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## Modelling nutrient–periphyton dynamics in streams: the importance of transient storage zones

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### Abstract

The dynamics of a nutrient-limited periphyton community in a segment of stream was modeled. The stream segment was assumed to consist of two zones, free-flowing water and a boundary zone of zero water flow, which acted as a transient storage zone for nutrients. Studies with a biologically unreactive tracer solute (sodium chloride) were used to obtain parameters for diffusion of solute into the transient storage zone. Two simple alternative functional responses representing nutrient-limited periphyton growth were formulated, one with only nutrient limitation on periphyton growth and one that additionally included density-dependent limitation of periphyton growth.

Attempts to fit the two alternative functional responses for periphyton growth and to predict nutrient levels in the transient storage zone showed that the two alternatives had very different implications for the steady state and dynamics of the storage zone. Empirical studies of periphyton biomass and nutrient turnover give support for the second alternative function. The model results suggests some additional experiments that can be performed to test the two alternatives.

**Keywords:** Freshwater ecosystems; Nutrients; Periphyton

### 1. Introduction

Stream hydraulic characteristics are important in the ecology of streams. Of particular importance is the presence of hydraulic or transient storage zones (zones of zero or near-zero flow) in stream channels. These zones are refuges for many organisms not adapted to high water veloci-

ties. They are also places where the nutrient cycling regime in the biological community is likely to be quite different from that in the free-flowing part of the stream. In the free-flowing stream, nutrient concentration in any relatively short reach is largely controlled by the nutrient concentration of incoming water from upstream, in contrast to the storage zones, where the biological communities can influence the local nutrient concentrations via uptake and conversion to organic matter. The fact that nutrients released from organic matter may remain long enough in the transient storage zone to be taken up by the

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biota more than once also influences the level of nutrient concentration there, as well as the nutrient supply to biota.

Fig. 1a shows a sketch of a stream reach short enough to be longitudinally uniform and Fig. 1b shows a schematic of the processes involving nutrient transport through that segment. This will be referred to as a “stream segment” from now on, divided into a storage zone and a free-flowing water zone, with the storage zone along the bottom, where water movement can be approximated as zero-flow. Bottom friction, especially from irregularities such as rocks, create these areas of zero-flow water. In addition, interstitial waters in sediments or within algal mats, backwater areas, and pools can also act as transient storage zones (e.g., Bencala and Walters, 1983; Triska et al., 1990; Mulholland et al., 1994), but here we will lump all of these storage zones together into the bottom layer of the stream.

In this paper we focus on the effect of the transient storage zone on the dynamics of a limiting nutrient in small streams with simple periphy-

ton communities. We use a mathematical model to predict how changes in various physical properties of the transient storage zone can affect measurable properties of biomass in this zone. These conclusions are compared to experimental evidence.

## 2. Estimating the transient storage zone of a stream

What evidence is there that segments of a stream can be described as consisting of two components: free-flowing water and a transient storage zone? Many studies have used this conceptualization and fit tracer injection data of experimental tracer injections to two-component models (e.g., Bencala and Walters, 1983). In these experiments a conservative tracer, such as a chloride or tritium solution, is injected at a constant rate into a stream point for a known period of time. At a site sufficiently below the injection point that the tracer can be assumed completely

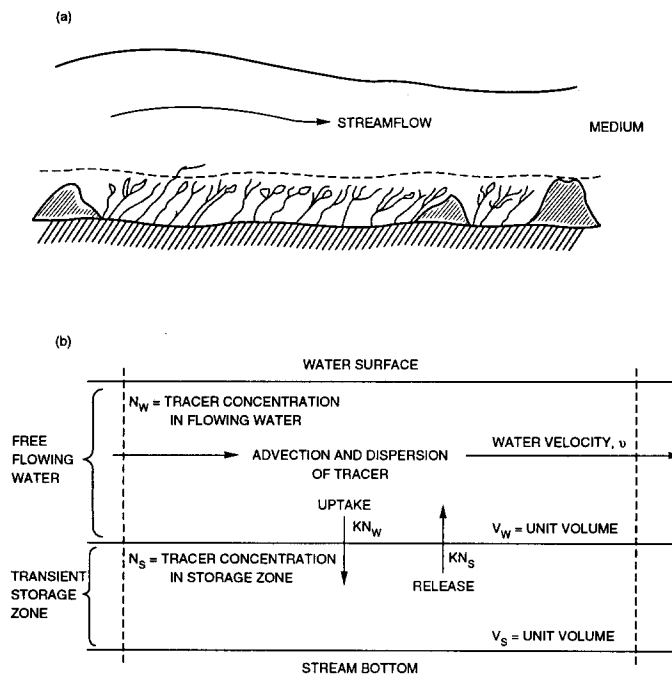


Fig. 1. (a) Longitudinal sketch of a stream segment, showing the free-flowing water and transient storage zones. (b) Schematic of the stream segment, indicating the movements of a solute tracer or nutrient.

mixed into the stream water, the tracer concentration is measured. This is called the upstream point and the concentration is essentially constant during the injection period. The concentration of the tracer is also measured as it reaches a point downstream, say 100 meters below the upstream measurement point. The tracer is injected for a time sufficient for its concentration to reach steady-state at the downstream site. Assuming there is no loss of tracer along this segment, or dilution by input of water from stream tributaries or groundwater, the shape of the measured concentration through time is determined by longitudinal dispersion and by diffusional transport (consisting of both molecular diffusion and turbulent diffusion) of tracer particles back and forth across the boundary between the free-flowing water and the transient storage zone. Tracer particles that enter the transient storage zone will stay for some period of time before being released back to the free-flowing water. This leads to a measured downstream concentration that is somewhat spread out temporally (compared to the square pulse input of 250 min) and is usually characterized by a long tail (Fig. 2).

