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.