*CO* Colorado, *COL* Columbia, *MO* Missouri, *MISS* Mississippi).

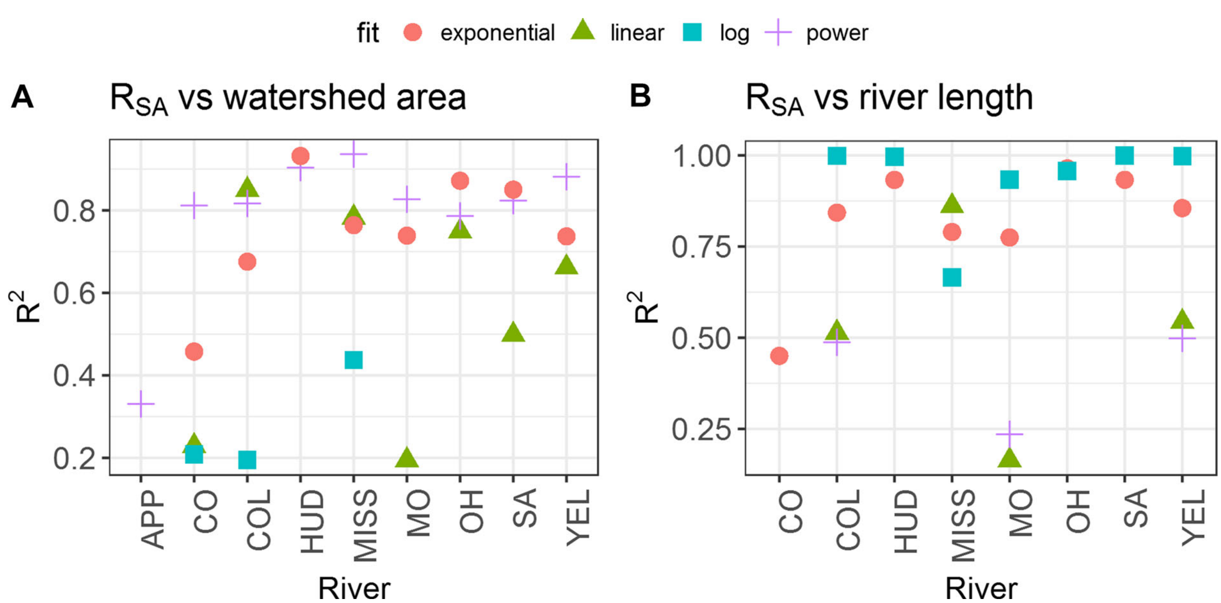

Figure 5. The *R*2 values of different functions (exponential, linear, logarithmic, and power) with significant fits of **A** R_{SA} versus watershed area and **B** R_{SA} vs distance downstream. Note the Potomac is not shown in either plot because none of the fits were significant due to too few data points, also the Apalachicola is not shown in figure **B** due to lack of significance.

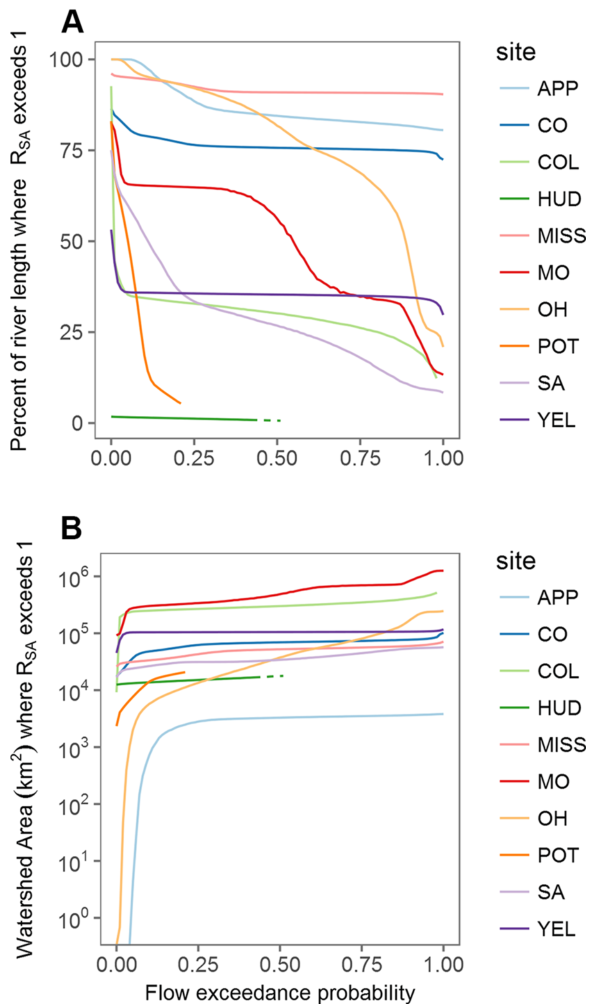

Figure 7. **A** The percent of the main stem river length where R_{SA} exceeded 1 versus flow exceedance probability. **B** The upstream watershed area at the location in the river where R_{SA} exceeded 1 versus flow exceedance probability. The Hudson and Potomac Rivers do not extend across the range of flows because R_{SA} was only exceeded at high flows (that is, lower exceedance probabilities).