Fig. 2 also shows a typical model fit of data, collected on Walker Branch, a first-order stream located on the Oak Ridge Reservation. The diffu-

sional transport constants across the boundary,  $k_s$  and  $k_w$ , and the longitudinal dispersion coefficient,  $D$ , can be calculated from fitting the model. The fact that the model fits the data very closely is an indication that the simple two-component model is a good approximation of reality, at least for this particular stream. This does not mean that there are actually two sharply distinct regions in the stream. In fact, the situation in a real stream is more complex, with a spectrum of possible transient storage zones, both in terms of size and diffusional transport rates. The point is, however, that with respect to tracer movement this stream segment as a whole behaves effectively very much like a two-component system. Note that because the steady state diffusional transport rate across the boundary must be the same in both directions, it must be true that  $k_w V_w = k_s V_s$ , so that the ratio of storage zone water volume to free-flowing water volume in the stream segment is  $V_s/V_w = k_w/k_s$ .

The studies shown here are for conservative tracers, which are not selectively taken up by biota. These tracers enable us to determine some stream physical characteristics; the size of the effective transient storage zone, the solute diffusional transport rates across the interface, and the longitudinal dispersion rate of the free-flowing water. The behavior of a solution of an essential nutrient in the stream will be different, because it takes part in and affects biological processes of growth and mortality. The purpose of this work is to predict the nutrient dynamics within the transient storage zone of streams.

### 3. Periphyton biomass and nutrient dynamics in transient storage zone

In this study it is assumed that the storage zone is a fixed abiotic feature of the stream that exists prior to the development of periphyton biomass. This is only approximately true. In a recent study we showed that the growth of periphyton biomass itself can positively influence the effective size of the storage zone (Mulholland et al., 1994). However, it is assumed here that the physical features of the stream alone determine

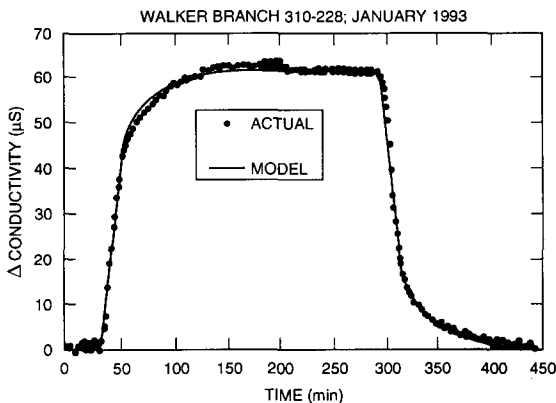


Fig. 2. Conservative tracer experiment data from a 4-h injection to Walker Branch stream. Solid points are conservative tracer concentrations, measured as changes in electrical conductance relative to pre-injection values, through time at a site approximately 70 m downstream from the point of injection. The best model fit to downstream data is shown.

the transient storage zone volume. The emphasis will be on how the size and other characteristics of the storage zone affect nutrient–periphyton dynamics within streams.

Another assumption made in this paper is that the periphyton community (algae and microbes) is located only within the transient storage zone. Past studies (e.g., Kim et al., 1992) have considered the biological processes of the stream to be independent of the transient storage zone processes. However, we consider the biological activity to be taking place within the storage zone. In this sense our concept of the transient storage zone is just an extension of the concept of a bottom boundary layer in flowing water systems.

The nutrient cycling characteristics of a stream segment will be studied using a model and empirical measurements of stream systems.

#### 4. Model formulation

In the model the periphyton community is lumped into one biomass component and the

detritus is also one component (Fig. 3). The model used here simulates a short, homogeneous, longitudinal segment, or unit length, of stream and assumes that there are four components:

$N_w$  = nutrient concentration in dissolved, biologically reactive inorganic form in the free-flowing water.

$N_s$  = nutrient in dissolved inorganic form in the water of the hydraulic or transient storage zone.

$B$  = concentration of nutrient tied up in the living biomass, that is, the concentration of biomass in the storage zone times the nutrient per unit biomass.

$D$  = nutrient tied up in the detritus, that is, the concentration of detritus in the storage zone times the nutrient per unit detritus.

The input flux of nutrient is  $I_n$  ( $I_n = QN_0$ ), where  $Q$  is the influx of water (liters/day) and  $N_0$  is the nutrient concentration arriving to the stream segment.

