Effects of bacterial dynamics on organic matter decomposition and nutrient release from sediments: A modeling study

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Abstract

Nutrient inputs to lakes, reservoirs, estuaries, and continental shelf waters are often dominated by nutrient release from sediments. Rates of nutrient release from the decomposition of sedimentary organic matter are determined by bacterial demands for food and energy. This dependence of decomposition kinetics on bacterial dynamics, however, is not explicitly considered in current models of early diagenesis. Here, we present a new model of early diagenesis that is based on soil decomposition models and that explicitly includes bacterial biomass as a state variable. Using the new model, we perform steady-state sensitivity analyses and integrate two time-dependent scenarios to determine the major controls on the abundance of bacteria in sediments and on sediment nutrient release. First, we test the sensitivity of bacterial biomass and nutrient release to substrate quantity and quality, and to bacterial growth parameters, growth efficiency and mortality. The model predicts that bacterial abundance in the sediments and nutrient release rates increase significantly with higher substrate inputs and higher quality of organic substrate. High growth efficiencies, on the other hand, reduce nutrient release rates and lead to more nutrient immobilization into bacterial biomass. Efficiency driven increases in bacterial abundances must be counteracted by higher mortality rates, if bacterial pool sizes are to remain within the range of values reported in the literature. Second, we simulate eutrophication and lake recovery over a 20-year period and the effect of a short-term peak in substrate input from an algal bloom. The model predicts that nutrient immobilization in the bacterial pool during eutrophication reduces nutrient release, while the decline of bacterial biomass in response to reduced substrate loadings prolongs lake recovery. The model further suggests that bacterial dynamics dampen the response of nutrient release to short-term peak inputs of organic matter. When bacterial biomass is allowed to vary over time, nutrient release rates are suppressed at their peak but remain elevated for a longer time. Models that do not consider the role of bacterial growth dynamics for organic matter decomposition are not able to simulate the potentially important effects of nutrient immobilization and variable decomposition rates on nutrient release.

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1. Introduction

Decomposition and burial of organic matter in sediments are key processes for biogeochemical cycles in lakes, reservoirs, and the ocean. Global and local carbon and nutrient cycles are closed by decomposition and burial of organic matter in sediments on time scales ranging from geologic times to seasonal fluctuations. Furthermore, rates of organic matter decomposition in sediments and subsequent nutrient release have a major influence on the trophic status of aquatic habitats and thus on ecosystems and water quality. In fact, sediment nutrient release can account for up to 80% of total nutrient inputs to some lakes (Larsen et al., 1981), and if external nutrient loads are reduced in an effort to restore surface-water quality, lake recovery can be significantly retarded by persistently high sediment release rates (cf. Larsen et al., 1981; Welch et al., 1986; Rossi and Premazzi, 1991). Quantitative knowledge of organic matter decomposition in sediments and of nutrient release to the water column is needed for comprehensive surface-water quality modeling and management decisions.

Biological processes mediate the decomposition of organic matter in sediments. Sediment microbiota oxidize organic matter to satisfy their carbon, nitrogen, and energy requirements and generate carbon dioxide and inorganic nutrients as metabolic by-products (Capone and Kiene, 1988). Consequently, decomposition rates are dependent on bacterial abundance. In a set of phytoplankton decomposition experiments, increases in bacterial biomass were shown to coincide with high metabolic activities and greatest loss of particulate organic carbon (Harvey et al., 1995). Moreover, bacterial biomass itself can account for a significant fraction of organic matter in surface sediments (1–20%; Gächter et al., 1988; Schallenberg et al., 1989; Törnblom and Bostrom, 1995). As a result, bacteria act simultaneously as sinks and sources for organic substrates and for inorganic nutrients (e.g., NH₄⁺; Tupas and Koike, 1990, 1991).

Despite the central role of sediment microbiota for organic matter decomposition and nutrient release, traditional surface-water quality models do not explicitly parameterize microbial dynamics (Thomann and Mueller, 1987; Schnoor, 1996; Chapra, 1997). Similarly, groundwater models do not explicitly consider microbial biomass, but they often incorporate Monod-type kinetics to explain microbial degradation of contaminants or nutrient uptake (e.g., Hunter et al., 1998). Activated sludge models used in wastewater treatment, on the other hand, explicitly include microbial biomass and growth kinetics (e.g., Dold et al., 1980; Gujer et al., 1999; Henze et al., 1999; Gujer, 2006), but knowledge gained in this field has not yet been applied to more dilute surface and groundwater environments. In surface-water and groundwater models, bacterial biomass is usually assumed to be at steady state and is implicitly included in reaction rate constants. This simplification might be valid in systems that do not experience any rapid changes in conditions and for long-term studies where seasonal and interannual variations can be ignored. In more dynamic systems and on shorter time scales, we expect to find transient responses of bacterial biomass to changed conditions, but their effect on sediment nutrient release is largely unknown.

Lake eutrophication and restoration over several years or decades and seasonal fluctuations in lake productivity are examples of dynamically changing conditions that trigger varying bacterial biomass concentrations in sediments. Short-term increases in bacterial abundance have been observed as a result of spring algal blooms (Törnblom and Bostrom, 1995; Goedkoop et al., 1997; Kirschner and Velimirov, 1999). For bacterial biomass to increase, a larger fraction of nutrients must be immobilized into the bacterial pool, which leads to reduced release rates of dissolved nutrients to the water column. However, increased bacterial concentrations enhance decomposition rates and thus nutrient release. The pivotal role of the ratio of bacterial biomass to food supply is well recognized in the wastewater field (e.g., Dold et al., 1980; Gujer et al., 1999; Henze et al., 1999; Gujer, 2006). The opposing effects of bacterial biomass on nutrient release cannot be studied with simulation models if bacterial biomass is assumed to be constant.

Here, we present a new model of early diagenesis (BIOSED), in which bacterial biomass varies as a function of substrate input and bacterial growth kinetics. Decomposition rates and nutrient immobilization and release are modeled as a function of the variable biomass pool. The new model combines the traditional multi-G model (Westrich and Berner, 1984) with mechanistic elements from soils models. In contrast to water quality models, many simulation models in soil science explicitly include microbial biomass as a state variable and decomposition rates of any substrate are commonly assumed to be proportional to the growth rate of its decomposers (Parnas, 1975; and review by Van Veen et al., 1981). The soils models and the new BIOSED model do not depict as many microbial processes nor with as much detail as the current wastewater decomposition models (e.g., Dold et al., 1980; Gujer et al., 1999; Henze et al., 1999; Gujer, 2006); a lack of field data for verification renders incorporation of all of these features into a diagenesis model premature.

The overall objective of this study is to present the new model (BIOSED) and to contrast it to the traditional multi-G framework. First, we assess the steady-state response of the two models to variations in substrate quantity and quality. Second, we examine how variations in bacterial growth efficiency and recycling of bacterial biomass alter nutrient release in the BIOSED model. Finally, we explore how the differences in the two models are reflected in predictions of nutrient release in two time-dependent scenarios: (1) lake eutrophication and recovery and (2) an algal bloom. These analyses give insights into what factors drive nutrient release from sediments and the impact of variations in bacterial biomass on this release.

