

A theoretical investigation of the organic carbon-microbial biomass relation in muddy sediments

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ABSTRACT: A population/diagenetic model is developed to describe the behavior/dynamics of the microbial biomass in aquatic sediments. This model is analyzed in order to establish the dominant terms, i.e. processes, in that balance. The result of this analysis shows that production-removal processes, i.e. growth, death, grazing, transformation to inactive or active, etc., are essentially in balance to the best (lowest order) approximation, while all varieties of transport processes, i.e. motility, chemotaxis, bioturbation, burial, etc., contribute only higher order corrections to this balance. The balance between production-removal processes is shown to imply a linear relation between the size of the microbial biomass and the concentration of organic substrate, as advanced by Rublee (1982; *Estuarine comparisons*, Academic Press, p. 159–182), based on empirical evidence.

KEY WORDS: Organic matter · Microbial biomass · Modelling · Diagenesis

INTRODUCTION

The existence of a quantitative relation between the organic matter content of muddy sediments and the size of the microbial biomass has intrigued biogeochemists and benthic ecologists for some time. For example, Dale (1974) and Rublee (1982) both report significant linear correlations between these 2 variables; however, Bird & Duarte (1989) argue that such correlations are potentially spurious. The nature of this criticism lies with the standardized mode of reporting biomass and carbon concentrations, and neither more measurements nor further statistical analyses will necessarily resolve this issue. A different approach, one based on independent theoretical considerations, can shed some light on the reality of this relation, and it is the aim of this paper to present such an analysis.

The size and evolution of a microbial population are governed by the interaction of various processes that can be formulated as a mathematical model. Models of this type have been employed to describe the dynamics of natural microbial populations in terrestrial

aquifers, soils and rivers (e.g. Bazin et al. 1976, Hattori & Hattori 1976, Hino 1981, Tan & Bond 1995), but this approach has not, to this author's knowledge, been applied to aquatic sediments. The underlying principle behind these models is conservation of mass, and this is achieved by correct balancing of inputs, outputs and accumulations. Successful descriptions and predictions of the distribution of both dissolved and solid components, including organic matter, have been possible with this methodology (Berner 1971, 1980, Lerman 1977, 1978, 1979, Van Cappellen et al. 1993, Thibodeaux 1996, Van Cappellen & Gaillard 1996, Boudreau 1997), and no reason exists to believe that it should not produce equally favorable results in dealing with sedimentary microbial biomass.

THE MODEL

The microbial biomass in a sediment is admittedly not a single quantity (variable). It is composed of various species (e.g. Nealson 1997) and of metabolically active and inactive organisms (e.g. Novitsky 1987). Differentiation of the different, largely bacterial species is probably not worthwhile for the purposes of this

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paper, but the total biomass can be divided into an active component of concentration b_a (in mass C per unit volume of solid sediment) and an 'inactive' (not growing) component, b_d . In addition, the active cells may be found in the porewater and on the solid sediment surfaces. Rublee (1982) has argued that most cells adhere with varying degrees of tenacity to the solids, and only a small fraction is truly present in the solution. This paper follows Tan & Bond (1995) by assuming that a linear equilibrium exists between free, b_f , and surface-dwelling cells, for simplicity b_s .

Dynamic mass balance for the components of the biomass at each point and time in a sediment is governed by differential equations for the surface active, porewater active and inactive cells, respectively (Lin & Segel 1974, Berner 1980, Okubo 1980, Boudreau 1997)

$$\underbrace{\frac{\partial \varphi_s b_s}{\partial t}}_{\text{Accumulation with time}} = \underbrace{-\frac{\partial J_s}{\partial x}}_{\text{Change of the flux with depth}} + \underbrace{\sum \varphi_s R_s}_{\text{Net creation or destruction}} \quad (1)$$

$$\frac{\partial \varphi b_f}{\partial t} = -\frac{\partial J_f}{\partial x} + \sum \varphi R_f \quad (2)$$

and

$$\frac{\partial \varphi_s b_d}{\partial t} = -\frac{\partial J_d}{\partial x} + \sum \varphi_s R_d \quad (3)$$

where t is time (years), x is depth into the sediment relative to the sediment-water interface (cm), φ is porosity, φ_s is solid volume-fraction ($1 - \varphi$), J_s , J_f and J_d are respectively the fluxes of surface-active, free-active and dead organisms at depth x and time t caused by the action of various transport processes ($\text{g C cm}^{-2} \text{ yr}^{-1}$), and $\sum R$ represents the net effect of all processes that create or destroy 1 of these model components ($\text{g C cm}^{-3} \text{ yr}^{-1}$). Simply stated, each equation says that if there is a change in the flux of a component with depth, this must be due to creation/loss by processes in $\sum R$ or net accumulation (either positive or negative) with time, i.e. the time-derivative term on the left-hand side of these equations. Eq. (3) indicates that the inactive cells are all treated as if they were attached, which is probably not true; however, the conclusions of this paper would not be altered by a significant free fraction of inactives, and the added simplicity from this assumption outweighs any small inaccuracy from this source.

