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THE SIMPLE CHEMOSTAT WITH WALL GROWTH*

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Abstract. A model of the simple chemostat which allows for growth on the wall (or other marked surface) is presented as three nonlinear ordinary differential equations. The organisms which are attached to the wall do not wash out of the chemostat. This destroys the basic reduction of the chemostat equations to a monotone system, a technique which has been useful in the analysis of many chemostat-like equations. The adherence to and shearing from the wall eliminates the boundary equilibria. For a reasonably general model, the basic properties of invariance, dissipation, and uniform persistence are established. For two important special cases, global asymptotic results are obtained. Finally, a perturbation technique allows the special results to be extended to provide the rest point as a global attractor for nearby growth functions.

Key words. chemostat, wall growth, global stability

AMS subject classifications. 34A34, 34D20, 92D25

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1. Introduction.

The chemostat plays an important role as a model in mathematical biology. In its simplest form it is a model of a simple lake where the populations compete for the available nutrient in a purely exploitative manner. It is also a laboratory model of the bioreactor, used to manufacture products by microorganisms. With some modifications it is used as the starting point for models of a waste-water treatment process. Finally, a strong case has been made, Freter [5], [6], that it is an appropriate starting point for the model of the mammalian large intestine. The derivation and analysis of a large number of chemostat-like models can be found in the monograph of Smith and Waltman [13] or the survey of Fredrickson and Stephanopoulos [7].

In the simple chemostat, one of the basic assumptions is that the flow rate is fast enough that wall growth is not a factor. Yet, it does occur and is a problem in bioreactors. Freter [5], [6] also makes the case that it is the ability to adhere to the wall of the large intestine that accounts for the diversity of the microflora there. The earliest model of wall growth seems to be that of Baltzis and Fredrickson [1].

In this work, we take the simplest chemostat model and modify it to account for wall growth. There are essentially three major modifications. A term is added to account for the adherence of the organism to the wall and a term for shearing from the wall. Finally, since the population on the wall does not wash out of the system, the corresponding term is removed from the equations. Although these may seem to be minor modifications, their effect is large. First of all the basic conservation principle of the chemostat is lost. This in turn does not allow the system to be reduced to one which exhibits monotone dynamics. The use of monotone dynamics has been one of the key ingredients in the analysis of many chemostat-like models [13]. A complete description of monotone dynamical systems can be found in the monograph of Smith [11].

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In section 2, the model is presented and basic properties are discussed. Section 3 presents a local analysis of the system where rest points are found and their stability determined. A persistence result is established in section 4. Sections 5 and 6 contain the global analysis of two important special cases. Section 7 presents a perturbation argument. A discussion section completes the paper.

2. The model. The simple chemostat consists of three vessels: the feed bottle, the culture vessel or reactor, and the overflow vessel. Medium, containing all of the nutrients needed for growth of the microorganism in surplus except one, is pumped at a constant rate into the culture vessel. The culture vessel is charged with one or more populations of microorganisms. The contents of the culture vessel—medium, organisms, and any products—are pumped into the overflow vessel at a constant rate, keeping the volume of the reactor constant. The organisms compete for the nutrient in a purely exploitative manner. The vessel is well mixed and all other parameters (temperature, pH, etc.) are strictly controlled. It is usually assumed that the flow rate is sufficient to preclude wall growth or the accumulation of metabolic products. Let $S(t)$ denote the concentration of the nutrient in the vessel and $x_i(t)$, $i = 1, 2$, denote the concentrations of the competitors. Let $S^{(0)}$ denote the concentration of the input nutrient and let D denote the dilution rate (flow rate/volume). If growth is assumed to be proportional to consumption, then the basic equations take the form

$$S' = (S^{(0)} - S)D - \frac{x_1}{\gamma_1} f_1(S) - \frac{x_2}{\gamma_2} f_2(S),$$

$$x_1' = x_1(f_1(S) - D),$$

$$x_2' = x_2(f_2(S) - D).$$

The parameters γ_i, $i = 1, 2$ are yield constants. Since the organism is the same in our model, one anticipates that the yield constants are equal, so we take $\gamma_1 = \gamma_2 = 1$.

Let $x_1(t)$ and $x_2(t)$ be the concentrations of microorganisms at a time t in the flow media and on the wall (or marked surface), respectively. We modify the above equations to account for the adhesion to and shearing from the wall by introducing parameters r_1 and r_2 for the rates. In addition, x_2 does not wash out of the chemostat. The equations of interest then are

$$S' = (S^{(0)} - S)D - f_1(S)x_1 - f_2(S)x_2,$$

$$x_1' = f_1(S)x_1 - Dx_1 - r_1x_1 + r_2x_2,$$

$$x_2' = f_2(S)x_2 + r_1x_1 - r_2x_2.$$

The usual scaling is to measure concentrations in units of $S^{(0)}$ and time in units of $1/D$. This yields the new system where the new $f_i(S)$ replaces $\frac{1}{D} f_i(S^{(0)}S)$, and the new r_i is r_i/D:

$$S' = 1 - S - f_1(S)x_1 - f_2(S)x_2,$$

$$x_1' = f_1(S)x_1 - x_1 - r_1x_1 + r_2x_2, \tag{2.1}$$

$$x_2' = f_2(S)x_2 + r_1x_1 - r_2x_2.$$

Most of the conclusions, particularly local theorems, hold for very general uptake functions. We require that $f_i(S)$, $i = 1, 2$, be the following:

(i) C^1-smooth with $f_i(0) = 0$;

(ii) a strictly monotone function of S;

(iii) bounded (i.e., $\lim_{S\to\infty} f_i(S) < \infty$),

for sections 2–4, although not all are required for all parts. Below we shall show that S eventually lies in a bounded interval, and thus we will have a uniform Lipschitz condition for $f_i(S)$ for large t. Global asymptotic results obtained in Theorems 5.1 and 6.1 hold for the system (2.1) with these general uptake functions f_i, although for the cases with n competing species we will have to restrict these functions to somewhat smaller class as will be indicated below.

Since the variables are concentrations, only nonnegative initial conditions are meaningful, and we are interested in the asymptotic behavior of solutions that remain nonnegative in forward time. Naturally, since the right-hand side of the system (2.1) is at least C^1-smooth in x_1, x_2, S, local existence and uniqueness follow immediately.

LEMMA 2.1. *The positive octant* $\Omega = \{(S, x_1, x_2) \in \mathbb{R}^3 | S > 0, x_1 > 0, x_2 > 0\}$ *is positively invariant for the system* (2.1).

Proof. On the part of $\partial\Omega$ where $S = 0$ the vector field is directed strictly inside Ω since $S' \equiv 1 > 0$. Moreover, whenever $x_i = 0$ with $x_j > 0$, $i \neq j$, then $x_i' = r_jx_j > 0$, and so the vector field points inside Ω along the whole boundary of Ω without the line $l = \{x_1 = x_2 = 0,\ S > 0\}$. The line l itself is invariant under the system (2.1); thus it consists of full trajectories. ∎

LEMMA 2.2. *All nonnegative solutions of* (2.1) *are uniformly bounded in forward time, and thus exist for all positive times. Moreover, the system* (2.1) *in* $\overline{\Omega}$ *is dissipative.*

Proof. Since x_i, $S > 0$ in Ω, any solution $u(t) = (S(t), x_1(t), x_2(t))$ of (2.1) satisfies the differential inequality $S' \leq 1 - S$. Thus, for every solution u in Ω

$$\limsup_{t\to\infty} S(t) \leq \limsup_{t\to\infty} (1 + (S(0) - 1)e^{-t}) = 1$$

because Ω is positively invariant with respect to (2.1).

