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A model for short-term control of the bacterioplankton by substrate and grazing

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Abstract

Substrate supply and grazing are the factors with the greatest potential for short-term control of planktonic bacterial density and productivity. A model was developed based on Monod kinetics, where growth rates are limited by food supply in a saturation type equation. In the model, substrate, bacteria, heterotrophic flagellates and zooplankton are state variables linked by trophic transfer and expressed as carbon. The steady state assumption allows calculation of equations indicating the following: (1) bacterial density is determined primarily by the ratio of substrate input to grazing rate; (2) bacterial production is balanced by a combination of losses due to maintenance, death and grazing, and occurs at a rate determined by the rate of substrate input and the growth yield; (3) ambient substrate concentration is directly related to grazing rate.

Sensitivity analysis of the model on a computer demonstrates some differences between grazer-controlled and substrate-controlled bacterial systems, and predictions of the model are listed for possible validation in natural systems. The model is potentially useful in evaluating the 'link vs. sink' question, as it provides a framework for investigating energy flow through the microbial food web as a function of controlling factors.

Heterotrophic bacterioplankton are the primary users of dissolved organic compounds, converting them into new cellular material or mineralizing them into constituent inorganic chemicals (Larsson & Hagstrom, 1982; see Wright, 1984 for a review). For some time it was assumed that these bacteria were controlled by the availability of substrate (typically at very low concentrations in natural waters), existing in a semi-starved (Sieburth *et al.*, 1974) or dormant state (Stevenson, 1978) and turning over only slowly. This view gave rise to the concept of the heterotrophic bacteria as mineralizers of dissolved organic matter; their place in aquatic systems was conceived of as a sink for energy but certainly of importance in regenerating nutrients.

Recently it has become clear that the bacteria are being grazed by planktonic protozoa (Fenchel, 1982; Azam *et al.*, 1983). Measurements have indicated that grazing on the bacteria is primarily traced to very small heterotrophic flagellates and ciliates (Sherr & Sherr, 1983), and occurs at rates in the same magnitude as rates of production of the bacteria (Wright & Coffin, 1984b). Because of these findings the planktonic bacteria have taken on new significance as a potential link between the dissolved organic carbon pool and the classical grazing food chain. However, there is some question whether this link is important in a quantitative sense (Ducklow *et al.*, 1986), and the bacterial role is unresolved. Since the actual amount of energy cycling to bacteria through dissolved organic matter can be a substantial proportion (up to 50%) of the primary product of aquatic ecosystems, the question (are the bacteria a 'link' or a 'sink', as it has been expressed) is quite important in our overall understanding of how the aquatic food web functions (Pomeroy, 1984).

As presently posed, the question is a quantitative one; how much energy flows from the dissolved organic matter to higher organisms? However, the underlying context of this question is functional: how does the aquatic microbial food web work? Specifically, what factors control bacterial density and productivity? A number of factors have been cited: temperature (Pomeroy & Deibel, 1986), primary production (Fuhrman & Azam, 1980), dormancy (Novitsky & Morita, 1978), substrate supply (Wright, 1984) and grazing (Azam *et al.*, 1983). Of these, the latter two appear to have the greatest potential for exercising control of the bacteria over hourly or daily time spans, given the potential of the bacteria for rapid growth.

I would like to present in this paper a simple model of the aquatic microbial food web that has been of help in my attempts to understand how substrate and grazing interact in controlling bacterioplankton density and productivity. I do not claim originality in the structure of the model, but I hope to show that from the model one can derive steady state applications to the natural environment that are quite significant. I also feel that a clear, step-by-step presentation of the model might be of use to others who are also interested in these questions. I will present the basic elements of the model and show that as it deals with controlling factors the model also has the potential for resolving the uncertainty concerning the basic role of the bacterioplankton. Finally, I have developed a user-friendly computer program of the model (written for the Apple II series) that should be useful for both instruction and personal investigation. This is available on request.