Ohio) had a majority of their main stem length dominated by water column sediment surface area.

The upstream watershed area at the location where R_{SA} exceeded 1 showed consistent patterns with discharge across all rivers (Figure 7B). As discharge increased, watershed area decreased pushing the location where R_{SA} exceeded 1 upstream. At low flow (flow exceedance = 0.90), R_{SA} exceeded 1 over a range of watershed sizes from 3644 km^2 in the Apalachicola basin (7% of total basin area) to 847,906 km^2 in the Missouri basin (62% of total basin area). At the highest flow, the location where R_{SA} exceeded 1 occurred over a range of watershed sizes from less than 1 km^2 in the Ohio and Apalachicola Rivers to a watershed size of 100,000 km^2 in the Missouri River (7% of total watershed area). At the median discharge, the location where R_{SA} exceeded 1 ranged from a watershed size of 3290 km^2 in the Apalachicola (6% of total basin area) to 485,964 km^2 in the Missouri basin (36% of total basin area) with a mean watershed size of 122,924 km^2. Translating these results to stream order, the location where R_{SA} exceeded 1 at median discharge ranged from 5th to 9th order across the different river basins with a median of 7th (according to stream orders assigned by the National Hydrography Dataset-Plus, Horizon Systems Corporation).

Discussion

We presented a physical template for the surface area of sediment particles in the benthic and water column zones across the river continuum. Our analysis scaled from individual particles, to river reaches, and to river networks to describe broad patterns within and across river basins. We showed that the surface area ratio, R_{SA}, scaled as a power function of watershed area. There was more sediment surface area in the water column than the benthic zone (that is, R_{SA} exceeded 1) starting somewhere between 5 and 9th-order rivers depending on the river basin, suggesting that ecosystem processes could be occurring largely in the water column in rivers of 5th order or greater.

Transitions in material processing, such as carbon and nutrient cycling, have also been found to occur in ~ 5th-order rivers. For example, rivers shifted from heterotrophy to autotrophy in 5th-order rivers (Webster 2007), and it was suggested that nutrient uptake shifted from benthic to water column dominance in rivers greater than 5th order (Reisinger and others 2015). However, our results showed that spatial discontinuities such as dams and temporal variability due to discharge shifted where this benthic to water column transition occurs. Our discussion below expands upon the ecosystem implications of benthic and water column sediment surface area and is intended to stimulate discussion on the role of the water column in river ecosystems and how to scale water column versus benthic processes.

Spatial Discontinuities and Temporal Variability

Spatial discontinuities, such as dams (Ward and Stanford 1983), had a marked impact on sediment surface area ratio, R_{SA}. The rivers with the most frequent and largest discontinuities (Missouri, Mississippi, Colorado, and Columbia) also had the most dams (> = 50 feet tall or 5000 acre-feet of storage, according to National Inventory of Dams) within their basin as well as along the main stem (Table 2). The type and size of the dam may be important. Large storage dams trap sediment and regulate discharge more so than run-of-river dams (Csiki and Rhoads 2010), and therefore, storage dams will have a greater impact on patterns in R_{SA}. For example, both the Mississippi and Ohio Rivers have many navigational run-of-river dams along their main stem. Yet, there were fewer discontinuities in R_{SA} along these rivers compared to the Missouri and Columbia which have fewer dams along the main stem, but those dams are large storage dams. The storage dams on the Colorado River, particularly Hoover and Glen Canyon dams, effectively suppressed R_{SA} for hundreds of kilometers (Figure 3).

Discharge had a large impact on spatial and temporal variability in R_{SA}. For example, at a given location along a river, R_{SA} could vary over several orders of magnitude within a year, being less than or greater than 1 at different times depending on flow (Figures 2, 3). Thus, variability in discharge—annually, seasonally, and episodically during storms—affects where along the river water column sediment surface area is greater than benthic. Furthermore, from a river network perspective discharge adds spatial variability. Our data were presented along a river's main stem assuming that discharge in each reach was at the same exceedance probability. However, in a real river basin, discharge will not occur this evenly due to subcatchments with differing hydrologic regimes (Richter and others 1998; Montgomery 1999); therefore, spatial and temporal asynchrony in discharge across a river basin will create complex spatial patterns in R_{SA} and where it exceeds 1.

