CHAPTER 8

SIMPLE MODELS OF MICROBIAL GROWTH

In laboratory cultures bacteria and yeast follow the population models of the previous chapter more precisely than more complex organisms. This is not surprising, because microbes are more likely to behave as homogenous populations. Their life cycles are simpler and large numbers are usually involved in growth experiments. However, microbiologists seldom use the models of Chapter 7. The logistic model has been a starting point for biologists interested in more complex organisms and processes (e.g. predation and competition). Microbiologists have developed a number of models which are based on different assumptions.

Different models have been chosen probably because laboratory culture procedures differ. Water fleas, protozoans, flour beetles, fruit flies, and guppies were used in classic experiments describing logistic growth. Usually these animals were transferred regularly to containers of fresh medium to resupply food and remove waste products. When food was the limiting factor in the experiment, reproduction in populations grown to carrying capacity would halt until death released enough food for reproduction to resume.

The resupply of nutrients is difficult with microbial populations, which are generally grown in batch cultures or continuous cultures. So, while microbiologists have studied population growth intensively for decades, they have used a number of interesting models other than those we studied in the previous chapter. These models are the subject of this chapter.

8.1 The Monod Model of Microbial Growth

For a long time, microbiologists have recognized that microbes respond to their nutrient sources much like enzymes act on substrates. The most striking resemblance is the way growth rate of microbes responds to an increase in concentration of a limiting nutrient. Monod (1942) noticed that this response was hyperbolic, like the saturation behavior of enzymes (Figure 8.1).

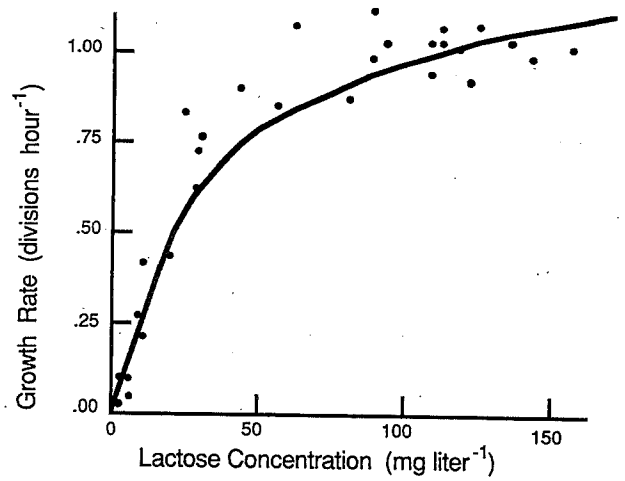


Figure 8.1. Graph of growth rate of the bacterial species *Escherichia coli* at different concentrations of lactose. Based on data from Monod (1942).

This behavior suggested that equations for enzymes could serve as models for some types of microbial growth, for example:

$$\frac{dB}{dt} = \mu B = \left(\mu_m \frac{[S]}{K_s + [S]}\right) B \tag{8.1}$$

where B is cell density, μ is the specific growth rate constant, S is the concentration of nutrient, and μ_m is the maximal growth rate when nutrient concentration is completely unlimited. K_s is the half-saturation constant, which represents the substrate concentration that permits growth at half the maximum rate; thus, $[S] = K_s$ when $\mu = \mu_m/2$. In effect, K_s determines how rapidly a hyperbolic curve such as Figure 8.1 approaches the asymptote. B may be measured as biomass (e.g. mg liter^{-1}), or as density of cells (e.g. number ml^{-1}) assuming uniform cell size. μ has units of biomass (unit biomass)$^{-1}$ time^{-1}.

A formal derivation of this equation is probably not possible, but it may be obtained by analogy to the Michaelis-Menten equation. An enzyme-substrate interaction may be diagrammed with:

$$E + S \underset{k_2}{\overset{k_1}{\rightleftharpoons}} ES \underset{k_4}{\overset{k_3}{\rightleftharpoons}} P + E$$

where E is free enzyme, S is the substrate, ES is the enzyme-substrate compound, P is the product, and k_1, k_2, k_3, and k_4 are rate constants for the reactions. As you saw in Section 2.2, these reactions can be modeled with the following equation:

$$v = V_{\max} \frac{[S]}{K_m + [S]} \tag{8.2}$$

You may recall that this equation was derived by assuming a steady-state concentration for ES and assuming that v approached $V_{\max}$ as ES approached E_{total}.