Given a solution in Ω, we define

$$\alpha(t) = \frac{x_1(t)}{x_1(t) + x_2(t)}.$$

According to its definition, $0 < \alpha(t) < 1$ holds along any solution in Ω, and α satisfies the following differential equation:

$$\alpha' = \alpha(1 - \alpha)\Big(f_1(S(t)) - 1 - f_2(S(t))\Big) + r_2(1 - \alpha) - r_1\alpha. \tag{2.2}$$

Since both functions $f_1(S)$ and $f_2(S)$ are uniformly bounded on $S \in [0, +\infty)$, that is, $0 \leq f_i(S) \leq m_i$ for $i = 1, 2$, and $S \in [0, +\infty)$, the following inequalities must hold:

$$\frac{d\alpha}{dt} \leq \alpha(1 - \alpha)M + r_2(1 - \alpha) - r_1\alpha,$$

$$\frac{d\alpha}{dt} \geq -\alpha(1 - \alpha)M + r_2(1 - \alpha) - r_1\alpha,$$

where the constant M is chosen so that $M \geq m_1 + m_2 + 1 > 0$. Let $F^+(\alpha) = \alpha(1-\alpha)M + r_2(1-\alpha) - r_1\alpha$; then $F^+(1) = -r_1 < 0$. Similarly, if $F^-(\alpha) = -\alpha(1-\alpha)M + r_2(1-\alpha) - r_1\alpha$, then $F^-(0) = r_2 > 0$. Consequently, there exist $0 < \eta, \delta < 1$, such that $\alpha' \geq \delta > 0$, whenever $0 \leq \alpha \leq \eta$, and $\alpha' \leq -\delta < 0$, whenever $1 - \eta \leq \alpha \leq 1$. In particular, for any solution there exists a $T > 0$, such that for $t \geq T$: $\eta \leq \alpha(t) \leq 1-\eta$. Consequently, for any solution $u(t)$ of (2.1) in Ω,

$$\eta \leq \liminf_{t\to\infty} \alpha(t) \leq \limsup_{t\to\infty} \alpha(t) \leq 1 - \eta. \tag{2.3}$$

It is clear that η can be chosen independently of the particular solution. Although the time T may vary from one solution u to another, the given η-bounds are uniform in Ω.

Let $z = x_1 + x_2 + S$. We add the three equations in (2.1) to show that for $t \geq T$,

$$z' = 1 - x_1 - S \leq 1 - \eta(x_1 + x_2) - \eta S = 1 - \eta z,$$

so $\limsup_{t\to\infty} z(t) = \limsup_{t\to\infty}(x_1 + x_2 + S) \leq \frac{1}{\eta}$.

Since all three components of a solution are nonnegative in Ω, we conclude that any positive solution is bounded, exists for all forward times, and enters the bounded set $\Lambda = \{x_1, x_2, S \geq 0\ ,\ x_1 + x_2 + S \leq \frac{1}{\eta}\}$. In other words, the system (2.1) is dissipative in $\overline{\Omega}$. □

Remark 2.1. We can reverse the previous inequality with $t \geq T$,

$$z' = 1 - x_1 - S \geq 1 - x_1 - x_2 - S = 1 - z,$$

so that

$$\liminf_{t\to\infty} z(t) = \liminf_{t\to\infty}(S(t) + x_1(t) + x_2(t)) \geq 1.$$

In particular, for any $\delta > 0$, and for any solution $u(t) = (S(t), x_1(t), x_2(t))$ there exists a $T_1 > 0$, such that for $t \geq T_1$:

$$z(t) = S(t) + x_1(t) + x_2(t) \geq 1 - \delta.$$

Remark 2.2. The upper bound in the definition of Λ can be estimated (crudely) to be less than $\frac{(1+m_1+m_2+r_1+r_2)}{r_2}$.

3. Equilibria and their stability. In this section we investigate the existence and stability of equilibria for (2.1). We use the terms stability and asymptotic stability in the sense of Liapunov. However, to emphasize stability determined by the linearization around a hyperbolic rest point, we say that the rest point is *hyperbolically stable* if it is hyperbolic and if the real parts of the eigenvalues of the linearization have negative real parts. A rest point is *hyperbolically unstable* if it is hyperbolic and if the linearization has at least one eigenvalue with positive real part.

An equilibrium point must satisfy the following equations:

$$\begin{aligned} 0 &= 1 - S - f_1(S)x_1 - f_2(S)x_2, \\ 0 &= f_1(S)x_1 - x_1 - r_1x_1 + r_2x_2, \\ 0 &= f_2(S)x_2 + r_1x_1 - r_2x_2. \end{aligned} \tag{3.1}$$

The system (3.1) always has a trivial solution $E_0 = (0, 0, 1)$ which belongs to the boundary, $\partial\Omega$, of Ω. The stability of E_0 is determined by the eigenvalues of the matrix

$$J(E_0) = \begin{pmatrix} -1 & -f_1(1) & -f_2(1) \\ 0 & f_1(1) - 1 - r_1 & r_2 \\ 0 & r_1 & f_2(1) - r_2 \end{pmatrix}.$$

Lemma 3.1. *E_0 is hyperbolically stable if*

$$f_1(1) - 1 - r_1 < 0,\ f_2(1) - r_2 < 0,\ (f_1(1) - 1 - r_1)(f_2(1) - r_2) > r_1 r_2.$$

If at least one of these inequalities is reversed and strict, E_0 is hyperbolically unstable. If E_0 is hyperbolically stable, then $f_1(1) < 1$.

Proof. Clearly, one eigenvalue, λ_3, of $J(E_0)$ is -1. The remaining two are the eigenvalues of a 2×2 submatrix

$$A = \begin{pmatrix} f_1(1) - 1 - r_1 & r_2 \\ r_1 & f_2(1) - r_2 \end{pmatrix}.$$

The eigenvalues λ_1 and λ_2 satisfy the quadratic equation $\lambda^2 - \mathrm{Tr}(A)\lambda + \mathrm{Det}(A) = 0$. By the Routh–Hurwitz criterion, both λ_1 and λ_2 have negative real parts if and only if $\mathrm{Tr}(A) < 0$ and $\mathrm{Det}(A) > 0$. Now, if $f_1(1)-1-r_1$ and $f_2(1)-r_2$ have different signs, then $\mathrm{Det}(A) = (f_1(1)-1-r_1)(f_2(1)-r_2)-r_1r_2 < 0$, and E_0 is hyperbolically unstable. If, both $f_1(1)-1-r_1$ and $f_2(1)-r_2$ are positive, $\mathrm{Tr}(A) = (f_1(1)-1-r_1)+(f_2(1)-r_2) > 0$, and E_0 is hyperbolically unstable. So, E_0 is hyperbolically stable if $f_1(1)-1-r_1 < 0$, $f_2(1) - r_2 < 0$, and $(f_1(1) - 1 - r_1)(f_2(1) - r_2) > r_1r_2$ and hyperbolically unstable if one of the reversed inequalities is strict.

The last statement is proved by contradiction. Suppose $f_1(1) \geq 1$ and E_0 is hyperbolically stable. By what has been shown above, neither $f_1(1) - 1 - r_1$ nor $f_2(1) - r_2$ can be zero; they cannot have opposite signs since then the third inequality in the lemma could be reversed. If $f_1(1) - 1 - r_1 < 0$, and $f_2(1) - r_2 < 0$, then

$$0 \leq (f_1(1) - 1 - r_1)(f_2(1) - r_2) - r_1r_2$$

$$= (f_1(1) - 1 - r_1)f_2(1) - r_2(f_1(1) - 1) \leq (f_1(1) - 1 - r_1)f_2(1) < 0.$$

Thus, if E_0 is hyperbolically stable, then $f_1(1) < 1$. □

The stability of E_0 is related to the existence of a second equilibrium $E_1 = (S^*, x_1^*, x_2^*)$ in the interior of Ω with all components positive.

Lemma 3.2. *The following statements are equivalent:*

a. *one of the reversed inequalities in Lemma* 3.1 *is strict (E_0 is hyperbolically unstable);*

b. *there exists a unique equilibrium $E_1 = (S^*, x_1^*, x_2^*)$ in the interior of* Ω.

