Insights on Nutrient Spiraling in Streams Based on a Simple Transport-Reaction Model

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1 Introduction

Schade and Power [unpublished notes] provide a lovely summary of nutrient spiraling and why stream ecologists care about spiraling: "Ecologists have long been interested in understanding the suite of factors that influence the movement of materials from mountaintop to ocean, particularly those processes that impede downstream fluxes. *Webster* [1975] developed the nutrient spiraling concept to integrate a traditional ecological focus on nutrient cycling in relatively closed ecosystems with this interest in downstream fluxes. Downstream movement effectively displaces nutrient cycles along a longitudinal axis, converting them into spirals. Nutrient spiraling theory developed from work on biogeochemistry of stream ecosystems, and recognizes the importance of understanding the balance of transport (i.e. hydrology) and retention processes (i.e. uptake of nutrients by plants, algae or microbes) in determining the rate of flux of materials to downstream ecosystems [*Newbold et al.*, 1982, 1983; *Newbold*, 1992]."

Within this context we choose a simple stream system to clarify the ingredients of the "uptake length" and "uptake speed," key nutrient spiraling metrics in stream ecology studies [e.g. *Doyle et al.*, 2003]. Namely, we focus on transport and spiraling of a nutrient as influenced by its uptake and release by benthic algae. Because we are interested in first-order behavior over large stream distances, we choose simple formulations of local nutrient production and consumption, and of algae growth. Moreover, for simplicity we purposefully avoid details of different nutrient species and how they are processed, and of different benthic algae involved in this processing.

Nutrient spiraling involves coupled (nonlinear) physical-biological processes, and the details of this spiraling therefore fundamentally control streamwise variations in nutrients and foodweb structure. Herein resides the beauty of spiraling: it contributes to a rich spatiotemporal nutrient-foodweb behavior. We illustrate a simple version of this in our description below of the two-part system involving a nutrient (e.g. nitrogen or phosphorus) and benthic algae.

2 Key Spiraling Metrics

Webster and Ehrman [1996] and *Doyle et al.* [2003] provide a summary of three key metrics in stream ecology. First, the uptake rate R [M L^{-2} t^{-1}] is the rate of nutrient uptake by plants, algae or microbes per unit area of streambed. Second, the uptake speed (or "uptake velocity" or "mass transfer coefficient" or "piston velocity") V_f [L t^{-1}] characterizes the rate of demand for a nutrient by plants, algae or microbes. *Doyle et al.* [2003] state that V_f is a "function" of the uptake rate and nutrient concentration c_N [M L^{-3}], namely,

$$V_f = \frac{R}{c_N} \tag{1}$$

Thus written, (1) takes the empirical viewpoint of estimating V_f from measurements of R and c_N. A biophysical viewpoint, in contrast, sees V_f as being a function of biological activity for given local stream conditions, whence functionally the uptake rate $R = V_f c_N$. The third metric is the uptake length λ [L]:

$$\lambda = \frac{hu}{V_f} \tag{2}$$

where h is the average flow depth and u is the average streamwise flow velocity. *Doyle et al.* [2003] describe λ as "the average distance a nutrient molecule travels in the water column before being sequestered in the benthic compartment, [thus representing] a whole-reach-scale measure of nutrient uptake." Thus, whereas R and V_f are local quantities, λ is spatially integrative.

Letting x [L] denote a streamwise coordinate, the uptake length λ normally is defined within the context of steady, uniform flow and steady concentration conditions as embodied in an exponential relation [*Stream Solute Workshop*, 1990; *Doyle et al.*, 2003]:

$$c_N(x) = c_{N0}e^{-x/\lambda} = c_{N0}e^{-V_f x/hu} \tag{3}$$

where $c_N(0) = c_{N0}$ is a steady upstream (inflow) boundary concentration. Here, λ is an e-folding lengthscale. From a transport perspective, as elaborated below, (3) obtains from a simple advective-reactive model of the form:

$$u\frac{\partial c_N}{\partial x} = -\frac{V_f}{h}c_N \tag{4}$$

which is expressed per unit channel width.