This paper's aim is to show that Eqs. (1) to (3) contain important information about the organic carbon-microbial biomass relation; however, in order to extract this information, the exact forms of the fluxes, J , and the reactions, $\sum R$, in each of these equations must first be specified. Secondly, the relative importance of each term in the resulting equations must be calculated. Fortunately, a formal mathematical solution of these equations is not needed to achieve the stated goal.

In order to make the following development more transparent, the porosity will be treated as a constant. This assumption is clearly wrong in most sediments, but its adoption has no effect whatsoever on the conclusions of this study.

Flux terms

All biomass, whether free or attached, appears to advect down the sediment column as more sediment is added by accumulation and the reference frame moves up (Berner 1980); this process creates an apparent downward flux, J_{adv} , of organisms relative to the sediment-water interface. Such a term will appear in the balance equations for all microbial fractions.

Free-active microbes in the porewaters can also move/be moved as a result of Brownian motion (bm), motility (mo), chemotaxis (ct), bioturbation (bio) and hydrological dispersion (dis), each of which contributes a component to the flux of free biomass, J_f , i.e.

$$J_f = (J_{bm})_f + (J_{mo})_f + (J_{ct})_f + (J_{bio})_f + (J_{dis})_f + (J_{adv})_f \quad (4)$$

Following Hattori & Hattori (1976), Corapcioglu & Haridas (1984, 1985), Tan & Bond (1995), and Boudreau (1997), Brownian motion is the random movement of small suspended particles due to the constant bombardment by water molecules, motility is the motion of microbes induced by their own 'random' movements, chemotaxis is the directed movement of organisms towards (or away from) a source of stimulation, e.g. food, bioturbation is the mixing of sediments by the actions of macrofauna (burrowing, ingestion-egestion, plowing, etc., but not irrigation which is modelled differently, as described below), and hydrodynamic dispersion is a diffusionlike scattering which results when a flow occurs in a porous medium. The mathematical forms of these fluxes are displayed in Table 1, along with parameter value estimates. All but advection are diffusion-type relations.

Some entries in Table 1 deserve comment. In particular, muddy sediments generally have modest porewater velocities that do not engender any appreciable dispersion, i.e. small Peclet numbers (Boudreau 1997); consequently, J_{dis} is made null by setting the dispersion coefficient (D_{dis}) to zero. Secondly, the fraction of motile organisms, θ_f , is probably small, as argued by Rublee (1982); however, the maximum influence of these transport terms will be obtained by setting this variable to unity.

Active microorganisms on sediment surfaces can move/be moved by burial, surface Brownian motion/diffusion (surf), motility, chemotaxis, and bioturbation, i.e.

$$J_s = (J_{surf})_s + (J_{surf})_s + (J_{ct})_s + (J_{bio})_s + (J_{adv})_s \quad (5)$$

Table 1. Mathematical forms and parameter values for the flux terms in Eqs. (1) to (3)