The variables  $N_w$ ,  $N_s$ ,  $B$ , and  $D$  have units of nutrient concentration (mg/l),  $V_w$  and  $V_s$  are the volumes of the free-flowing water column and the

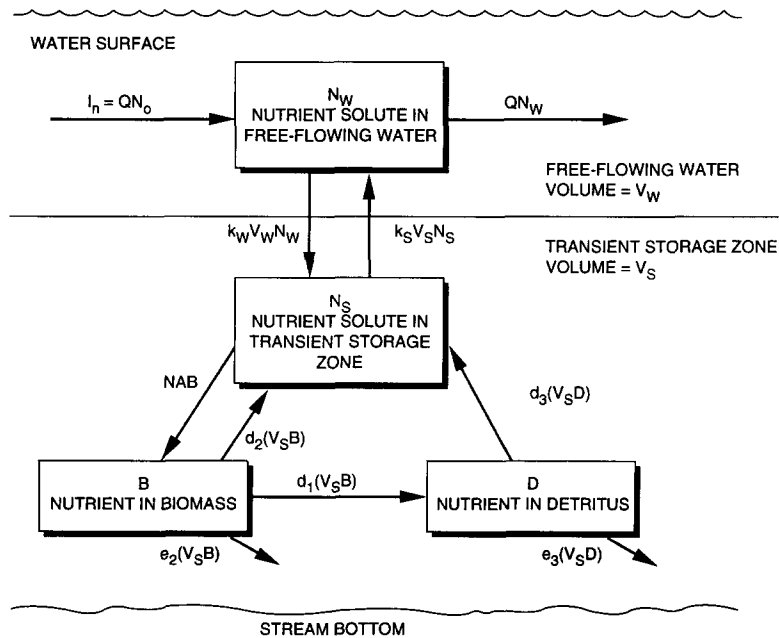


Fig. 3. Schematic of model for nutrient movement within the transient storage zone and between it and the free-flowing water. The transient storage zone is assumed to contain all of the living biomass and detritus.

storage zone per unit length of stream (l),  $k_w$  and  $k_s$  are transfer coefficients (1/day) from the water column to the storage zone and vice versa (it must always be true that  $k_w V_w = k_s V_s$ ),  $d_1$  is the transfer coefficient (1/day) of live biomass to detritus,  $d_2$  and  $d_3$  are the rate coefficients (1/day) of loss of nutrient from biomass and detritus back to water in the transient storage zone, and  $e_2$  and  $e_3$  are rate coefficients (1/day) of loss of biomass and detritus as export (e.g., drift from the system). The model assumes that the transient storage zone is perfectly mixed, so there are no diffusion gradients of nutrient within the zone.

Note from Fig. 3 that the flux to the living organic matter, or rate of accumulation of nutrient into living biomass, which is proportional to biomass growth, has not been assigned a functional form at this point, but is simply called NAB (nutrient assimilation into biomass). Part of the goal of this paper is to determine what functional form is a reasonable description of this assimilation rate. The equations for the general model can be written out as

$$\frac{d(V_w N_w)}{dt} = QN_0 - QN_w - k_w V_w N_w + k_s V_s N_s \quad (1)$$

$$\frac{d(V_s N_s)}{dt} = k_w V_w N_w - k_s V_s N_s - [\text{NAB}] + d_2(V_s B) + d_3(V_s D) \quad (2)$$

$$\frac{d(V_s B)}{dt} = [\text{NAB}] - d_2(V_s B) - d_1(V_s B) - e_2(V_s B) \quad (3)$$

$$\frac{d(V_s D)}{dt} = d_1(V_s B) - d_3(V_s D) - e_3(V_s D) \quad (4)$$

where NAB = rate of nutrient assimilation by living biomass.

A reasonable initial formulation for NAB might be the Monod-type growth function,  $r(V_s B)N_s/[b + N_s]$ , where  $r$  and  $b$  are constants. The growth rate per unit periphyton biomass approaches the constant  $r$  when the concentration of limiting nutrient,  $N_s$ , is very large. This function implicitly assumes that the growth of biomass in the storage zone is limited only by

nutrient availability. With this growth rate assumption, the steady state solution to Eqs. 1,2,3,4 becomes

$$N_s^* = \frac{b(d_1 + d_2 + e_2)}{r_1 - d_1 - d_2 - e_2} \quad (5)$$

$$N_w^* = \frac{1}{Q + k_w V_w} [N_0 Q + k_s V_s N_s^*] \quad (6)$$

$$B^* = \left[ \frac{d_3 + e_3}{e_2(d_3 + e_3) + e_3 d_1} \right] \times \left[ \frac{Q}{Q + k_w V_w} \right] k_s [N_0 - N_s^*] \quad (7)$$

$$D^* = \frac{d_1}{d_3 + e_3} B^* \quad (8)$$

where the asterisk denotes a steady state solution. We will call this functional response 1.

A second possible function for NAB is  $r(V_s B)N_s/(b_1 + N_s + cB)$ . This is a modification of the traditional Monod-type growth, which has been analyzed by Beddington (1975) and DeAngelis et al. (1975). In the present function, the additional  $cB$  term in the denominator represents a form of self-limitation of growth resulting from possible limitation of nutrient availability through a decrease in diffusion rate as biomass increases. The Monod-type growth function can be recovered from the present function by setting the parameter  $c = 0$ .