The model is based on kinetics introduced by Monod (1949), where the growth rate of a population is a function of the concentration of food in a saturation type equation. This approach was applied by Williams and co-workers to predator-prey systems (Williams, 1980; Wilcox & MacCluer, 1979), and by Graham & Canale to a microbial food chain under batch culture conditions (1982). Following Williams, I call it the saturation kinetics model. The Monod equation is also at the heart of the equations used to describe chemostat operations (Herbert *et al.*, 1956); Thingstad & Pengerud (1985) have recently employed Monod kinetics in a chemostat simulation of the microbial food web. Laake *et al.* (1983) have presented a saturation kinetics model for the microbial food web which parallels the present one in many ways; it employs the same four trophic levels, and in some ways is more sophisticated. Fenchel (1982) and Anderson & Fenchel (1985) have developed a predator-prey model employing the classical Lotka-Volterra equations. This model behaves in many ways like the Monod-base models, but does not deal quantitatively with substrate input and ambient concentration over time.

The saturation kinetics model differs from those mentioned above in two significant ways. First, it employs the concept of maintenance energy (Pirt, 1965). This represents a constant energy demand on the bacteria that must be met regardless of growth rate. Maintenance energy is a concept that emerged from chemostat growth studies of bacteria, but as yet has not been amenable to measurement in the bacterioplankton. Pirt (1982) has demonstrated that because of maintenance energy demand, growth yield varies with the specific (actual) growth rate in a saturation-type fashion; it is highest when the actual growth rate is also high, which occurs when the system is not substrate-limited. As substrate becomes increasingly limiting, actual growth rate and actual growth yield decline. If maintenance energy were zero, the growth yield would have a maximum, constant value. These relationships are shown in equation 5, Table 1.

Most important, although the model deals with changes in the state variables, its most useful applications at present are when steady state conditions are assumed, i.e., when the state variables are unchanging. In support of the steady state, numerous workers have reported a remarkable constancy of numbers of the planktonic bacteria (e.g., Ducklow, 1983; Wright & Coffin, 1983) and heterotrophic flagellates (Sherr *et al.*, 1984). If our purpose in developing models is to understand how the food web works in nature, we must obviously employ them to investigate steady state conditions. The steady state approach was used by Billén *et al.* (1980) in a simpler two-member model of bacterial growth based on uptake kinetics and a 'death rate' as the final sink for the bacteria. As we will see, some of the predictions of Billén's model are identical with the present one.

Table 1. Symbols and equations for the saturation kinetics model.

Symbol	Units	Explanation
B	$\mu g\ C\ l^{-1}$	Bacterial biomass (for cell density, assume 24 μg C/l equals 10^9 bacteria)
B_{max}	$\mu g\ C\ l^{-1}$	Upper limit of bacterial biomass in a given system
μ	hr^{-1}	Maximum specific growth rate, or growth rate constant
μ_a	hr^{-1}	Actual growth rate under conditions of substrate limitation
g	hr^{-1}	Grazing rate of heterotrophic protozoa on bacteria
P	$\mu g\ C\ l^{-1}\ hr^{-1}$	Rate of input of usable DOC into system
S	$\mu g\ C\ l^{-1}$	Ambient concentration of useful DOC substrate
m	hr^{-1}	Maintenance coefficient; ratio of substrate used per hr for maintenance to cell biomass
d	hr^{-1}	Death rate for bacteria, heterotrophic flagellates or zooplankton
Y	(no units)	Actual growth yield for bacteria, heterotrophic flagellates or zooplankton
Y_g	(no units)	Maximum growth yield for bacteria, heterotrophic flagellates or zooplankton
K	$\mu g\ C\ l^{-1}$	Half-saturation constant for bacteria, heterotrophic flagellates or zooplankton
F	$\mu g\ C\ l^{-1}$	Heterotrophic flagellate grazer biomass, in carbon
Z	$\mu g\ C\ l^{-1}$	Zooplankton biomass (grazers on flagellates)

Equations

1. Subrate equation: $\Delta S = P - \left(\frac{\mu_b B_{t-1}}{K_b + S_{t-1}}\right) S_{t-1}$

2. Bacteria equation:

$$\Delta B = \left(\frac{\mu_b S_{t-1}}{K_b + S_{t-1}} - \frac{\mu_f F_{t-1}}{(K_f + B_{t-1})Y_f} - m_b - d_b\right) B_{t-1}$$

3. Heterotrophic flagellate equation:

$$\Delta F = \left(\frac{\mu_f B_{t-1}}{K_f + B_{t-1}} - \frac{\mu_z Z_{t-1}}{(K_z + F_{t-1})Y_z} - m_f - d_f\right) F_{t-1}$$