In a similar way, the growth of cells in a culture may be described by a "reaction" like the following:

$$S + B \underset{k_2}{\overset{k_1}{\rightleftharpoons}} SB \underset{k_4}{\overset{k_3}{\rightleftharpoons}} B + P$$

In this hypothetical and not very precise description, B refers to living cells, S is the limiting nutrient, SB is the combination of cells plus absorbed but unassimilated nutrient, and P is the new cell biomass derived from the metabolized nutrient. k_1 is rate of nutrient intake, k_2 is the rate of nutrient loss through excretion, and k_3 is rate of formation of new cellular material that includes the nutrient. In this scheme, k_4 is zero because P is new cell biomass and is not distinguishable from B. (k_4 might take on a positive value in the case of cannibalism.) Because of metabolic requirements, more S must be used by the cells than appears in the amount of new biomass, P. The process may exhibit the positive feedback characteristics of the autocatalytic enzyme reaction (see Section 6.5).

As with enzymes, new cell material is formed fastest when cell biomass and associated systems are saturated with nutrient in the form of SB. Considerable evidence for the validity of the Monod model has accumulated since it was first proposed (Dugdale 1967, Powers and Canale 1975). In practice, values of μ are found for different nutrient concentrations S in experiments. The curve-fitting techniques of Chapter 3 are then used with the hyperbolic equation to find values for K_s and μ_m, the constants in Equation 8.1.

In many experiments, the occurrence of respiration, mortality and autolysis have been found to decrease growth rates independently of nutrient

concentration (Herbert 1958). For these cases, Equation 8.1 is modified to include an additional term to account for these losses:

$$\frac{dB}{dt} = \mu B = \left(\mu_m \frac{[S]}{K_s + [S]} - R\right) B \tag{8.3}$$

where R is a rate constant describing loss of biomass.

8.2 Batch Culture of Microorganisms

Batch cultures are started with a few microorganisms introduced into a container of sterile nutrient solution. The population grows until the nutrient supply is depleted; then it begins to decline as organisms die or become dormant. The typical S-shaped portion of the growth curve may be logistic. However, when a microorganism in a batch culture dies, it may not release nutrients that other microbes can use for reproduction to replace the dead microbe. Hence, batch cultures may not conform to logistic assumptions. A population that does meet these assumptions will neither decline nor increase when it is at carrying capacity.

Exercise 8-1: Use Equation 8.3 in a simulation of bacterial growth in a batch culture with a limiting nutrient. Assume a fixed amount of nutrient, $[S]_{\text{total}}$. The nutrient found in cells, free nutrient concentration $[S]$ in the culture medium, and total nutrient concentration follow this simple relationship:

$$[S]_{\text{total}} = [S] + aB \tag{8.4}$$

where a is the proportion of biomass concentration B that is made up of absorbed nutrient. Use the following values for constants in your simulation:

$$R = 0.03\ \text{hr}^{-1} \qquad a = 0.03 \qquad \mu_m = 0.3\ \text{hr}^{-1}$$
$$[S]_{\text{total}} = 100\ \text{mg liter}^{-1} \qquad K_s = 25\ \text{mg liter}^{-1}$$

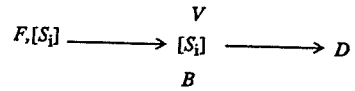
Assume an initial biomass of 1 mg liter^{-1} and allow the simulation to proceed to steady-state. Be sure to adjust your initial value of $[S]$ to include the amount of nutrient contained in the initial inoculum. Use the usual two-stage Euler method to perform the integration. Because of the potential for instability with numerical integration, use an Improved Euler integration with $\Delta t = 0.1$, or a simple Euler with $\Delta t = 0.01$. Output for your simulation should be B and $[S]$ plotted on the same graph through time.

8.3 Continuous Cultures in Chemostats

Chemostatic cultures are used both in laboratory research and in industrial production of the useful results of microbial growth (e.g. antibiotics). Some sewage treatment plants are designed as chemostats.

A chemostat is set up with the microorganisms in a container (reactor) of liquid nutrient medium. The medium in the container is usually stirred or agitated continuously to prevent development of nutrient gradients and settling of the microorganisms. At a carefully controlled rate, fresh nutrient medium is put continuously into the reactor from a reservoir. Medium is removed from the container at the same rate as it is added; this effluent contains unused medium, microbial cells, and metabolic products. The approach used here follows the description of Novick and Szilard (1950*a*,*b*).