The steady-state values of  $N_w$ ,  $N_s$ ,  $B$ , and  $D$  are now (for what we will call functional response 2)

$$N_s^* = \frac{\frac{k_s Q N_0}{Q + k_w V_w} + \frac{b}{c} \left[ \frac{d_1 e_3}{d_3 + e_3} + e_2 \right]}{\frac{Q k_s}{Q + k_w V_w} + \left[ \frac{d_1 e_3}{d_3 + e_3} + e_2 \right] \frac{r - d_1 - d_2 - e_2}{c(d_1 + d_2 + e_2)}} \quad (9)$$

$$N_w^* = \frac{N_0 Q + k_s V_s N_s^*}{Q + k_w V_w} \quad (10)$$

$$B^* = \frac{(r - d_1 - d_2 - e_2) N_s^*}{c(d_1 + d_2 + e_2)} - \frac{b_1}{c} \quad (11)$$

$$D^* = \frac{d_1}{d_3 + e_3} B^* \quad (12)$$

## 5. Implications and tests of the model

Using the steady state results of the above two functional responses, one can examine the effects of a range of different assumptions on relationships between the free-flowing water and the hydraulic storage zone that might occur in different stream systems.

The parameter values in Table 1 were chosen to fit a set of experiments (Mulholland et al., 1994) done in the presence and absence of grazing by snails, resulting in low and high periphyton biomasses, respectively. (Note, the snail grazer density is considered an exogenously controlled component and does not have to be treated as a variable in the model.) The experimental values of the steady state values  $N_w^*$ ,  $N_s^*$ , and  $B^*$  in the high biomass case and the best model fits are compared in Table 2. Loss rates of nutrient from the periphyton, measured using samples of periphyton tagged with  $^{33}\text{P}$ , are shown in Table 3. These were measured under conditions of both ambient streamwater P and enhanced P (about twenty times the concentration of ambient). There was no experimentally detectable difference between the loss rates under these two conditions. This is what is expected from both models, since this loss rate is merely  $d_2 + d_3$ . With both functions the model was able to give good fits to

Table 1  
Parameter values used to fit functional responses (FR) 1 and 2 to data for an artificial stream described in Mulholland et al. (1994)

|       | FR 1    | FR 2    | Units             |
|-------|---------|---------|-------------------|
| $N_0$ | 0.005   | 0.005   | mg/l              |
| $Q$   | 31680.0 | 31680.0 | l/day             |
| $k_w$ | 97.2    | 97.2    | day <sup>-1</sup> |
| $k_s$ | 388.8   | 388.8   | day <sup>-1</sup> |
| $V_w$ | 0.8     | 0.8     | l                 |
| $V_s$ | 0.2     | 0.2     | l                 |
| $d_1$ | 0.07    | 0.009   | day <sup>-1</sup> |
| $d_2$ | 0.03    | 0.004   | day <sup>-1</sup> |
| $d_3$ | 0.04    | 0.005   | day <sup>-1</sup> |
| $e_2$ | 0.03    | 0.004   | day <sup>-1</sup> |
| $e_3$ | 0.03    | 0.004   | day <sup>-1</sup> |
| $r$   | 0.5     | 0.5     | day <sup>-1</sup> |
| $b$   | 0.01    | 0.01    |                   |
| $c$   | 0.0     | 0.02    |                   |

Table 2

Experimental values of  $N_w^*$ ,  $N_s^*$ , and  $B^*$  and model fits for the two functions responses (FR). AFDM is ash-free dry matter, which corresponds to  $(B^* + D^*)/3$  in the model (NM = not measured)

|               | Experiment | FR 1    | FR 2    | Units              |
|---------------|------------|---------|---------|--------------------|
| High Biomass: |            |         |         |                    |
| $N_w^*$       | 0.006      | 0.005   | 0.005   | mg/l               |
| $N_s^*$       | NM         | 0.00351 | 0.00487 | mg/l               |
| AFDM          | 4.75       | 6.41    | 4.28    | mg/cm <sup>2</sup> |

ash-free dry matter. However, functional response 1 could not be fit to ash-free dry matter and nutrient turnover rate simultaneously because of the constraints that fitting the ash-free dry matter put on  $d_2 + d_3$ .

By comparing further implications of the two models, as embodied in the steady state results (Eqs. 5–8 and 9–12), we can see which model is better corroborated by other characteristics. We will explore the model behavior for the variations of four parameters:

1. The volume of the storage zone,  $V_s$ .
2. The diffusional transfer rates,  $k_w$  and  $k_s$ .
3. The input nutrient concentration,  $N_0$ .
4. The loss rate of biomass from the system,  $e_2$ .

### 5.1. Effects of the transient storage zone size, $V_s$

Change in the volume of the storage zone,  $V_s$ , causes an inverse change in  $k_s$ , such that the product  $k_s V_s$  remains constant. The reason for this is that a change in  $V_s$  is interpreted as a change the depth of the storage zone. This should not affect the diffusional transport rate at the

Table 3

Values of phosphorus loss rate from periphyton in the experiment (using whole stream radiotracer addition approach) and as predicted by the two functional responses (FR1 and FR2) under different conditions of phosphorus concentration

|  | Experiment | FR 1  | FR 2  | Units             |
|--|------------|-------|-------|-------------------|
| High biomass, ambient P                  | 0.017      | 0.130 | 0.017 | day <sup>-1</sup> |
| High biomass, enhanced P ( $\times 20$ ) | 0.017      | 0.130 | 0.017 | day <sup>-1</sup> |