These results suggest spatial discontinuities such as dams and temporal variability due to floods/droughts shift rivers between benthic and water column control of sediment-mediated processes. If we generally conceptualize processes in small streams as dominated by the benthic zone (Covich and others 1999; McKnight and others 2004) and those in large rivers by the water column (Ochs and others 2009; Reisinger and others 2015; Reisinger and others 2016), rivers oscillate between benthic (stream-like) and water column control (river-like) over time and space. Large storage dams decreased R_{SA} in downstream reaches. In these reaches, there are less suspended sediment surface area, more light penetration, and likely increased primary production and benthic biology. In contrast, high discharge events make streams function more like rivers, although only episodically. As discharge and R_{SA} increase, less light reaches the benthic zone, in-channel and watershed-derived materials are added to the water column (Wolman and Miller 1960), and benthic organisms are entrained within the water column (Poff and Ward 1991; Gibbins and others 2007).

Ecosystem Implications

Sediment-mediated ecosystem processes shifting between benthic and water column dominance

Table 2. Table of Basic Characteristics of the River Basins Evaluated Including the Number of Reaches Evaluated Along Each River, Number of Dams Along Main Stem, Number of Dams in the Watershed, Range of Watershed Sizes Represented by the Evaluated Reaches, Main Stem Length, and Stream Order Where R_{SA} Exceeded 1 at Median Discharge

Rivers	# of reaches	# dams within main stem*	# dams within basin*	range in watershed area at reaches (km^2)	length of main stem (km)	Stream order where R_{SA} = 1 (at Q50)
Apalachicola (APP)	11	10	19	388–49727	783	5
Colorado (CO)	15	8	144	165–638950	2137	9
Columbia (COL)	16	31	142	1258–665368	2198	8
Hudson (HUD)	5	4	–	65–2953	248	7
Missouri (MO)	22	13	269	818–1357155	3938	9
Mississippi (MISS)	15	35	716	2667–2926689	3250	7
Ohio (OH)	8	27	341	642–525768	2087	6
Potomac (POT)	5	3	17	802–24996	342	–
Sacramento (SA)	7	4	55	297–70000	556	7
Yellowstone (YEL)	7	0	1	80–178965	969	8

**Dams of > = 50 feet tall or 5000 acre-feet of storage according to National Hydrography Dataset from the National Inventory of Dams.*

have implications for how to measure, model, and manage ecosystems. First, we need to highlight key differences between the benthic and water column zones. The benthic zone is largely stationary, disturbed only by events of a threshold size (Buffington and Montgomery 1997; Lake 2000), whereas the water column is under continuous turbulent motion downstream. Another key difference is the range and timescales of variability of the physical environment. For example, variability in temperature, light, and current velocity occurs at a higher frequency and over a wider range in the water column compared to the benthic zone (Gardner and Doyle unpublished data). The benthic zone has more consistent thermal and light regimes that are dampened by upwelling groundwater (Malcolm and others 2002), attenuation of light/heat through the water column (Kirk 1994; Ji 2017), and less frequent downstream transport. These key differences demonstrate how the physical environment, timescales of variability, and the controls of ecosystem processes may differ between the benthic and water column zones.

Considering these key differences, scaling ecosystem processes across a river basin requires different methods for benthic versus water column processes if both zones are appreciably contributing to the whole ecosystem. For example, in river network models of material processing, nutrient and carbon uptake rates are scaled from headwater streams to large rivers based on the wetted perimeter-to-discharge ratio or similar metrics that assume benthic processing (Seitzinger and others 2002; Alexander and others 2009; Bertuzzo and others 2017; Helton and others 2018; Ye and others 2017). Applications of nutrient spiraling theory have been explicitly benthic (Newbold and others 1981; Fisher and others 1998; Ensign and Doyle 2006). However, there is no physical basis for scaling water column processes using the same metrics as benthic processes. Rather, suspended sediment concentration, suspended sediment surface area, and/or the properties of suspended materials should be used to develop functional relationships for scaling water column material processing.

In the context of material spiraling (Newbold and others 1981; Fisher and others 1998), integrating water column and benthic processing would conceptually be two concomitant material spirals. One spiral is the traditional cycling of materials between water column and benthic zones, assuming water column materials are mineralized and benthic forms are assimilated by biota and particulates. The second spiral occurs exclusively in the water column where materials cycle between mineralized and biotic/particulate forms without entering the benthic zone. Water column spirals are potentially longer due to continuous downstream advection; however, rivers respond quickly to material inputs likely due to heterotrophic activity in the water column (Cotner and Biddanda 2002). These two concomitant spirals are coupled as materials are exchanged between the benthic and water column spirals. The questions become what are the water column versus benthic spiraling uptake rates/lengths, how coupled are these spirals, and how do the rates, lengths, and degree of coupling scale with river size?