For reference below, let t denote time and note that the (Lagrangian) rate of change $\mathrm{d}c_N/\mathrm{d}t$ in concentration $c_N(t)$ as viewed by an observer moving with the flow along $x(t)$ at speed $u = \mathrm{d}x/\mathrm{d}t$ is $\mathrm{d}c_N/\mathrm{d}t = (\partial c_N/\partial x)\mathrm{d}x/\mathrm{d}t = u\partial c_N/\partial x$, which, using (3), gives

$$\frac{\mathrm{d}c_N}{\mathrm{d}t} = -\frac{1}{\tau}c_N \tag{5}$$

where $\tau = \lambda/u = h/V_f$ is an e-folding timescale. This illustrates simply that, according to (3) or (4), the net rate of uptake (consumption) of a nutrient from the fluid column is directly proportional to the concentration c_N [e.g. *Webster and Ehrman*, 1996]. This rate, of course, must be related to biological activity. If it is assumed that the level of activity, hence uptake, is locally a function of biomass per unit area of streambed c_A [M L^{-2}], then to obtain (5) requires that $1/\tau$ be directly proportional to c_A. This, in turn, means that (3) and (4) are restricted to the simplest possible prescription of nutrient uptake, namely, $\mathrm{d}c_N/\mathrm{d}t \propto c_A c_N$, which excludes possible differences in uptake behavior under, say, nutrient limited versus nutrient unlimited conditions. We clarify these points below.

The next section introduces a basic model of nutrient transport and "reaction" (production and consumption) together with a simple description of benthic algae growth. This forms the basis for further clarifying key ingredients of the uptake length λ and the uptake speed V_f in subsequent sections.

3 Basic Model of Nutrient Transport and Reaction with Benthic Algae

Momentarily neglecting hyporheic exchanges, conservation of nutrient mass in a stream requires that:

$$\frac{\partial}{\partial t}(bhc_N) = -\frac{\partial}{\partial x}(bhuc_N) + \frac{\partial}{\partial x}\left(bhD\frac{\partial c_N}{\partial x}\right) + P(x,t) + C(x,t) + S(x,t) \tag{6}$$

Here, c_N [M L^{-3}] is the nutrient concentration, b [L] is the local channel width, h [L] is the local average channel depth, u [L t^{-1}] is the local average flow velocity, D [L^2 t^{-1}] is a hydrodynamic dispersion coefficient, P [M L^{-1} t^{-1}] is the rate of nutrient production per unit channel length, C [M L^{-1} t^{-1}] is the rate of nutrient consumption per unit channel length, S [M L^{-1} t^{-1}] is a source/sink of the nutrient per unit channel length related to, say, atmospheric deposition or net input/loss with groundwater, x is the streamwise coordinate and t is time.

In (6) the production and consumption terms, P and C, define the (local) cycling of the nutrient. Indeed, setting the flow velocity u and the hydrodynamic dispersion D to zero, the advection and dispersion terms in (6) vanish, and the rate of change in c_N per unit channel length, namely

$$\frac{\partial}{\partial t}(b h c_N) = P(x,t) + C(x,t) + S(x,t) \tag{7}$$

effectively describes the cycling behavior of c_N in a "box" without water motion. The advection and dispersion terms in (6), representing transport with water flow, therefore transform this cycling into downstream spiraling.

The rate of nutrient consumption C is equivalent to the rate of nutrient uptake by benthic algae, and the rate of production P describes the remobilization of this nutrient, temporarily sequestered by benthic algae, back into the fluid column in relation to remineralization and algae death. These rates are set by the standing stock (biomass) of benthic algae, so we also require a dynamic model of the algae biomass c_A [M L^{-2}], namely

$$\frac{\partial}{\partial t}(b c_A) = R(x,t) - M(x,t) \tag{8}$$

where R [M L^{-1} t^{-1}] is the benthic algae growth rate per unit channel length and M [M L^{-1} t^{-1}] is the algae mortality rate per unit channel length.

The nutrient consumption/uptake rate C is assumed to follow a modified Michaelis-Menten function (or a Beddington type II function [*Beddington*, 1975; *DeAngelis et al.*, 1975; see *Getz et al.*, 2003]):

$$C = -\frac{b c_A}{\tau_{NC}} \frac{c_N}{k_{NC} + c_N + \gamma \dfrac{c_A}{h}} \tag{9}$$

where τ_{NC} is an uptake time constant, k_{NC} is a half-saturation constant and γ is an interference parameter. This phenomenological relation says that the nutrient is consumed at a rate that is proportional to the standing stock of algae c_A. When the nutrient concentration c_N is unlimiting ($c_N \gg k_{NC}$), the uptake rate is limited only by interference inasmuch as the algae biomass c_A is not insignificant. When the nutrient concentration becomes limiting ($c_N \sim k_{NC}$), the uptake rate overall is increasingly controlled by the nutrient level.