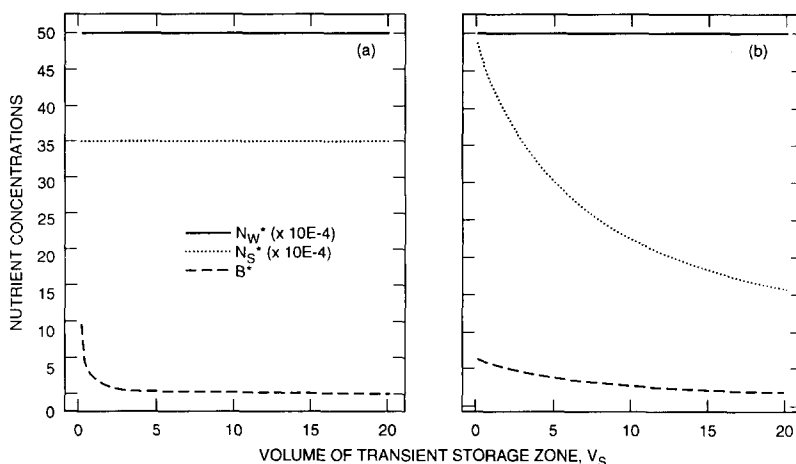


Fig. 4. Effects of changes in the fraction of stream that is part of the transient storage zone,  $V_s$ , on  $B^*$ ,  $N_w^*$ , and  $N_s^*$ ; for (a) functional response 1, high biomass, (b) functional response 2, high biomass.

interface between the free-flowing water and the storage zone,  $k_s V_s (=k_w V_w)$ , so these remain constant. The effects on each model following such changes are as follows.

*Functional response 1*

Fig. 4a shows the effects of a range of values of  $V_s$  from 0.0 to 20.0 l in the stream segment (keeping  $V_w$  constant). Note that  $N_s^*$  and  $N_w^*$

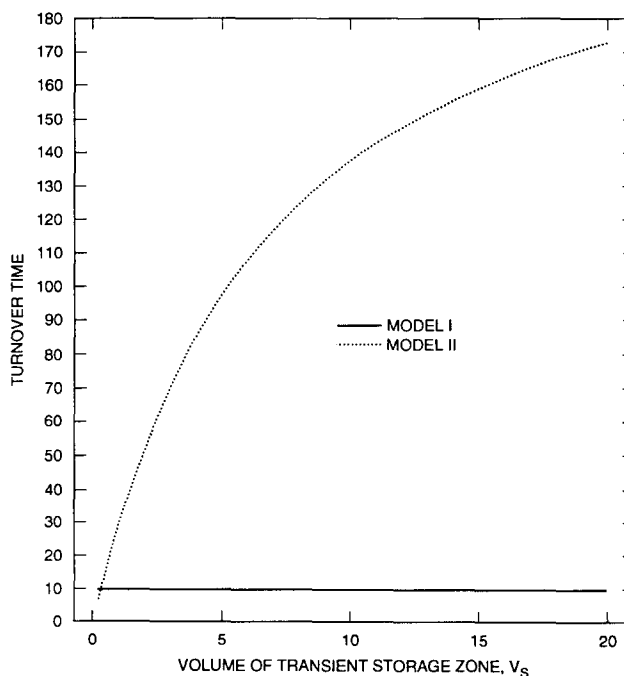


Fig. 5. Effects of changes in the fraction of stream that is part of the transient storage zone,  $V_s$ , on nutrient turnover time within the transient storage zone,  $T$ ; high biomass.

stay constant with increasing  $V_s$  ( $N_s^*$  is controlled by the periphyton), but  $B^*$  decreases (in this and all other cases,  $D^*$  changes in direct proportion to  $B^*$ ). This is a result of the fact that the overall amount of biomass-bound nutrient in the storage zone,  $V_s B^*$ , stays constant, because it is limited by the diffusion of new nutrient into the storage zone. Thus, the concentration,  $B^*$ , decreases. However, note that  $B^*$  is presented as a concentration here, so that total biomass is  $B^* V_s$  and would tend to increase with increasing  $V_s$ .

*Functional response 2*

The effects of  $V_s$  on the model variables are shown in Fig. 4b. In particular, when  $V_s$  is very small,  $N_s^*$  is dominated by the effects of diffusion from the free-flowing water and is approximately equal to  $N_0$  (and  $N_w^*$ ). When  $V_s$  is very large, the effects of diffusion of nutrient from the free-flowing water are small and  $N_s^*$  is dominated by the effects of periphyton. Thus, for increasing  $V_s$ ,  $N_s^*$  approaches

$$N_s^* = \frac{b(d_1 + d_2 + e_2)}{r_1 - d_1 - d_2 - e_2} \tag{13}$$

As  $V_s$  increases,  $N_w^*$  decreases from its maximum value of  $N_0$ , but for the parameter values being used, this effect is negligible and is not seen in Fig. 4b. The living biomass nutrient concentra-

tion,  $B^*$ , decreases with increasing  $V_s$  because of the decrease in  $N_s^*$ .