Flux (process)	Form	Parameter value	Units of parameter	Source
Advection in porewater	$(J_{adv})_l = \varphi u b_l$	$10^{-4} \leq u < 10^0$	cm yr^{-1}	Berner (1980)
Advection of solids	$(J_{adv})_s = \varphi_s w b_s$	$10^{-4} \leq u < 10^0$	cm yr^{-1}	Berner (1980)
Brownian motion	$(J_{bm})_l = -\varphi D_{bm} \frac{\partial b_l}{\partial x}$	$D_{bm} = 0.03$	$\text{cm}^2 \text{yr}^{-1}$	Segel et al. (1977)
Motility	$(J_{mo})_l = -\varphi D_{mo} \frac{\partial \theta_l b_l}{\partial x}$	$D_{mo} \leq 30$	$\text{cm}^2 \text{yr}^{-1}$	Lovely & Dahlquist (1975) Segel et al. (1977) Berg (1993)
Chemotaxis	$(J_{ct})_l = \varphi \theta_l b_l \frac{(D_{ct})_l}{g} \frac{\partial g}{\partial x}$	all $D_{ct} \approx 2 D_{mo}$	$\text{cm}^2 \text{yr}^{-1}$	Rosen (1983)
Porewater bioturbation	$(J_{bio})_l = -\varphi D_{bio} \frac{\partial b_l}{\partial x}$	$10^{-2} \leq D_{bio} \leq 10^1$	$\text{cm}^2 \text{yr}^{-1}$	Berner (1980)
Dispersion	$(J_{dis})_l = -\varphi D_{dis} \frac{\partial b_l}{\partial x}$	$D_{dis} = 0$	$\text{cm}^2 \text{yr}^{-1}$	Tan & Bond (1995)
Surface diffusion	$(J_{surf})_s = -\varphi_s D_{surf} \frac{\partial b_s}{\partial x}$	$D_{surf} \approx D_{bm}$	$\text{cm}^2 \text{yr}^{-1}$	Carberry (1976)
Motility on solids	$(J_{mo})_s = -\varphi_s (D_{mo})_s \frac{\partial \theta_s b_s}{\partial x}$	$(D_{mo})_s \leq D_{mo}$	$\text{cm}^2 \text{yr}^{-1}$	Analogy to Lovely & Dahlquist (1975)
Chemotaxis on solids	$(J_{ct})_s = \varphi_s \theta_s b_s \frac{(D_{ct})_s}{g} \frac{\partial g}{\partial x}$	$D_{cts} \approx D_{ct}$	$\text{cm}^2 \text{yr}^{-1}$	Analogy to Rosen (1983)
Bioturbation of solids	$(J_{bio})_s = -\varphi_s (D_{bio})_s \frac{\partial b_s}{\partial x}$	$(D_{bio})_s = D_{bio}$	$\text{cm}^2 \text{yr}^{-1}$	Boudreau (1997)

Notes:
 u = advective velocity of the porewater
 w = burial velocity of solid sediment ($u = w$ if $\varphi = \varphi_s$ and with no externally forced hydrological flow)
 D_{bm} = diffusion coefficient for Brownian motion in porewater
 D_{mo} = diffusion coefficient for motility in porewater
 θ_l = fraction of the free-active population that is motile/chemotactic (assumed to be a constant)
 $(D_{mo})_s$ = diffusion coefficient for motility of microorganisms on sediment particle surfaces
 D_{surf} = Brownian motion diffusion coefficient on the surface of particles
 θ_s = fraction of the surface-active population that is motile/chemotactic (assumed to be a constant)
 $(D_{ct})_l$ = diffusion coefficient for chemotaxis of free microorganisms in porewater
 $(D_{ct})_s$ = diffusion coefficient for chemotaxis of microorganisms on sediment particle surfaces
 D_{bio} = diffusion coefficient for bioturbation of microorganisms in porewater
 $(D_{bio})_s$ = diffusion coefficient for bioturbation of microorganisms on sediment particles
 g_i = concentration of the i th labile type of organic matter available to microorganisms for growth

The form and parameter values for these processes are also presented in Table 1. Diffusion coefficients for all these processes are set to their values in porewater; in reality, the surface Brownian motion, motility, and chemotaxis constants are probably smaller than the values in porewater, maybe significantly so, but no empirical data exists to resolve these conjectures; thus, $(D_{ct})_s = (D_{ct})_l \equiv D_{ct}$, etc., but also $\theta_s = \theta_l \equiv \theta$, etc.

In contrast, inactive organisms are treated as attached to solids (not a crucial assumption), such that they move only due to the processes of bioturbation

and burial, i.e.

$$J_d = (J_{bio})_d + (J_{adv})_d \quad (6)$$

and that these components are identical in form and parameter values to those associated with the active surface biomass, $(J_{bio})_s$ and $(J_{adv})_s$, respectively.

Source-sink terms

The sources and sinks represented by the 3 ΣR terms account for the appearance and removal of microor-

ganisms at each depth and time and from each class defined above by biological and physical processes. The specific formulation of the growth/maintenance process into a mathematical statement is pivotal to the present analysis; consequently, some detail is needed in this respect. Microbial biomass can be created by net heterotrophy, photosynthesis and chemo-autotrophy. Net chemo-autotrophy is a process dominant in certain microbial mats and is not central to this study; therefore, it will be ignored hereafter. Net heterotrophy, i.e. oxidation of organic matter in geochemical terms, is the more common form of biomass creation in sediments, although photosynthesis by microphytobenthos is known where sufficient light is available.

The literature on modelling the growth of microbial populations is immense; however, much of it refers to microbial populations that are actually growing in size and not starved for food resources. Under such conditions the rate of growth/maintenance, R_{het} , can be described by an unstructured model of the generic form (Williams 1971, Humphrey 1972, Blanch 1981, Tan & Bond 1995)

$$R_{\text{het}} = y k_{\text{het}} b g \quad (7)$$

where k_{het} is a rate constant, g is the concentration of the limiting nutrient (essentially equivalent to labile C in sediments), y is the yield for this reaction (i.e. mol C incorporated in b per mol C in g consumed), b is a generic variable for b_l or b_s , and the effect of oxidants or nutrients is ignored for the moment.