2. Model framework

Models of early diagenesis vary in the spatial representation of the sediment system as well as the level of complexity with which biological, chemical, and physical processes are parameterized. In most models, diagenetic processes such as chemical reactions, diffusion, advection, adsorption, burial, and compaction are represented as a system of coupled one-dimensional partial differential equations (Berner, 1980; Boudreau, 1996). Numerical solutions to these equations yield
concentration profiles of solid species, such as organic matter, FeS, and Fe(OH)$_2$, and of dissolved species, such as O$_2$, NO$_3^-$, SO$_4^{2-}$, NH$_4^+$, and CH$_4$ (e.g., Billen, 1982; Klump and Martens, 1989; Soetaert et al., 1996; Van Cappellen and Wang, 1996; Hunter et al., 1998; Kelly-Gerreyn et al., 1999; Park and Jaffé, 1999). Concentration gradients of dissolved species at the sediment-water interface are then converted to nutrient fluxes into the overlying water column using Fick’s first law. Some models also explicitly consider the effects of bioturbation and bioirrigation on the transport of solid and dissolved species (e.g., Boudreau and Marinelli, 1994; Van Cappellen and Wang, 1996).

An alternative to depth-resolved models of early diagenesis are simple box models that are particularly useful for the prediction of sediment nutrient fluxes. Fluxes of dissolved species between adjacent boxes can be calculated as a function of average concentrations within each box; resultant fluxes are independent of heterogeneities and microstructure within the boxes of interest. One of the advantages over depth-resolved models is that steady-state solutions for concentrations and fluxes can oftentimes be derived analytically. This facilitates computationally inexpensive sensitivity analyses and comparison of different kinetic formulations. DiToro (2001) utilized a simple two-layer sediment model with a thin surface box and an underlying bulk sediment box. In this study, we follow the approach of DiToro (2001), but only consider processes within and fluxes into and out of the surface sediment box. Our model can easily be extended to a two-box system by adding a bulk sediment box and additional mass transfer terms (Schultz, 2002).

2.1. Box model

In the following section, we derive the differential equations for a one-box model of the surface sediment layer. We describe mass transfer terms, contrast two kinetic formulations, discuss the choice of parameters, and develop a reference scenario that allows for the comparison of the two kinetic formulations. A list of all variables and parameters is given in Appendix I and the full sets of equations for both kinetic formulations are given in Appendix II.

For non-reactive solids, S, the concentration inside the surface box changes as a function of sedimentation rate and burial:

$$\frac{dS}{dt} = \frac{J_S}{H} - \frac{wS}{H}$$  

(1)

where $J_S$ (g Sc m$^{-2}$ year$^{-1}$) is the sedimentation flux of non-reactive solids S, w (cm year$^{-1}$) the burial velocity, and H (cm) is the thickness of the box. The diffusive flux of a dissolved species, $J_D$ (g Dc m$^{-2}$ year$^{-1}$), across the sediment-water interface is proportional to the difference in concentration between the surface sediment box and the overlying water:

$$J_D = -T_D(D_{sed} - D_{aq})H \approx -T_D D_{sed}H$$  

(2)

where $T_D$ (year$^{-1}$) is a mass transfer coefficient, H (cm) the thickness of the box, and $D_{sed}$ and $D_{aq}$ are the concentrations of D in the sediment box and in the overlying water, respectively. If $D_{sed} \gg D_{aq}$, diffusion can be approximated as a function of $D_{sed}$ only. Mass transfer coefficients, $T_D$ (year$^{-1}$), are a function of molecular diffusivity or bioturbation rates as appropriate for the specific location (Bird et al., 1960; in DiToro, 2001).

The magnitude of the total sedimentation flux, $J_{tot}$ (g cm$^{-2}$ day$^{-1}$), and the average organic carbon content of the settling solids, $f_{org}$, are determined by catchment size, lake morphometry, trophic status, and hydraulic regime of the lake (Gorham et al., 1974, 1983; Tartari and Biasci, 1997). The concentration of solids (bulk density), $\rho$ (g cm$^{-3}$), depends on particle properties (e.g., particle size distribution and density) and deposition processes (DiToro, 2001). In this study, we used a concentration of solids measured in a local lake ($m = 0.2$ g cm$^{-3}$; Schultz, 2002) and a burial velocity, w, of 0.72 cm year$^{-1}$. Being in the upper range of literature values (0.1–1.0 cm year$^{-1}$; DiToro, 2001), this burial velocity is representative of a mesotrophic to eutrophic system. The residence time of particles in the surface box is a function of burial velocity and box thickness. We chose an arbitrary residence time of 150 days, which, at a burial velocity of 0.72 cm year$^{-1}$, corresponds to a box thickness of 0.3 cm.

2.2. Decomposition kinetics

Decomposition of organic matter by bacteria in sediments is a complicated stepwise process and many metabolic pathways are not fully understood. Mutualistic consortia of bacteria breakdown a complex mixture of biochemical substrates, and, in the process, release inorganic nutrients (Fenchel et al., 1998). Decomposition models are always based on simplifying assumptions. The objective of this study is to compare the decomposition kinetics of the commonly used multi-G model (Westrich and Berner, 1984) with the newly developed BIOSED model.

2.2.1. Multi-G

Westrich and Berner (1984) argued that sedimentary organic matter can be divided into a labile fraction, $C_l$ (g labile organic C cm$^{-3}$), and a stable fraction, $C_s$ (g stable organic C cm$^{-3}$), with significantly different reactivities, and a refractory fraction, $C_r$, that is not decomposed at all on time scales relevant to water quality modeling. The decomposition of organic matter follows first-order kinetics:

$$\frac{dC_l}{dt} = -k_l C_l$$  

(3)

where subscript $i$ indicates the particular fraction of organic carbon (labile, stable or refractory), $C_l$ (g C cm$^{-3}$ year$^{-1}$) are carbon substrate concentrations, and $k_l$ (year$^{-1}$) are first-order decomposition rates that express the different reactivities of the three substrate fractions.

2.2.2. BIOSED

The BIOSED model (Fig. 1) extends the multi-G framework and explicitly considers the effect of variable bacterial biomass concentrations on decomposition kinetics. This new approach is based on soil decomposition models that commonly parameterize bacterial biomass as a state variable
and explicitly consider processes such as nutrient mineralization, immobilization, and nutrient-limited growth (e.g., Parnas, 1975; McGill et al., 1981; Paul and Juma, 1981; Van Veen et al., 1981; Blagodatsky and Richter, 1998; Abrahamsen and Hansen, 2000). More specifically, the BIOSED model combines the following four assumptions into a model of early and explicit diagenesis:

1. Organic matter is subdivided into labile, stable, and refractory substrate pools according to the multi-G model.
2. Breakdown rate of organic matter is proportional to the concentration of decomposers, $C_b$ (g C cm$^{-3}$), in the system.
3. A constant bacterial growth efficiency, $e$, determines the fraction of substrate carbon respired.
4. The size of the biomass pool is limited by a constant first-order mortality rate, $m$, which integrates such factors as competition, death, and predation. Bacterial biomass is assumed to be recycled back into the labile substrate pool.