Proof. To find the criterion for existence of an interior equilibrium of (2.1) we seek to solve the algebraic system (3.1) and add the three equations in (3.1) to show that $0 = 1 - S - x_1$ must be satisfied. Since only nonnegative solutions are relevant, x_1 is restricted to the interval $[0, 1]$. From the first equation in (3.1), we obtain

$$x_1 - x_1 f_1(S) = x_2 f_2(S),$$

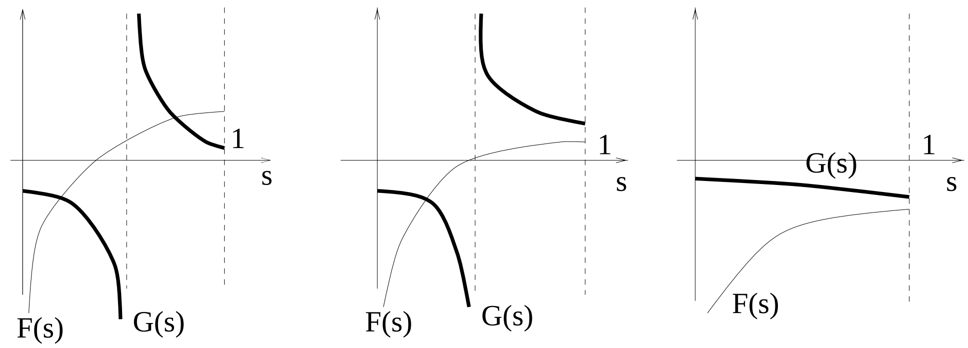

FIG. 3.1. *Possible intersections of F(S) and G(S).*

or

$$x_2 = x_1 \frac{1 - f_1(S)}{f_2(S)}$$

which, when substituted into the second equation, yields

$$x_1 \Big((f_2(S) - r_2) \frac{1 - f_1(S)}{f_2(S)} + r_1 \Big) = 0.$$

After cancelling x_1, which yields E_0 as a solution, and dividing by $1 - f_1(S)$ we obtain the equation

$$\frac{(f_2(S) - r_2)}{f_2(S)} = \frac{r_1}{f_1(S) - 1}.$$

Since $f_2(S) = 0$ is equivalent to $S = 0$, it does not solve the system. We can divide by $f_1(S) - 1$ because $f_1(S) - 1 = 0$ forces $x_2 = 0$ which, in turn, implies that $S = 1$.

Let $F(S) = \frac{(f_2(S) - r_2)}{f_2(S)}$, and $G(S) = \frac{r_1}{f_1(S) - 1}$ for $0 < S \leq 1$. $F(S)$ is a monotone increasing function of S that has $\lim_{S \to 0^+} F(S) = -\infty$. $G(S)$ is a monotone decreasing function of S with $G(0) = -r_1$. An interior equilibrium exists if and only if the graphs of F and G intersect at some point S^*, $0 < S^* < 1$. Note that it is necessary that $f_2(S^*) < r_2$, or $F(S^*) \leq 0$, since, otherwise, x_2 will be negative.

When $0 < S^* < 1$ is found, we set $x_1^* = 1 - S^* > 0$ and $x_2^* = \frac{r_1 x_1^*}{r_2 - f_2(S^*)} > 0$, and so $E_1 = (x_1^*, x_2^*, S^*)$ has positive components.

We observe that whenever $f_1(1) \geq 1$, $G(S)$ has a vertical asymptote at $S = f_1^{-1}(1) < 1$ where it tends to minus infinity. This and the continuity of both F and G provide for the needed point of intersection S^*. Moreover, the graphs of F and G intersect at most once in the region where $F(S) < 0$ which implies uniqueness of the positive equilibrium; see Figure 3.1.

Now, if E_0 is hyperbolically stable, then necessarily $f_1(1) - 1 < 0$ and $f_2(1) - r_2 < 0$ $(F(1) < 0)$, and $(f_1(1) - 1 - r_1)(f_2(1) - r_2) > r_1 r_2$. Since $f_1(1) - 1 < 0$, the last condition is equivalent to

$$G(1) - F(1) = \frac{r_1}{f_1(1) - 1} - 1 + \frac{r_2}{f_2(1)} = \frac{f_2(1)[f_1(1) - 1 - r_1] - r_2[f_1(1) - 1]}{(1 - f_1(1)) f_2(1)} > 0,$$

so the graphs of F and G do not intersect before $S = 1$, and E_1 does not exist. Conversely, if E_1 does not exist, then necessarily $F(1) < G(1) < 0$ and $f_1(1) < 1$. Thus, $f_1(1) - 1 - r_1 < 0$, $f_2(1) - r_2 < 0$ and $(f_1(1) - 1 - r_1)(f_2(1) - r_2) > r_1 r_2$. □

LEMMA 3.3. *If E_1 exists it is locally hyperbolically stable.*

Proof. The local stability of $E_1 = (S^*, x_1^*, x_2^*)$ is determined by the eigenvalues of the matrix:

$$J(E_1) = \begin{pmatrix} -1 - x_1^* f_1'(S^*) - x_2^* f_2'(S^*) & -f_1(S^*) & -f_2(S^*) \\ x_1^* f_1'(S^*) & f_1(S^*) - 1 - r_1 & r_2 \\ x_2^* f_2'(S^*) & r_1 & f_2(S^*) - r_2 \end{pmatrix}.$$

The previous lemma guarantees the existence of E_1 when E_0 is hyperbolically unstable. We will show that whenever E_1 exists, it is hyperbolically stable by showing that all eigenvalues of $J(E_1)$ have negative real parts.

We compute the coefficients of the characteristic polynomial P of $J(E_1)$. Let $P(\lambda) = \lambda^3 + a_1\lambda^2 + a_1\lambda + a_3$. Then

$$a_1 = -\mathrm{Tr}(J(E_1)) = \Big(1 + r_1 - f_1(S^*)\Big) + \Big(r_2 - f_2(S^*)\Big) + 1 + x_1^* f_1'(S^*) + x_2^* f_2'(S^*),$$

$$a_3 = -\mathrm{Det}(J(E_1)) = -x_1^* f_1'(S^*)\Big[-r_1 f_2(S^*) - f_1(S^*)(r_2 - f_2(S^*))\Big]$$

$$+x_2^* f_2'(S^*)\Big[(1 + r_1 - f_1(S^*))f_2(S^*) + r_2 f_1(S^*)\Big]$$

$$+\Big(1 + x_1^* f_1'(S^*) + x_2^* f_2'(S^*)\Big)\Big[(1 + r_1 - f_1(S^*))(r_2 - f_2(S^*)) - r_1 r_2\Big],$$

which can be further simplified using the following fact. The third term in the expansion of a_3 is zero because the corresponding minor is zero. This follows from the existence of a nontrivial solution (x_1^*, x_2^*) to the corresponding linear system of the last two equations in (3.1) with $S = S^*$. Thus,

$$a_3 = -\mathrm{Det}(J(E_1)) = -x_1^* f_1'(S^*)\Big[-r_1 f_2(S^*) - f_1(S^*)(r_2 - f_2(S^*))\Big]$$

$$+x_2^* f_2'(S^*)\Big[(1 + r_1 - f_1(S^*))f_2(S^*) + r_2 f_1(S^*)\Big].$$

Now,

$$a_2 = \Big[(1 + r_1 - f_1(S^*))(r_2 - f_2(S^*)) - r_1 r_2\Big]$$

$$+\Big[(r_2 - f_2(S^*))(1 + x_1^* f_1'(S^*) + x_2^* f_2'(S^*)) + x_2^* f_2(S^*) f_2'(S^*)\Big]$$

$$+\Big[(1 + r_1 - f_1(S^*))(1 + x_1^* f_1'(S^*) + x_2^* f_2'(S^*)) + x_1^* f_1(S^*) f_1'(S^*)\Big],$$

where the first term in the square brackets is also zero; therefore,

$$a_2 = \Big[(r_2 - f_2(S^*))(1 + x_1^* f_1'(S^*) + x_2^* f_2'(S^*)) + x_2^* f_2(S^*) f_2'(S^*)\Big]$$

$$+\Big[(1 + r_1 - f_1(S^*))(1 + x_1^* f_1'(S^*) + x_2^* f_2'(S^*)) + x_1^* f_1(S^*) f_1'(S^*)\Big].$$

