



A Mathematical Model of the Chemostat with Periodic Washout Rate

G. J. Butler; S. B. Hsu; Paul Waltman

SIAM Journal on Applied Mathematics, Vol. 45, No. 3. (Jun., 1985), pp. 435-449.

Stable URL:

<http://links.jstor.org/sici?sici=0036-1399%28198506%2945%3A3%3C435%3AAMMOTC%3E2.0.CO%3B2-V>

SIAM Journal on Applied Mathematics is currently published by Society for Industrial and Applied Mathematics.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/siam.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

A MATHEMATICAL MODEL OF THE CHEMOSTAT WITH PERIODIC WASHOUT RATE*

G. J. BUTLER†, S. B. HSU‡ AND PAUL WALTMAN§

Abstract. In its simplest form, the chemostat consists of several populations of microorganisms competing for a single limiting nutrient. If the input concentration of nutrient and the washout rate are constant, theory predicts and experiment confirms that at most one of the populations will survive. In nature, however, one may expect the input concentration and washout rate to vary with time. In this paper we consider a model for the chemostat with periodic washout rate. Conditions are found for competitive exclusion to hold, and bifurcation techniques are employed to show that under suitable circumstances there will be coexistence of the competing populations in the form of positive periodic solutions.

1. Introduction. Under the simplest of circumstances, when two or more populations compete exploitatively for a single limiting substrate in a chemostat, all but one of the populations become extinct [10]. Built into the analysis of this competition in the chemostat are, however, a number of assumptions which are certainly not always met in nature and which might not be met even in the laboratory. Since competitive exclusion is a key concept in ecology, it is important to understand exactly which assumptions imply competitive exclusion. This seems to be particularly compelling since there is much theoretical literature demonstrating competitive exclusion but many examples in nature demonstrating coexistence.

In the traditional chemostat equations two "constants" are under the control of the experimenter, the concentration of the input nutrient and the overflow rate (the pump rate). In nature one anticipates that both of these vary with time. The variable nutrient chemostat has been investigated by Hsu [9], Smith [14], and Hale and Somolinos [7], when the input concentration is periodic, and coexistence of the competing predator population was established in the form of a periodically oscillating solution.

In this paper we study the other control parameter—the "washout" rate—and consider the question of coexistence. We might note that a variable washout rate can even occur unexpectedly in the laboratory if the pump's efficiency changes with fluctuations in the line voltage.

A bifurcation theorem is used to establish the existence of a periodic solution corresponding to the coexistence of the competitors within appropriate parameter ranges. We also determine parameter regions where competitive exclusion holds. Previous work on this question can be found in Stephanopoulos, Frederickson and Aris [15] where the focus of their attention is somewhat different from ours.

General background on the chemostat can be found in the survey articles [6], [16], [17].

We present the model in § 2 together with some preliminary results and results pertaining to competitive exclusion. Section 3 contains our principal theorems concerning coexistence, with a discussion of stability in § 4. In § 5 we consider our results in

* Received by the editors August 2, 1983, and in revised form June 21, 1984.

† Department of Mathematics, University of Alberta, Edmonton, Alberta, Canada, T6G 2G1. The research of this author was supported by the Natural Sciences and Engineering Research Council of Canada under grant A-8130.

‡ Department of Applied Mathematics, National Chiao Tung University, Hsinchu, Taiwan, Republic of China. The research of this author was supported by the National Science Council of the Republic of China.

§ Department of Mathematical and Computing Science, Emory University, Atlanta, Georgia 30322. The research of this author was supported by the National Science Foundation under grant MCS-8120380.

the light of recent work of Hirsch [8] and Hale and Somolinos [7]. This general approach may also be applied when other parameters in the model are allowed to vary periodically.

2. The model—preliminary results and extinction. If we assume that nutrient uptake is described by Michaelis–Menten kinetics, the model equations are

$$\begin{aligned}
 S'(t) &= (S^0 - S(t))D(t) - \left(\frac{m_1}{y_1}\right)\frac{S(t)x_1(t)}{a_1 + S(t)} - \left(\frac{m_2}{y_2}\right)\frac{S(t)x_2(t)}{a_2 + S(t)}, \\
 x_i'(t) &= x_i(t)\left(\frac{m_i S(t)}{a_i + S(t)} - D(t)\right), \quad i = 1, 2, \\
 x_i(0) &= x_{i0} \geq 0, \quad S(0) = S_0 \geq 0.
 \end{aligned}$$

S^0 is the constant input concentration of substrate S , $D(t)$ is a positive continuous periodic function with period $\omega > 0$, representing the washout rate. y_i, m_i, a_i are positive constants which are the yield, intrinsic growth rate and Michaelis–Menten constant, respectively, for the i th competitor.

The variables in the above system may be rescaled by measuring S in units of S^0 , x_1 in units of $S^0 y_1$ and x_2 in units of $S^0 y_2$. If time is then measured in units of the mean value $(1/\omega) \int_0^\omega D(t) dt$ of $D(t)$, the system takes the form

$$\begin{aligned}
 (2.1) \quad S'(t) &= (1 - S(t))D(t) - \frac{m_1 S(t)x_1(t)}{a_1 + S(t)} - \frac{m_2 S(t)x_2(t)}{a_2 + S(t)}, \\
 x_i'(t) &= x_i(t)\left(\frac{m_i S(t)}{a_i + S(t)} - D(t)\right), \quad i = 1, 2, \\
 x_i(0) &= x_{i0} \geq 0, \quad S(0) = S_0 \geq 0,
 \end{aligned}$$

where m_i and a_i have also been rescaled and $D(t)$ has mean value 1. The period of D has also been rescaled, but we shall again label it ω .