While the assumptions above do increase the level of detail beyond that of the multi-G model, the BIOSED model does not incorporate additional levels of complexity that are included in models of organic matter decomposition utilized in the wastewater field (e.g., Dold et al., 1980; Gujer et al., 1999; Henze et al., 1999; Gujer, 2006). Specifically, the BIOSED model:

1. Does not invoke hydrolysis of the stable organic matter to create the labile organic matter.
2. Depicts mortality (recycling) of bacteria as conversion of biomass solely into labile organic matter and does not transfer some of the microbial biomass into the recalcitrant pool.

(3) Does not describe the demand for oxidants but assumes that electron acceptors are always available in non-growth-limiting concentrations.
(4) Does not explicitly model nitrification.
(5) Assumes that bacteria are carbon-limited rather than N- or P-limited.

Clearly, there is room for further evolution of the BIOSED model as data become available with which to examine the need for further improvements.

Given the assumptions above, bacterial breakdown of organic matter is described as a second-order reaction that depends both on the substrate concentration and on the abundance of bacteria in the system:

$$\frac{dC_i}{dt} = -k_i^* C_i C_b$$

(4a)

where $k_i^*$ is a second-order rate constant in year$^{-1}$ (g C cm$^{-3}$)$^{-1}$. In order to simplify the comparison of the two models, we assume that $k_i^*$ is the product of $k_i$ (year$^{-1}$), which describes the dependence on substrate quality and which is identical to the rate constants used in the multi-G model, and a factor $b$ in (g C cm$^{-3}$)$^{-1}$, which describes the dependence on bacterial biomass and which includes the effect of bacterial growth efficiency. Bacterial growth efficiency is the ratio of carbon assimilation to organic carbon uptake and is equivalent to a yield coefficient for organic carbon. We can further rewrite $b = 1/eC_{bo}$, where $e$ is bacterial growth efficiency and $C_{bo}$ can be viewed as a normalization biomass. Thus, the differential equations that describe breakdown of organic matter in the BIOSED model become:

$$\frac{dC_i}{dt} = -\frac{C_b}{C_{bo}} k_i C_i$$

(4b)

(For the labile substrate pool, the equation above would include the recycling of bacterial biomass, $+mC_b$, which is assumed to be first order with respect to bacterial biomass). Bacterial carbon biomass changes as a function of carbon uptake from the decomposition of labile and stable substrate and bacterial mortality/recycling:

$$\frac{dC_b}{dt} = \frac{C_b}{C_{bo}} (k_1 C_1 + k_2 C_2) - mC_b$$

(5)

Again in Eq. (5), the pseudo-first-order rate constants ($k_1, k_2$) may be viewed as second-order rate constants when divided by a bacterial biomass, $C_{bo}$. A schematic of the model is shown in Fig. 1, and the mass-balance equations involving the kinetic expressions above are summarized in Appendix II.

Only a few experimental studies have determined in situ bacterial growth efficiencies in sediments, and reported values range from $-10\%$ to $-40\%$ (Bell and Ahlgren, 1987 and references therein; Goedkoop et al., 1997; Kirschner and Velimirov, 1999; Bastviken et al., 2003). In an extensive review of the literature on bacterial growth efficiencies in planktonic communities, del Giorgio and Cole (1998) reported an observed range from 5% to as high as 60%. The controls on this important physiological factor are poorly known, but it has been hypothesized that the interaction of the rate of energy supply,
substrate quality, and energetic demand of the bacterial cells can explain the wide range of values (del Giorgio and Cole, 1998).

Energy supply and substrate quality vary along trophic gradients. Biddanda et al. (2001) indeed showed a correlation between trophic status and bacterial growth efficiency for bacterioplankton with the highest efficiencies in eutrophic systems. They also reported a correlation between C:N ratios of the substrate (a proxy for substrate quality) and bacterial growth efficiency; other studies, however, have not observed this correlation (seston: Tezuka, 1990; soils: Devevre and Horwath, 2000). High energetic demands of bacterial cells and thus low efficiencies can be expected (1) when cells must actively transport solutes against a large gradient, (2) when large amounts of extracellular enzymes must be produced to breakdown particulate substrates and macromolecules, (3) when a wide array of different enzymes must be produced and different transport systems must be maintained simultaneously, and (4) when a significant fraction of the population is metabolically inactive (del Giorgio and Cole, 1998). Low efficiencies are also expected for anaerobic relative to aerobic bacterial growth (e.g., Bastviken et al., 2003). For this study we chose a bacterial growth efficiency, $e$, of 10% and use this value as our starting point to examine the interaction between bacterial metabolism and nutrient release. The question of whether the bacterial population is nutrient-limited or limited by grazers is also addressed in the context of variable growth efficiencies.

2.2.3. Analytical solutions

We can analytically solve for the steady-state concentrations in the two models by setting all time-dependent terms ($d/dt$) to zero and simultaneously solving the system of equations. The solutions are given in Table 3. Comparison of Eqs. (3) and (4b) indicates that rates of organic matter breakdown are equal in the two models if

$$\frac{C_{b_0}}{C_{b_0} - k_1} = \frac{C_b - C_{b_0}}{C_{b_0}} = 1 \iff \frac{C_b}{C_{b_0}} = e$$

(6)

We refer to this special case as the reference scenario, and we use deviations from the reference scenario to determine the effects of environmental conditions on the multi-G and the BIOSED model. Using Eq. (6), the governing equations of the BIOSED model can be simplified, and the steady-state size of the biomass pool for the reference scenario can be calculated as a function of the substrate pool sizes and bacterial growth efficiency:

$$C_{b,ref} = \frac{(e - 1)Hk_bC_{l,ref} + eHk_bC_{s,ref} - wC_{l,ref} + fj_C}{w}$$

(7)

Table 1 summarizes all sediment and kinetic parameters for which constant values are used this study. In addition, Table 1 lists parameter values specific to the reference scenario. Deviations of parameter values from their reference scenario value for the purpose of steady-state sensitivity analysis and for non-steady-state simulations are clearly indicated in the text.