We use the Routh–Hurwitz criterion for the coefficients of P. In order for all eigenvalues to have negative real parts, the following conditions must be satisfied:

$$a_1 > 0,\ a_3 > 0,\ a_1 a_2 > a_3.$$

Since at E_1 both $(f_1(S^*) - 1 - r_1)$ and $(f_2(S^*) - r_2)$ are negative, a_1 is strictly positive. Similarly, a_3 is positive as a sum of two positive terms. To simplify the notation we drop the asterisks and the arguments in the following computation of $s = a_1 a_2 - a_3$:

$$s = x_1 f_1' \Big[-r_1 f_2 + f_1(f_2 - r_2)\Big] - x_2 f_2' \Big[f_2(1 + r_1 - f_1) + f_1 r_2\Big]$$

$$+\Big[(1 + r_1 - f_1) + (f_2 - r_2) + (1 + x_1 f_1' + x_2 f_2')\Big]$$

$$\times\Big[x_1 f_1 f_1' + x_2 f_2 f_2' + (-1 + f_1 - r_1 + f_2 - r_2)(-1 - x_1 f_1' - x_2 f_2')\Big]$$

$$\geq s' = x_1 f_1' \Big[-r_1 f_2 + f_1(f_2 - r_2)\Big] - x_2 f_2' \Big[f_2(1 + r_1 - f_1) + f_1 r_2\Big]$$

$$+\Big[(1 + r_1 - f_1) + (r_2 - f_2) + (1 + x_1 f_1' + x_2 f_2')\Big]$$

$$\times\Big[x_1 f_1 f_1' + x_2 f_2 f_2' + (1 - f_1 + r_1 - f_2 + r_2)\Big],$$

because $1 + x_1 f_1' + x_2 f_2' > 1$. Note that the first two terms in square brackets are negative while the third term (the product) is positive. Before going further, we collect several important observations. First, at E_1 it is necessary that $f_1 < 1$, and second, $(f_1 - 1 - r_1)(f_2 - r_2) - r_1 r_2 = 0$ implies that $-f_2 r_1 = r_2(f_1 - 1) - f_2(f_1 - 1) = (r_2 - f_2)(f_1 - 1)$. Also, $1 + r_1 - f_1 > 0$ and $r_2 - f_2 > 0$. Finally, $f_i, f_i' > 0$ for $i = 1, 2$. It follows that

$$s' = x_1 f_1' \Big[-r_1 f_2 + f_1(f_2 - r_2) + (1 + r_1 - f_1) + (r_2 - f_2)$$

$$+ f_1(1 - f_1 + r_1) + f_1(r_2 - f_2) + f_1\Big]$$

$$+ x_2 f_2' \Big[-f_2(1 + r_1 - f_1) - f_1 r_2 + (1 + r_1 - f_1) + (r_2 - f_2)$$

$$+ f_2(1 - f_1 + r_1) + f_2(r_2 - f_2) + f_2\Big]$$

$$+\Big(1 + r_1 - f_1 + r_2 - f_2\Big)^2 + 2\Big(x_1 f_1' + x_2 f_2'\Big)\Big(x_1 f_1 f_1' + x_2 f_2 f_2'\Big).$$

We eliminate nonnegative terms $(1+r_1-f_1+r_2-f_2)^2$ and $2(x_1f_1'+x_2f_2')(x_1f_1f_1'+x_2f_2f_2')$ and arrive at the following inequality:

$$s' \geq x_1f_1'\Big[-r_1f_2 + f_1(f_2-r_2) + (1+r_1-f_1) + (r_2-f_2)$$

$$+f_1(1-f_1+r_1) + f_1(r_2-f_2) + f_1\Big]$$

$$+x_2f_2'\Big[-f_2(1+r_1-f_1) - f_1r_2 + (1+r_1-f_1) + (r_2-f_2)$$

$$+f_2(1-f_1+r_1) + f_2(r_2-f_2) + f_2\Big]$$

$$= x_1f_1'\Big[-r_1f_2 + (1+r_1-f_1) + (r_2-f_2) + f_1(1-f_1+r_1) + f_1\Big]$$

$$+x_2f_2'\Big[-f_1r_2 + (1+r_1-f_1) + (r_2-f_2) + f_2(r_2-f_2) + f_2\Big]$$

$$= x_1f_1'\Big[(r_2-f_2)(f_1-1) + (1+r_1-f_1) + (r_2-f_2) + f_1(1-f_1+r_1) + f_1\Big]$$

$$+x_2f_2'\Big[r_2(1-f_1) + (1+r_1-f_1) + f_2(r_2-f_2)\Big]$$

$$= x_1f_1'\Big[(r_2-f_2)f_1 + (1+r_1-f_1) + f_1(1-f_1+r_1) + f_1\Big]$$

$$+x_2f_2'\Big[r_2(1-f_1) + (1+r_1-f_1) + f_2(r_2-f_2)\Big]$$

$$= x_1f_1'\Big[(1+r_2-f_2)f_1 + (1+f_1)(1-f_1+r_1)\Big]$$

$$+x_2f_2'\Big[r_2(1-f_1) + (1+r_1-f_1) + f_2(r_2-f_2)\Big] > 0.$$

This is a sum of two positive terms, so s' is positive, and thus $s > 0$. By the Routh–Hurwitz criterion all three eigenvalues have negative real parts, and therefore E_1 is hyperbolically stable. ◻

One expects (and we conjecture) that the interior rest point is globally asymptotically stable whenever it exists. This is established below in two biologically important special cases.

4. Uniform persistence. We first remind the reader of the basic definitions. A system of ordinary differential equations for which the closure of the positive octant is positively invariant is called *persistent* if for every solution $x(t)$ with positive coordinates there exists an $\eta > 0$ so that $\liminf_{t\to\infty} x_i(t) \geq \eta$ for every coordinate of the solution $x(t)$. The system is called *uniformly persistent* if $\eta > 0$ can be chosen uniformly for all positive solutions.

The usual route to uniform persistence is to use the theorems which yield the existence of the above lower bound on the components of the flow. However, it is more satisfying to actually exhibit them and this is the route we take. This appears in the literature [2] as *practical persistence*.

THEOREM 4.1. *If either* $f_1(1) - 1 - r_1 > 0$ *or* $f_2(1) - r_2 > 0$ *or* $(f_1(1) - 1 - r_1)(f_2(1) - r_2) < r_1 r_2$, *then the system* (2.1) *is uniformly persistent in* Ω.

THEOREM 4.2. *Under the hypotheses of Theorem* 4.1, *there exists a global attractor for* (2.1) *in* Ω.

Proof of Theorem 4.2. Lemma 2.2 is sufficient for the existence of the global attractor [8, Thm. 3.4.8]. Theorem 4.1 guarantees that the attractor is in the open set Ω. ◻

Proof of Theorem 4.1. $M > 0$ denotes the common upper bound on $\limsup_{t\to\infty} x_i(t)$ for $i = 1, 2$. It follows from Lemma 2.2 that $M < \infty$. Let $L_i > 0$ be a Lipschitz constant for f_i, $i = 1, 2$ and let $L = L_1 + L_2$. (As noted previously, since S is bounded and f_i is continuously differentiable, such constants exist.)

We show first that there exists a uniform lower bound on $\liminf_{t\to\infty} S(t)$. Let $\nu_1 = \frac{1}{2(1+ML)}$. The inequality

$$S' = 1 - S - f_1(S)x_1 - f_2(S)x_2 \geq 1 - S(1 + ML) \geq \frac{1}{2} > 0$$

with $S \leq \nu_1$ implies that $\liminf_{t\to\infty} S(t) \geq \nu_1$ along any solution $u(t)$ of (2.1) in Ω.

In addition, from the proof of Lemma 2.2 we know that for sufficiently large times $\eta \leq \frac{x_1(t)}{x_1(t)+x_2(t)} \leq 1 - \eta$. This is equivalent to

$$\frac{\eta}{1-\eta} \leq \frac{x_1(t)}{x_2(t)} \leq \frac{1-\eta}{\eta};$$

therefore we conclude that either both $\liminf_{t\to\infty} x_i(t) = 0$ for $i = 1, 2$ or both $\liminf_{t\to\infty} x_i(t) \geq \nu_2 > 0$.