It is not hard to show that the solutions of (2.1) are nonnegative and bounded, as the following lemma indicates:

LEMMA 2.1. (i) *The nonnegative (S, x_1, x_2) -cone Ω is positively invariant for (2.1) as are the bounding faces $x_1 = 0$ and $x_2 = 0$.*

(ii) *Solutions of (2.1) are uniformly asymptotically bounded as $t \rightarrow \infty$, i.e. the system is dissipative. In fact, $\lim_{t \rightarrow \infty} (S(t) + x_1(t) + x_2(t)) = 1$, and the rate of convergence is exponential.*

(iii) *There is a constant $\eta > 0$ such that $\underline{\lim}_{t \rightarrow \infty} S(t) \geq \eta$ for all solutions $S(t)$.*

Proof. (i) and (ii) Since the arguments are quite standard, we omit the details, save to note that if $z(t) = S(t) + x_1(t) + x_2(t)$, then

$$(2.2) \quad z(t) = 1 + (z_0 - 1) \exp \int_0^t -D(s) ds.$$

Since $D(t)$ is a positive continuous periodic function, $d_1 = \min D(t)$ exists and is positive. It follows from (2.2) that $S(t) + x_1(t) + x_2(t) \rightarrow 1$ exponentially as $t \rightarrow \infty$.

(iii) In fact

$$\underline{\lim}_{t \rightarrow \infty} S(t) \geq \eta = \frac{d_1}{d_1 + m_1/a_1 + m_2/a_2}.$$

For suppose that $\underline{\lim}_{t \rightarrow \infty} S(t) < \eta$. Since $\overline{\lim}_{t \rightarrow \infty} x_i(t) \leq 1$, by (2.2), we may find $t_n \rightarrow \infty$

and η_0 with $0 < \eta_0 < \eta$ such that $S(t_n) < \eta_0$, $S(t_n)x_i(t_n) < \eta_0$ for $i = 1, 2$, and $S'(t_n) \rightarrow 0$ as $n \rightarrow \infty$. But then

$$S'(t_n) \cong (1 - \eta_0)d_1 - \eta_0 \left(\frac{m_1}{a_1} + \frac{m_2}{a_2} \right) > d_1 - \eta \left\{ d_1 + \left(\frac{m_1}{a_1} + \frac{m_2}{a_2} \right) \right\} = 0,$$

a contradiction.

COROLLARY 2.2. *The triangular region $\Delta: S + x_1 + x_2 = 1$, $S, x_1, x_2 \geq 0$; is a global attractor for (2.1), and solutions of (2.1) approach Δ exponentially as $t \rightarrow \infty$.*

Proof. Immediate from the proof of the preceding lemma.

It will be convenient to use the notation $\langle f \rangle$ for the mean value of any continuous, ω -periodic function f , i.e. $\langle f \rangle = (1/\omega) \int_0^\omega f(s) ds$.

Analogously to the case in which (2.1) is autonomous, we define λ_i to be $a_i/(m_i - 1)$, ($m_i \neq 1$), $i = 1, 2$. In the autonomous case, the relative values of the λ_i completely determine the outcome [10]; in the periodic case, this is not always the case as we shall see.

If the mean washout rate is too high, one or both of the competing populations will go to extinction. This is the content of the next lemma:

LEMMA 2.3. *A necessary condition for both competitors to go extinct is that*

$$\frac{m_i}{a_i + 1} \leq 1, \quad i = 1, 2.$$

A sufficient condition for x_i to go extinct is that $m_i/(a_i + 1) < 1$.

Proof. Assume that x_1 and x_2 go extinct, that is to say, $\lim_{t \rightarrow \infty} x_1(t) = \lim_{t \rightarrow \infty} x_2(t) = 0$ for all solutions of (2.1). Suppose that we had $m_i/(a_i + 1) > 1$ for some i . Choosing a solution of (2.1) with $x_i(0) > 0$, so that $x_i(t) > 0$ for all $t \geq 0$, we have

$$(2.3) \quad \frac{x'_i(t)}{x_i(t)} = \frac{m_i S(t)}{a_i + S(t)} - D(t).$$

By Corollary 2.2, $S(t) \rightarrow 1$ as $t \rightarrow \infty$, and so we may choose t_0 sufficiently large that $m_i S(t)/(a_i + S(t)) \geq \langle D \rangle$ for all $t \geq t_0$. Integrating (2.3) from $t = t_0$ to $t = t_0 + m\omega$, we have

$$x_i(t_0 + m\omega) = x_i(t_0) \exp \int_{t_0}^{t_0 + m\omega} \left\{ \frac{m_i S(t)}{a_i + S(t)} - D(t) \right\} dt \geq x_i(t_0) > 0.$$

Letting $m \rightarrow \infty$, we find $\overline{\lim}_{t \rightarrow \infty} x_i(t) > 0$, contrary to supposition. This proves the first part of the lemma. For the second part let $1 - m_i/(a_i + 1) = 2\varepsilon_i > 0$. Since $\overline{\lim}_{t \rightarrow \infty} S(t) \leq 1$, we have $m_i S(t)/(a_i + S(t)) \leq m_i/(a_i + 1) + \varepsilon_i$ for $t \geq t_i$, say, and so $x'_i(t)/x_i(t) \leq 1 - \varepsilon_i - D(t)$, for $t \geq t_i$. Upon integrating both sides of this inequality, it then follows that $\lim_{t \rightarrow \infty} x_i(t) = 0$, since $\langle D \rangle = 1$.

Lemma 2.3 dealt with extinction that occurs regardless of competition. In the following result, extinction occurs as a result of competition.

LEMMA 2.4. *Let $\lambda_1 < \lambda_2 < 1$, $m_1 \geq m_2$. Then for all solutions of (2.1) with positive initial conditions, we have $x_2(t) \rightarrow 0$ as $t \rightarrow \infty$. Furthermore, for any given compact set of initial conditions which is disjoint from the x_1 -axis, convergence of x_2 to zero occurs at a uniform exponential rate.*

Proof. The proof proceeds very much along the lines of that of [10, Lemma 4.3]; hence we give only an outline. It is possible, under the hypotheses of the lemma and Lemma 2.1(iii), to choose $\xi > 0$ such that $\xi(m_2 S/(a_2 + S) - 1) - (m_1 S/(a_1 + S) - 1) <$

$-\eta_1 < 0$ for some $\eta_1 > 0$. Since

$$\frac{\xi x_2'(t)}{x_2(t)} - \frac{x_1'(t)}{x_1(t)} = \left[\xi \left(\frac{m_2 S(t)}{a_2 + S(t)} - 1 \right) - \left(\frac{m_1 S(t)}{a_1 + S(t)} - 1 \right) \right] + (\xi - 1)(1 - D(t))$$

and $\int_0^t (1 - D(s)) ds$ is bounded for all t , an integration gives

$$(x_2(t))^\xi \leq c_0 e^{-\eta_1 t} x_1(t) \exp \left[(\xi - 1) \int_0^t (1 - D(s)) ds \right]$$

for some $c_0 > 0$ depending upon initial conditions, where c_0 may be chosen uniformly for initial conditions in any compact set disjoint from the x_1 -axis. From Lemma 2.1, $x_1(t)$ is bounded (again uniformly for any compact set of initial conditions) and so the result follows.