Literature values for the relative sizes and properties of labile, stable, and refractory substrate pools are inconsistent and strongly depend on environmental parameters. For the multi-G model, relative abundances of the three substrates in the sedimentation flux were taken from Westrich and Berner (1984) and rounded to the next multiple of five. First-order decomposition rate constants in both models, $k_l$ and $k_s$, were taken from the same publication. The same stable and refractory substrate pool sizes are used in the BIOSED model as in the multi-G model, and the size of the labile substrate pool is adjusted such that the bacterial biomass in the sediment (as a fraction of total sediment organic carbon) remains within the

| Table 1 – Parameters for one-box multi-G and BIOSED models |
|----------------------------------|----------------|-----------|---------|-----|---|---|
| **Parameter** | **Symbol** | **Value** | **Units** | **Source** |
| Sediment bulk density | $\rho$ | 0.2 | g cm$^{-1}$ | Schultz (2002) |
| Box thickness | $H$ | 0.3 | cm | See text |
| Mass transfer coefficient CO$_2$ | $T_{CO_2}$ | 2.55 | day$^{-1}$ | Bird et al. (1960) in DiToro (2001) |
| Mass transfer coefficient NH$_3$ | $T_{NH_3}$ | 3.03 | day$^{-1}$ | Bird et al. (1960) in DiToro (2001) |
| Rate constant labile pool | $k_l$ | 24 | year$^{-1}$ | Westrich and Berner (1984) |
| Rate constant stable pool | $k_s$ | 1.4 | year$^{-1}$ | Westrich and Berner (1984) |
| Stable C:N ratio | $C_{CN_s}$ | 65 | g C(gN)$^{-1}$ | See text |
| Labile C:N ratio | $C_{CN_l}$ | 26 | g C(gN)$^{-1}$ | See text |
| Refractory C:N ratio | $C_{CN_r}$ | 15 | g C(gN)$^{-1}$ | See text |
| Bacterial C:N ratio | $C_{CN_b}$ | 65 | g C(gN)$^{-1}$ | See text |
| Normalization biomass | $C_{b0}$ | 0.016 | g C cm$^{-3}$ | See text |
| Burial velocity | $\omega$ | 0.72 | cm year$^{-1}$ | DiToro (2001) |
| Residence time | $\tau$ | 150 | day | $r = H/\omega$ |
| Total sedimentation flux | $J_{tot}$ | 0.144 | g cm$^{-2}$ year$^{-1}$ | Westrich and Berner (1984) |
| Labile fraction of $J_{tot}$ | $f_l$ | 60 | % | Westrich and Berner (1984) |
| Stable fraction of $J_{tot}$ | $f_s$ | 15 | % | Westrich and Berner (1984) |
| Refractory fraction of $J_{tot}$ | $f_r$ | 25 | % | Westrich and Berner (1984) |
| Bacterial growth efficiency | $e$ | 10 | % | See text |
| Bacterial mortality | $m$ | 0.33 | year$^{-1}$ | See text |

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range of literature values (Gächter et al., 1988; Schallenberg
and Kalff, 1993; Törnblom and Boström, 1995). In the BIOSED
model the labile substrate pool is slightly larger than in the
multi-G model because recycled biomass contributes to the
labile pool in addition to the input from the sedimentation
flux. Pool sizes and fluxes of dissolved nutrients for the two
models under reference scenario conditions are summarized in
Table 2.

2.2.4. Coupling of C and N cycles
In both models, C and N cycles are coupled using fixed but
distinct C:N ratios, $r_{CN,i}$, for the three substrate pools and for
the biomass pool:

$$\frac{dN_i}{dt} = \frac{1}{r_{CN,i}} \frac{dC_i}{dt}, \quad i = l, s, r, b$$

(8)

Thus, in the multi-G model, N mineralization is directly propor-
tional to C mineralization, and in BIOSED the breakdown of
organic N in the stable and labile pools is proportional to the
respective rates of organic carbon decomposition (Fig. 1). How-
ever, it is the balance between organic matter breakdown and
bacterial N uptake that determines N mineralization in the BIOSED
model. This balance is a function of substrate C:N ratios and bacterial
growth requirements as determined by bacterial growth efficiency and
bacterial C:N ratio. Equations for total C and N mineralization are given in
Appendix II.

Labile substrate can be described as a conglomerate of easily
decomposable organic macromolecules such as simple
sugars and amino acids (Burdige, 1991; Hedges et al., 2001), but
is oftentimes equated to fresh algal material. Eucaryotic and
prokaryotic algae synthesize biomass with molar C:N ratios
is oftentimes equated to fresh algal material. Eucaryotic and
sugars and amino acids (Burdige, 1991; Hedges et al., 2001), but
easily decomposable organic macromolecules such as simple
}

<table>
<thead>
<tr>
<th>Variable</th>
<th>Symbol</th>
<th>Multi-G</th>
<th>BIOSED</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Labile substrate</td>
<td>C_{l,ref}</td>
<td>1.64 x 10^{-3}</td>
<td>1.66 x 10^{-3}</td>
<td>g C cm^{-3}</td>
</tr>
<tr>
<td>Stable substrate</td>
<td>C_{s,ref}</td>
<td>2.84 x 10^{-3}</td>
<td>2.84 x 10^{-3}</td>
<td>g C cm^{-3}</td>
</tr>
<tr>
<td>Refractory substrate</td>
<td>C_{r,ref}</td>
<td>7.50 x 10^{-3}</td>
<td>7.50 x 10^{-3}</td>
<td>g C cm^{-3}</td>
</tr>
<tr>
<td>Bacterial biomass</td>
<td>C_{b,ref}</td>
<td>1.60 x 10^{-3}</td>
<td>1.60 x 10^{-3}</td>
<td>g C cm^{-3}</td>
</tr>
<tr>
<td>Sediment organic carbon content</td>
<td>CO_{2} flux</td>
<td>6.0</td>
<td>6.8</td>
<td>%</td>
</tr>
<tr>
<td></td>
<td>NH_{4} flux</td>
<td>1.2 x 10^{-4}</td>
<td>1.1 x 10^{-4}</td>
<td>g C cm^{-2} year^{-1}</td>
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<td></td>
<td>Labile substrate</td>
<td>2.0 x 10^{-5}</td>
<td>1.8 x 10^{-5}</td>
<td>g C cm^{-2} year^{-1}</td>
</tr>
</tbody>
</table>

Table 2 – Pools and fluxes at steady-state for reference conditions

Assuming that after sufficient time all labile and stable organic
matter is completely mineralized, organic C:N ratios of deep
deposits correspond to the refractory C:N ratio. Most lake
deposits have depth profiles that asymptote to C:N ratios
between 11 and 15 (Urban, unpubl. data). We assign a constant
C:N of 15 to the refractory substrate pool. Since neither the
fractions nor the properties of the different pools can be based
directly on experimental data, model sensitivity to changes in
these parameters is evaluated.

3. Results

3.1. Steady state

In this section, the sensitivity of the two models to key
parameters is assessed, and the two kinetic formulations are
compared with respect to their predicted N release rates in
response to different organic matter inputs. Organic matter
input is varied both in quantity (sedimentation flux) and in
quality (fraction of labile substrate) over a wide range from
oligotrophic to eutrophic and from mostly allochthonous to
mostly autochthonous material. Analytical steady-state solu-
tions for the multi-G and the BIOSED model are summarized in
Table 3.

Sedimentation fluxes of organic carbon are closely linked to
trophic status and range over three orders of magnitude
(Tartari and Biasci, 1997). Both models predict an almost linear
correlation of N and C mineralization rates with the rate of
 settling organic matter. At low inputs, however, the BIOSED
model the labile substrate pool is slightly larger than in the
multi-G model because recycled biomass contributes to the
labile pool in addition to the input from the sedimentation
flux. Pool sizes and fluxes of dissolved nutrients for the two
models under reference scenario conditions are summarized in
Table 2.