Water column material processing may only be important in the largest rivers. In addition to our results on sediment surface area, as river size increases there are other biophysical changes that suggest an increase in water column processes relative to the benthic zone. As a river grows in size, a smaller proportion of the water volume interacts with the benthic zone and less frequently (Gomez-Velez and Harvey 2014; Gomez-Velez and others 2015), concentrations of suspended materials increase (Meybeck 1982; Meybeck and others 2003), the sources of carbon inputs can shift from allochthonous to autochthonous (Vannote and others 1980; Thorp and Delong 1994; Finlay 2001; Oliver and Merrick 2006; Battin and others 2008; Hall and others 2015; Hotchkiss and others 2015; Raymond and others 2016), and primary production can shift from largely benthic periphyton to largely drifting phytoplankton (Vannote and others 1980; Finlay 2001; Oliver and Merrick 2006; Battin and others 2008; Hall and others 2015; Hotchkiss and others 2015; Raymond and others 2016). However, even in small headwater streams, Rovelli and others (2017) showed that 28% of ecosystem respiration occurred in the water column on average, and there was transient dominance of water column gross primary productivity. Similarly, Reisinger and others (2015) showed water column ammonium uptake occurred in all stream sizes. Water column processes are rarely partitioned from the whole ecosystem (Giorgio and Williams 2005) especially across a gradient of river size, yet evidence is growing that at a certain river size our conceptual and numerical models must incorporate water column processes and their controls.

Measurement and management strategies may also need to be reassessed depending on the relative influence of the benthic and water column zones. For example, consider the case of a river with almost no benthic biota due to light limitation and/or perpetual disturbance where a majority of the biology is mobile. In such a river, a traditional fixed-site approach will not capture the ecosystem and biogeochemical dynamics. Instead, synoptic or flowpath approaches should be adopted that are spatially explicit or follow a water mass and its biological community downstream (Doyle and Ensign 2009; Volkmar and others 2011; Hensley and others 2014; Ensign and others 2017). Management strategies may also shift. For example, if benthic processes are dominant, water quality management should focus on increasing vertical exchange within riverbed structures (Gomez-Velez and Harvey 2014; Gomez-Velez and others 2015). If water column processes are dominant, management of river velocity by dams could be used to maintain enough suspended materials in the water column, but without significantly reducing residence time, to maximize the contact area and time between suspended materials and solutes within the water column.

Biogeochemical Context of Sediments

The biogeochemical context of benthic and water column sediment is also important; however, our analysis was limited to the physical template. Sediment facilitates biological processes not only due to contact surface area and contact residence time, but also due to biogeochemical conditions such as redox gradients, abundance of microbial communities (Hosen and others 2017; Mendoza-Lera and others 2017), concentrations of organic matter, nutrients, and other elements (Wotton 2007). The biogeochemical context could be conceptually integrated with our model of the surface area ratio by defining a ‘‘reactivity ratio,’’ R_R. The reactivity ratio represents the ratio of water column to benthic concentration or mass of nutrients, organic matter, or microbes per sediment surface area. The product of the surface area ratio (R_{SA}) and reactivity ratio (R_R) is the ratio of water column to benthic ‘‘biogeochemical potential.’’

$$\text{``}\textit{Biogeochemical Potential''}\ \textit{or``Mass Flux''} = R_{SA} R_R \tag{10}$$

R_R could also represent areal rates of sediment-mediated heterotrophic processes such as respiration or denitrification, and the product of R_{SA} and R_R is the ratio of water column to benthic mass flux (mass time^{-1}). The benthic zone likely has higher rates of heterotrophic processes and greater mass of organic matter. Yet, according to our results, benthic rates would have to be 1–3 orders of magnitude greater than water column rates for the ‘‘mass flux’’ to be largely benthic in rivers of 5th order or larger.

In practice, assessing the biogeochemical potential or mass flux is a particle-centric view of rivers that requires detailed field sampling. However, a particle-centric view could provide valuable insights, particularly in turbid rivers, since the properties and role of suspended materials in riverine ecosystems have not been well studied (Dodds and Whiles 2004; Wotton 2007; Battin and others 2008). Suspended materials have been well studied in marine systems (Alldredge and Silver 1988), and similar processes such as particle aggregation (marine or river ‘‘snow’’) and denitrification in the interstitial spaces of suspended materials have been observed in rivers (Droppo and others 1997; Droppo 2001; Zimmermann-Timm 2002; Wotton 2007; Liu and others 2013). Battin and others (2008) highlighted the importance of suspended materials and aggregates asserting that they can structure water column chemistry as a result of their formation, existence, and degradation that consumes, transforms, and releases materials and solutes. A recent study of rivers in North Carolina found one drop of surface water contains over one billion nanoparticles (River and Richardson 2018a, b), illustrating that there remains much to discover on the properties and function of suspended materials in rivers.