The nutrient turnover time within the transient storage zone increases as a function of  $V_s$  for functional response 1 but not 2 (Fig. 5). Nutrient turnover time is defined as the total nutrient in the transient storage zone in steady state divided by the input flux,

$$T \approx \frac{(N_s^* + B^* + D^*)V_s}{k_w V_w N_w^*} = \frac{N_s^* + B^* + D^*}{k_s N_w^*} \tag{14}$$

The turnover time  $T$  approaches an asymptote in functional response 2, because  $B^*$  and  $D^*$  decrease with increasing  $V_s$  in that case.

*5.2. Effects of diffusional transport rates,  $k_w$  and  $k_s$*

If the coefficients  $k_w$  and  $k_s$ , which measure the effectiveness of transport of nutrients between the zones, are changed simultaneously, while  $V_w$  and  $V_s$  are held constant, then  $k_w V_w$  and  $k_s V_s$  (which must remain equal) will change in proportion.

*Functional response 1*

As the coefficients  $k_w$  and  $k_s$  simultaneously increase,  $N_s^*$  and  $N_w^*$  remain constant, while  $B^*$

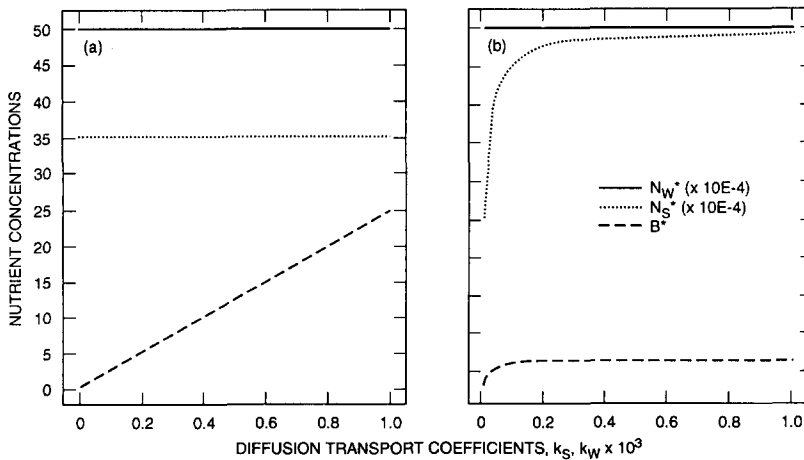


Fig. 6. Effects of change in the nutrient transfer coefficients,  $k_w$  and  $k_s$ , on  $B^*$ ,  $N_w^*$ , and  $N_s^*$ ; for (a) functional response 1, high biomass, (b) functional response 2, high biomass.



increases almost linearly from zero (Fig. 6a), although it would eventually reach an asymptote if the coefficients continued to increase. Thus, increasing diffusional transport permits a greater amount of nutrients within the segment to be incorporated into periphyton biomass.

*Functional response 2*

With no nutrient diffusion between zones ( $k_s$  and  $k_w$  equalling zero),  $N_s^*$  is entirely dominated by the periphyton and its value is the same as in Eq. 5, while  $N_w^*$  is equal to  $N_0$  (Fig. 6b). As this diffusional transport is increased to high values,  $N_s^*$  approaches the value

$$N_s^* = \frac{\frac{k_s N_0 Q}{k_w V_w} + \frac{b}{c} \left[ \frac{d_1 e_3}{d_3 + e_3} + e_2 \right]}{\frac{Q k_s}{k_w V_w} + \left[ \frac{d_1 e_3}{d_3 + e_3} + e_2 \right] \frac{r - d_1 - d_2 - e_2}{c(d_1 + d_2 + e_2)}} \quad (15)$$

The asymptote of  $N_s^*$  depends on other parameters, such as  $Q$  and  $V_w$ , but for the parameter

values of this model it is very close to  $N_0$ . The periphyton biomass,  $B^*$ , asymptotes at lower values of  $k_s$  ( $k_w$ ) than in functional response 1.

The turnover time is constant for functional response 1, because  $B^*$  and  $D^*$  increase linearly with  $k_s$  ( $k_w$ ), although  $N_s^*$  stays constant (Fig. 7). For functional response 2,  $N_s^*$ ,  $B^*$ , and  $D^*$  all asymptote as  $k_s$  ( $k_w$ ) increases. Therefore, turnover time is a decreasing function of the diffusional transport rate.

*5.3. Effects of changes in upstream nutrient concentration,  $N_0$*

*Functional response 1*

Changes in  $N_0$  are predicted to have no effect on  $N_s^*$ , but  $N_w^*$  and  $B^*$  are both roughly proportional to  $N_0$  (Fig. 8a). The reason that there is no effect on  $N_s^*$  is that this value is held constant by periphyton uptake (Eq. 5).