4. Zooplankton grazer equation: $\Delta Z = \left(\frac{\mu_z F_{t-1}}{K_z + F_{t-1}} - d_z\right) Z_{t-1}$

6. Growth yield eqation (from Pirt, 1982): $Y = \frac{Y_G \mu_a}{\mu_a + Y_G m}$

In nature, of course, we do not expect the steady state to be all that steady. We have presented evidence (Wright & Coffin, in press) that in a salt marsh estuary the density of the planktonic bacteria may be quite constant from one tide to the next, but that this balance depends on a very close coupling of bacterial growth and grazing that may not always occur. Fenchel (1986) described reciprocal shifts in bacteria and microflagellates occurring in 10 day cycles. It will be seen that the model deals effectively with the consequences of a perturbation of the steady state.

Table 1 presents the symbols and equations employed in the model, and Fig. 1 is a diagrammatic presentation of the model. Substrate, bacteria, heterotrophic microflagellates and microzooplankton are state variables linked by trophic transfer and expressed in terms of their carbon content. Substrate input (P) is the basic driving function in the model and represents the rate at which new labile organic carbon enters the substrate pool from all sources in the system. The model is programmed at the present time to generate a time series for the 4 major state variables, with observer-selected time-steps for computation, sampling interval and length of time run.

Figure 2 presents the standard run of the microbial food web model; values for the constants are in the figure legend, and the figure presents changes in several state variables over time. Given a constant rate of substrate input, the system assumes a steady state with oscillations occurring as a result of the dynamic nature of the predator-prey relationship between the zooplankton and the heterotrophic flagellates. The impact of the oscillations is lessened moving down the trophic levels in the food web. This behavior is well-known for such systems and has re-

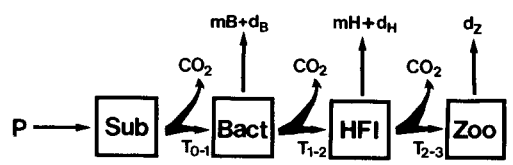

Fig. 1. Saturation kinetic model for planktonic microbial food web. Boxes represent trophic levels as carbon pools, and arrows represent carbon transfer between trophic levels and to respiration, maintenance and death sinks. Symbols are as defined in Table 1.

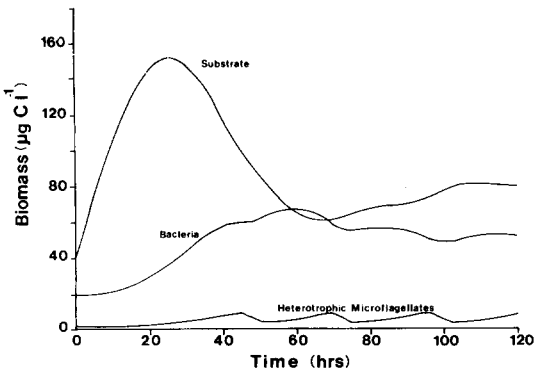

Fig. 2. Standard computer run of saturation kinetic model. Parameters as follows: Substrate input (P) = 200 μg C l^{-1} day^{-1}. Starting levels for pools, in μg C l^{-1}: substrate, 40; bacteria, 20; flagellates, 2; zooplankton, 0.2. Maximum growth rates, in hr^{-1}: bacteria, 0.2; flagellates, 0.15; zooplankton, 0.08. Half-saturation constants, in μg C l^{-1}: bacteria, 120; flagellates, 24; zooplankton, 10. Maintenance coefficients, in hr^{-1}: 0.04 for all populations. Death rates, in hr^{-1}: bacteria, 0.01; flagellates, 0.015; zooplankton, 0.03. Growth yields: 0.4 for all populations. System reached steady state by 120 hours.

cently been shown to occur in natural waters (Fenchel, 1986).

Assuming steady state conditions it is possible to derive an expression for bacterial density as a function of substrate input and grazing.

From equation 1, Table 1, at steady state:

$$\mu_b \cdot B \left(\frac{S}{K_b + S}\right) = P \cdot Y_b \tag{1}$$

setting grazing as a single rate, from equation 2, Table 1:

$$g = \frac{\mu_f \cdot F}{K_f + B} \cdot \frac{1}{Y_f} \tag{2}$$

and applying this equation back to equation 2, Table 1, assuming steady state:

$$\mu b \cdot B \left(\frac{S}{K_b + S}\right) = m \cdot B + d \cdot B + g \cdot B \tag{3}$$

combining equations (1) and (3):

$$B = \frac{P \cdot Y_b}{m + d + g} \tag{4}$$

Assuming that growth yield, maintenance coefficient and death rate are parameters that will not undergo radical change, equation (4) indicates that a given bacterial density at steady state is determined primarily by the ratio of substrate input to grazing rate. The steady state system of Billén *et al.* (1980) yielded the identical equation except that the loss factors in the denominator were represented by a single mortality constant.