An intuitively obvious case of Lemma 2.4 occurs when competitor x_1 out-competes x_2 at all pertinent levels of nutrient density, i.e. if $m_1 S / (a_1 + S) > m_2 S / (a_2 + S)$ for all $S > 0$. For this case, provided that $\lambda_2 \leq 1$, we have $1 = (m_1 + \lambda_1) / (a_1 + \lambda_1) = (m_2 + \lambda_2) / (a_2 + \lambda_2) < m_1 \lambda_2 / (a_1 + \lambda_2)$, which implies that $\lambda_1 < \lambda_2$. Letting $S \rightarrow \infty$ in the inequality $m_1 S / (a_1 + S) > m_2 S / (a_2 + S)$, we also have $m_1 \geq m_2$; so Lemma 2.4 shows that $\lim_{t \rightarrow \infty} x_2(t) = 0$. If $\lambda_2 > 1$ (or is undefined), Lemma 2.3 gives the same result.

If one of the competitors is absent, we obtain the 2-dimensional subsystem

$$(2.4) \quad S'(t) = (1 - S(t))D(t) - \frac{m x(t) S(t)}{a + S(t)}, \quad x'(t) = x(t) \left(\frac{m S(t)}{a + S(t)} - D(t) \right)$$

where x represents the remaining competitor (with $m = m_i$, $a = a_i$ for $i = 1$ or 2 , as appropriate).

By Lemma 2.1, for any solution of (2.4), $S(t) + x(t) = 1 + R(t)$ where $R(t) = O(e^{\alpha t})$ as $t \rightarrow \infty$, for some $\alpha < 0$. (Repeat the proof of Lemma 2.1, using (2.4) in place of (2.1).) Fix such a solution $(S_i(t), x_i(t))$. Then $x_i(t)$ solves an equation of the form

$$(2.5) \quad y'(t) = y(t) \left(\frac{m(1 - y(t))}{1 + a - y(t)} - D(t) \right) + r(t)$$

where $r(t) = O(e^{\alpha t})$ as $t \rightarrow \infty$ and depends on the choice of $x_i(t)$. For the moment rewrite (2.5) as

$$(2.6) \quad y' = F(t, y) + r(t)$$

which in turn is viewed as a perturbation of

$$(2.7) \quad z' = F(t, z).$$

Equation (2.7) has a unique positive ω -periodic solution $\phi(t)$ which is globally asymptotically stable for positive solutions of (2.7). This was shown in [1] using Massera's theorem. It is not difficult to show, by linearizing about $\phi(t)$, that the convergence is uniformly exponential on compact sets of initial conditions. In particular $\phi(t)$ is exponentially asymptotically stable. A simple Gronwall's inequality argument shows that if $y(t)$ is any solution of (2.6) then

$$y(t) = \phi(t) + O(e^{\beta t}) \quad \text{for some } \beta < 0.$$

Note that $\phi(t)$ is independent of the choice of $x_i(t)$, although (2.6) is not; in particular $x_i(t)$ converges exponentially to $\phi(t)$ as $t \rightarrow \infty$. Define $\psi(t) = 1 - \phi(t)$. Then $S_i(t)$

converges exponentially to $\psi(t)$ as $t \rightarrow \infty$. Now

$$\phi'(t) = F(t, \phi(t)) = \phi(t) \left[\frac{m(1 - \phi(t))}{1 + a - \phi(t)} - D(t) \right] = \phi(t) \left[\frac{m\psi(t)}{a + \psi(t)} - D(t) \right]$$

and

$$\psi'(t) = -\phi'(t) = (1 - \psi(t))D(t) - \frac{m\phi(t)\psi(t)}{a + \psi(t)}.$$

Thus $(\psi(t), \phi(t))$ is a solution of (2.4) and is globally exponentially asymptotically stable for strictly positive solutions. This is just the analogue of the global stability result for the simple chemostat with constant washout rate D .

Referring back to (2.4) with $m = m_i, a = a_i, i = 1$ or 2 , we have shown the following:

LEMMA 2.5. Assume that $m_i/(1 + a_i) > 1$ ($\lambda_i < 1$). There are positive ω -periodic functions $S_i(t), \phi_i(t)$, such that the solutions $(S_i(t), \phi_i(t))$ of (2.4) (with $m = m_i, a = a_i$) are exponentially asymptotically stable for (2.4), and $x = \phi_i$ is globally asymptotically stable for (2.7).

Returning to the full 3-dimensional system, we see that there may be three periodic solutions of (2.1) on the boundary of Ω , the constant solution $E_0 = (1, 0, 0)$ and the solutions

$$E_1 = (S_1, \phi_1, 0), \quad E_2 = (S_2, 0, \phi_2).$$

E_0 is globally asymptotically stable for (2.1) if $\max_{i=1,2} m_i/(a_i + 1) < 1$ ($\min_{i=1,2} \lambda_i > 1$). This follows from Lemma 2.3. If $\lambda_1 < 1 < \lambda_2$, E_0 has a 2-dimensional stable manifold (the (S, x_2) -plane) and a 1-dimensional unstable manifold. If $\lambda_1 < \lambda_2 < 1$, E_0 has a 1-dimensional stable manifold (the S -axis) and 2-dimensional unstable manifold (the (x_1, x_2) -plane).

Assuming that $\lambda_1 < \lambda_2 < 1$, each of the solutions $E_i, i = 1, 2$, has at least a 2-dimensional stable manifold (the (S, x_i) -plane).