Applications

Practical applications of our results and modeling framework include the design of field studies and scaling of field and laboratory measurements. For design of field studies, our results suggest the type of river, discharge, and location along a river where it is appropriate to focus on suspended materials. For example, in river basins with high concentrations of fine suspended materials (for example, Apalachicola), measurements of water column processes and materials should begin around 5th-order rivers. However, in other river basins with coarser bed sediments and deeper hyporheic depths water column process rates may not be important relative to the benthic zone. A quick assessment of R_{SA}, using empirical data and the model (equation 6), may be indicative of the relative role of benthic and suspended sediments in the fate and transport of materials and solutes. For example, sediment surface area has been correlated with metal and pollutants loads (Tessier and others 1980; Horowitz and Elrick 1987; Rügner and others 2013), and estimating R_{SA} prior to sampling can guide whether to collect water column or benthic samples.

Coupling our sediment surface area model with biogeochemical, enzymatic, or weathering rates derived from laboratory or field experiments could be used to scale up to ecosystems or river networks. A conceptual example (equation 10) was presented for scaling up mass flux or biogeochemical potential across river size. However, more detailed models and sampling efforts will be required to partition water column and benthic ecosystem processes. With new sampling techniques, such as eddy covariance for benthic metabolism (Berg and others 2003; Rovelli and others 2017), we can better measure and partition benthic and water column processes. In addition, our frugal modeling approach (Carpenter 2003) can be easily modified with different assumptions to better represent specific rivers and generate hypotheses. The model could incorporate different channel shapes, different functions for representing downstream patterns in sediment size, hyporheic depth, and hydraulic geometry and could include functions that link parameters with discharge.

Conclusions

We presented a physical template for sediment-mediated ecosystem processes and compared the sediment–water contact area in the benthic and water column zones across river size. The surface area ratio, R_{SA}, scaled as a power function of watershed area, and there was more sediment surface area in the water column than the benthic zone in rivers equal to or greater than 5–9th order depending on the river basin. Dams and variation in discharge caused spatial discontinuities and temporal variability that shifted the location along a river where water column sediment surface area was dominant; therefore, rivers oscillated between water column and benthic dominance over time and space. Our results suggest at a certain river size water column processes should be incorporated into models of material processing. Water column processes require different scaling metrics than benthic processes (for example, not wetted perimeter) that integrate the properties of suspended materials. Field measurements of water column and benthic processes from headwaters to coasts are needed to better understand how these different zones influence the whole river ecosystem.

ACKNOWLEDGEMENTS

Thanks to conversations with Emily Bernhardt, Jim Heffernan, Scott Ensign, and all members of the Duke River Center as well as 2 anonymous reviewers and the editors who substantially contributed to the improvement of this manuscript.

FUNDING

NSF-IGERT Grant #DGE-1068871.

REFERENCES

Alexander RB, Böhlke JK, Boyer EW, David MB, Harvey JW, Mulholland PJ, Seitzinger SP, Tobias CR, Tonitto C, Wollheim WM. 2009. Dynamic modeling of nitrogen losses in river networks unravels the coupled effects of hydrological and biogeochemical processes. Biogeochemistry 93:91–116.

Alexander RB, Boyer EW, Smith RA, Schwarz GE, Moore RB. 2007. The role of headwater streams in downstream water quality. J Am Water Resour Assoc 43:41–59.

Alldredge AL, Silver MW. 1988. Characteristics, dynamics and significance of marine snow. Prog Oceanogr 20:41–82.

Asselman N. 2000. Fitting and interpretation of sediment rating curves. J Hydrol 234:228–48.

Avnimelech Y, Ritvo G, Meijer LE, Kochba M. 2001. Water content, organic carbon and dry bulk density in flooded sediments. Aquac Eng 25:25–33.

Battin TJ, Kaplan LA, Findlay S, Hopkinson CS, Marti E, Packman AI, Newbold JD, Sabater F. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. Nat Geosci 1:95–100.

Berg P, Røy H, Janssen F, Meyer V, Jørgensen BB, Huettel M, de Beer D. 2003. Oxygen uptake by aquatic sediments measured with a novel non-invasive eddy-correlation technique. Mar Ecol Prog Ser 261:75–83.