Table 3 – Analytical expressions for steady-state pools
for multi-G and BIOSED models

<table>
<thead>
<tr>
<th>Multi-G model</th>
<th>BIOSED model</th>
</tr>
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<tbody>
<tr>
<td>Labile substrate</td>
<td>$C_{l,ss} = \frac{C_{l,ref}}{r_{CN,l}}$</td>
</tr>
<tr>
<td>Stable substrate</td>
<td>$C_{s,ss} = \frac{C_{s,ref}}{r_{CN,s}}$</td>
</tr>
<tr>
<td>Refractory substrate</td>
<td>$C_{r,ss} = \frac{C_{r,ref}}{r_{CN,r}}$</td>
</tr>
</tbody>
</table>
| Bacterial biomass | $C_{b,ss} = \frac{C_{b,ref}(e^{C_{b,ref} - 

(1 - \frac{1}{r_{CN,b}})(C_{l,ss} + C_{s,ss} - C_{r,ss})}}{1 - \frac{1}{r_{CN,b}}}$ |
Fig. 2 – Model predicted response of N mineralization and bacterial biomass to inputs of organic C. Both the BIOSED (short dash) and multi-G (long dash) models predict an increasingly smaller N mineralization rate as the input of organic C to the sediments is decreased. However, the BIOSED prediction decreases more rapidly than does the multi-G model prediction such that the ratio (solid line) declines precipitously at organic C contents below 20% in the settling flux. The BIOSED model predicts that bacterial biomass increases in a nonlinear fashion with increasing input of organic C to the sediment.

Fig. 3 – Model predicted response of N mineralization and microbial biomass to the quality of sedimenting organic matter. Both the BIOSED (short dash) and multi-G (long dash) models predict that N mineralization increases as the labile fraction of settling organic matter increases. However, the ratio of the model predictions (solid line) shows that the models diverge quickly at labile fractions below 30%. The BIOSED model predicts that bacterial biomass increases as the labile fraction of settling material increases.

Turnover of bacterial biomass in the BIOSED model depends upon growth rate, respiration, and death rate (mortality, m). The ratio of growth to respiration is determined by bacterial growth efficiency and is reflected in variable nutrient release rates. Fig. 4a and b shows the steady-state response of N release and of the fraction of bacterial biomass in the surface sediment to different bacterial growth efficiencies and recycling rates. Bacterial biomass increases with increasing bacterial growth efficiency; the rate of increase, however, is determined by the recycling rate. Low recycling rates lead to a strong dependence of bacterial biomass on bacterial growth efficiency, while high recycling rates tend to weaken this dependence. Consequently, N release is low at high bacterial growth efficiencies while recycling rates modulate the balance between nutrient uptake and nutrient release. Using literature values as a theoretical upper limit for the bacterial fraction in sediments (15%; solid horizontal line), maximum growth efficiencies can be estimated as a function of the recycling rate.

The model predictions discussed above are not affected by the arbitrary dimensions selected for the surface sediment layer. The surface layer is defined by the independent variables (w, \( \rho \) and \( H \)) that together define the residence time of...
material in the layer. As the residence time increases (caused by an increase in $H$ or $\rho$ or by a decrease in $w$), the organic matter within the box becomes more degraded and therefore has a larger fraction of stable relative to labile organic matter. In the BIOSED model, an increase in residence time also results in a decrease in bacterial carbon concentration ($C_b$). However, the rates of mineralization (and the fluxes out of the surface layer) of both C and N (Figs. 2a and 3a) are not affected by changes in residence time (e.g., increasing $H$) if the carbon influx remains constant; the decreased concentration of organic matter in the box associated with increased residence time is offset by a larger mass of sediment in the box ($H\rho$).

3.2. Time-dependent simulations

Differences in the dynamic behavior of the two kinetic formulations were examined in two non-steady-state simulations that were solved numerically using a first-order forward Euler method. Identical results were obtained with a fourth-order Runge–Kutta as well as with a second-order Rosenbrock formula. The objective of the study was not to mimic reality, but to show the effect of a variable bacterial biomass pool on decomposition kinetics and nutrient release rates in simplified but reasonable scenarios.

The first scenario simulates the effects of prolonged eutrophication over 10 years and subsequent recovery over another 10-year period. Increased nutrient loadings lead to increased phytoplankton growth and thus to higher rates of organic matter input to the sediment. Eutrophication is therefore simulated as an increase in labile organic matter input, which represents the additional sinking phytoplankton biomass. Inputs of stable (allochthonous) material and refractory material are assumed to be constant. Over the 10-year period, the sedimentation flux increases continually from $\sim 0.15 \text{ g cm}^{-2} \text{ year}^{-1}$ to $\sim 0.17 \text{ g cm}^{-2} \text{ year}^{-1}$, the total organic matter content of the settling particles increases from 11.4% to 25%, and the fraction of labile material increases from 50% to 65% of settling organic carbon. This translates into an overall increase in organic matter input of 10% per year. Lake recovery is assumed to be the exact inverse of eutrophication. Organic matter input decreases at similar rates and reaches the initial values after another 10 years. In our scenario, sediment properties such as concentration of solids (bulk density), $\rho$, are unaffected by eutrophication and recovery. Therefore, increases in the sedimentation flux, $J_{\text{tot}}$, are paralleled by increases in the burial velocity, $w$, which, in turn, leads to a reduction of the residence time in the surface box (with $H = \text{constant}$).

In our attempt to estimate an upper limit for the differences between the two model-predicted N release rates, we chose a high efficiency, high turnover system as discussed below. Bacterial growth efficiency was set at a constant value of 40% and the recycling rate was fixed at 3.3 year$^{-1}$ (10 times the reference scenario value). The analysis focuses on lake recovery over the second half of the simulation.

Both models show decreases in C and N release with decreasing organic matter input; the absolute difference in release rates between the two models decreases as lake recovery progresses (Fig. 5). Note that nutrient release rates are smaller in the BIOSED model for the entire simulation period. Integrated over a 10-year period of lake recovery this difference in N release rates amounts to a 31% lower total N release in the BIOSED compared to the multi-G estimate. Lower rates and lower overall nutrient release in the BIOSED model are
the result of our choice of a high efficiency, high turnover system; the scenario represents an upper limit for the model differences. Even at steady state, nutrient release would not be equal for the two models under these conditions. Instead of releasing most of the decomposed C and N, a significant fraction of the nutrients in the BIOSED model is instead rapidly recycled within the system as a result of high bacterial growth efficiency and recycling rate. It is possible that this enhanced biomass pool is not maintained deeper in the sediments where bacterial growth efficiency is probably lower due to anaerobic conditions.