A chemostat may be diagrammed in this way:



V is the volume of the chemostat culture vessel, F is the flow rate through the chemostat, and B is cell biomass density. $[S_i]$ is the concentration of nutrient entering the chemostat, and $[S]$ is concentration of nutrients in the container and in the outflow. D is the dilution rate, found by F/V, with a dimension of time^{-1}. The rate of growth (or decline) of cells in the chemostat is described by

$$\frac{dB}{dt} = \mu B - DB \tag{8.5}$$

where μ is the growth rate constant, and can be obtained from Equation 8.1 for any given $[S]$. When the chemostat population is at steady state, $dB/dt = 0$ and $\mu = D$.

The change in substrate concentration in the chemostat is defined with the equation:

$$\frac{d[S]}{dt} = D[S_i] - D[S] - \mu Ba \tag{8.6}$$

Here, $D[S_i]$ defines the rate of nutrient input to the chemostat and $D[S]$ is the rate at which unused nutrients are washed out. The constant a is the fraction of cell biomass that is comprised of nutrient (see Equation 8.4), so that μBa represents the rate of uptake of nutrients by the cells.

Equations 8.5 and 8.6, coupled with 8.1, allow a complete simulation of chemostat behavior. A variety of objectives are possible for different combinations of input data. For example, it is possible to determine

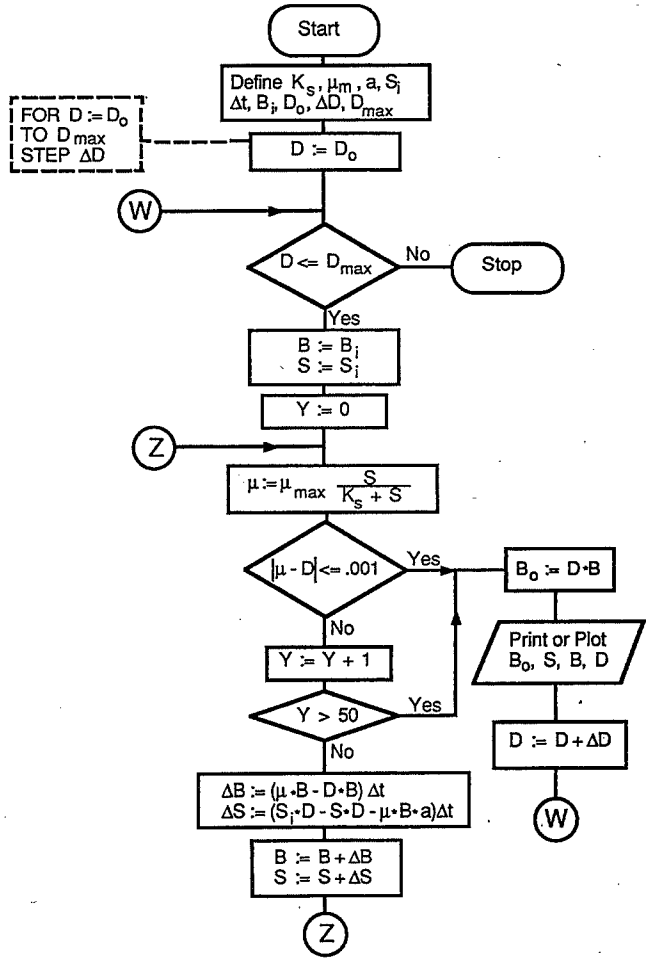


Figure 8.2. Flowchart for program for steady-state simulation of chemostat (Exercise 8-3).

dilution rates that will maximize cell biomass output, B_o, from the system for a given $[S_i]$.

Exercise 8-2: Use Equations 8.5, 8.6 and 8.1 to simulate growth of a microorganism in a chemostat. Assume an input nutrient concentration, $[S_i] = 100$ mg liter^{-1}. Set initial biomass $B = 10$, and initial nutrient concentration $[S] = [S_i]$ in the chemostat. Set the constants of the system as follows:

$$K_s = 75 \qquad \mu_m = 1.5 \qquad a = 0.013$$

Examine the effects on B and $[S]$ of different dilution rates: 0.05, 0.25, 0.50, and 0.70. Your output should consist of two graphs, the first showing B for the 4 levels of D, and the second showing $[S]$ for the 4 levels. Show these plotted over about 50 units of time. Numerical integration can be unstable at low rates of dilution, so use the simple two-stage Euler procedure with $\Delta t = 0.1$.