*Functional response 2*

With this functional response all three variables,  $N_s^*$ ,  $N_w^*$ , and  $B^*$ , should increase as  $N_0$  is

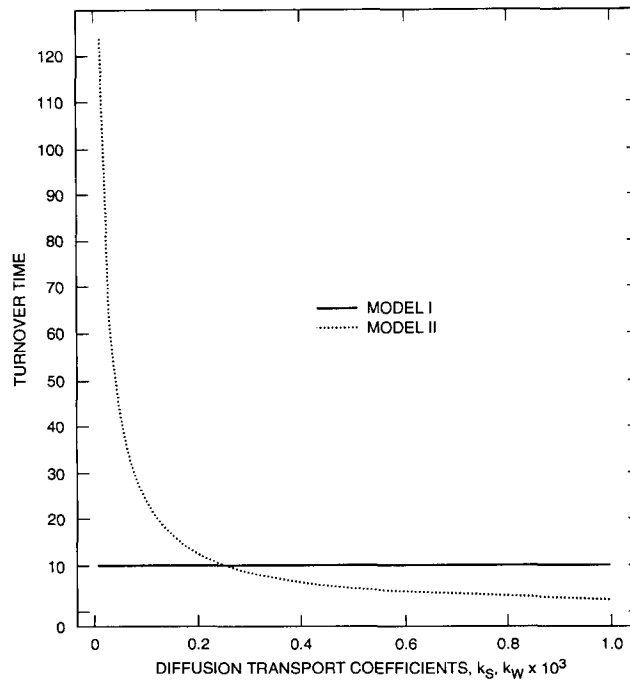


Fig. 7. Effects of changes in the nutrient transfer coefficients,  $k_w$  and  $k_s$ , on the nutrient turnover time in the transient storage zone,  $T$ ; high biomass.

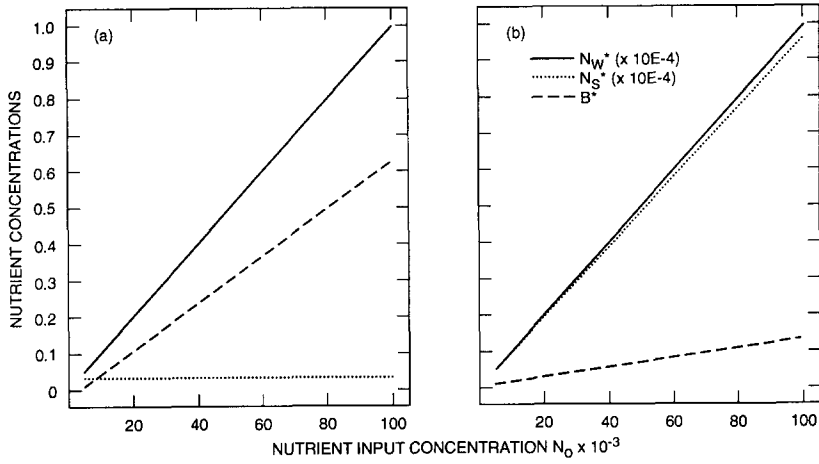


Fig. 8. Effects of changes in the input nutrient concentration,  $N_0$ , on  $B^*$ ,  $N_w^*$ , and  $N_s^*$ ; for (a) functional response 1, high biomass, (b) functional response 2, high biomass.

increased (Fig. 8b). Periphyton is somewhat self-limited and cannot control the transient zone nutrient concentration,  $N_s^*$ , at a constant level.

The nutrient turnover time,  $T$ , is relatively constant with respect to changes in  $N_0$  in functional response 2 but increases for functional

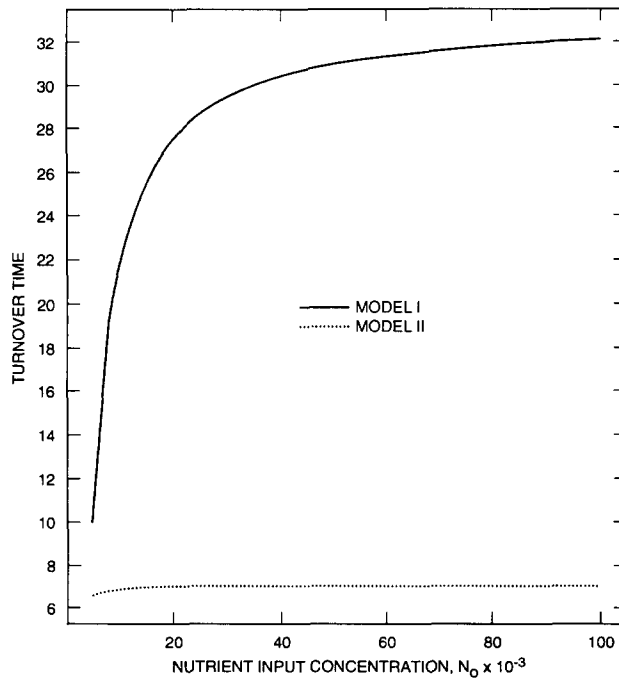


Fig. 9. Effects of changes in the input nutrient concentration,  $N_0$ , on the nutrient turnover time,  $T$ , in the transient storage zone; high biomass.