Eq. (7) creates a nonlinear response to additions of labile carbon because b is also a function of labile g , and b and g are multiplied together in Eq. (7). If g is altered, then the biomass will respond by some change, such that the rate, R_{het} , will be different than that calculated by the change in g alone. Even if g and b are always in linear equilibrium, then a quadratic response is expected. The dynamics of carbon additions to sediments do not exhibit such a nonlinear response; specifically, Westrich & Berner (1984) have provided clear evidence of a linear response of sedimentary heterotrophic rates to additions of labile carbon. Boudreau (1992) has provided a quasi-reaction mechanism that explains this response. As a result R_{het} is more accurately described by the simpler expression

$$R_{\text{het}} = y k_{\text{het}} g \quad (8)$$

Again, no overall dependence on oxidant concentration appears in this equation because total decomposition is being considered¹. Only 1 type of labile organic

matter is assumed to maintain the biomass in the upper 10 to 20 cm of sediments, and its reactivity must be on the order of a month or two in order to do so. This reactivity is consistent with that of fresh phytoplankton (e.g. Westrich & Berner 1984).

The surface-active biomass, b_s , is subject to growth by heterotrophy, possible photosynthesis, activation of inactive biomass, and is subject to loss by death, grazing, transformation to inactive, and attachment-detachment, i.e. respectively,

$$\begin{aligned} \Sigma R_s = & (R_{\text{het}})_s + (R_{\text{photo}})_s + (R_{\text{act}})_d \\ & - (R_{\text{death}})_s - (R_{\text{graze}})_s - (R_{\text{trans}})_s + (R_{\text{a-d}})_s \end{aligned} \quad (9)$$

where the precise forms of each of these source-sink terms is to be found in Table 2. Death transfers organisms to the g pool. While the active-free biomass in the porewater changes due to these same processes, irrigation can also have an effect. Irrigation is the biologically mediated exchange of water accomplished by tube-dwelling macrofauna (see Aller 1982, 1988). This exchange leads to 3-dimensional diffusion patterns that appear as a source-sink term in a 1-dimensional model (Boudreau 1984), i.e. R_{irrig} , so that

$$\begin{aligned} \Sigma R_t = & (R_{\text{het}})_t + (R_{\text{photo}})_t - (R_{\text{death}})_t \\ & - (R_{\text{graze}})_t - (R_{\text{trans}})_t - (R_{\text{a-d}})_t + R_{\text{irrig}} \end{aligned} \quad (10)$$

Finally, inactive biomass is increased by transformation from the active pool and decreased by death, grazing, and reactivation,

$$\Sigma R_d = (R_{\text{trans}})_d - (R_{\text{death}})_d - (R_{\text{graze}})_d - (R_{\text{act}})_d \quad (11)$$

The value for the yield in the heterotrophy terms is something of a question. Yields for various organic substrates are known, e.g. 0.5 for glucose (Lauffenburger 1983), and 0.29 to 0.68 for various other carbon sources (Gaudy & Gaudy 1972, Corapcioglu & Haridas 1984). Linley & Newell (1984) and Blackburn (1987) present evidence that y for natural microbial population acting on natural organic matter is much lower; consequently, a value of 0.2 is adopted, keeping in mind that the conclusions of this paper do not depend strongly on its exact value.

Attachment-detachment equilibrium

A discussion of attachment-detachment as an equilibrium process can be found in Tan & Bond (1995) and is not repeated here. A linear relation (isotherm) is assumed to exist between the active biomass in the porewater and on the solid sediment, i.e.

$$b_l = (K_{\text{ads}} b_s \varphi_s) / \varphi \quad (12)$$

where K_{ads} is an appropriate adsorption coefficient, assumed to be a constant. Rublee (1982) has argued that

¹This statement can be verified by considering Eqs. (4.199) to (4.203) in Boudreau (1997). By adding these equations and setting the Monod and inhibition constant equal for a given oxidant, the total rate of organic matter decay becomes oxidant independent

Table 2. Mathematical forms and parameter values for the source and sink terms in Eqs (1) to (3)