Following the success of chemostat experiments with algae, there is merit in assuming that benthic algae growth follows a modified Droop formulation [*Droop*, 1968, 1973; *Lange and Oyarzun*, 1992]. Specifically, per unit channel length the rate of growth is a hyperbolic function [e.g. *Power and Dietrich*, 2002; *Getz et al.*, 2003]:

$$R = \frac{b c_A}{\tau_R}\left(1 - \frac{K_Q}{Q}\right) \tag{10}$$

where τ_R is a growth time constant, $Q(x, t)$ [M M^{-1}] is the nutrient storage "quota" of algae tissue and K_Q is the minimum amount of nutrient stored per unit algae biomass. In turn, per unit biomass the quota Q satisfies:

$$\frac{\partial Q}{\partial t} = \frac{1}{\tau_{NC}} \frac{c_N}{k_{NC} + c_N + \gamma \dfrac{c_A}{h}} - \frac{Q}{\tau_R}\left(1 - \frac{K_Q}{Q}\right) - \frac{Q}{\tau_P}\left(1 - \frac{K_Q}{Q}\right) \tag{11}$$

That is, the rate of change in nutrient storage in cell tissue is equal to the uptake rate minus the rate at which the nutrient is used in cell reproduction, minus any direct loss from tissue after uptake (not involving reproduction or death), where τ_P is a loss-rate time constant.

Momentarily neglecting grazing, the algae mortality rate M is assumed to be proportional to the standing stock c_A, whence

$$M = \frac{b c_A}{\tau_M} \tag{12}$$

where τ_M is a mortality time constant. This formulation also neglects, for now, effects of changing flow, sediment transport, and temperature, etc. on algae mortality.

Turning to the production P, if the nutrient mass temporarily sequestered by benthic algae is proportional to the standing stock, then we may assume that, per unit channel length, production P is proportional to this standing stock [e.g. *Fong et al.*, 1994], namely

$$P = \beta_M \frac{b c_A(t - \tau_D) Q}{\tau_M} + \beta_P \frac{b c_A Q}{\tau_P}\left(1 - \frac{K_Q}{Q}\right) \tag{13}$$

where τ_D is a characteristic delay constant. This says that algae releases back to the streamflow a part of the nutrient mass it previously consumed but has not yet used in reproduction, and that full release of stored nutrient mass following death is delayed by a time τ_D required for tissue decay. In the absence of an ancillary model for cellular nutrient processing (e.g. leading to generation of different nutrient species), the factors β_M and β_P (where $0 \le \beta_M, \beta_P \le 1$) are heuristically introduced here to represent the proportions of the nutrient which, when released, are in a form that is readily available for uptake downstream.

4 Steady, Uniform Flow

It is important to first consider the simple case of steady, uniform flow with $S = 0$. Then b, h, u and D are constants and (6) through (9) give

$$\frac{\partial c_N}{\partial t} = -u \frac{\partial c_N}{\partial x} + D \frac{\partial^2 c_N}{\partial x^2} + \frac{\beta_M c_A(t - \tau_D) Q}{h \tau_M} + \frac{\beta_P c_A Q}{h \tau_P}\left(1 - \frac{K_Q}{Q}\right) - \frac{c_A}{h \tau_{NC}} \frac{c_N}{k_{NC} + c_N + \gamma \dfrac{c_A}{h}} \tag{14}$$

and

$$\frac{\partial c_A}{\partial t} = \frac{c_A}{\tau_R}\left(1 - \frac{K_Q}{Q}\right) - \frac{c_A}{\tau_M} \tag{15}$$