Exercise 8-3: Considerable insight into the behavior of a chemostat can be obtained from a simulation of steady-state conditions. The basic simulation of Exercise 8-2 can be inserted into a program which varies D, and allows the simulation to iterate to a steady state. The program can show the steady-state values for different characteristics of the chemostat. Write a program that will vary

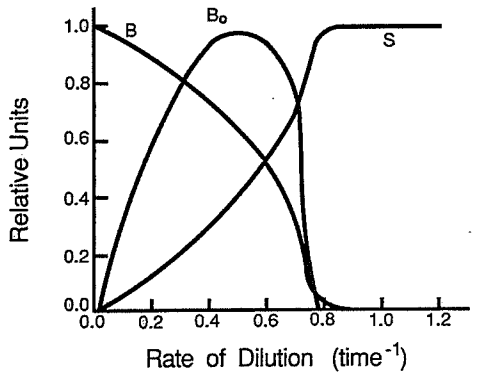


Figure 8.3. Graph of data from simulation of steady-state conditions in a chemostat at various rates of dilution. See Exercise 8-3.

dilution rate from 0.02 to 1.2 in increments of 0.02. Use $\Delta t = 1.0$. Plot out the results as in Figure 8.3, which shows typical steady-state results. A flowchart for the simulation is given in Figure 8.2.

8.4 Multiple Limiting Nutrients

The Monod equation for microbial growth has been used in a variety of simulation studies. The Monod equation may not be precisely correct, but it provides a convenient starting point for modeling populations of cells and even rather complex animals, e.g. rotifers (Boraas 1983) and daphnids (Vyhnalek 1987). Because it is an analogue of the Michaelis-Menten equation, modelers are able to draw upon a large body of literature that deals with enzyme kinetics. Chen (1970) used the Monod equation as a starting point for describing the effect of multiple nutrients:

$$\mu = \mu_m \left(\frac{[S]}{K_s + [S]}\right)\left(\frac{[N]}{K_n + [N]}\right)\left(\frac{[P]}{K_p + [P]}\right) \qquad (8.7)$$

This equation could be employed as a model for the growth of diatoms, for example, where S, N, and P might represent the three most likely limiting nutrients: silicon, nitrogen, and phosphorus. The half-saturation constants for each of these elements would then be given with K_s, K_n, and K_p. The growth rate μ_m is presumably determined with all three elements in saturating concentrations. The origin of this and similar equations is evidently Cleland's (1970) equation for enzyme kinetics with multiple substrates.

The free nutrients in this system at any time may be determined from a set of three equations, each following Equation 8.4. For example:

$$[S]_{\text{free}} = [S]_{\text{total}} - a_s B$$

where $a_s B$ represents the fractional biomass of the organism that is derived from S. B is the biomass density, and a is the coefficient relating a nutrient to biomass. We will assume that a is constant, although this is probably not the case in many circumstances (Boraas 1983). The use of Equation 8.4 implies a batch culture procedure, rather than the continuous chemostatic culture of the preceding section.

Equation 8.7 may be used to simulate an ecological or agricultural principle, Liebig's Law of the Minimum. Briefly, this law states that growth of a population will be limited by the factor which exists in least supply relative to the need of the population. Liebig's idea was that the factors limiting the yield of crops could be identified and removed in turn (Hutchinson 1973).

Exercise 8-4: Write and implement a program to simulate multiple nutrient limitation of diatom growth based on Equation 8.7. (See also Equations 8.3 and 8.4.) For the first part of the batch culture simulation, set up your simulation with the following constants and initial values:

Total nutrient concentrations (mg liter^{-1}):

$S_t = 10.0 \qquad N_t = 1.00 \qquad P_t = 0.10$

Fractional composition of diatom biomass:

$a_s = 0.15 \qquad a_n = 0.10 \qquad a_p = 0.005$

Half-saturation constants (mg liter^{-1}):

$K_s = 0.10 \qquad K_n = 0.15 \qquad K_p = 0.04$

Initial diatom biomass (mg liter^{-1}):

$B = 0.10$

Rate of loss for mortality, etc. (hr^{-1}):

$R = 0.005$

Maximum growth rate at saturation (hr^{-1}):

$\mu_m = 0.120$

Use a two-stage simple Euler integration in this simulation, with $\Delta t = 1$. Let the simulation proceed for about 120 hours, and plot 4 lines on the same graph, showing B, $[S]$, $[N]$ and $[P]$. Based on these simulation results, identify the nutrient that is "limiting" in this system.