Bertuzzo E, Helton AM, Hall Jr RO, Battin TJ. 2017. Scaling of dissolved organic carbon removal in river networks. Adv Water Resour 110:136–46.

Buffington JM, Montgomery DR. 1997. A systematic analysis of eight decades of incipient motion studies, with special reference to gravel-bedded rivers. Water Resour Res 33:1993–2029.

Carpenter SR. 2003. The need for fast-and-frugal models. Princeton: Princeton University Press.

Carpenter SR, Turner MG. 2017. Twenty years of ecosystems: emerging questions and challenges. Ecosystems 20:1–3.

Caspers H. 1981. The functioning of freshwater ecosystems. In: Le Cren ED, Lowe-McConnell RH. International biological programme, 22, 588 pp. Cambridge: Cambridge University Press 1980. ISBN 0 521 22507 8. £ 40.00. Internationale Revue der gesamten Hydrobiologie und Hydrographie 66: 908–909.

Cotner JB, Biddanda BA. 2002. Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems. Ecosystems 5:105–21.

Covich AP, Palmer MA, Crowl TA. 1999. The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. Bioscience 49:119–27.

Csiki S, Rhoads BL. 2010. Hydraulic and geomorphological effects of run-of-river dams. Prog Phys Geogr 34:755–80.

Descy J-P, Gosselain V. 1994. Development and ecological importance of phytoplankton in a large lowland river (River

Meuse, Belgium). Phytoplankton in turbid environments: rivers and shallow lakes. Berlin: Springer. pp 139–55.

Dodds WK, Whiles MR. 2004. Quality and quantity of suspended particles in rivers: continent-scale patterns in the United States. Environ Manag 33:355–67.

Doyle MW, Ensign SH. 2009. Alternative reference frams in river system science. Bioscience 59:499–510.

Droppo I, Leppard G, Flannigan D, Liss S. 1997. The freshwater floc: a functional relationship of water and organic and inorganic floc constituents affecting suspended sediment properties. Water Air Soil Pollut 99:43–54.

Droppo IG. 2001. Rethinking what constitutes suspended sediment. Hydrol Process 15:1551–64.

Ensign SH, Doyle MW. 2006. Nutrient spiraling in streams and river networks. J Geophys Res 111:G04009.

Ensign SH, Doyle MW, Gardner JR. 2017. New strategies for measuring rates of environmental processes in rivers, lakes, and estuaries. Freshw Sci 36:000.

Finlay JC. 2001. Stable carbon isotope ratios of river biota: implications for energy flow in lotic food webs. Ecology 82:1052–64.

Fisher SG, Grimm NB, Martí E, Holmes RM, Jones JB Jr. 1998. Material spiraling in stream corridors: a telescoping ecosystem model. Ecosystems 1:19–34.

Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ Manag 10:199–214.

Gibbins C, Vericat D, Batalla RJ. 2007. When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. Freshwater Biol 52:2369–84.

Giorgio PA, Williams PJB. 2005. Respiration in aquatic ecosystems. Oxford, USA: Oxford University Press.

Gomez-Velez JD, Harvey JW. 2014. A hydrogeomorphic river network model predicts where and why hyporheic exchange is important in large basins. Geophys Res Lett 41:6403–12.

Gomez-Velez JD, Harvey JW, Cardenas MB, Kiel B. 2015. Denitrification in the Mississippi River network controlled by flow through river bedforms. Nat Geosci 8:941–5.

Hall RO, Tank JL, Baker MA, Rosi-Marshall EJ, Hotchkiss ER. 2015. Metabolism, gas exchange, and carbon spiraling in rivers. Ecosystems 19:73–86.

Helton AM, Hall RO, Bertuzzo E. 2018. How network structure can affect nitrogen removal by streams. Freshwater Biol 63:128–40.

Hensley RT, Cohen MJ, Korhnak LV. 2014. Inferring nitrogen removal in large rivers from high-resolution longitudinal profiling. Limnol Oceanogr 59:1152–70.

Horowitz AJ, Elrick KA. 1987. The relation of stream sediment surface area, grain size and composition to trace element chemistry. Appl Geochem 2:437–51.

Hosen JD, Febria CM, Crump BC, Palmer MA. 2017. Watershed urbanization linked to differences in stream bacterial community composition. Front Microbiol 8:1452.

Hotchkiss E, Hall R Jr, Sponseller R, Butman D, Klaminder J, Laudon H, Rosvall M, Karlsson J. 2015. Sources of and processes controlling CO_2 emissions change with the size of streams and rivers. Nat Geosci 8:696–9.