Linearizing (2.1) about E_1 yields the matrix

$$(2.8) \quad \begin{pmatrix} -D(t) - \frac{m_1 a_1 \phi_1(t)}{(a_1 + S_1(t))^2} & \frac{m_1 S_1(t)}{a_1 + S_1(t)} & \frac{-m_2 S_1(t)}{a_2 + S_1(t)} \\ \frac{m_1 a_1 \phi_1(t)}{(a_1 + S_1(t))^2} & \frac{m_1 S_1(t)}{a_1 + S_1(t)} - D(t) & 0 \\ 0 & 0 & \frac{m_2 S_1(t)}{a_2 + S_1(t)} - D(t) \end{pmatrix}$$

with a similar expression for E_2 .

Thus the Floquet exponent that determines local stability for E_1 is $I = \langle m_2 S_1 / (a_2 + S_1) \rangle - 1$, i.e. E_1 is exponentially locally asymptotically stable if $\langle m_2 S_1 / (a_2 + S_1) \rangle < 1$ and unstable if $\langle m_2 S_1 / (a_2 + S_1) \rangle > 1$.

In the cases that one or both of the competitors x_i go extinct, as given by Lemmas 2.3 and 2.4, we are able to obtain the following results.

THEOREM 2.6. Let $\lambda_1 < \lambda_2 < 1$ and let $m_1 \geq m_2$. Then all solutions of (2.1) with positive initial conditions satisfy $S(t) \rightarrow S_1(t), x_1(t) \rightarrow \phi_1(t), x_2(t) \rightarrow 0$ as $t \rightarrow \infty$, where S_1, ϕ_1 are given by Lemma 2.5. The rate of convergence is exponential.

To deal with the case that x_1 out-competes x_2 , we could employ the ideas of Hale and Somolinos [7], where they give a general discussion of dissipative systems, applying

this to chemostat equations with a periodically varying input. We prefer, however, to give the following alternative argument:

Consider two systems

$$(2.9) \quad x' = x \wedge F(t, x, y), \quad y' = y \wedge G(t, x, y), \quad x(0), y(0) \geq 0,$$

$$(2.10) \quad x' = x \wedge F(t, x, 0), \quad x(0) \geq 0.$$

Here x is a vector in \mathbf{R}^k ($k = 1$ or 2), y is a vector in \mathbf{R}^{n-k} , and for r -dimensional vectors $u = (u_1, \dots, u_r)$, $v = (v_1, \dots, v_r)$, the notation $u \wedge v$ indicates the vector $(u_1 v_1, \dots, u_r v_r)$. (See [3], where this notation is introduced.) Assume that F and G are, respectively, continuous k -vector-valued and $(n - k)$ -vector-valued functions which are ω -periodic in t and C^1 in (x, y) . Identify the x variable with points of \mathbf{R}^k , the y variable with points of \mathbf{R}^{n-k} , and (x, y) with points of $\mathbf{R}^n = \mathbf{R}^k \times \mathbf{R}^{n-k}$, so that (2.9), (2.10) are defined, respectively, on the nonnegative cones $\mathcal{C}_n, \mathcal{C}_k$ of $\mathbf{R}^n, \mathbf{R}^k$. Note that the interior of \mathcal{C}_n , its bounding $(n - 1)$ -dimensional faces and all lower dimensional boundaries are invariant for (2.9), with a similar statement holding for (2.10).

LEMMA 2.7. *Assume the following hypotheses hold:*

- (i) (2.10) has a finite number of periodic solutions, all of which are hyperbolic (have no Floquet exponents with zero real part) when considered, together with $y = 0$, as solutions of (2.9).
- (ii) All solutions of (2.10) are periodic or asymptotically periodic as $t \rightarrow \infty$.
- (iii) There is a solution ψ of (2.10) which is globally asymptotically stable for all solutions of (2.10) with positive initial conditions.
- (iv) The solution $(\psi, 0)$ of (2.9) is asymptotically stable.
- (v) All solutions (x, y) of (2.9) with positive initial conditions are bounded and satisfy $y(t) \rightarrow 0$ as $t \rightarrow \infty$.

Then $(\psi, 0)$ is globally asymptotically stable for solutions of (2.9) with positive initial conditions.

Proof. Consider the discrete dynamical systems (2.9)', (2.10)' obtained from (2.9) and (2.10) by use of the period map. Thus (2.9)' is defined by the map $T: \mathcal{C}_n \rightarrow \mathcal{C}_n$ given by

$$T(a, b) = (x(0, a, b; \omega), y(0, a, b; \omega))$$

where $(x(s, a, b; t), y(s, a, b; t))$ denotes the solution (x, y) of (2.9) with initial conditions $x(s) = a, y(s) = b$. (2.10)' is defined by the restriction of T to \mathcal{C}_k .

Let $a, b > 0$. By (v), the orbit $\{T^n(a, b)\}_{n=0}^\infty$ of (2.9)' has a nonempty positive omega limit set $\Omega \subset \mathcal{C}_k$. Let $p \in \Omega$. Then the orbit of (2.9)' through p is also contained in Ω . If $p \in \text{int } \mathcal{C}_k$, then $T^n p \rightarrow p_0 = (\psi(0), 0)$, by (iii), and so $p_0 \in \Omega$. It now follows from (iv) that $\Omega = \{p_0\}$. Thus we have

$$(x(0, a, b; t), y(0, a, b; t)) \rightarrow (\psi(t), 0) \quad \text{as } t \rightarrow \infty.$$

If $p \in \partial \mathcal{C}_k$, the boundary of \mathcal{C}_k , it follows from (ii) that the positive omega limit set of the orbit $\{T^n p\}_{n=0}^\infty$ is a fixed point q of T , lying in $\partial \mathcal{C}_k$. Thus $q \in \Omega$. By (i), q is a hyperbolic, unstable fixed point of T and possesses an unstable manifold $W^u(q)$ and a stable manifold $W^s(q)$ ($W^s(q)$ may be the single point $\{q\}$). Since the bounding faces and all lower dimensional boundaries of \mathcal{C}_n are invariant under T , it is easily seen that the stable and unstable manifolds of q must lie in $\partial \mathcal{C}_n$. Thus the orbit $\{T^n(a, b)\}_{n=0}^\infty$ is disjoint from $W^s(q)$. Since $q \in \Omega$, it follows from Hartman's theorem [12] (see p. 80 and discussion on p. 88) that Ω must contain some point q_1 , of $W^u(q)$, $q_1 \neq q$. q_1 cannot lie in that part of $W^u(q)$ (if any) which is not in \mathcal{C}_k , otherwise Ω