The second scenario represents the effects of seasonal variations in organic matter inputs. Short-term peaks in organic matter inputs occur in many lakes, reservoirs, and the oceans as a result of algal blooms. Nutrient release is modeled over a 1-year period. The long-term average concentration of organic matter in settling particles, \(J_{\text{org}}\), is set to 10%; between days 120 and 160 this value linearly increases over 10 days to a maximum concentration of 30%, remains at this value for 20 days, and is linearly reduced to its original value over another 10 days. For this simulation, bacterial growth efficiency and recycling rate were fixed at the reference scenario values. Variations in these two parameters can modify the observed difference between the two models.

Both models respond to the seasonal peak in organic matter input with enhanced N release and both return back to the steady-state release rate after the end of the pulse (Fig. 6). Cumulative amounts of additional N release due to the sedimentation peak (areas under the curves) are equal and show the validity of the mass balance in both models. The temporal pattern of the two model responses, however, is markedly different. Growth and decline of biomass in the BIOSED model act as a buffer for nutrient release and prolong the time period affected by the sedimentation event while reducing peak release rates. Excluding biomass from the decomposition model can therefore lead to overpredictions of the maximum N release rate of more than 70%. These overpredictions in maximum release rates are coupled to underpredictions of the duration of increased N release. The multi-G model returns to steady state approximately 60 days after the end of the pulse, whereas the BIOSED model shows enhanced N release rates for more than 200 days.

4. **Discussion**

4.1. **What controls bacterial biomass in sediments?**

A balance between bacterial growth and loss (e.g., burial, mortality, grazing) controls the abundance of bacteria in sediments. All of these factors are functions of the complex interplay between substrate availability, metabolic adaptation to changing environmental conditions, and external factors such as abundance of grazers. The BIOSED model explicitly considers substrate-limited growth and burial of bacterial biomass; all other biomass losses are parameterized as a ‘closure’ term and lumped into the first-order recycling rate, \(m\). Variation of one parameter at a time allows us to examine independently the effects of substrate quantity, substrate quality, bacterial growth efficiencies, and bacterial recycling rates on bacterial biomass. Field evidence points to an upper bound on bacterial abundances in sediments of about 15% of total organic carbon (Gächter et al., 1988; Schallenberg and Kalff, 1993; Törnblom and Boström, 1995). Higher concentrations of up to 20% have been reported, but they seem to be special cases that require limited grazing pressure as expected in anoxic systems (cf. Gächter et al., 1988). Comparing our results to this apparent maximum enables us to assess possible limiting mechanisms for bacteria in sediments.

Cole et al. (1988) summarized data from 70 experimental studies and found that production of heterotrophic biomass was positively correlated to sediment organic C content. The BIOSED model captures this dependence of bacterial production (the product of growth rate and bacterial biomass) on organic matter concentration in the sediments; the specific first-order bacterial growth rate remains constant, while bacterial biomass and thus production increase by more than 15-fold in response to a 10-fold increase in organic matter input (Fig. 2b).

In the BIOSED model, bacterial production not only depends on the total input of organic matter, but on the relative contributions of labile, stable, and refractory material to the total substrate pool. By definition, labile material is broken down at a higher rate than stable material. Thus, if more labile material is available, bacteria can incorporate substrate into their biomass at a higher rate. An increase in the fraction of labile substrate from 5% to 70% leads to an increase in bacterial production by a factor of 8.8. As in the response to total organic matter input (Fig. 2b), bacterial biomass increases while the biomass-specific growth rate remains constant (Fig. 3b). The effects of substrate quantity and quality constitute direct, bottom-up limitations on bacterial biomass.

The abundance of bacteria can also be limited indirectly through the effects of system trophic status on bacterial growth efficiency. Biddanda et al. (2001) showed an increase in planktonic bacterial growth efficiency along a trophic gradient from oligotrophic to eutrophic waters. This suggests that cellular maintenance requirements (as a percentage of total C uptake) increase with decreasing nutrient supply. In sediments, this trend might be reversed; increasing anoxia as a result of eutrophication might lead to lower bacterial growth efficiencies and thus increase nutrient recycling efficiency. Fig. 4b shows the dependence of bacterial biomass on bacterial growth efficiency and recycling (i.e., all processes that return bacterial biomass to the substrate pool). High recycling rates counterbalance high bacterial growth rates and thus allow for higher growth efficiencies without exceeding a maximum bacterial concentration. Similar biomass pool sizes are possible in both low efficiency, low recycling systems and in high efficiency, high recycling systems. For low recycling rates, bacterial biomass strongly varies as a function of bacterial growth efficiency (steep slope), which indicates the dominance of bottom-up limitation of the biomass pool. High recycling rates, on the other hand, reduce the response of bacterial biomass to bacterial growth efficiency (gentle slope), and reflect a condition of top-down limitation for the bacterial pool.

Measurements of sediment bacterial C and bacterial growth efficiency across a trophic gradient are too few to allow trends to be observed, but it seems possible that top-down regulation dominates in nutrient-rich sediments that are
characterized by high efficiency and high bacterial biomass. Sediments of oligotrophic lakes are more difficult to classify because the lines in Fig. 4b converge as growth efficiency declines. In these low efficiency systems both bottom-up and top-down regulation could be important in limiting the abundance of bacteria in sediments.

4.2. What determines sediment nutrient release?

For both models, the rate of supply of organic matter strongly influences the rate of N release (Fig. 2a). The processes driving this dependence, however, differ significantly between the two models. For the multi-G model, the dependence of nutrient release on organic matter input is straightforward: an increase in organic matter inputs leads to an increase in concentration in the surface sediment layer that, in turn, causes a proportional increase in decomposition rates (Eq. (4)).

In contrast, decomposition rates in the BIOSED model are proportional to bacterial biomass as well as to organic matter concentration. Bacterial biomass also is proportional to the organic matter concentration as long as the recycling rate remains constant. Thus an increase in inputs of organic matter to the surface sediments stimulates organic matter decomposition through two mechanisms: a higher substrate supply and a larger bacterial pool. Under steady-state conditions, a 10-fold increase in organic matter inputs will cause a 10-fold increase in mineralization rates in the multi-G model and a 15-fold increase in the BIOSED model. The difference between the models is not as large as might be expected. Besides stimulating organic matter decomposition, the increase in bacterial biomass also enhances immobilization that leads to a decoupling of decomposition rates and nutrient release rates and shifts the relative sizes of the organic matter pools. The increase in decomposition rates is counterbalanced by decreases in the relative sizes of the labile and stable pool. Labile substrate decreases from 29% to 4% of total sedimentary organic matter, stable substrate from 22% to 12%, whereas refractory material and bacterial biomass increase from 42% to 67% and from 7% to 16%, respectively. Instead of accumulating in the sediment as predicted in the multi-G model, a fraction of the additional organic substrate is incorporated into the biomass pool.

The second factor influencing nutrient release rates is organic matter quality. Bacterial nutrient mineralization rates have been shown to be proportional to substrate quality (e.g., Egli et al., 1993), which is often associated with the sources of the organic matter (autochthonous versus allochthonous). A possible explanation for this dependence is a thermodynamic interpretation of the theoretical concept of organic matter quality: the number of enzymatic steps required for complete mineralization of organic carbon to carbon dioxide defines quality (Bosatta and Ågren, 1999). For the purpose of our modeling exercise we distinguish three substrate pools with distinct decomposition rates and C:N ratios, and their relative abundances define the overall quality (reactivity) and the overall C:N ratio of the organic matter.