Reaction	Form	Parameter value	Unit of parameter	Source
Heterotrophy	$R_{\text{het}} = y k_{\text{het}} g$	$k_{\text{het}} \approx 10$ $y = 0.2$	yr^{-1} $\text{mol C mol}^{-1} \text{C}$	Westrich & Berner (1984) See body of text
Photosynthesis	$R_{\text{photo}} = k_{\text{photo}} I b_s$	$k_{\text{photo}} I \approx k_{\text{death}}$	yr^{-1}	An assumption ^a
Death	$R_{\text{death}} = k_{\text{death}} b$	$k_{\text{death}} \approx 5.5$ $k_{\text{death}} \approx 4.4$	yr^{-1} yr^{-1}	Corapcioglu & Haridas (1984) Lauffenburger et al. (1981)
Grazing	$R_{\text{graze}} = k_{\text{graze}} b$	$k_{\text{graze}} = k_{\text{death}}$	yr^{-1}	An assumption
Transformation to dormant	$R_{\text{trans}} = k_{\text{trans}} b_s$	$k_{\text{trans}} \approx k_{\text{death}}$	yr^{-1}	An assumption
Transformation to active	$R_{\text{act}} = k_{\text{act}} b_d$	$k_{\text{act}} \approx k_{\text{trans}}/10$	yr^{-1}	An assumption
Irrigation	$R_{\text{irrig}} = k_{\text{irrig}} b_f$	$k_{\text{irrig}} \leq 200$	yr^{-1}	Boudreau (1997)

Notes:
 I = intensity of light; since k_{photo} and I always appear as the combination $k_{\text{photo}}I$, they are treated as a single parameter; the author fully realizes that the variable I is strongly attenuated with depth in sediments, but this point has no effect on the outcome of this present study
 b = generic biomass concentration that can represent b_d , b_f or b_s as appropriate
 $k_{\text{act}} \approx k_{\text{trans}}/10$ in order to be consistent with the idea that most of the live biomass is dormant
^aAssumptions are discussed in the text

most of the biomass is adsorbed; therefore, K_{ads} is a relatively small number dimensionless number, i.e. <1 . Note that K_{ads} is the inverse of the adsorption coefficient as it normally defined, e.g. Tan & Bond (1995), but using this form leads to cleaner, easier to read equations.

Final equations

Substitution of the forms in Tables 1 & 2 and assuming constant porosity produces the new equations

$$\begin{aligned} \frac{\partial b_s}{\partial t} &= (D_{\text{bm}} + \theta D_{\text{mo}} + D_{\text{bio}}) \frac{\partial^2 b_s}{\partial x^2} - \theta D_{\text{ct}} \frac{\partial}{\partial x} \left(\frac{b_s}{g} \frac{\partial g}{\partial x} \right) \\ &- w \frac{\partial b_s}{\partial x} + (1 - K_{\text{ads}}) y k_{\text{het}} g + k_{\text{act}} b_d \\ &+ (k_{\text{photo}} I - k_{\text{death}} - k_{\text{graze}} - k_{\text{trans}}) b_s + \frac{R_{\text{a-d}}}{\phi_s} \end{aligned} \quad (13)$$

$$\begin{aligned} \frac{\partial b_f}{\partial t} &= (D_{\text{bm}} + \theta D_{\text{mo}} + D_{\text{bio}}) \frac{\partial^2 b_f}{\partial x^2} - \theta D_{\text{ct}} \frac{\partial}{\partial x} \left(\frac{b_f}{g} \frac{\partial g}{\partial x} \right) \\ &- w \frac{\partial b_f}{\partial x} + \frac{K_{\text{ads}} \phi_s}{\phi} y k_{\text{het}} g \\ &+ (k_{\text{photo}} I - k_{\text{death}} - k_{\text{graze}} - k_{\text{trans}} - k_{\text{irrig}}) b_f - \frac{R_{\text{a-d}}}{\phi} \end{aligned} \quad (14)$$

and

$$\begin{aligned} \frac{\partial b_d}{\partial t} &= D_{\text{bio}} \frac{\partial^2 b_d}{\partial x^2} - w \frac{\partial b_d}{\partial x} + k_{\text{trans}} \left(b_s + \frac{\phi b_f}{\phi_s} \right) \\ &- (k_{\text{death}} + k_{\text{graze}} + k_{\text{act}}) b_d \end{aligned} \quad (15)$$