would not be contained in \mathcal{C}_k . If $k = 1$, this forces q_1 to lie in $\text{int } \mathcal{C}_k$ and so $\Omega \subset \text{int } \mathcal{C}_k \neq \emptyset$, allowing us to complete the argument as before. If $k = 2$, either $q_1 \in \text{int } \mathcal{C}_k$ or $q_1 \in \partial \mathcal{C}_k$. In the latter case, the positive omega limit set of $\{T^n q_1\}_{n=0}^\infty$ is a fixed point q_2 of T , with $q_2 \in \partial \mathcal{C}_k$. From (i) and (iii), it follows that q_2 is a hyperbolic unstable fixed point of T which possesses a stable manifold in the 1-dimensional set $\partial \mathcal{C}_k$ since it is the positive omega limit set of the orbit through q_1 . Note that this forces $W^u(q_2)$ to be disjoint from $\partial \mathcal{C}_k$. As before, Ω must contain some point q_3 of the unstable manifold $W^u(q_2)$ of q_2 , with $q_3 \neq q_2$, $q_3 \in \mathcal{C}_k$. Since q_3 cannot lie in $\partial \mathcal{C}_k$, it must be interior to \mathcal{C}_k . Now we may finish the argument as before. This completes the proof of the lemma.

LEMMA 2.8. *Let $x = \psi$ be a positive periodic solution of (2.10) which is exponentially asymptotically stable. Suppose that for each compact set K of initial conditions disjoint from the set $x = 0$, there exist $M, \beta > 0$ such that for each solution of (2.9) with initial conditions in K , we have*

$$|y(t)| \leq M|y(0)| e^{-\beta t}.$$

Then $(\psi, 0)$ is exponentially asymptotically stable for (2.9).

Proof. Put $\xi = x - \psi$, $\eta = y$ in the first equation of (2.9) to obtain

$$(2.11) \quad \xi'(t) = A(t)\xi(t) + B(t)\eta(t) + r(t, \xi, \eta)$$

where $A(t)$ is an ω -periodic $k \times k$ matrix, $B(t)$ an ω -periodic $k \times (n - k)$ matrix and $r(t, \xi, \eta)$ satisfies $r \rightarrow 0$ uniformly in t as $(\xi, \eta) \rightarrow (0, 0)$.

Since $x = \psi$ is exponentially asymptotically stable for (2.10), the fundamental matrix $Y(t)$ associated with the linear system

$$(2.12) \quad \xi'(t) = A(t)\xi(t)$$

satisfies $\|Y(t)Y^{-1}(s)\| \leq C e^{-\alpha(t-s)}$, $0 \leq s \leq t < \infty$, for some $C, \alpha > 0$ [2].

Let $\varepsilon > 0$ be given. Choose $\sigma = \sigma(\varepsilon)$ so that $|\xi| + |\eta| \leq \sigma$ implies $|r(t, \xi, \eta)| \leq \varepsilon(|\xi| + |\eta|)$. Let $\|B(t)\| \leq C_1$ for all t . By the variation of constants formula, we have

$$\xi(t) = Y(t)\xi(0) + \int_0^t Y(t)Y^{-1}(s)\{B(s)\eta(s) + r(s, \xi(s), \eta(s))\} ds$$

and so

$$(2.13) \quad |\xi(t)| \leq C e^{-\alpha t}|\xi(0)| + \int_0^t C e^{-\alpha(t-s)}\{C_1|\eta(s)| + \varepsilon(|\xi(s)| + |\eta(s)|)\} ds$$

provided that $|\xi(s)| + |\eta(s)| \leq \sigma$, $0 \leq s \leq t$.

Let $0 < \sigma_0 < \psi(0)$ and let

$$K = \{(x_0, y_0) \in \mathbf{R}^n : |x_0 - \psi(0)| \leq \sigma_0, |y_0| \leq \sigma_0\}.$$

By hypothesis, there exist $M, \beta > 0$ such that any solution (x, y) of (2.9) with $(x(0), y(0)) \in K$ satisfies $|y(t)| \leq M|y(0)| e^{-\beta t}$. Without loss of generality, we may assume that $\alpha < \beta$.

Suppose that $|\xi(0)| \leq \sigma_0, |\eta(0)| \leq \sigma_0$. Then (2.13) gives

$$(2.14) \quad |\xi(t)| \leq C e^{-\alpha t}|\xi(0)| + \int_0^t C e^{-\alpha(t-s)}\{(C_1 + \varepsilon)M|\eta(0)| e^{-\beta s} + \varepsilon|\xi(s)|\} ds,$$

provided that $|\xi(s)| + |\eta(s)| \leq \sigma$, $0 \leq s \leq t$.

Put $z(t) = |\xi(t)| e^{\alpha t}$. Then we have

$$\begin{aligned}
 (2.15) \quad z(t) &\leq Cz(0) + \int_0^t C_{\varepsilon} z(s) ds + \int_0^t (C_1 + \varepsilon) M |\eta(0)| e^{(\alpha - \beta)s} ds \\
 &\leq \left(Cz(0) + \frac{(C_1 + \varepsilon) M |\eta(0)|}{\beta - \alpha} \right) + \int_0^t C_{\varepsilon} z(s) ds.
 \end{aligned}$$

Gronwall's inequality yields

$$\begin{aligned}
 (2.16) \quad z(t) &\leq \left(Cz(0) + \frac{(C_1 + \varepsilon) M |\eta(0)|}{\beta - \alpha} \right) e^{C_{\varepsilon} t}, \quad \text{i.e.} \\
 |\xi(t)| &\leq \left(C |\xi(0)| + \frac{(C_1 + \varepsilon) M |\eta(0)|}{\beta - \alpha} \right) e^{(C_{\varepsilon} - \alpha)t},
 \end{aligned}$$

provided that $|\xi(s)| + |\eta(s)| \leq \sigma, 0 \leq s \leq t$. We also have

$$(2.17) \quad |\eta(t)| \leq M |\eta(0)| e^{-\beta t} \leq M |\eta(0)|.$$

Fix $\varepsilon < \alpha/C$ and let

$$\delta = \min \left(\sigma_0, \frac{1}{2} \sigma \left[C + \frac{(C_1 + \alpha/C) M}{\beta - \alpha} + M \right]^{-1} \right).$$