Physical folks are fond of casting the governing equations of a system into dimensionless form. One reason is that this process leads to important dimensionless numbers, in this case a Peclet number and four Damkohler numbers. So begging indulgence, let

$$c_N = k_{NC}\hat{c}_N,\ c_A = k_{NC}H\hat{c}_A,\ Q = K_Q\hat{Q},\ h = H\hat{h},\ u = U\hat{u},\ x = X\hat{x},\ t = \frac{X}{U}\hat{t} \text{ and } \tau_D = \frac{X}{U}\hat{\tau}_D \quad (16)$$

where circumflexes denote dimensionless quantities and H, U and X respectively denote a characteristic depth, velocity and reach length. Substituting these into (14), (15) and (11) then gives

$$\frac{\partial \hat{c}_N}{\partial \hat{t}} = -\hat{u}\frac{\partial \hat{c}_N}{\partial \hat{x}} + \frac{1}{Pe}\frac{\partial^2 \hat{c}_N}{\partial \hat{x}^2} + \frac{\beta_M Da_M K_Q}{\hat{h}}\hat{c}_A(t^*)\hat{Q} + \frac{\beta_P Da_P K_Q}{\hat{h}}\hat{c}_A(\hat{Q}-1) - \frac{Da_{NC}}{\hat{h}}\frac{\hat{c}_A\hat{c}_N}{1+\hat{c}_N+\frac{\gamma}{\hat{h}}\hat{c}_A} \quad (17)$$

$$\frac{\partial \hat{c}_A}{\partial \hat{t}} = Da_R\hat{c}_A\left(1-\frac{1}{\hat{Q}}\right) - Da_M\hat{c}_A \quad (18)$$

and

$$\frac{\partial \hat{Q}}{\partial \hat{t}} = \frac{Da_{NC}}{K_Q}\frac{\hat{c}_N}{1+\hat{c}_N+\frac{\gamma}{\hat{h}}\hat{c}_A} - (Da_R + Da_P)(\hat{Q}-1) \quad (19)$$

Here, $Pe = XU/D$ is a Peclet number, and $Da_M = \tau_A/\tau_M$, $Da_P = \tau_A/\tau_P$, $Da_{NC} = \tau_A/\tau_{NC}$ and $Da_R = \tau_A/\tau_R$ are Damkohler numbers, each the ratio of the residence time of flow within X, namely $\tau_A = X/U$, and a biological "reaction" timescale (τ_M, τ_P, τ_{NC} and τ_R). In addition, $t^* = \tau_A(\hat{t} - \hat{\tau}_D)$.

Here is an easy way to "read" these Damkohler numbers: The rate of a particular process (identified by the subscript on its Damkohler number), relative to another process, increases directly with the Damkohler number. For example, the condition $Da_R/Da_{NC} \ll 1$ implies that the rate of algae reproduction is insignificant relative to the rate of nutrient uptake (an assumption that typically is applied in short-term nutrient addition experiments.)

5 Steady Conditions

There is considerable value in considering the case of steady conditions, both for the purpose of revealing important structure in the model and for comparison with the abstraction represented by the simplified model (3). Under steady conditions with $Pe \gg 1$ (see *Gandolfi et al.* [2001] for details regarding this assertion), (17), (18) and (19) yield:

$$\hat{u}\frac{\partial \hat{c}_N}{\partial \hat{x}} = -\alpha_0 + \alpha_1\hat{c}_N \quad (20)$$

$$\hat{Q} = \frac{Da_R}{Da_R - Da_M} \quad (21)$$

and

$$\hat{c}_A = \frac{\hat{h}}{\gamma}\left(\left[\frac{Da_{NC}(Da_R - Da_M)}{K_Q Da_M(Da_R + Da_P)} - 1\right]\hat{c}_N - 1\right) \quad (22)$$

where

$$\alpha_0 = \frac{K_Q}{\gamma} \frac{Da_M}{Da_R - Da_M} \left[(\beta_M - 1) Da_R + (\beta_P - 1) Da_P \right] \tag{23}$$

and

$$\alpha_1 = \alpha_0 \left[\frac{Da_{NC}(Da_R - Da_M)}{K_Q Da_M (Da_R + Da_P)} - 1 \right] \tag{24}$$

Lovely. This suggests several important items that are entirely consistent with physical intuition.

Inasmuch as $\tau_R \ll \tau_M$ ($Da_M \ll Da_R$), the nutrient quota $Q \to K_Q$ such that reproduction proceeds at a (slow) pace that matches mortality. For a given nutrient level the standing stock c_A increases with increasing uptake rate (Da_{NC}) and decreasing mortality rate (Da_M), and decreases with increasing interference (γ). Note that in the absence of interference ($\gamma \to 0$), the steady standing stock c_A is unbounded.