Eqs. (13) & (14) still contain the attachment-detachment rate terms that are technically undefined, i.e. we have assumed the equilibrium given by Eq. (12). This indeterminacy is resolved by adding Eqs. (13) & (14) and substituting Eq. (12) in order to obtain equations solely for b_s and b_d , (e.g. see Berner 1980, Chapter 4)

$$\begin{aligned} \frac{\partial b_s}{\partial t} &= (D_{\text{bm}} + D_{\text{bio}} + \theta D_{\text{mo}}) \frac{\partial^2 b_s}{\partial x^2} - \theta D_{\text{ct}} \frac{\partial}{\partial x} \left(\frac{b_s}{g} \frac{\partial g}{\partial x} \right) \\ &- w \frac{\partial b_s}{\partial x} + \frac{y k_{\text{het}} g}{(1 + K_{\text{ads}})} + k_{\text{act}} b_d \\ &+ (k_{\text{photo}} I - k_{\text{death}} - k_{\text{graze}} - k_{\text{trans}}) b_s - \frac{K_{\text{ads}}}{(1 + K_{\text{ads}})} k_{\text{irrig}} b_s \end{aligned} \quad (16)$$

and

$$\begin{aligned} \frac{\partial b_d}{\partial t} &= D_{\text{bio}} \frac{\partial^2 b_d}{\partial x^2} - w \frac{\partial b_d}{\partial x} + k_{\text{trans}} (1 + K_{\text{ads}}) b_s \\ &- (k_{\text{death}} + k_{\text{graze}} + k_{\text{act}}) b_d \end{aligned} \quad (17)$$

THE ANALYSIS

In order to address the question of the existence of a biomass-carbon relation, neither Eq. (15) nor Eq. (16) needs to be solved in any formal sense. Instead, an answer can be developed simply by considering which terms dominate the balance in each equation; by this, I mean that the terms in these equations are not of equal numerical size, which indicates that some terms/processes are more important than others in achieving the stated balance.

The object of the analysis that follows is to discover the relative size of the terms and to establish rigorously which terms could be neglected to the lowest order of accuracy. This process of finding the relative magnitude of terms in an equation is called scaling. To paraphrase Lin & Segel (1974), scaling attempts to select reference quantities so that introduction of these quantities into each term in the dimensional equations transforms it into the product of a constant dimensional factor (usually a parameter grouping), which estimates the term's actual order of magnitude, and a function of dimensionless variable(s) of unit order of magnitude. This is somewhat different than the usual meaning of scaling used in biological sciences (e.g. Schmidt-Nielsen 1984), but it is not totally unrelated.

The depth variable x is scaled by the total depth interval of interest, L . Microbial populations exhibit large changes on depth scales of 10 cm (e.g. Rublee 1982, Novitski & Karl 1986, Novitski 1987), and this is chosen as the value for L . Dividing x by L produces a new dimensionless depth variable (coordinate), $\xi \equiv x/L$. The time variable, t , is scaled by the time, t_m , it takes for the microbes to move over the interval depth L . The diffusionlike transport processes of bioturbation, Brownian motion and motility will produce a t_m of

$$t_m = \frac{L^2}{(D_{bio} + D_{bm} + \theta D_{mo})} \quad (18)$$

which results in a value of about 3 yr with the parameter values in Table 1. By comparison, the time to bury (advect) microbes over this distance is certainly no less than 10 yr if the sediment accumulates at an atypical rate of 1 cm yr⁻¹ and no less than 100 yr for more reasonable accumulation rates. Consequently, Eq. (18) defines the appropriate value of t_m , and division of t by t_m produces a new dimensionless time variable, $\tau \equiv t/t_m$. Finally, the biomass concentrations b_s and b_d are scaled with their values at the sediment-water interface, $(b_s)_o$ and $(b_d)_o$, and the concentration of the reactive organic carbon is also scaled with the concentration at this surface, g_o . The new nondimensional concentrations are then $B_s \equiv b_s/(b_s)_o$, $B_d \equiv b_d/(b_d)_o$, and $G \equiv g/g_o$.

Substitution of these scales and new variables, and some simple re-arrangement, produces the following 2 equations:

$$\begin{aligned} \frac{\partial B_s}{\partial \tau} = & \frac{\partial^2 B_s}{\partial \xi^2} - \frac{\theta D_{ct}}{(D_{bm} + D_{bio} + \theta D_{mo})} \frac{\partial}{\partial \xi} \left(\frac{B_s}{G} \frac{\partial G}{\partial \xi} \right) \\ & - \frac{wL}{(D_{bm} + D_{bio} + \theta D_{mo})} \frac{\partial B_s}{\partial \xi} \\ & + \frac{y k_{net} L^2}{(1 + K_{ads})(D_{bm} + D_{bio} + \theta D_{mo})} \frac{g_o}{(b_s)_o} G \\ & + \frac{k_{act} L^2}{(D_{bm} + D_{bio} + \theta D_{mo})} \frac{(b_d)_o}{(b_s)_o} B_d \\ & + \frac{(k_{photo} I - k_{death} - k_{graze} - k_{trans}) L^2}{(D_{bm} + D_{bio} + \theta D_{mo})} B_s \\ & - \frac{K_{ads} k_{irrig} L^2}{(1 + K_{ads})(D_{bm} + D_{bio} + \theta D_{mo})} B_s \end{aligned} \quad (19)$$