Then if $|\xi(0)| + |\eta(0)| \leq \delta$ and provided that $|\xi(s)| + |\eta(s)| \leq \sigma, 0 \leq s \leq t$, we have by (2.16) and (2.17),

$$\begin{aligned}
 |\xi(t)| &\leq \left(C + \frac{(C_1 + \alpha/C) M}{\beta - \alpha} \right) \delta \leq \frac{\sigma}{2}, \\
 |\eta(t)| &\leq M \delta \leq \frac{\sigma}{2}, \quad \text{i.e.}
 \end{aligned}$$

$|\xi(t)| + |\eta(t)| \leq \sigma$. From this it follows that (2.16) and (2.17) are valid for all $t \geq 0$ for all solutions (ξ, η) with $|\xi(0)| + |\eta(0)| \leq \delta$. The lemma now follows from (2.16) and (2.17), since $C_{\varepsilon} - \alpha < 0$.

Proof of Theorem 2.6. In (2.4), put $m = m_1, a = a_1, y = S + x - 1$, and rewrite the equations as

$$(2.18) \quad x' = x \left(\frac{m_1(1 + y - x)}{1 + a_1 + y - x} - D(t) \right), \quad y' = -D(t)y.$$

Consider also the system

$$(2.19) \quad x' = x \left(\frac{m_1(1 - x)}{1 + a_1 - x} - D(t) \right).$$

The periodic solutions of (2.18) are $(0, 0)$ and $(\phi_1, 0)$. By Lemma 2.5, all solutions of (2.19), except for $x = 0$, approach ϕ_1 as $t \rightarrow \infty$, and $(\phi_1, 0)$ is exponentially asymptotically stable for (2.18). It is easily verified that $(0, 0)$ is a hyperbolic unstable periodic solution of (2.18), and clearly $y(t) \rightarrow 0$ for all solutions of (2.18) with positive initial conditions. Lemma 2.1 gives boundedness of solutions. Applying Lemma 2.7, it follows that $(\phi_1, 0)$ is globally asymptotically stable for solutions of (2.18) with positive initial conditions.

Next we put $x_1 = x$, $S + x_1 + x_2 - 1 = y_1$, $x_2 = y_2$, $y = (y_1, y_2)$, and rewrite (2.1) as

$$(2.20) \quad \begin{aligned} x' &= x \left(\frac{m_1(1 + y_1 - y_2 - x)}{1 + a_1 + y_1 - y_2 - x} - D(t) \right), \\ y_1' &= -D(t)y_1, \\ y_2' &= y_2 \left(\frac{m_2(1 + y_1 - y_2 - x)}{1 + a_2 + y_1 - y_2 - x} - D(t) \right). \end{aligned}$$

We also consider

$$(2.21) \quad x' = x \left(\frac{m_1(1 - x)}{1 + a_1 - x} - D(t) \right).$$

The periodic solutions of (2.20) are $(0, 0, 0)$, $(\phi_1, 0, 0)$, $(0, 0, \phi_2)$, corresponding to E_0 , E_1 and E_2 , respectively. Now $(\phi_1, 0)$ is exponentially asymptotically stable for the subsystem of (2.20) with $y_2 = 0$, and by Lemma 2.4, $y_2 \rightarrow 0$ uniformly exponentially for solutions of (2.20) with initial conditions in any given compact set disjoint from the x -axis. Lemma 2.8 shows that $(\phi_1, 0, 0)$ is exponentially asymptotically stable for (2.20). Again it is easily verified that $(0, 0, 0)$ is a hyperbolic unstable periodic solution of (2.20). Since $y = (y_1, y_2) \rightarrow 0$ as $t \rightarrow \infty$ for any solution of (2.20) with positive initial conditions and solutions are bounded, we again apply Lemma 2.7 and obtain the theorem.

3. Coexistence results. Throughout this section, we shall assume that $0 < \lambda_1 < 1$. Since $\langle D \rangle = 1$, this means that $m_1 > 1$. Our main purpose in this section is to prove the following:

THEOREM 3.1. *Let m_1, a_1 be given (such that $0 < \lambda_1 < 1$). There exists $\alpha = \alpha(m_1, a_1)$ such that for any $a_2 > \alpha$, m_2 (the bifurcation parameter) can be chosen such that $\lambda_1 < \lambda_2$ and (2.1) possesses on ω -periodic solution $(S(t), x_1(t), x_2(t))$ near E_1 and bifurcating from it, in which S, x_1 and x_2 are all positive.*

THEOREM 3.2. *Let m_1, a_1, a_2 be as above. There exists a continuous one-parameter family of positive ω -periodic solutions of (2.1) connecting the solutions E_1 and E_2 .*

The approach used in this section and the next is similar to that used by Cushing [3], [4], [5].

Proof of Theorem 3.1. As a result of Lemma 2.1, in considering (2.1) we may restrict our attention to the invariant triangle $\Delta: S + x_1 + x_2 = 1; S, x_1, x_2 \geq 0$. Eliminating S from (2.1) restricted to Δ , leads to the equations

$$(3.1) \quad x_1' = x_1 f_1(t, x_1, x_2), \quad x_2' = x_2 f_2(t, x_1, x_2)$$

where $f_i(t, x_1, x_2) = (m_i(1 - x_1 - x_2) / (1 + a_i - x_1 - x_2) - D(t))$, $i = 1, 2$. Denote $(\partial f_i / \partial x_j)$ by f_{ij} , and note that for $i \neq j$, $f_{ij}(t, x_1, x_2) < 0$ on $\mathbf{R} \times \Delta$, i.e. (3.1) is *competitive*. We also have $f_{ii}(t, x_1, x_2) < 0$ on $\mathbf{R} \times \Delta$, $i = 1, 2$.