The model also provides a context for dealing with bacterial production. Several methods for measuring bacterial productivity have been advanced (see Newell & Fallon, 1982, for a comparison of methods). All have in common the measurement of the actual rate of increase or growth of the standing stock of bacteria, and then finding production by multiplying together density and the growth rate. In terms of the model, this rate of growth (μ_a) is some fraction of the maximum specific growth rate (μ) because of the effects of substrate limitation:

$$\mu_a = \mu_b \left(\frac{S}{K_b + S}\right) \tag{5}$$

At steady state, where B is not changing, the following equalities exist [equations (3), (4) and (5)]:

$$B \cdot \mu_a = B\,(m + d + g) = P \cdot Y_b \tag{6}$$

These equalities indicate that at steady state, bacterial production is balanced by a combination of losses due to maintenance, death and grazing, and occurs at a rate determined by the rate of input of substrate and the efficiency of use of that substrate.

The steady state concentration of ambient substrate, according to the model, can be derived from equation 2, Table 1 and equation (2) above:

$$S = K_b \left(\frac{m + d + g}{\mu}\right) - 1 \tag{7}$$

The parameter most likely to vary in this equation is again the grazing rate, and the equation indicates that ambient substrate will be strongly influenced by

changes in the grazing rate.

Sensitivity analysis of the model is illustrated for grazing and substrate input, the two most important variables in the model. For this simulation, equation (2) was used to determine grazing. Figure 3A is a replication of the standard run (Fig. 2) with the grazing rate set at 0.03/hr, and the higher trophic levels omitted. Figure 3B demonstrates the outcome of a 75% decrease in grazing rate on the standard run, and Fig. 3C demonstrates the outcome of a doubling of substrate input. Both perturbations produced an increase in bacterial density, but with opposite effects on bacterial production. The reduction in grazing (3B) led to a new steady state where ambient substrate concentration was reduced, bacterial density increased, and bacterial production declined as energy usage shifted away from the grazers and towards meeting the maintenance needs of the larger bacterial biomass. The new levels of the state variables and rates were consistent with the predictions of equations (4) and (6).

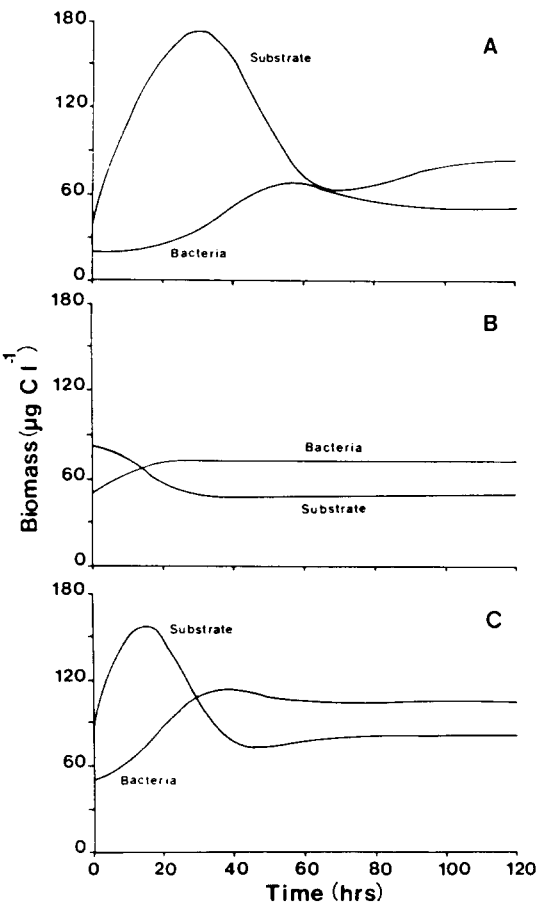

Fig. 3. 3A: Computer run of saturation kinetic model, where flagellates and zooplankton removed and grazing simulated by setting grazing rate at 0.03 hr^{-1} (see equation 2, text). Substrate input, starting levels and constants for bacteria as in Fig. 2. 3B: Outcome of a 75% reduction in grazing rate, starting at steady state levels as at the end of Fig. 3A run. 3C: Outcome of a doubling in rate of substrate input (P), starting at steady state levels as at the end of Fig. 3A run.