Exercise 8-5: Modify the simulation of Exercise 8-4 to test your identification of the limiting nutrient. First plot B over time using the values for S_t, N_t and P_t given in Exercise 8-4. Then rerun the simulation using 100 times each of the baseline nutrient concentrations in turn, to discover which nutrient is limiting to this hypothetical diatom population.

You should discover that one of the nutrients limits the final level of B, but another limits rate of growth. This distinction between different limits for Monod-Herbert models of Leibig's Law is discussed in O'Brien (1972, 1973), Holmes (1973), and Kelly and Hornberger (1973).

8.5 Competition for Limiting Nutrients

In Chapter 7 we discussed competitive interactions among organisms, using equations for interaction based on the logistic limits to population

growth. The Monod-Herbert model (Equation 8.3) has been used for some time in equivalent models to describe the interaction of two or more species competing for some nutrients.

Powers and Canale (1975) developed a model of green algae and blue-green algae (cyanobacteria) competing for nitrogen and phosphorus, two important limiting nutrients for plants in lakes. Some blue-green algae differ significantly from green algae because some species can "fix" molecular nitrogen. These blue-green algae are able to use the atmospheric nitrogen gas dissolved in water as a source of nitrogen that is not available to the green algae. The interaction between these two groups is important, because blue-green algae are capable of causing "problems" for humans when they are abundant in water. The following description of this model is simplified from the original and omits many factors known to be significant in determining nutrient dynamics, including runoff, mixing, sinking of algae, and predation by herbivorous zooplankton. However, it still proves to be an interesting and challenging simulation.

We will assume a lake with two types of algae, blue-green and green, and assume that they respond as homogeneous populations. We will further assume that their growth is limited by nitrogen and phosphorus dissolved in the water, and that we can treat the lake as a batch culture, with the initial nutrients either remaining dissolved in the lake water or incorporated in the algae. We will assume that algal growth rates can be described with equations for multiple limiting nutrients (see Equation 8.7):

$$\mu_G = \mu_{mG}\left(\frac{[P]}{K_{pG}+[P]}\right)\left(\frac{[N]}{K_{nG}+[N]}\right) \tag{8.8}$$

$$\mu_B = \mu_{mB}\left(\frac{[P]}{K_{pB}+[P]}\right)\left(\frac{[N]+[n]}{K_{nB}+[N]+[n]}\right) \tag{8.9}$$

The inclusion of $[n]$ as an extra term in Equation 8.9 is to permit a rough simulation of the fixation of dissolved molecular nitrogen gas by the blue-green algae. The terms in these two equations are defined as follows:

μ_G is growth rate of green algae;
μ_B is growth rate of blue-green algae;
μ_{mG} is growth rate of green algae at saturation with N and P;
μ_{mB} is growth rate of blue-green algae at saturation with N and P;
$[P]$ is concentration of available phosphorus;
$[N]$ is concentration of available nitrogen;
$[n]$ is concentration of dissolved molecular nitrogen gas;
K_{pG} is the half-saturation constant for phosphorus and green algae;

K_{pB} is the half-saturation constant for phosphorus and blue-green algae;
K_{nG} is the half-saturation constant for nitrogen and green algae;
K_{nB} is the half-saturation constant for nitrogen and blue-green algae.

In this simplified model, light and temperature variation are assumed to be negligible, although Powers and Canale (1975) considered them to have important impacts on μ_{mG} and μ_{mB}. The equations describing change in biomass will be based on the Monod-Herbert model (Equation 8.3):

$$\frac{dG}{dt} = \mu_G G - R_G G \tag{8.10}$$

$$\frac{dB}{dt} = \mu_B B - R_B B \tag{8.11}$$

where G and B refer to the biomass concentrations of the green and blue-green algae, and R_G and R_B are the mortality and respiration loss constants for each algal type. Unlike the description of bacterial growth of Section 8.2 above, algal death and respiration will release the nutrients P and N to the lake water. As a result, the available phosphorus concentrations can be found with

$$[P] = [P]_t - a_{pG}G - a_{pB}B \tag{8.12}$$

where $[P]_t$ is concentration of total phosphorus, a_{pG} is the fraction of phosphorus in green algal biomass, and a_{pB} is the fraction of phosphorus in blue-green algal biomass.