For both models N release changes as a function of substrate quality. Fig. 3a shows the steady-state response of the two models to a range of C:N ratios of 15–26 corresponding to a range of labile substrate fractions of 5–75%. As for the dependence on substrate quantity, the basic patterns look similar for the two kinetic formulations, but the driving processes are different. In the multi-G model, N release changes linearly with $C_t$ and $C_s$. In the BIOSED model there is a much more complicated interplay between variable decomposition rates, bacterial growth efficiency ($\eta$), bacterial biomass recycling (m), and sediment substrate pool sizes that determines N release.

Besides the direct effects of substrate quantity and quality, bacterial growth efficiency also exerts an indirect effect on nutrient release rates. High growth efficiencies lead to a decrease in N release rates, because more substrate is immobilized in bacterial biomass and a smaller fraction of decomposed organic matter is remineralized and released (Fig. 4a). The reduction in N mineralization as bacterial growth efficiency increases is determined by the degree of recycling of bacterial biomass. For any given recycling rate of bacterial biomass, nutrient release decreases with increasing efficiency (Fig. 4a).

Sediment properties in most lakes and reservoirs are spatially heterogeneous (e.g., Rudd et al., 1986; Snopek et al., 1996; Urban et al., 1997). Spatial variability may be manifested as differences in substrate quality (more allochthonous inputs in littoral areas), different bacterial abundances (lower in littoral regions), and potentially in different bacterial growth efficiencies (lower in anaerobic pelagic sediments). Spatial variability in these parameters results in spatially variable mineralization rates and ratios. In eutrophic Lake Sempach (Urban et al., 1997) the ratio of (HCO$_3^-$ + CH$_4$) to NH$_4^+$ release decreased from 5.5 to 4.3 from the littoral to the pelagic region of the lake; such a decrease is consistent with a decrease in microbial growth efficiency in the more anaerobic sediments of the pelagic region. Similarly, the ratio of HCO$_3^-$ to NH$_4^+$ release decreased from 6.3 to 0.7 between littoral and pelagic regions of Little Rock Lake (Sherman et al., 1994). Spatially variable bacterial biomass and efficiencies as well as variable substrate quantity and quality affect the overall rate of organic matter decomposition and nutrient release rates. While the multi-G model captures some of the variability in nutrient release in response to variable organic matter quantity and quality, heterogeneities in decomposition and immobilization rates as a result of the spatially variable bacterial pool are not captured.

Time-dependent model simulations show the importance of bacterial loss and growth processes for the prediction of sediment N release. The two simulations examine simultaneous changes in substrate quantity and quality over time. In the case of lake recovery over a 10-year period, both models capture the expected decrease in nutrient release rates in response to reduced sediment loadings. As a result of our attempt to estimate an upper limit on the differences in nutrient release rates between the model, nutrient release rates are consistently smaller for the BIOSED model for the entire length of the simulation due to enhanced internal recycling of nutrients. However, the effect of remineralization of bacterial biomass is clearly reflected in the decreasing absolute difference between the predicted release rates as lake recovery progresses. The biomass pool, shrinking from initially ~15% of organic C in the surface sediment to ~8% at the end of the simulation, accounts for a sizeable fraction of released N.

In agreement with observations (Cole et al., 1988), the model predicts that increases in organic matter inputs are...
coupled to increases in bacterial biomass. Bacterial growth requires nutrients that are immobilized from the substrate pool instead of being mineralized as inorganic nutrients. For a continuous increase in organic matter input (e.g., prolonged eutrophication), the reduction of mineralization rates due to bacterial nutrient immobilization continues until a maximum biomass pool size is reached. If there is a limit to sediment bacterial biomass, further increases in organic matter input result either in higher bacterial turnover rates or in increased burial of undecomposed organic matter. Reductions in the size of the bacterial pool as a result of lake recovery release the immobilized nutrient pool over time, which causes a decoupling of decomposition rates and nutrient release rates. This effect increases the nutrient release rate relative to a constant-biomass system. The smaller slope for the BIOSED model in Fig. 5 indicates that bacterial dynamics prolong the time required for a lake to recover from eutrophication.

In our simulation of a short-term peak in organic matter inputs (algal bloom), bacterial dynamics dampen the response in nutrient release rates. After the onset of increased substrate input, immobilization decreases the rate at which nutrients are mineralized. Part of the additional substrate is converted to bacterial biomass. After the initial (pre-pulse) sedimentation rates are restored, the additional bacterial biomass cannot be sustained by the substrate inputs and the immobilized nutrients are eventually released as inorganic nutrients (Fig. 6). Field data qualitatively consistent with these model predictions were reported by Sherman et al. (1994) who measured regular seasonal fluctuations in C:N ratios of mineralization products released from sediments; high C:N ratios occurred in summer when bacterial populations might have expanded in response to increased food inputs. A definitive field study to validate the model will require measurements of bacterial abundances, bacterial growth efficiency, and bacterial mortality.

The overall effect of growth and decline of the bacterial pool on nutrient release is the net result of two different effects of changes in bacterial biomass. As discussed above, increases in bacterial biomass are directly reflected in increased decomposition rates, but the increase in biomass requires nutrients that, in turn, decrease release rates. With our set of parameters, nutrient immobilization is a stronger factor than enhanced decomposition, and a net dampening of nutrient release is predicted. In systems where the initial biomass concentration is a much smaller fraction of decomposable organic matter the “buffering capacity” of the bacterial pool is strongly reduced. Small absolute changes in the bacterial pool do not require large immobilization fluxes, but cause relatively large changes in decomposition rates. It is, therefore, conceivable that algal blooms could result in enhanced nutrient release compared to constant-biomass models in such systems.

Incorporation of microbial biomass into models of early diagenesis therefore has important implications for modeling the seasonal cycle of organic matter input and the resultant seasonality in nutrient release. In our example, the magnitudes of peak release rates and the duration of enhanced mineralization rates strongly differ between the two models, whereas the cumulative N release is not affected by incorporation of a variable biomass pool into the model framework. Hence, a long-term N mass balance on the lake might not be influenced as strongly by the predicted differences in N release rates over time. Comprehensive surface-water quality models that are used to determine reservoir management decisions on a daily or weekly basis, however, will respond differently to the prediction of N release from a multi-G sediment model versus the BIOSED model.