We have shown (Lemma 2.5) that if $x_2 \equiv 0$, so that (3.1) reduces to $x_1' = x_1 f_1(t, x_1, 0)$, then there is a positive periodic solution $x_1 = \phi_1$ which is globally attracting for positive solutions of that equation. We shall find conditions for which there is a bifurcation of this periodic solution into a periodic solution of (3.1) lying in the positive (x_1, x_2) -quadrant. First we set $\xi_1 = x_1 - \phi_1$, $\xi_2 = x_2$ to write (3.1) in the form

$$(3.2) \quad \begin{aligned} \xi_1' &= \{f_1(t, \phi_1, 0) + \phi_1 f_{11}(t, \phi_1, 0)\} \xi_1 + \phi_1 f_{12}(t, \phi_1, 0) \xi_2 + g_1(t, \xi_1, \xi_2), \\ \xi_2' &= f_2(t, \phi_1, 0) \xi_2 + g_2(t, \xi_1, \xi_2) \end{aligned}$$

where $g_i = g_i(t, \xi_1, \xi_2) = O(\xi_1^2 + \xi_2^2)$ as $(\xi_1, \xi_2) \rightarrow (0, 0)$, uniformly with respect to t .

Denote $f_1(t, \phi_1, 0) + \phi_1 f_{11}(t, \phi_1, 0)$ by a_{11} , $\phi_1 f_{12}(t, \phi_1, 0)$ by a_{12} , and observe that

$$\langle a_{11} \rangle = \langle \phi_1 f_{11}(t, \phi_1, 0) \rangle < 0.$$

Now

$$f_2(t, \phi_1, 0) = \frac{m_2(1 - \phi_1(t))}{1 + a_2 - \phi_1(t)} - D(t).$$

We put

$$a_{22} = -D(t), \quad b(t) = \frac{1 - \phi_1(t)}{1 + a_2 - \phi_1(t)}, \quad \mu = m_2,$$

and note that $\langle a_{22} \rangle < 0$. With this notation, (3.2) may be written as

$$(3.3) \quad \begin{aligned} \xi'_1 &= a_{11}\xi_1 + a_{12}\xi_2 + g_1(t, \xi_1, \xi_2, \mu), \\ \xi'_2 &= a_{22}\xi_2 + \mu b(t)\xi_2 + g_2(t, \xi_1, \xi_2, \mu). \end{aligned}$$

Let B denote the Banach space of continuous ω -periodic scalar functions on R with the uniform norm. We require a lemma on the Fredholm alternative which we state in a form used by Cushing [4].

LEMMA 3.3 [4]. Let $a_{ij} \in B$, $i, j = 1, 2$.

(a) If $\langle a_{11} \rangle \neq 0 \neq \langle a_{22} \rangle$, then the system

$$(3.4) \quad y'_1 = a_{11}y_1 + a_{12}y_2, \quad y'_2 = a_{22}y_2$$

has no nontrivial periodic solution, in which case, if $h_1, h_2 \in B$, the system

$$(3.5) \quad \xi'_1 = a_{11}\xi_1 + a_{12}\xi_2 + h_1, \quad \xi'_2 = a_{22}\xi_2 + h_2$$

has a unique solution $(\xi_1, \xi_2) \in B \times B$. The operator $L: (B \times B) \rightarrow (B \times B)$ defined by $(\xi_1, \xi_2) = L(h_1, h_2)$ is a compact, linear operator, and may be decomposed as follows: $L(h_1, h_2) = (L_1(a_{12}L_2h_2 + h_1), L_2h_2)$ where $L_1, L_2: B \rightarrow B$ are compact linear operators.

(b) If $\langle a_{22} \rangle = 0$ and $\langle a_{11} \rangle \neq 0$, then (3.4) has exactly one independent solution in $B \times B$.

(c) If $b \in B$ with $\langle b \rangle = 0$, and $f \in B$, then $\xi' = b\xi + f$ has a solution $\xi \in B$ iff $\langle f(t) \exp(-\int_0^t b(s) ds) \rangle = 0$.

Since a_{11}, a_{22} satisfy the conditions of Lemma 3.3(a), we may define the compact linear operators L, L_1, L_2 , given by that lemma and reformulate the problem of finding nontrivial periodic solutions of (3.3) as that of finding a nontrivial solution in $B \times B$ of the operator equation

$$(3.6) \quad (\xi_1, \xi_2) = \mu L^*(\xi_1, \xi_2) + G(\xi_1, \xi_2, \mu).$$

Here L^* and G are operators from $B \times B$ to $B \times B$ given by

$$\begin{aligned} L^*(\xi_1, \xi_2) &= (L_1(a_{12}L_2(b(t)\xi_2)), L_2(b(t)\xi_2)), \\ G(\xi_1, \xi_2, \mu) &= (L_1(a_{12}L_2g_2 + g_1), L_2g_2) \end{aligned}$$

where g_1 and g_2 are given in (3.3). L^* is a compact linear operator and G is continuous and compact with $G(\xi_1, \xi_2, \mu) = o(\|(\xi_1, \xi_2)\|)$ as $\|(\xi_1, \xi_2)\| \rightarrow 0$.

The next two lemmas are a basic bifurcation theorem, and a global bifurcation theorem due to Rabinowitz:

LEMMA 3.4 [11]. Let $T_\mu = \mu A + N$ be a continuous one parameter family of operators from a Banach space X to itself, such that A is compact and linear and N satisfies

$\|Nx - Ny\| = o(\|x - y\|)$. Then a bifurcation of the zero solution of the equation $T_\mu x = x$ ($x \in X$) can only occur at a characteristic value μ^* (reciprocal of a nonzero eigenvalue) of A , and will occur if μ^* has odd multiplicity. In this case, the bifurcation point corresponds to a continuous branch of eigenvectors of T_μ in a neighbourhood of the zero of X .

LEMMA 3.5 [13]. Let T_μ, A, N, X be as above, and let Σ be the closure of the set of all nontrivial solutions of $T_\mu x = x$ as μ ranges over \mathbf{R} . If μ^* is a simple characteristic value of A , then Σ contains two subcontinua $\Sigma_\infty^+, \Sigma_\infty^-$ whose only point in common for μ near μ^* is $(\mu^*, 0)$, and each of which either

- (a) is unbounded, or
- (b) contains $(\mu, 0)$ where $\mu \neq \mu^*$ is a characteristic value of A .

