the determination of the presence or absence of limit cycles. It is often easier to test a steady state for its local stability (linearized stability analysis) than for its global stability.

With this background, we will consider some representative examples.

Example 16.1.

Competition of two species for the same growth-rate-limiting substrate is common. Determine when the two organisms may stably coexist if both *A* and *B* follow Monod kinetics.

Solution For this situation, the following equations describe the dynamic situation:

$$\frac{dX_A}{dt} = -DX_A + \frac{\mu_{mA} S}{K_{SA} + S} X_A \tag{16.1}$$

$$\frac{dX_B}{dt} = -DX_B + \frac{\mu_{mB} S}{K_{SB} + S} X_B \tag{16.2}$$

$$\frac{dS}{dt} = D(S_0 - S) - \frac{1}{Y_{X_{A/S}}} \frac{\mu_{mA} S X_A}{K_{SA} + S} - \frac{1}{Y_{X_{B/S}}} \frac{\mu_{mB} S}{K_{SB} + S} X_B \tag{16.3}$$

If both *A* and *B* coexist, we would require from eqs. 16.1 and 16.2 that

$$D = \frac{\mu_{mA} S}{K_{SA} + S} = \frac{\mu_{mB} S}{K_{SB} + S} \tag{16.4}$$

Equation 16.4 can be solved to yield

$$S = \frac{\mu_{mB} K_{SA} - \mu_{mA} K_{SB}}{\mu_{mA} - \mu_{mB}} \tag{16.5}$$

Equation 16.5 is meaningful only if $S \geq 0$. Consider the two cases in Fig. 16.1. In case (a), $\mu_{mA} K_{SB} > \mu_{mB} K_{SA}$ and $\mu_{mA} > \mu_{mB}$; consequently, S is always less than zero, and coexistence is impossible. In case (b), however, a value of S can be found from eq. 16.5 that will allow the populations to coexist. The corresponding D for the crossover point is D_c.

Although this coexistence is mathematically obtainable, it is not physically attainable in real systems. In real systems, the dilution rate will vary slightly with time, and, in fact, the variation will show a bias. Using an analysis more sophisticated than appropriate for this text, it can be demonstrated that one competitor will be excluded from the chemostat if the intensity of the "noise" (random fluctuations) in D and the bias of the mean of D away from D_c are not both zero. Also, it is possible for either competitor to be excluded, depending on how D varies.[†]

Two competitors can coexist if we modify the conditions of the experiments. Examples of such modifications include allowing spatial heterogeneity (the system is no longer well mixed or wall growth is present) or another level of interaction is added (e.g., adding a predator or interchange of metabolites). Also, operation of the chemostat in a dynamic mode (D is a function of time) can sometimes lead to coexistence. It is also interesting to note that the use of other rate expressions (e.g., substrate inhibition) can lead to multiple crossover points and potentially multiple steady states.

[†]G. N. Stephanopoulos, R. Aris, and A. G. Fredrickson, *Math Biosci. 45:*99 (1979).