Let $A(q)$ be defined as

$$A(q) = \begin{pmatrix} f_1(q) - r_1 - 1 & r_2 \\ r_1 & f_2(q) - r_2 \end{pmatrix}.$$

It follows from Lemma 3.1 that $A(1)$ has a positive eigenvalue. By continuity, there exists $\lambda < 1$, such that for $\lambda \leq q \leq 1$, $A(q)$ still has a positive eigenvalue $\rho > 0$. Let $\mu = \frac{1}{8}(1 - \lambda)$, and $\delta = \mu$. It follows from Remark 2.1 that for $t \geq T$

$$x_1' = \Big(f_1(S(t)) - r_1 - 1\Big)x_1 + r_2 x_2 \geq \Big(f_1(1 - \mu - x_1 - x_2) - r_1 - 1\Big)x_1 + r_2 x_2,$$

$$x_2' = \Big(f_2(S(t)) - r_2\Big)x_2 + r_1 x_1 \geq \Big(f_2(1 - \mu - x_1 - x_2) - r_2\Big)x_2 + r_1 x_1.$$

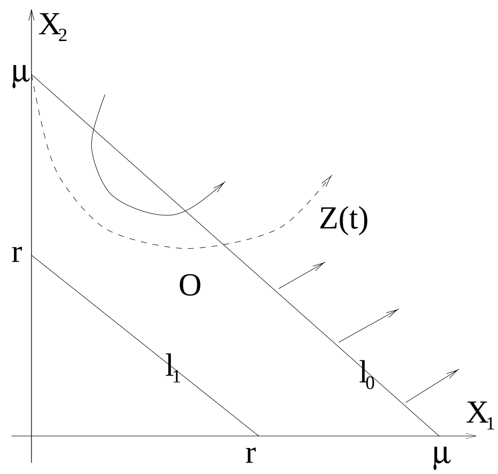

FIG. 4.1. *Behavior of solutions of the system* (4.1).

Consider the region $O = \{x_1 + x_2 \leq \mu, x_i \geq 0\}$, and consider the linear system

$$X' = AX \tag{4.1}$$

with $A = A(1-2\mu)$. The system (4.1) is cooperative because the off-diagonal entries of A are positive. Then [10] A has a positive eigenvalue $\rho > 0$ and the corresponding eigenvector $w = (w_1, w_2)$ with positive coordinates. Thus, the system (4.1) has solutions of the form $V(t) = C\ w\ \exp(\rho t)$ which tend to infinity and therefore leave the region O in finite time. In particular, for any solution $X(t)$ of (4.1) such that $X(0)$ is positive, there exists $C > 0$ such that $X_1(0) \geq Cw_1$ and $X_2(0) \geq Cw_2$. Since (4.1) is monotone, these inequalities hold for all $t \geq 0$.

Consider the segment $l_0 = \{x_1 + x_2 = \mu, x_i \geq 0\}$. If $X_1 + X_2 = \mu$, $\frac{d}{dt}(X_1 + X_2) \geq (f_1(\lambda) - 1)X_1 + f_2(\lambda)X_2$. If $f_1(\lambda) - 1 \geq 0$, then $\frac{d}{dt}(X_1 + X_2) \geq 0$ on l_0, so no solution of (4.1) can enter the region $X_1 + X_2 \leq \mu$. If $f_1(\lambda) - 1 < 0$, then solutions of (4.1) can enter this region only with $X_1 \leq \frac{f_2(\lambda)}{1 - f_1(\lambda)} X_2$. Consider the solution $Z(t)$ with initial condition $(0, \mu)$, and suppose it enters O. At $t = 0$, $Z_1' > 0$, so $Z(t)$ has positive coordinates for $t > 0$; therefore, it must leave the region O in finite time. There exists $t_0 > 0$ such that $Z(t_0) \in l_0$ and $Z(t) \in O$ for $0 \leq t \leq t_0$. In particular, there exists a lower bound $r > 0$ on $Z_1(t) + Z_2(t)$ for $0 \leq t \leq t_0$. The system (4.1) is two-dimensional, so by uniqueness of solutions, any solution X of (4.1) with initial conditions on l_0 either does not enter O, or stays above the curve $Z(t)$, $t \in [0, t_0]$. This and the fact that no solution stays in O imply that $\liminf_{t\to\infty}[X_1(t) + X_2(t)] \geq r$; see Figure 4.1.

Now we return to the behavior of positive solutions of (2.1). Let $t \geq T$; then

$$x_1' \geq \Big(f_1(1 - \mu - x_1 - x_2) - r_1\Big)x_1 + r_2 x_2, \tag{4.2}$$

$$x_2' \geq \Big(f_2(1 - \mu - x_1 - x_2) - r_2\Big)x_2 + r_1 x_1.$$

In the region O, one has further that

$$x_1' \geq \Big(f_1(1 - 2\mu) - r_1 - 1\Big)x_1 + r_2 x_2, \tag{4.3}$$

$$x_2' \geq \Big(f_2(1-2\mu) - r_2\Big)x_2 + r_1 x_1$$

since $S \geq 1-\mu-x_1-x_2 \geq 1-2\mu \geq \lambda$. The comparison of solutions of (4.3) with the corresponding positive solution $X(t)$ of (4.1) yields that r is a lower bound on $x_1(t)+x_2(t)$ for sufficiently large t. Since (4.1) is a linear system with constant coefficients, r may be computed explicitly. Using (2.3) it follows that $\liminf_{t\to\infty} x_1(t) \geq r\eta > 0$ and $\liminf_{t\to\infty} x_2(t) \geq r\eta > 0$. From (2.2) one can obtain a lower estimate on η in terms of system parameters as $\frac{r_2}{1+f_1(1)+f_2(1)+r_1+r_2}$ which gives the "practical" uniform persistence. ∎

5. The case of equal uptake. Usually one thinks of the population in the liquid medium and the population adhering to the wall as the same organism, simply classified by its compartment. For such it is reasonable that the growth functions be the same. In other terms, their fitness is identical. However, since we are assuming that growth is proportional to nutrient uptake, one could question this assumption. Recent results on the structure of microfilm show that the film has many channels [3, 4] for the liquid. Hence it is not unreasonable to assume that the same level of nutrient is available to both populations. Freter [5, 6] makes a case for this assumption in his models of the large intestine. We will weaken this assumption slightly through a perturbation argument in section 7, below, so that the uptake functions need not be identical, but need only to be "close."

The conclusions of Theorem 5.1 are true for any uptake function f satisfying the conditions listed in section 2. The Liapunov function argument used in the proof of Theorem 5.2 requires the restriction that $f_i(S) = \frac{m_i S}{a_i+S}$. An extension based on the results of the work of Wolkowicz and Lu [15] is noted; it requires that f_i in (5.4) belong to a class of functions that includes, for instance, Lotka–Volterra, Monod, and sigmoidal uptake functions.

It is convenient to change variables by letting $z = x_1 + x_2$, and $\alpha = \frac{x_1}{x_1+x_2}$ in Ω. The equations may be rewritten as

$$S' = 1 - S - z(\alpha f_1(S) + (1-\alpha)f_2(S)),$$

$$z' = z(\alpha f_1(S) + (1-\alpha)f_2(S) - \alpha),$$

$$\alpha' = \alpha(1-\alpha)(f_1(S) - f_2(S) - 1) - \alpha(r_1+r_2) + r_2.$$

For $f_1(S) \equiv f_2(S)$, denote the common value by $f(S)$. The equations simplify to

$$S' = 1 - S - zf(S),$$

$$z' = z(f(S) - \alpha), \tag{5.1}$$

$$\alpha' = -\alpha(1-\alpha) - \alpha(r_1+r_2) + r_2.$$

THEOREM 5.1. *If $f(1) > 1$, E_1 is a global attractor of Ω.*

Proof. Note that the third equation for the variable α does not involve the other two variables. Hence one can "solve" for α as a function of time and substitute that function into the remaining two equations resulting in a nonautonomous system of one dimension less. If it should happen that $\alpha(t)$ has a limit as time tends to infinity, then the lower-dimensional system falls under the theory of asymptotically autonomous systems. We first show that this is the case.