and

$$\begin{aligned} \frac{\partial B_d}{\partial \tau} = & \frac{D_{bio}}{(D_{bm} + D_{bio} + \theta D_{mo})} \frac{\partial^2 B_d}{\partial \xi^2} \\ & - \frac{wL}{(D_{bm} + D_{bio} + \theta D_{mo})} \frac{\partial B_d}{\partial \xi} \\ & + \frac{k_{trans}(1 + K_{ads}) L^2}{(D_{bm} + D_{bio} + \theta D_{mo})} \frac{(b_s)_o}{(b_d)_o} B_s \\ & - \frac{(k_{death} + k_{graze} + k_{act}) L^2}{(D_{bm} + D_{bio} + \theta D_{mo})} B_d \end{aligned} \quad (20)$$

These last 2 equations are now scaled, as defined above, i.e. each term is a product of a parameter/parameter grouping (including unity) and a dimensionless variable or derivative.

The last step of the analysis is to substitute actual values for all the parameters in Eqs. (19) & (20). Most of these are in Tables 1 & 2, with the exception K_{ads} , θ , and the ratios of the initial concentrations. As explained above, K_{ads} is a small number and its exact value is essentially immaterial to the following results; without great prejudice, its value can be set to zero. The mobile fraction θ has also been argued to be small, but this paper's conclusion remains unaltered even if it is set to its maximum possible value of 1. Finally the ratio $(b_s)_o/(b_d)_o$ is a small number, say 0.1, if the microbial population is mostly inactive with respect to growth, as advanced by Novitski (1987); conversely, the ratio $g_o/(b_s)_o$ is a large number, as the live biomass is normally a small fraction of the concentration of total organic matter in sediments. This ratio is set to a maximum value of 0.1; smaller values will only reinforce the conclusions. Substituting all values produces the following order-of-magnitude balance for surface-active biomass,

$$\begin{aligned}
 \underbrace{\mathbf{O}(1) \frac{\partial B_s}{\partial \tau}}_{\text{Transient accumulation}} &= \underbrace{\mathbf{O}(1) \frac{\partial^2 B_s}{\partial \xi^2}}_{\text{Various diffusions}} - \underbrace{\mathbf{O}(1) \frac{\partial}{\partial \xi} \left(\frac{B_s}{G} \frac{\partial G}{\partial \xi} \right)}_{\text{Chemotaxis}} - \underbrace{\mathbf{O}(10^{-4} - 10^0) \frac{\partial B_s}{\partial x}}_{\text{Advection}} \\
 &\quad \underbrace{+ \mathbf{O}(10^2) G + \mathbf{O}(10^2) B_d + \mathbf{O}(10^1 - 10^2) B_s - \mathbf{O}(10^2) B_s}_{\text{Sources and Sinks}} \\
 &\quad \underbrace{\text{Production from O&L} \quad \text{Re-activation of dormant} \quad \text{Net death} \quad \text{Irrigative loss}}
 \end{aligned} \quad (21)$$

and for dormant biomass,

$$\begin{aligned}
 \underbrace{\mathbf{O}(1) \frac{\partial B_d}{\partial \tau}}_{\text{Transient accumulation}} &= \underbrace{\mathbf{O}(10^{-3} - 10^0) \frac{\partial^2 B_d}{\partial \xi^2}}_{\text{Various diffusions}} - \underbrace{\mathbf{O}(10^{-4} - 10^0) \frac{\partial B_d}{\partial \xi}}_{\text{Advection}} \\
 &\quad \underbrace{+ \mathbf{O}(10^1) B_s - \mathbf{O}(10^2) B_d}_{\text{Sources and sinks}} \\
 &\quad \underbrace{\text{Source from free biomass} \quad \text{Loss by death, grazing and activation}}
 \end{aligned} \quad (22)$$

respectively, for Eqs. (19) & (20), and where the symbol $\mathbf{O}(\text{number})$ indicates the size of the coefficient that multiplies the adjoining term, e.g. $\mathbf{O}(10^{-2})$ means a term of magnitude 0.01 (dimensionless). The $\mathbf{O}(\text{number})$ symbols have a one-to-one correspondence with the parameter groupings at the beginning of each term in Eqs. (19) & (20). When a range rather than a number is found in the $\mathbf{O}(\)$ symbol, this indicates that the parameter grouping has a large possible range based on the values quoted in Tables 1 & 2.