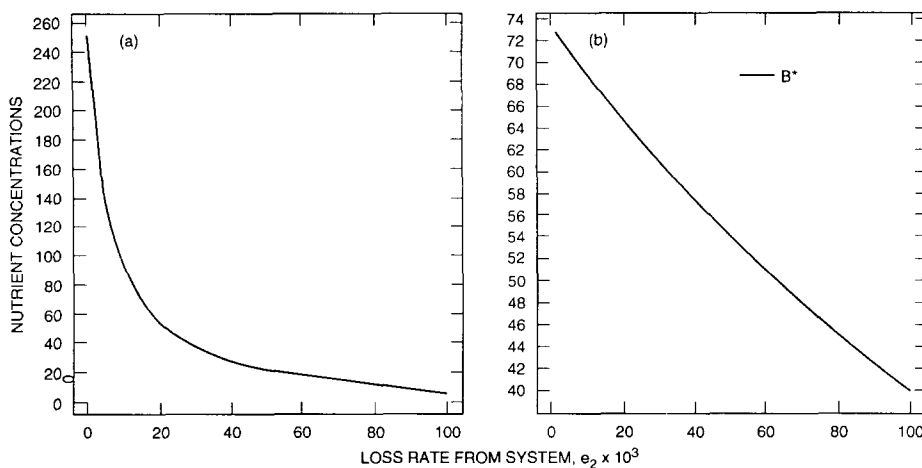


Fig. 10. Effects of changes in the loss rate coefficient of biomass,  $e_2$ , on  $B^*$ , for (a) functional response 1, high biomass and (b) functional response 2, high biomass.

response 1 (Fig. 9). The increase with functional response 1 reflects the fact that  $B^*$  and  $D^*$  increase much more rapidly with increasing  $N_0$  than these variables do with functional response 2, due to the self-limitation in the latter model.

5.4. Effects of changes in biomass loss rate from system,  $e_2$

Functional response 1

Increases in the loss rate,  $e_2$ , of periphyton biomass from the system result in a decrease in the periphyton biomass,  $B^*$  (Fig. 10a). The tran-

sient storage zone nutrient concentration,  $N_s^*$ , however, increases (Fig. 11a). The reason for this increase can be seen directly in Eq. 5, in which the parameters for the periphyton govern the nutrient concentration in the storage zone, and Eq. 7, in which  $B^*$  and  $N_s^*$  are negatively related.

Functional response 2

In this case, an increase in  $e_2$  leads again to a decrease in periphyton biomass,  $B^*$  (Fig. 10b). However, there is a simultaneous decrease in  $N_s^*$

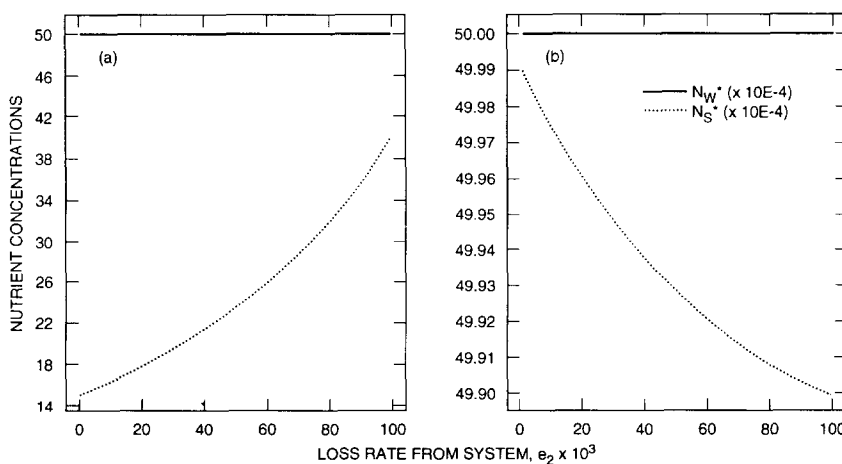


Fig. 11. Effects of changes in the loss rate coefficient of biomass,  $e_2$ , on  $N_w^*$  and  $N_s^*$ , for (a) functional response 1, high biomass and (b) functional response 2, high biomass.

(Fig. 11b). This positive correlation between  $B^*$  and  $N_s^*$  is evident in Eq. 11.

## 6. Discussion and conclusions

Which of these models is the superior representation of nutrient–periphyton dynamics in a stream segment can only be decided through comparisons with empirical studies. Available data on the loss rate as a function of periphyton biomass and of  $N_0$  (Mulholland et al., 1994; our Table 3) favors functional response 2. In addition, the predicted changes within the transient storage zone in response to changes  $V_s$  and  $k_s$  and  $k_w$  appear to be better described by functional response 2 than by 1. In particular, functional response 2 predicts that  $N_s^*$  should be affected by changes in these quantities, while functional response 1 does not. While no specific data are available, it seems unreasonable that  $N_s^*$  would be completely dominated by the periphyton, especially in the limit when  $V_s$  is miniscule compared to  $V_w$  and the nutrient transfer rate is large. It seems almost certain that the free-flowing water concentration will dominate the storage zone concentration, resulting in values approximating  $N_0$ . The decline in turnover time in the transient storage zone as a function of  $k_w$  ( $k_s$ ), as predicted by functional response 2, seems reasonable, because diffusion processes between zones increasingly disrupt the recycling.

The above comparisons suggest that functional response 2 better represents behavior within the stream segment. The difference between functional response 1 and 2 is that the latter contains a term for self-limitation of periphyton in the denominator of the biomass growth rate term, NAB. Of course, the mere presence of an additional parameter in functional response 2 should make a better fit to data possible, but this parameter of self-limitation is also a reasonable one for biological reasons. The comparisons of functional

responses 1 and 2 with respect to changes in the loss rate of biomass from the system,  $e_2$ , show a clear difference in the direction  $N_s^*$  is predicted to change. We have not yet been able to obtain reliable measurements of  $N_s^*$  in stream systems. However, this measurement will be the object of future studies, which may help us evaluate further the accuracy of the model.

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