**Acknowledgments**

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**Appendix I. List of all symbols**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\rho$</td>
<td>Concentration of solids (sediment bulk density)</td>
<td>g cm$^{-3}$</td>
</tr>
<tr>
<td>$w$</td>
<td>Burial velocity</td>
<td>cm year$^{-1}$</td>
</tr>
<tr>
<td>$H$</td>
<td>Thickness of surface sediment box</td>
<td>cm</td>
</tr>
<tr>
<td>$\tau$</td>
<td>Residence time in surface sediment box: $\tau = H/w$</td>
<td>year</td>
</tr>
<tr>
<td>$S$</td>
<td>Concentration of non-reactive solids</td>
<td>g S cm$^{-3}$</td>
</tr>
</tbody>
</table>
Appendix I (Continued)

$D_{\text{sed}}$ Concentration of dissolved species in sediment porewater \( \text{g D cm}^{-3} \)

$D_{\text{aq}}$ Concentration of dissolved species in water column \( \text{g D cm}^{-3} \)

$C_{i}, \ i \in [l, s, r]$ Concentration of labile, stable, refractory organic carbon substrate \( \text{g C cm}^{-3} \)

$C_{\text{org}}$ Concentration of total organic carbon substrate: \( C_{\text{org}} = \sum C_{i} \) \( \text{g C cm}^{-3} \)

$C_{b}$ Concentration of bacterial biomass \( \text{g C cm}^{-3} \)

$\text{CO}_{2}$ Concentration of dissolved inorganic carbon in sediment porewater \( \text{g C cm}^{-3} \)

$NH_{3}$ Concentration of dissolved inorganic nitrogen in sediment porewater \( \text{g N cm}^{-3} \)

$c_{i,i}, \ i \in [l, s, r, b]$ Concentrations under steady-state conditions \( \text{g C cm}^{-3} \)

$c_{i,ref}, \ i \in [l, s, r, b]$ Concentrations for the reference scenario \( \text{g C cm}^{-3} \)

$j_{tot}$ Total sedimentation flux: \( j_{tot} = j_{s} + j_{org} \) \( \text{g cm}^{-2} \text{year}^{-1} \)

$j_{s}$ Sedimentation flux of non-reactive solids S \( \text{g S cm}^{-2} \text{year}^{-1} \)

$j_{org}$ Sedimentation flux of organic carbon substrate $C_{\text{org}}$ \( \text{g C cm}^{-2} \text{year}^{-1} \)

$f_{org}$ Average organic carbon content of total sedimentation flux: \( f_{org} = j_{org}/j_{tot} \) \( \% \)

$f_{i}, \ i \in [l, s, r]$ Relative contribution of substrate $i$ to organic carbon substrate flux $j_{org}$ \( \% \)

$dCO_{2}$ Diffusive flux of dissolved species $D$ across sediment–water interface \( \text{g D cm}^{-2} \text{year}^{-1} \)

$dCO_{2}$ Diffusive flux of CO$_2$ across sediment–water interface \( \text{g C cm}^{-2} \text{year}^{-1} \)

$dNH_{3}$ Diffusive flux of NH$_3$ across sediment–water interface \( \text{g N cm}^{-2} \text{year}^{-1} \)

$D_{\text{sed}}$ Concentration of dissolved species in sediment porewater \( \text{g D cm}^{-3} \)

$T_{i}$ Mass transfer coefficient for dissolved species $D$ \( \text{year}^{-1} \)

$T_{CO_{2}}$ Mass transfer coefficient for CO$_2$ \( \text{year}^{-1} \)

$T_{NH_{3}}$ Mass transfer coefficient for NH$_3$ \( \text{year}^{-1} \)

$k_{i}, \ i \in [l, s, r]$ First-order decomposition rates for organic carbon substrates $i$ \( \text{year}^{-1} \)

$k^{*}_{i}, \ i \in [l, s, r]$ Second-order decomposition rates for substrate $i$: \( k^{*}_{i} = k_{i}/eC_{b0} \) \( \text{g C cm}^{-3} \text{year}^{-1} \)

$e$ Bacterial growth efficiency \( \% \)

$C_{b0}$ “Normalization biomass” used to quantify dependence of second-order decomposition rates $k^{*}_{i}$ on concentration of bacterial biomass $C_{b}$ \( \text{g C cm}^{-3} \)

$m$ First-order mortality/recycling rate for bacterial biomass \( \text{year}^{-1} \)

$r_{CN_{i}}, \ i \in [l, s, r, b]$ Carbon to nitrogen ratio in organic substrate and bacterial biomass \( \text{g C (g N)}^{-1} \)

$N_{i}, \ i \in [l, s, r, b]$ Labile, stable, refractory, or biomass nitrogen pool: \( N_{i} = r_{CN_{i}}C_{i} \) \( \text{g N cm}^{-3} \)

**Appendix II. Full set of equations**

**B.1. Multi-G model**

Labile substrate:

\[
\frac{dC_{l}}{dt} = -k_{l}C_{l} - \frac{wC_{l}}{H} + \frac{f_{l}J_{C}}{H}
\]

Stable substrate:

\[
\frac{dC_{s}}{dt} = -k_{s}C_{s} - \frac{wC_{s}}{H} + \frac{f_{l}J_{C}}{H}
\]

Refractory substrate:

\[
\frac{dC_{r}}{dt} = -\frac{wC_{r}}{H} + \frac{f_{l}J_{C}}{H}
\]

Remineralized carbon:

\[
\frac{dCO_{2}}{dt} = -k_{l}C_{l} + k_{s}C_{s} - \frac{J_{CO_{2}}}{H}
\]

Remineralized nitrogen:

\[
\frac{dNH_{3}}{dt} = \frac{1}{r_{CN_{i}}}k_{l}C_{l} + \frac{1}{r_{CN_{i}}}k_{s}C_{s} - \frac{j_{NH_{3}}}{H}
\]

**B.2. BIOSED model**

Labile substrate:

\[
\frac{dC_{l}}{dt} = -\frac{C_{b0}}{C_{b0}}k_{l}C_{l} - \frac{wC_{l}}{H} + \frac{f_{l}J_{C}}{H} + mC_{b}
\]

Stable substrate:

\[
\frac{dC_{s}}{dt} = \frac{C_{b0}}{C_{b0}}k_{s}C_{s} - \frac{wC_{s}}{H} + \frac{f_{l}J_{C}}{H}
\]

Refractory substrate:

\[
\frac{dC_{r}}{dt} = \frac{wC_{r}}{H} + \frac{f_{l}J_{C}}{H}
\]

Bacterial biomass:

\[
\frac{dC_{b}}{dt} = \frac{C_{b0}}{C_{b0}}(k_{l}C_{l} + k_{s}C_{s}) - \frac{wC_{b}}{H} - mC_{b}
\]

Remineralized carbon:

\[
\frac{dCO_{2}}{dt} = \frac{(1 - C_{l}C_{b0})(k_{l}C_{l} + k_{s}C_{s}) - J_{CO_{2}}}{H}
\]

Remineralized nitrogen:

\[
\frac{dNH_{3}}{dt} = \frac{C_{b0}}{C_{b0}}\left[k_{l}C_{l}\left(\frac{1}{r_{CN_{l}}} - \frac{1}{r_{CN_{b}}}ight) + k_{s}C_{s}\left(\frac{1}{r_{CN_{b}}} - \frac{1}{r_{CN_{b}}}ight)\right] - \frac{j_{NH_{3}}}{H}
\]

**References**