Examination of the components of Eq. (21) shows that the source-sink terms constitute the lowest order balance and that the transport and transient accumulation terms are next order (smaller) corrections to that balance, i.e. we could write Eq. (16) as:

$$\begin{aligned}
 &\left(k_{\text{death}} + k_{\text{graze}} + k_{\text{trans}} + \frac{K_{\text{ads}} k_{\text{irrig}}}{1 + K_{\text{ads}}} - k_{\text{photo}} I \right) b_s - k_{\text{act}} b_d \\
 &= \frac{y k_{\text{net}}}{1 + K_{\text{ads}}} g + \sigma_1(x, t) \quad (23)
 \end{aligned}$$

where $\sigma_1(x, t)$ is a correction term that accounts for the effects of transport and temporal variations as found in Eq. (16), i.e. all the terms in Eq. (21) multiplied by $\mathbf{O}(1)$ and smaller. $\sigma_1(x, t)$ is not only a function of x and t , but also b_s and its spatial and temporal derivatives, as dictated by the full balance in Eq. (16). The preceding analysis would argue that this latter correction is, nevertheless, small. Likewise, Eq. (22) suggests that, to the lowest order of accuracy,

$$b_s = \frac{(k_{\text{death}} + k_{\text{graze}} + k_{\text{act}})}{k_{\text{trans}}(1 + K_{\text{ads}})} b_d + \sigma_2(x, t) \quad (24)$$

where $\sigma_2(x, t)$ is another transport-transient correction term, again relatively small in magnitude. Substitution of Eq. (24) into Eq. (23) generates the equation

$$\alpha b_d = \beta g + \sigma_3(x, t) \quad (25)$$

where $\sigma_3(x, t)$ is a relatively small, combined, transport-transient correction term,

$$\alpha \equiv \left[\left[k_{\text{death}} + k_{\text{graze}} + k_{\text{trans}} + \frac{K_{\text{ads}} k_{\text{irrig}}}{(1 + K_{\text{ads}})} - k_{\text{photo}} I \right] \times \frac{(k_{\text{death}} + k_{\text{graze}} + k_{\text{act}})}{k_{\text{trans}}(1 + K_{\text{ads}})} - k_{\text{act}} \right] \quad (26)$$

and

$$\beta \equiv \frac{y k_{\text{net}}}{1 + K_{\text{ads}}} \quad (27)$$

The correlation advanced by Rublee (1982) is based upon total organic carbon and total cell numbers; this latter quantity can be converted to mass concentration by using a nominal bacterial size and density to biomass, while accepting the probable imprecisions of such a calculation. On the other hand, Eq. (25) established a lowest order link between the metabolically inactive biomass, b_d , and the labile organic matter, g . Fortunately, according to Novitski (1987), most of the biomass is inactive in sediments, so that b_d is a good approximation of total biomass, b_T , i.e.

$$b_d \approx b_T \quad (28)$$

Furthermore, total organic matter, g_T , can be expressed as the sum of the labile, g , and refractory, g_r , components,

$$g_T = g + g_r \quad (29)$$

Substitution of Eqs. (28) & (29) into Eq. (25) produces the final result:

$$b_T \approx \frac{\beta}{\alpha} g_T + \sigma_4(x, t) \quad (30)$$

where $\sigma_4(x, t)$ is yet another correction term that includes the added effects of the refractory component on the relation, as well as the effects of transport processes and transients.

Eq. (30) establishes a linear (lowest order) relation between organic matter and microbial biomass concentration, in agreement with the findings of Rublee (1982). Best fits to any data may still be colored by the potential artifact identified by Bird & Duarte (1989), but the existence of the linear correlation is now established. Nevertheless, the factor $\sigma_4(x, t)$ in Eq. (30) is not a constant (as in Rublee 1982), but a complex function of space, time, the derivatives of the active and inactive biomasses and the refractory organic matter concentration. A linear regression, as in Rublee (1982), approximates the effects of $\sigma_4(x, t)$ as a single constant, i.e. its mean value for all the sediment locations and depth intervals included in his data base. Rublee's linear fit explained only 63% of the variability in his data, and part of the reason is the approximation of $\sigma_4(x, t)$ as a constant. The take-home message here is not that

Rublee's particular relation is necessarily universal, simply that exploration of this type of data by means of linear regression appears to be a theoretically justified approach.

To this author's knowledge, Eqs. (13) to (15) represent collectively the first mathematical balance model for microbial biomass in aquatic sediments. While the application presented here has been rather modest, the use of such equations in engineering and hydrological problems has proven to be fruitful, and the same may be true for the study of early diagenetic problems.

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