For steady upstream loading at concentration c_{N0}, the solution of (20) is logarithmic in form whereas the solution of (22) is exponential. Thus (4) can be only a rough approximation of steady conditions, and there is no simple mapping of the characteristic quantities in (20) to the metrics V_f and λ in (3). More importantly, inasmuch as (9) through (13) are phenomenologically and experimentally defensible, (3) and (4) do not capture the basic essence of the biological dynamic involved in nutrient spiraling.

Consider the special case where $\beta_M = \beta_P = 1$, implying that the nutrient, when released from algae (by direct loss or following death), is in a form that is readily available for uptake downstream. Then $\alpha_1 = \alpha_2 = 0$ and (20) reduces to

$$\frac{\partial \hat{c}_N}{\partial \hat{x}} = 0 \tag{25}$$

For steady upstream nutrient loading at concentration c_{N0}, the solution of (25) is $c_N(\mathrm{x}) = c_{N0}$. That is, nutrient uptake is everywhere balanced by production, and the nutrient concentration remains uniform downstream. In turn, according to (21) and (22) the quota $Q(x)$ and the standing stock $c_A(x)$ are uniform. This scenario approximately mimics in one case the behavior of phytoplankton in the Neuse River, North Carolina where, following initial upstream loading of nitrogen that caused a blue-green algal bloom, continuous release/remineralization of nitrogen as ammonium following decomposition sustained the bloom [*Stanley*, 1983].

Consider the special case where $\beta_M = \beta_P = 0$, implying that the nutrient, when released, is in a form that is unavailable for uptake downstream. Then

$$\alpha_0 = -\frac{K_Q}{\gamma} \frac{Da_M (Da_R + Da_P)}{Da_R - Da_M} \tag{26}$$

and

$$\alpha_1 = -\frac{Da_{NC}}{\gamma} - \alpha_0 \tag{27}$$

Solutions of (20) and (22) for steady upstream loading at concentration c_{N0} indicate a downstream decline in both $c_N(x)$ and $c_A(x)$. But as in the first case above, the decline in c_N is far from an exponential form. We now turn to other special cases of (20) and (22) to clarify these points.

5.1 Nutrient Unlimited Conditions

For conditions where $k_{NC} \ll c_N$ and $\gamma c_A/h \ll c_N$, no bounded steady solution of c_A exists. Algae growth is a runaway process.

5.2 Nutrient Limited Conditions with Small Variations in c_N

Consider the addition of a small deviation in the nutrient loading under initially steady conditions, where it is assumed that the loading occurs over a period that is shorter than the reproduction, mortality and remineralization timescales. This is like a nutrient addition experiment, or a change in the loading from an upstream point source, following a steady state. Let $c_N(x) = C_N(x) + c_N'(x)$ and $c_A(x) = C_A(x)$, where C_N and C_A denote the basic (initial) state and c_N' denotes the small deviation in the nutrient. Then C_N satisfies (20) and c_N' satisfies the linearized equation:

$$\hat{u}\frac{\partial \hat{c}_N'}{\partial \hat{x}} = -\frac{Da_{NC}\hat{C}_A\Gamma}{\hat{h}}\hat{c}_N' \tag{28}$$

where

$$\Gamma = \frac{1}{1 + \hat{C}_N + \frac{\gamma}{\hat{h}}\hat{C}_A}\left(1 - \frac{\hat{C}_N}{1 + \hat{C}_N + \frac{\gamma}{\hat{h}}\hat{C}_A}\right) \tag{29}$$

For small interference this reduces to $\Gamma \approx 1/(1 + C_N)^2$.

In dimensional form with small interference (28) becomes

$$u\frac{\partial c_N'}{\partial x} = -\frac{C_A}{\tau_{NC}h}\frac{k_{NC}}{(k_{NC} + C_N)^2}c_N' \tag{30}$$

which maps nicely to the metric V_f in (4). Namely,

$$V_f = \frac{C_A}{\tau_{NC}}\frac{k_{NC}}{(k_{NC} + C_N)^2} \tag{31}$$

with units [L t^{-1}]. In turn, the uptake length λ [L] is

$$\lambda = \frac{hu\tau_{NC}}{C_A}\frac{(k_{NC} + C_N)^2}{k_{NC}} \tag{32}$$

Note that these metrics are explicitly a function of the local standing stock C_A, as they should be. Moreover, (32) suggests that the uptake length depends on the ambient initial concentration C_N. Because $C_N(x)$ varies downstream, the length scale λ must also.

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