Equations 16.13b and 16.14 determine whether eqs. 16.6 to 16.9 allow the potential existence of a purely mutualistic steady state.

The stability of such a coexistent state has been examined, where μ_A and μ_B were represented by various growth functions. Using a linear stability analysis, it can be shown that this pure mutualistic state results in a saddle point, and the system is unstable for all physically accessible values of *D*. If, however, the growth-rate-limiting substrate for either *A* or *B* is *S,* then a stable coexistent state can be found.

Example 16.3.

Consider the growth of a protozoa (predator) on bacteria (prey) in a chemostat. Write appropriate equations for this system.

Solution Here bacteria constitute a substrate for protozoa. In a chemostat culture, the following balances can be written for substrate, prey, and predator.

$$\text{Substrate:} \qquad \frac{dS}{dt} = D(S_0 - S) - \frac{1}{Y_{X_b/S}} \frac{\mu_{mb} S}{K_b + S} X_b \tag{16.15}$$

$$\text{Prey:} \qquad \frac{dX_b}{dt} = -DX_b + \frac{\mu_{mb} S}{K_b + S} X_b - \frac{1}{Y_{X_p/b}} \frac{\mu_{mp} X_b X_p}{K_p + X_b} \tag{16.16}$$

$$\text{Predator:} \qquad \frac{dX_p}{dt} = -DX_p + \frac{\mu_{mp} X_b X_p}{K_p + X_b} \tag{16.17}$$

where $Y_{X_b/S}$ and $Y_{X_p/b}$ are the yield coefficients for the growth of prey on substrate and the growth of predator on prey, respectively.

This model was used to describe the behavior of *Dictyostelium discoideum* and *E. coli* in a chemostat culture and was found to predict experimental results quite well. A variety of types of coexistence behavior have been revealed by stability analysis. These include no oscillations, damped oscillations, and sustained oscillations (see Fig. 16.2).

A classical model that describes oscillations in a prey–predator system is the Lotka–Volterra model, in which growth rates are expressed by the following equations:

$$\text{Prey:} \qquad \frac{dX_b}{dt} = \mu'_b X_b - \frac{\mu'_p X_b X_p}{Y_{p/b}} \tag{16.18}$$

$$\text{Predator:} \qquad \frac{dX_p}{dt} = -k'_d X_p + \mu'_p X_b X_p \tag{16.19}$$

The first term in eq. 16.18 describes the growth of prey on substrate and the second the consumption of prey by predators. The first and second terms in eq. 16.19 describe the death of predator in the absence of prey and the growth of predator on prey, respectively. $Y_{p/b}$ is the yield of predators on prey (g/g), μ'_b is the specific growth rate of prey on a soluble substrate (h^{-1}), μ'_p is the growth rate of predator on prey (l/g-h), and k'_d is the specific death rate of the predator (h^{-1}).

Equations 16.18 and 16.19 allow a steady-state solution for batch growth, where dX_b/dt and $dX_p/dt = 0$. Under these conditions $X_{bF} = k'_d/\mu'_p$ and $X_{pF} = \mu'_b Y_{p/b}/\mu'_p$.