By definition $0 < \alpha(t) < 1$, and this is reflected in the equation for α by the fact that $\alpha'(0) > 0$, and $\alpha'(1) < 0$. For our variable then, this is a positively invariant region. Inside this interval there is a unique rest point given by

$$\alpha^* = \frac{r_1 + r_2 + 1 - \sqrt{r_1^2 + 2r_1 + 2r_1 r_2 + (r_2 - 1)^2}}{2}.$$

Since it is a scalar equation, all solutions tend to α^*.

Indeed, since α' is a quadratic function in α with its highest coefficient positive, and since $\alpha'(0) > 0$ and $\alpha'(1) < 0$, the interval $(0, 1)$ contains only the smaller root of $\alpha' = 0$, while the larger root has to be greater than 1. Moreover, $\alpha = \alpha^*$ is a hyperbolically stable equilibrium of the scalar equation.

Eliminating the final equation of the system (5.1) reduces the question to that of the asymptotic stability of the equilibrium $\hat{E}_1$ of the reduced system:

$$S' = 1 - S - zf(S),$$

$$z' = z(f(S) - \alpha^*). \tag{5.2}$$

The system (5.2) has two equilibria, $\hat{E}_0 = (1, 0)$ and $\hat{E}_1 = (S^*, z^*)$ with $S^* = f^{-1}(\alpha^*)$ and $z^* = \frac{1-S^*}{\alpha^*}$. The coordinates of $\hat{E}_0$ and $\hat{E}_1$ coincide with the first two coordinates of corresponding equilibria of the full system (5.1). $\hat{E}_1$ exists because $f(1) > 1$. The matrix $J(\hat{E_0})$ of the system has one negative eigenvalue $\lambda_1 = -1$ and one positive eigenvalue $\lambda_2 = f(1) - \alpha^* \geq f(1) - 1 > 0$, so $\hat{E}_0$ is unstable.

Also, note that the segment $\{z = 0, 0 \leq S \leq 1\}$ is positively invariant with respect to (5.2). If a particular solution starts from $z(0) = 0$, it stays in that segment. We evaluate the matrix $J = \frac{\partial F}{\partial(z,S)}$ at $\hat{E}_1$:

$$J(\hat{E}_1) = \begin{pmatrix} -1 - zf'(S^*) & -f(S^*) \\ zf'(S^*) & 0 \end{pmatrix}.$$

Since Tr $J(\hat{E}_1) < 0$ and Det $J(\hat{E}_1) > 0$, it follows that both eigenvalues of J have strictly negative real parts, so $\hat{E}_1$ is locally hyperbolically stable.

To prove global stability of $\hat{E}_1$ under (5.2), we introduce the following Liapunov function:

$$V(z, S) = \int_{S^*}^{S} \frac{f(\eta) - \alpha^*}{f(\eta)} d\eta + \int_{z^*}^{z} \left(1 - \frac{z^*}{\eta}\right) d\eta. \tag{5.3}$$

The derivative $\frac{dV}{dt}$ with respect to (5.2) is given by

$$\begin{aligned}\frac{dV}{dt} &= \frac{f(S) - \alpha^*}{f(S)}(1 - S - zf(S)) + (z - z^*)(f(S) - \alpha^*) \\ &= \frac{f(S) - \alpha^*}{f(S)}(1 - S) - z^*(f(S) - \alpha^*) \\ &= \frac{f(S) - \alpha^*}{f(S)}(1 - S - z^* f(S)).\end{aligned}$$

Since f is a strictly monotone function of S, it follows that $\frac{dV}{dt} \leq 0$ for $S > 0$ with inequality being strict unless $S = S^*$. Thus V is a Liapunov function for (5.2), and all positive solutions of (5.2) converge to some invariant set with $S = S^*$, that is, to $\hat{E}_1$. In particular, there are no cyclic orbits, and all of the conditions of [14] or [13, Appendix F] are met, so one can conclude that the asymptotic behavior of the system (5.1) is the same as that of the system (5.2). Therefore, all solutions of (5.1) with positive initial conditions tend to E_1. □

This situation can be generalized to the case of n competing populations in the chemostat. Suppose that each population has the same growth rate both in the media and on the wall. In addition, assume that the wall is equally available to all competitors, and the capacity of the wall is unlimited. We denote by x_{i1} and x_{i2} the quantities of bacteria of ith type in the media and on the wall, respectively. In the system that follows, $f_i(S) = \frac{m_i S}{a_i + S}$ denotes the universal growth rate of the ith competitor:

$$S' = 1 - S - \sum_{i=1}^{n}(x_{i1} + x_{i2})f_i(S),$$

$$x'_{i1} = x_{i1}(f_i(S) - 1) - r_{i1}x_{i1} + r_{i2}x_{i2},\ i = 1, \ldots, n, \tag{5.4}$$

$$x'_{i2} = x_{i2}f_i(S) + r_{i1}x_{i1} - r_{i2}x_{i2},\ i = 1, \ldots, n.$$

This system is similar to (5.1); the biologically relevant region where all coordinate functions are nonnegative is positively invariant.

We let α_i^* denote the positive solution of the quadratic

$$0 = -\alpha(1 - \alpha) - \alpha(r_{i1} + r_{i2}) + r_{i2},\ i = 1, \ldots, n,$$

which we have already shown to exist. Now, under additional assumption that $m_i > 1$ for $i = 1, \ldots, n$, the following exclusion result holds.

THEOREM 5.2. *Suppose that* $f_i(S) = \frac{m_i S}{a_i + S}$. *Let* $S_i^* = f_i^{-1}(\alpha_i^*)$ *for* $i = 1, \ldots, n$, *and suppose that*

$$0 < S_1^* < S_2^* \leq S_3^* \leq \cdots \leq S_n^* \tag{5.5}$$

and that $S_1^* < 1$. *Then any positive solution of* (5.4) *reaches an equilibrium*

$$E = (S_1^*, x_{11}^*, x_{12}^*, 0, \ldots, 0)\ ,\ i = 1, \ldots, n,$$

where x_{11}^*, x_{12}^*, *and* S_1^* *are positive.*

Proof. After the change of coordinates $z_i = x_{i1} + x_{i2}$, $\alpha_i = \frac{x_{i1}}{z_i}$, the system may be rewritten in terms of z_i, α_i, and S as

$$S' = 1 - S - \sum_{i=1}^{n} z_i f_i(S),$$

$$z'_i = z_i(f_i(S) - \alpha_i),\ i = 1, \ldots, n,$$

$$\alpha'_i = -\alpha_i(1 - \alpha_i) - \alpha_i(r_{i1} + r_{i2}) + r_{i2},\ i = 1, \ldots, n.$$

All equations for α_i are separated from the system, so they can be solved independently. For any positive solution, its α_i–coordinates reach their steady state level exponentially fast, namely,

$$\lim_{t\to\infty} \alpha_i(t) = \alpha_i^*, \; i = 1, \ldots, n,$$

and the limit is independent of the initial conditions.

The limiting system becomes

$$S' = 1 - S - \sum_{i=1}^{n} z_i f_i(S),$$

$$z_i' = z_i(f_i(S) - \alpha_i^*), \; i = 1, \ldots, n. \tag{5.6}$$

If the uptake functions are of the form $f_i(S) = \frac{m_i S}{a_i + S}$ (Monod model), this system is of the type studied in Hsu [9]. For a system like this, it has been shown that if the break-even concentrations S_i^* satisfy the inequality (5.5), then the corresponding exclusion result holds. Thus, any positive solution reaches an equilibrium $E = (S_1^*, x_{11}^*, x_{12}^*, 0, \ldots, 0)$, $i = 1, \ldots, n$, where x_{11}^*, x_{12}^*, and S_1^* are positive.