Jackson CR, Millar JJ, Payne JT, Ochs CA. 2014. Free-living and particle-associated bacterioplankton in large rivers of the Mississippi River Basin demonstrate biogeographic patterns. Appl Environ Microbiol 80:7186–95.

Ji Z-G. 2017. Hydrodynamics and water quality: modeling rivers, lakes, and estuaries. New York: Wiley.

Jia X, Williams R. 2001. A packing algorithm for particles of arbitrary shapes. Powder Technol 120:175–86.

Kirk JT. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge: Cambridge University Press.

Lake P. 2000. Disturbance, patchiness, and diversity in streams. J N Am Benthol Soc 19:573–92.

Lamberti GA, Steinman AD. 1997. A comparison of primary production in stream ecosystems. J N Am Benthol Soc 16:95–104.

Leopold LB, Maddock T. 1953. The hydraulic geometry of stream channels and some physiographic implications: quantitative measurement of some of the hydraulic factors that help to determine the shape of natural stream channels: depth, width, velocity, and suspended load, and how they vary with discharge as simple power functions; teir interrelations are described by the term ''hydraulic geometry'': U.S. Government Printing Office.

Liu T, Xia X, Liu S, Mou X, Qiu Y. 2013. Acceleration of denitrification in turbid rivers due to denitrification occurring on suspended sediment in oxic waters. Environ Sci Technol 47:4053–61.

Malcolm I, Soulsby C, Youngson A. 2002. Thermal regime in the hyporheic zone of two contrasting salmonid spawning streams: ecological and hydrological implications. Fish Manag Ecol 9:1–10.

Marzadri A, Dee MM, Tonina D, Bellin A, Tank JL. 2017. Role of surface and subsurface processes in scaling N_2O emissions along riverine networks. Proc Natl Acad Sci 114:4330–5.

McCluney KE, Poff NL, Palmer MA, Thorp JH, Poole GC, Williams BS, Williams MR, Baron JS. 2014. Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. Front Ecol Environ 12:48–58.

McKnight DM, Runkel RL, Tate CM, Duff JH, Moorhead DL. 2004. Inorganic N and P dynamics of Antarctic glacial meltwater streams as controlled by hyporheic exchange and benthic autotrophic communities. J N Am Benthol Soc 23:171–88.

Mendoza-Lera C, Frossard A, Knie M, Federlein LL, Gessner MO, Mutz M. 2017. Importance of advective mass transfer and sediment surface area for streambed microbial communities. Freshwater Biol 62:133–45.

Meybeck M. 1982. Carbon, nitrogen, and phosphorus transport by world rivers. Am J Sci 282:401–50.

Meybeck M, Laroche L, Dürr H, Syvitski J. 2003. Global variability of daily total suspended solids and their fluxes in rivers. Glob Planet Change 39:65–93.

Millar JJ, Payne JT, Ochs CA, Jackson CR. 2015. Particle-associated and cell-free extracellular enzyme activity in relation to nutrient status of large tributaries of the Lower Mississippi River. Biogeochemistry 124:255–71.

Montgomery DR. 1999. Process domains and the river continuum. J Am Water Resour Assoc 35:397–410.

Mulholland PJ, Helton AM, Poole GC, Hall RO, Hamilton SK, Peterson BJ, Tank JL, Ashkenas LR, Cooper LW, Dahm CN, Dodds WK, Findlay SE, Gregory SV, Grimm NB, Johnson SL, McDowell WH, Meyer JL, Valett HM, Webster JR, Arango CP, Beaulieu JJ, Bernot MJ, Burgin AJ, Crenshaw CL, Johnson

LT, Niederlehner BR, O'Brien JM, Potter JD, Sheibley RW, Sobota DJ, Thomas SM. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. Nature 452:202–5.

Newbold JD, Elwood JW, O'Neill RV, Winkle WV. 1981. Measuring nutrient spiralling in streams. Can J Fish Aquat Sci 38:860–3.

Ochs CA, Capello HE, Pongruktham O. 2009. Bacterial production in the Lower Mississippi River: importance of suspended sediment and phytoplankton biomass. Hydrobiologia 637:19–31.

Oliver RL, Merrick CJ. 2006. Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). Freshwater Biol 51:1131–48.

Parker G. 1991. Selective sorting and abrasion of river gravel. I: theory. J Hydraul Eng 117:131–47.

Peterson BJ, Wollheim WM, Mulholland PJ, Webster JR, Meyer JL, Tank JL, Marti E, Bowden WB, Valett HM, Hershey AE, McDowell WH, Dodds WK, Hamilton SK, Gregory S, Morrall DD. 2001. Control of nitrogen export from watersheds by headwater streams. Science 292:86–90.