Because the blue-green algae can fix molecular nitrogen, $[N]_t$ will not be constant, but will increase as the concentration of blue-green biomass increases. In addition, $[N]$ may be lost from the system by bacterial breakdown of nitrogenous compounds to molecular nitrogen, a process termed denitrification. $[N]_t$ must be adjusted to account for these two processes:

$$\frac{d[N]_t}{dt} = -D[N] + a_{nB}B\mu_{mB}\left(\frac{[N]+[n]}{k_{nB}+[N]+[n]} - \frac{[N]}{k_{nB}+[N]}\right) \tag{8.13}$$

where $[N]_t$ is the total nitrogen concentration, D is the rate constant for denitrification, and the parenthetical expression accounts for the increase of blue-green algal biomass that is attributable to the fixation of molecular nitrogen. Because most lake waters are saturated with molecular nitrogen, $[n]$ may be considered a constant for the lake. After adjusting the total amount of nitrogen $[N]_t$ for changes due to nitrogen fixation and

denitrification, the concentration of available nitrogen can then be found following the form of Equation 8.12:

$$[N] = [N]_t - a_{nG}G - a_{nB}B \tag{8.14}$$

Exercise 8-6: Use the information and equations above to write and implement a computer program to simulate the competition between green and blue-green algae for limiting P and N. Use the following constants:

$K_{pG} = 0.05$ mg liter^{-1} $\quad a_{pG} = 0.01$ mg P (mg biomass)$^{-1}$
$K_{pB} = 0.03$ mg liter^{-1} $\quad a_{pB} = 0.01$ mg P (mg biomass)$^{-1}$
$K_{nG} = 0.30$ mg liter^{-1} $\quad a_{nG} = 0.08$ mg N (mg biomass)$^{-1}$
$K_{nB} = 0.20$ mg liter^{-1} $\quad a_{nB} = 0.08$ mg N (mg biomass)$^{-1}$
$\mu_{mG} = 2.0$ day^{-1} $\quad R_G = 0.06$ day^{-1}
$\mu_{mB} = 1.0$ day^{-1} $\quad R_B = 0.04$ day^{-1}
$D = 0.05$ day^{-1}

Set the constant concentrations as follows:

$$[n] = 0.02 \text{ mg liter}^{-1} \qquad [P]_t = 0.05 \text{ mg liter}^{-1}$$

Set the variable concentrations with these initial values:

$$G = 0.01 \text{ mg liter}^{-1}$$
$$B = 0.01 \text{ mg liter}^{-1} \qquad [N]_t = 0.1 \text{ mg liter}^{-1}$$

Use the two-stage simple Euler integration for this simulation, with $\Delta t = 1.0$. The output for this simulation could take many different forms. As a minimum, show $[N]_t$ and the concentrations of B, G and available N over a simulated 240 days.

8.6 Toxic Inhibition of Microbial Growth

As concern about the occurrence of toxic materials in the environment has risen in recent years, so has the number of attempts to model the effect of toxic materials on microbial populations (e.g. Bates et al. 1982, Rai et al. 1981, Vaccaro et al. 1977). Modifications of the elementary Monod model for microbial growth can approximate the effect of toxic materials in some circumstances.

Most biochemistry textbooks describe ways of modifying the basic Michaelis-Menten enzyme model (Equation 8.2) to show different types of inhibition or interference with enzyme activity. The Monod model for microbial growth may be modified similarly. For example, the following equation modifies the growth rate constant for the Monod model (Equation 8.1) to describe a reaction to toxicants similar to non-competitive enzyme inhibition:

$$\mu = \left(\frac{1}{1 + [T]/K_T}\right) \mu_m \left(\frac{[S]}{K_s + [S]}\right) \tag{8.15}$$

K_s, $[S]$, μ_m and μ are defined as in the Monod model (Equation 8.1), and $[T]$ is the concentration of toxicant. K_T is a toxicity constant and is equal to the concentration of toxicant that causes a halving of the value of μ_m. The action of the toxicant is to reduce the value of μ_m so that regardless of the concentration of nutrient $[S]$, the population cannot grow as rapidly with the toxicant present as it can without the toxicant.