We apply the results on asymptotically autonomous systems again to conclude that the asymptotic behavior of the full system (5.4) is the same as the behavior of the reduced $(n+1)$-dimensional system with $\alpha_i = \alpha_i^*$ for $i = 1, \ldots, n$. ◻

Unfortunately, the result is not known to be true for general monotone uptake functions. However, Wolkowicz and Lu [15] have generalized the result of Hsu [9] to a class of nonlinear uptake functions which includes the above Monod model, sigmoidal models, and many other commonly used uptake functions. This class is not easy to describe briefly, so the interested reader is referred to [15, 16] for the details. Theorem 5.2 can be shown to hold for this class.

6. The case of a pure refuge. In this section we consider the situation where the wall serves only as a spatial refuge for the population. Specifically, it is assumed that the populations do not consume nutrient and hence do not proliferate while attached to the wall. This is equivalent to the assumption that $f_2(S) \equiv 0$ in the original system (2.1). The system becomes

$$S' = 1 - S - x_1 f(S),$$

$$x_1' = x_1(f(S) - 1) - r_1 x_1 + r_2 x_2, \tag{6.1}$$

$$x_2' = r_1 x_1 - r_2 x_2,$$

where $f(S)$ is the original $f_1(S)$.

This system always has a trivial equilibrium on the boundary of the positive octant, namely, $E_0 = (1, 0, 0)$. The general results from section 3 still apply here, although in Theorem 6.2 we will require that f_i again belong to a smaller functional class, so that we can apply a Liapunov-type argument to prove global stability in case of n competing species. The condition $f(1) \geq 1$ remains necessary and sufficient for the existence of a nontrivial equilibrium in the interior of the positive octant, that is, $E_1 = (S^*, x_1^*, x_2^*,) = (S^*, 1 - S^*, \frac{r_1}{r_2}(1 - S^*))$ with $S^* = f^{-1}(1)$.

E_0 is unstable since the linearization of the system evaluated at E_0, that is, $J(E_0)$, has a positive eigenvalue $\lambda = f(1) - 1 > 0$. We use a Liapunov function to show global asymptotic stability of E_1 in $\Omega = \{S, x_1, x_2 > 0\}$.

THEOREM 6.1. *E_1 is a global attractor in Ω.*

Proof. Let

$$V(x_1, x_2, S) = \int_{S^*}^{S} \frac{f(z)-1}{f(z)} dz$$

$$+ \int_{x_1{}^*}^{x_1} \left(1 - \frac{x_1{}^*}{z}\right) dz + \int_{x_2{}^*}^{x_2} \left(1 - \frac{x_2{}^*}{z}\right) dz. \tag{6.2}$$

The derivative $\frac{dV}{dt}$ with respect to (6.1) is given by

$$\frac{dV}{dt} = \frac{f(S)-1}{f(S)}(1 - S - x_1 f(S)) + \left(1 - \frac{x_1^*}{x_1}\right)(x_1(f(S)-1) - r_1 x_1 + r_2 x_2)$$

$$+ \left(1 - \frac{x_2^*}{x_2}\right)(r_1 x_1 - r_2 x_2).$$

Thus,

$$\frac{dV}{dt} = \left[\frac{f(z)-1}{f(z)}(1 - S - x_1 f(S)) + \left(1 - \frac{x_1^*}{x_1}\right)(x_1(f(S)-1)\right]$$

$$+ \left[\left(1 - \frac{x_2^*}{x_2}\right)(r_1 x_1 - r_2 x_2) - \left(1 - \frac{x_1^*}{x_1}\right)(r_1 x_1 - r_2 x_2)\right] = A + B.$$

We analyze A and B separately:

$$B = (r_1 x_1 - r_2 x_2)\frac{1}{x_1 x_2}(x_1(x_2 - x_2^*) - x_2(x_1 - x_1^*))$$

$$= (r_1 x_1 - r_2 x_2)\frac{1}{x_1 x_2}(x_2 x_1^* - x_1 x_2^*) = -\frac{x_1^*}{r_2}(r_1 x_1 - r_2 x_2)^2 \frac{1}{x_1 x_2}.$$

It is clear that $B < 0$ in Ω, unless $r_1 x_1 = r_2 x_2$. Now, analysis similar to that in the proof of Theorem 5.1 shows that A is strictly negative unless $S = S^*$. Thus, $\frac{dV}{dt} < 0$, unless $S = S^*$, and $r_1 x_1 = r_2 x_2$.

It follows that V is a Liapunov function for the system (6.1) in Ω, therefore any positive solution has its ω-limit set in the set $\frac{dV}{dt} = 0$, the point E_1. Consequently, E_1 is the global attractor. $\square$

This result generalizes to the case of n competitors. For n competing populations the system takes the form:

$$S' = 1 - S - \sum_{i=1}^{n} x_{i1} f_i(S),$$

$$x_{i1}' = x_{i1}(f_i(S) - 1) - r_{i1} x_{i1} + r_{i2} x_{i2}, \; i = 1, \ldots, n,$$

$$x'_{i2} = r_{i1}x_{i1} - r_{i2}x_{i2},\ i = 1, \dots, n.$$

We first assume that $f_i(S) = \frac{m_i S}{a_i + S}$, $i = 1, \dots, n$. For this system, the following exclusion result holds.

THEOREM 6.2. *Let $S_i^* = f_i^{-1}(1)$ for $i = 1, \dots, n$. Suppose that $m_i > 1$ for $i = 1, \dots, n$ and that*

$$0 < S_1^* < S_2^* \le S_3^* \le \cdots \le S_n^*.$$

Suppose also that $S_1^* < 1$. Then any positive solution tends to the equilibrium

$$E = (S_1^*, x_{11}^*, x_{12}^*, 0, \dots, 0),\ i = 1, \dots, n,$$

where x_{11}^*, x_{12}^*, and S_1^* are positive. In particular, $x_{11}^* = 1 - S_1^*$ and $x_{12}^* = \frac{r_{11}}{r_{12}}(1 - S_1^*)$.

Proof. The region where all coordinates are nonnegative is positively invariant for this system. Clearly, the system has a rest point $E = (S_1^*, 1 - S_1^*, \frac{r_{11}}{r_{12}}(1 - S_1^*), 0, \dots, 0)$. In the region where all coordinates are positive we define the function V:

$$V(x_{i1}, x_{i2}, S) = \int_{S^*}^{S} \left(1 - \frac{S^*}{z}\right) dz + c_1 \int_{x_{11}^*}^{x_{11}} \left(1 - \frac{{x_{11}}^*}{z}\right) dz$$

$$+ c_1 \int_{{x_{12}}^*}^{x_{12}} \left(1 - \frac{{x_{12}}^*}{z}\right) dz + \sum_{i=2}^{n} c_i (x_{i1} + x_{i2}),$$

where $c_i = \frac{m_i}{m_i - 1} > 0$ for $i = 1, \dots, n$.

We differentiate V with respect to the system as follows:

$$\frac{dV}{dt} = \left(1 - \frac{S_1^*}{S}\right)(1 - S - x_{11}f_1(S) - x_{21}f_2(S) - \cdots - x_{n1}f_n(S))$$

$$+ c_1 \left(1 - \frac{x_{11}^*}{x_{11}}\right)(x_{11}(f_1(S) - 1) - r_{11}x_{11} + r_{12}x_{12})$$

$$+ c_1 \left(1 - \frac{x_{12}^*}{x_{12}}\right)(r_{11}x_{11} - r_{12}x_{12}) + \sum_{i=2}^{n} c_i x_{i1}(f_i(S) - 1).$$

This sum is similar to the sum in the proof of Theorem 5.1, but it has several extra terms, that is,

$$\frac{dV}{dt} = \left(1 - \frac{S_1^*}{S}\right)(1 - S - x_{11}f_1(S)) + c_1 \left(1 - \frac{x_{11}^*}{x_{11}}\right) x_{11}(f_1(S) - 1)$$

$$+ c_1 \left(\left(1 - \frac{x_{12}^*}{x_{12}}\right) - \left(1 - \frac{x_{11}^*}{x_{11}}\right)\right)(r_{11}x_{11} - r_{12}x_{12})$$

$$+ \sum_{i=2}^{n} x_{i1}\left(c_i(f_i(S) - 1) - \left(1 - \frac{S_1^*}{S}\right) f_i(S)\right) = A + B + C.$$