For purposes of discussion it may be appropriate to refer to two modes of operation of the microbial food web: grazer control (Fig. 3A, 3C), and substrate control (Fig. 3B). Table 2 suggests the basic characteristics of the microbial food web according to these two modes of control. The characteristics are relative, and assume a common rate of substrate input. It is evident from equation (4) that the major outcome of a shift in substrate input is a change in bacterial density, and if grazer control can be assumed to be the normal mode, then relative bacterial density is a useful reflection of substrate input. Indeed, if the constants in equations 4 or 6 can be evaluated reliably, the equation may be useful in estimating substrate input in different systems.

Validation of the model is of course limited to those state and rate variables that are currently amenable to measurement: densities of the bacteria, heterotrophic flagellates and zooplankton; growth rates of these members of the food web, and grazing rates. Beyond these, it might be possible to obtain a rough estimate of ambient substrate concentration from the response of a bacterial assemblage to short-term incubation (Wright & Coffin, in press). To examine natural systems for possible validation of the

Table 2. Characteristics of microbial food web under grazer control versus substrate control.

Parameter	Grazer control	Substrate control
Bacterial density	moderate	high
Bacterial growth rate	high	low
Grazer density	moderate to high	low
Grazing rate	high	low
Ambient substrate conc.	relatively high	low

model, the following predictions derived from the model are suggested:

1. It should be possible to find samples from the same environment which demonstrate at different times the characteristics of the two modes of control outlined in Table 2.

2. Bacterial production and grazing should be positively correlated.

3. Ambient substrate concentration and grazing should be positively correlated.

4. If shifts in the mode of control occur, then bacterial density might not be correlated very highly with substrate input, bacterial production, grazing and heterotrophic microflagellates.

5. Athough this is obvious, grazing rate and heterotrophic microflagellate density should be positively correlated.

It is not the intent of this paper to explore these predictions; evidence for all five of the predictions has been presented in Wright (in press) and Wright & Coffin (in press). Other workers are beginning to report data that also agree with the above predictions (e.g., Bell, 1986; Hobbie, pers. comm.), and it seems safe to conclude that the model presented above – in particular in its steady form – is a useful tool in understanding the workings of the microbial food web. Much more work is needed to establish the limits and variations in many of the constants employed in the model. In particular, the relationships between net and gross bacterial production, growth yield and maintenance energy losses need to be explored in detail.

It is obvious that these considerations are applicable to the 'link or sink' question. A microbial food web where the bacteria are predominantly substrate-controlled is clearly acting as a sink for organic matter. Conceivably, a major increase in forms that feed on the flagellate grazers might lead to the establishment of this mode. It is possible, however, that the most common mode of control is grazer control, owing to the rapid ability of the heterotrophic microflagellates to increase (Sherr *et al.*, 1984) and to the substantial unused carbon pool represented by high bacterial densities under substrate control. Fenchel (1986) argues that grazing in eutrophic systems tends to keep bacterial densities well below the substrate limit, while in more oligotrophic systems the bacteria come closer to their substrate limit owing to the existence of a threshold bacterial density for support of grazer populations.

The grazer-controlled system is linking the flux of dissolved organic matter to higher trophic levels, although more data is needed in order to evaluate how efficient this transfer is. The information on grazing by the microflagellates is accumulating rapidly (Wright & Coffin, 1984a, 1984b; Servais *et al.*, 1985; Sanders & Porter, 1986; Wiknar *et al.*, 1986; Fenchel, 1986), and the consensus seems to be that grazing is highly important.

It is unlikely that any single experiment (Ducklow *et al.*, 1986) or the study of one system will resolve the link vs. sink controversy. Major differences exist between planktonic systems, and variations in the relative impacts of substrate input and grazing are likely to occur in these different systems. These variations in the mode of control will undoubtedly be reflected in the pattern of energy flow through the microbial food web. More research is needed before we understand when and why such changes in the mode of control may be expected to occur. This model is offered as a tool for sorting these things out.

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