The Monod growth constant may be modified also to show another possible toxic effect, this one resembling the activity of competitive enzyme inhibition:

$$\mu = \mu_m \left(\frac{[S]}{[S] + K_s\,(1 + [T]/K_T)}\right) \tag{8.16}$$

Here the toxicant increases the concentration of limiting nutrient required to achieve a particular level of growth. In effect, K_T is equivalent to the concentration of the toxicant that will produce a doubling of the value of K_s.

In actual practice it is difficult to discriminate between these two modes of toxic effect. In most toxicity experiments, different levels of toxicant are added to replicate cultures of the microorganism, and observations are made of the decline in growth rate that results (e.g., Gillespie and Vaccaro 1978). If you wanted to decide experimentally which of the two modes of toxic activity a particular toxicant follows, you would add a range of toxicant concentrations across a range of substrate concentrations. This can be tricky because of the possibility of interactions between a toxicant and increased levels of nutrients. Molecules of toxic materials often become attached to organic molecules, which may serve to increase or decrease their toxicity in unexpected ways.

Exercise 8-7: Select either Equation 8.15 or 8.16 as the basis of a simulation of the effect of adding a toxicant to a batch culture (Exercise 8-1). Use the following constants:

$$\mu_m = 1 \quad K_s = 25 \quad R = 0.03 \quad a = 0.03 \quad K_T = 0.01$$

Initiate your batch cultures with biomass concentrations of 1 mg liter^{-1}. Make your simulation of two parts. First plot the rate of change of biomass, dB/dt, against toxicant concentration from 0 to 0.04 mg l^{-1}, in increments of 0.001 mg l^{-1}. Do this for at least 4 different values of $[S]$. These values should cover a fairly wide range, including much less than K_s, about equal to K_s, greater than K_s, and very much greater than K_s to simulate saturation. Secondly, plot the growth of the culture through time with at least six different concentrations of toxicant: 0, 0.001, 0.01, 0.1, 1, and 10. This log series of toxicant levels will approximate the first-trial procedure of an experimental determination of the reaction to various toxicant levels.

Conclusion

The Monod model provides an alternative to the logistic for describing how homogeneous populations grow in limited environments. Like the logistic, it is based on simple assumptions which are infrequently met even in carefully controlled experiments. A fair amount of printer's ink has been spilled describing the failures of the Monod model. For example, the concentrations of nutrients are known to differ among cells of different ages; some nutrients will affect growth of biomass and others affect rates of cell division; and, the "luxury consumption" of nutrients like phosphorus is not considered.

Like the Verhulst-Pearl logistic, the Monod model is used not because it is a "good" or a "bad" model, but because it is simple. In the present case, it serves as a tractable model that provides the basic starting point for models of microbial growth.

CHAPTER 9

POPULATION MODELS BASED ON AGE-SPECIFIC EVENTS

In the previous two chapters we studied homogeneous populations, with all members of populations assumed to be identical. We essentially ignored birth and death processes, lumping them together as "growth rate". However, age makes a difference in the performance of complex organisms, and this must be considered if we wish to make realistic models of their populations. Ability to reproduce depends on age, with some members of a population more likely to reproduce than others. Death rates change with age of organisms, and age is important in changing the impact of disease, parasitism, predation, etc. on an individual. Age-class models that consider these differences are the subject of this chapter.

9.1 Age-Specific Survival and Reproduction

Members of populations of most organisms do not all die at the same age. (The life insurance industry is based on this observation.) If enough data about age of death can be collected for a population, an overall pattern can be seen for age at death, also called age-specific mortality or survivorship. Three common patterns are diagrammed in Figure 9.1 (Pearl and Miner 1935, Deevey 1947, Slobodkin 1980). Type A is characteristic of species with relatively high death rates for very young individuals, low and constant mortality rates for intermediate ages, and higher mortality rates again for older individuals. This type of curve is found for most human populations and for many mammals. Type B is produced by a constant mortality rate, with a constant percentage of individuals dying for each unit of time. (This is identical with the exponential die-off simulation of Section 1.2.) Adults of some species of birds and bats may follow this curve (Deevey 1947, Keen and Hitchcock 1980). Type C is characteristic of most organisms, with a high rate of mortality early in life, and a relatively low rate for the later periods. This curve is typical of many fish