The three parts A, B, and C are treated separately. In the proof of Theorem 6.1 it was shown that $A < 0$ for all $S \neq S_1^*$, and that $A = 0$ if and only if $S = S_1^*$. Also, B was shown to be strictly negative, unless $r_{11}x_{11} = r_{12}x_{12}$. Now, since c_i is chosen in such a way that $c_i = \frac{f_i(S)(S-S_i^*)}{S(f_i(S)-1)}$, C can be rewritten as

$$C = \sum_{i=2}^{n} x_{i1} \frac{f_i(S)}{S}(S_1^* - S_i^*) = \sum_{i=2}^{n} x_{i1} \frac{m_i}{a_i + S}(S_1^* - S_i^*) \leq 0,$$

because $S_1^* - S_i^* < 0$ for all $i = 2, \ldots, n$. In fact, $C < 0$ unless $x_{i1} = 0$ for all $i = 2, \ldots, n$. Therefore, we conclude that V is a Liapunov function in the region where all coordinates are positive. So, any positive solution is asymptotic to the set $\frac{dV}{dt} = 0$, namely the point $E = (S_1^*, 1 - S_1^*, \frac{r_{11}}{r_{12}}(1 - S_1^*), 0, \ldots, 0)$. ◻

In the above argument, the assumption that the uptake functions were of Monod type was used only to assure that the specification of c_i yielded a constant. Clearly, the proof would work for any class of functions that allowed the conclusion that $C \leq 0$. Professor G. Wolkowicz has pointed out that if one chose $c_i = 1$ and the first term in (6.2) was changed to

$$\int_{S^*}^{S} \frac{(f(z) - 1)(1 - S^*)}{1 - z} dz,$$

a similar calculation would yield the same B, an A that is easily seen to be nonpositive, and

$$C = \sum_{i=2}^{n} x_{i1} \left(\alpha_i (f_i(S) - 1) - (f_1(S) - 1) f_i(S) \frac{(1 - S^*)}{(1 - S)} \right).$$

In Wolkowicz and Lu [15], it is shown that one can choose α_i's so that each term in C is nonpositive for a large class of monotone uptake functions. Thus Theorem 6.2 can be extended to this class.

7. Perturbation theorems. We extend the results obtained in sections 5 and 6 by using perturbation arguments to show that the "equal" uptake functions in section 5 can be replaced by "nearly equal," and the "pure refuge" assumption of section 6 can be replaced by a "low growth zone." In this section the functions $g_i(S)$ are assumed to satisfy the three conditions listed in section 2. Although the results below follow quite simply from the properties obtained earlier and a theorem already in the literature, they are important to give added content to the results of the previous two sections.

The theorem that we use is formulated in [12] for a more general situation. We state a special case that is sufficient for our needs. Consider two systems in R^n:

$$x' = f(x) \tag{7.1}$$

and

$$y' = f(y) + \epsilon g(y), \tag{7.2}$$

where ϵ is a small real parameter and f and g are C^1 functions. Let $\bar{x}$ denote a rest point for (7.1) with basin of attraction $B(\bar{x})$ and let $J(\bar{x})$ denote the Jacobi matrix evaluated at the rest point.

THEOREM 7.1 (see [12, Thm. 1]). *Suppose that the eigenvalues of $J(\bar{x})$ lie in the left-half plane. Then there is an ϵ_0 and a smooth family of rest points $\bar{y}(\epsilon)$ for $|\epsilon| < \epsilon_0$*

satisfying $\bar{y}(0) = \bar{x}$*;* $\bar{y}(\epsilon)$ *is uniformly asymptotically stable. Moreover, if* K *is any compact set in* $B(\bar{x})$*, there exists a positive number* ϵ_1 *such that if* $y_0 \in K$*,* $|\epsilon| < \epsilon_1$*, then the solution* $y(t,\epsilon)$ *with* $y(0,\epsilon) = y_0$ *satisfies* $lim_{t\to\infty}|y(t,\epsilon) - \bar{y}(\epsilon)| = 0$.

It is the last statement that will yield the global attractor as a rest point. The key step is to find the compact set K of the theorem. To do this we note that the absorbing set found in Lemma 2.2 depended only on the bounds on the two functions, m_1 and m_2, and the numbers r_1 and r_2 (Remark 2.2). Moreover, lower bounds found for uniform persistence also depended only on these quantities (section 4).

For the problem of equal uptake (section 5) the perturbed equations take the form

$$S' = 1 - S - (f(S) + \epsilon g_1(S))x_1 - (f(S) + \epsilon g_2(S))x_2,$$

$$x_1' = (f(S) + \epsilon g_1(S))x_1 - x_1 - r_1x_1 + r_2x_2, \tag{7.3}$$

$$x_2' = (f(S) + \epsilon g_2(S))x_2 + r_1x_1 - r_2x_2,$$

where $f(S)$, $g_1(S)$, and $g_2(S)$ satisfy the general conditions listed in section 2. For ϵ sufficiently small, there will be a unique perturbed rest point $E_1(\epsilon)$. (This follows directly from the implicit function theorem or use the first statement in Theorem 7.1.)

THEOREM 7.2. *Suppose that* $f(1) > 1$*. Then for sufficiently small* ϵ*,* $E_1(\epsilon)$ *will be a global attractor of solutions of* (7.3) *with initial conditions in the positive cone in* R^3*.*

Proof. For $\epsilon = 0$, Theorem 5.1 implies that E_1 is a global attractor of the positive cone in E^3. Hence any compact set K in the positive cone will be in $B(E_1)$ as required in Theorem 7.1. Fix $f(S)$ and $g_i(S)$, $i = 1, 2$. For ϵ sufficiently small, Theorem 4.1 (with $f_i(S) = f(S) + \epsilon g_i(S)$) implies that the system (7.3) is uniformly persistent. To simplify notation let η be any positive number less than the bounds given by uniform persistence of the three components. By Lemma 2.2, (7.3) (with ϵ as determined above) is uniformly dissipative—call the absorbing set Λ. Let $K = Cl\{(S, x_1, x_2)|S > \eta, x_1 > \eta, x_2 > \eta, (S, x_1, x_2) \in \Lambda\}$. In addition, choose ϵ so small that Theorem 7.1 applies with this choice of K. This completes the proof. □

We now perturb the case where the wall was a pure refuge (system (6.1)) to obtain the equations

$$S' = 1 - S - x_1(f(S) + \epsilon g_1(S)) - \epsilon g_2(S)x_2,$$

$$x_1' = x_1(f(S) + \epsilon g_1(S) - 1) - r_1x_1 + r_2x_2, \tag{7.4}$$

$$x_2' = \epsilon g_2(S) + r_1x_1 - r_2x_2.$$

THEOREM 7.3. *Suppose that* $f(1) > 1$*. Then for sufficiently small* ϵ*,* $E_1(\epsilon)$ *will be a global attractor of solutions of* (7.4) *with initial conditions in the positive cone in* R^3*.*

Proof. The proof is the same as Theorem 7.2 with Theorem 6.1 used instead of Theorem 5.1. □

8. Discussion. We have described a model of the chemostat with three nonlinear differential equations. The new feature was that the population could adhere to the wall (or other marked surface, for example, a slide inserted into the medium) and could shear from the wall into the medium. We consider this population as being in two classes or compartments and model the interactions accordingly. The population on the wall does not wash out of the chemostat, destroying one of the basic tenants of the usual model, a conservation principle. This principle, in turn, is one of the key steps in reducing many chemostat models to a monotone dynamical system where strong convergence properties are in evidence.

The model has only two rest points, a total washout state and an interior coexistence state. The stability properties of each were provided. Uniform persistence and boundedness were established leading to the existence of a global attractor in the interior of the positive cone. The key question is whether this global attractor is a simple rest point.

The global stability properties of the rest point were established in two biologically important special cases for strictly increasing growth functions. Later, a perturbation theorem of Smith was applied to extend the reach of the global stability results. We conjecture that the interior rest point is globally stable when it exists.

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