Pizzuto JE. 1995. Downstream fining in a network of gravel-bedded rivers. Water Resour Res 31:753–9.

Poff NL, Ward J. 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. Can J Fish Aquat Sci 48:1926–36.

Poole GC. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biol 47:641–60.

Raymond PA, Saiers JE, Sobczak WV. 2016. Hydrological and biogeochemical controls on watershed dissolved organic matter transport: pulse-shunt concept. Ecology 97:5–16.

Reisinger AJ, Tank JL, Hoellein TJ, Hall RO. 2016. Sediment, water column, and open-channel denitrification in rivers measured using membrane-inlet mass spectrometry. J Geophys Res Biogeosci 121:1258–74.

Reisinger AJ, Tank JL, Rosi-Marshall EJ, Hall RO, Baker MA. 2015. The varying role of water column nutrient uptake along river continua in contrasting landscapes. Biogeochemistry 125:115–31.

Richter BD, Baumgartner JV, Braun DP, Powell J. 1998. A spatial assessment of hydrologic alteration within a river network. Regul Rivers Res Manag 14:329–40.

River M, Richardson CJ. 2018a. Particle size distribution predicts particulate phosphorus removal. Ambio 47:124–33.

River M, Richardson CJ. 2018b. Stream transport of iron and phosphorus by authigenic nanoparticles in the Southern Piedmont of the US. Water Res 130:312–21.

Rovelli L, Attard KM, Binley A, Heppell CM, Stahl H, Trimmer M, Glud RN. 2017. Reach-scale river metabolism across contrasting sub-catchment geologies: effect of light and hydrology. Limnol Oceanogr 62:S1.

Rügner H, Schwientek M, Beckingham B, Kuch B, Grathwohl P. 2013. Turbidity as a proxy for total suspended solids (TSS) and particle facilitated pollutant transport in catchments. Environ Earth Sci 69:373–80.

Scholes RJ. 2017. Taking the mumbo out of the jumbo: progress towards a robust basis for ecological scaling. Ecosystems 20:4–13.

Seitzinger SP, Styles RV, Boyer EW, Alexander RB, Billen G, Howarth RW, Mayer B, Van Breemen N. 2002. Nitrogen retention in rivers: model development and application to watersheds in the northeastern USA. The Nitrogen cycle at regional to global scales. Berlin: Springer. pp 199–237.

Tessier A, Campbell P, Bisson M. 1980. Trace metal speciation in the Yamaska and St. Francois rivers (Quebec). Can J Earth Sci 17:90–105.

Thorp JH, Delong MD. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70:305–8.

Thorp JH, Thoms MC, Delong MD. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. River Res Appl 22:123–47.

Tucker ME. 2009. Sedimentary petrology: an introduction to the origin of sedimentary rocks. New York: Wiley.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Can J Fish Aquat Sci 37:130–7.

Volkmar EC, Dahlgren RA, Stringfellow WT, Henson SS, Borglin SE, Kendall C, Van Nieuwenhuyse EE. 2011. Using Lagrangian sampling to study water quality during downstream transport in the San Luis Drain, California, USA. Chem Geol 283:68–77.

Walling D, Moorehead P. 1989. The particle size characteristics of fluvial suspended sediment: an overview. Hydrobiologia 176:125–49.

Walling DE, Owens PN, Waterfall BD, Leeks GJ, Wass PD. 2000. The particle size characteristics of fluvial suspended sediment in the Humber and Tweed catchments, UK. Sci Total Environ 251:205–22.

Ward JV, Stanford J. 1983. The serial discontinuity concept of lotic ecosystems. Dyn Lotic Ecosyst 10:29–42.

Waters TF. 1977. Secondary production in inland waters. Adv Ecol Res 10:91–164.

Webster JR. 2007. Spiraling down the river continuum: stream ecology and the U-shaped curve. J N Am Benthol Soc 26:375–89.

Wetzel RG. 2001. Limnology: lake and river ecosystems. Houston: Gulf Professional Publishing.

Wolman MG, Miller JP. 1960. Magnitude and frequency of forces in geomorphic processes. J Geol 68:54–74.

Wotton RS. 2007. Do benthic biologists pay enough attention to aggregates formed in the water column of streams and rivers? J N Am Benthol Soc 26:1–11.

Ye S, Reisinger AJ, Tank JL, Baker MA, Hall RO, Rosi EJ, Sivapalan M. 2017. Scaling dissolved nutrient removal in river networks: a comparative modeling investigation. Water Resour Res 53:9623–41.

Zimmermann-Timm H. 2002. Characteristics, dynamics and importance of aggregates in rivers—an invited review. Int Rev Hydrobiol 87:197–240.