We see that μ^* is a characteristic value of L^* iff the system

$$(3.7) \quad \xi'_1 = a_{11}\xi_1 + a_{12}\xi_2, \quad \xi'_2 = (\mu^*b(t) - D(t))\xi_2$$

has a nontrivial ω -periodic solution. Since $\langle D \rangle = 1$, this is the case iff $\mu^* = [(1 - \phi_1)/(1 + a_2 - \phi_1)]^{-1}$ by Lemma 3.3(b), from which it follows that the eigenspace of $(\mu^*)^2 L^*$ is one-dimensional. Lemma 3.3(c) may now be used to show that μ^* is a simple characteristic root of L^* (see [1, p. 33]).

Since the two quadrants $x_1, x_2 > 0$ and $x_1 > 0 > x_2$, and the x_1 -axis, are invariant for (3.1), and since $(\phi_1, 0)$ is an isolated periodic solution of (3.1) restricted to the x_1 -axis, bifurcation theory (Lemmas 3.4 and 3.5) shows that as we vary m_2 through the critical value μ^* , positive nontrivial periodic solutions of (3.1) appear as a branch of solutions of (3.2) bifurcating from the zero solution. (There is also a branch of periodic solutions with $x_2(t) < 0$ which are not of biological significance.)

In order to show that we really can get coexistence of x_1, x_2 in the form of periodic oscillations, we must show that as m_2 passes through the value of μ^* , the ordering $\lambda_1 < \lambda_2$ is maintained. Otherwise it could be the case that $m_2 = \mu^*$ corresponds to $\lambda_1 = \lambda_2$ and we have a nongeneric bifurcation resulting in a continuum of periodic solutions for the same value $m_2 = \mu^*$ and no positive periodic solutions at all for $m_2 > \mu^*$ or $m_2 < \mu^*$.

We shall need the following result which may be of interest in its own right:

LEMMA 3.6. If $(S_1, \phi_1, 0)$ is a positive periodic solution of (2.1), then $\langle S_1 \rangle > \lambda_1$.

Proof. Let $(S_1(t), \phi_1(t), 0)$ be a solution which is periodic of period ω . Then

$$m_1 = \frac{1}{\langle S_1/(a_1 + S_1) \rangle}$$

since $\langle D \rangle = 1$;

$$\lambda_1 = \frac{a_1}{m_1 - 1} = \frac{\langle S_1/(a_1 + S_1) \rangle}{\langle 1/(a_1 + S_1) \rangle},$$

and

$$(3.8) \quad \langle S_1 \rangle - \lambda_1 = \langle S_1 \rangle - \frac{\langle S_1/(a_1 + S_1) \rangle}{\langle 1/(a_1 + S_1) \rangle}.$$

Hence the proof of Lemma 3.6 is complete if one shows that the right-hand side of (3.8) is positive. Since

$$\begin{aligned} \langle S_1 \rangle - \frac{\langle S_1/(a_1 + S_1) \rangle}{\langle 1/(a_1 + S_1) \rangle} &= \frac{\langle S_1 \rangle - (\langle S_1 \rangle + a_1)\langle S_1/(a_1 + S_1) \rangle}{1 - \langle S_1/(a_1 + S_1) \rangle} \\ &= \left[\frac{\langle S_1 \rangle}{\langle S_1 \rangle + a_1} - \langle S_1/(a_1 + S_1) \rangle \right] \frac{\langle S_1 \rangle + a_1}{1 - \langle S_1/(a_1 + S_1) \rangle}, \end{aligned}$$

this amounts to showing that the bracketed quantity is positive as the second factor is always positive (in fact bounded below by $a_1 > 0$).

Since

$$\left\langle \frac{S_1}{a_1 + S_1} \right\rangle = 1 - \frac{a_1}{\langle a_1 + S_1 \rangle}$$

and

$$\frac{\langle S_1 \rangle}{\langle a_1 + S_1 \rangle} = 1 - a_1 \langle 1/(a_1 + S_1) \rangle,$$

then

$$\frac{\langle S_1 \rangle}{\langle a_1 + S_1 \rangle} - \langle S_1/(a_1 + S_1) \rangle = \frac{a_1}{\langle a_1 + S_1 \rangle} [\langle 1/(a_1 + S_1) \rangle \langle a_1 + S_1 \rangle - 1].$$

From the Cauchy-Schwarz inequality it follows that

$$\langle 1/(a_1 + S_1) \rangle \langle a_1 + S_1 \rangle - 1 \geq 0$$

with equality only if S_1 is constant. The lemma follows.

Consider μ^* as a function of a_2 . Again denoting $1 - \phi_1(t)$ by $S_1(t)$, we have that

$$\mu^*(a_2) = \frac{1}{\langle S_1/(a_2 + S_1) \rangle} = \frac{1}{1 - a_2 \langle 1/(a_2 + S_1) \rangle}.$$

If λ^* is the value of λ_2 corresponding to $m_2 = \mu^*$ then

$$\lambda_2^*(a_2) = \frac{a_2}{\mu^*(a_2) - 1} = \frac{1 - a_2 \langle 1/(a_2 + S_1) \rangle}{\langle 1/(a_2 + S_1) \rangle} = \frac{\langle S_1/(a_2 + S_1) \rangle}{\langle 1/(a_2 + S_1) \rangle}.$$

Thus, $\lim_{a_2 \rightarrow \infty} \lambda_2^*(a_2) = \langle S_1 \rangle$, and $\langle S_1 \rangle > \lambda_1$ by Lemma 3.6. It follows that if a_2 is chosen sufficiently large, then $\lambda_1 < \lambda_2^*$, for the bifurcating periodic solutions of (2.1) near the bifurcation point. This completes the proof of Theorem 3.1.

Proof of Theorem 3.2. Applying Lemma 3.5 to (3.2) (and (3.1)), yields the following possibilities:

- (i) There are positive periodic solutions for all $m_2 < \mu^*$.
- (ii) There exists \hat{m}_2 such that there are positive periodic solutions corresponding to m_2 which become unbounded as $m_2 \rightarrow \hat{m}_2$.
- (iii) There are positive periodic solutions for all $m_2 > \mu^*$.
- (iv) There exist \bar{m}_2 and a continuum of positive periodic solutions of (3.1) which connect $(\phi_1, 0)$ with $m_2 = \mu^*$ to some periodic solution in the x_2 -axis with $m_2 = \bar{m}_2$.

Note that case (b) of Lemma 3.5 cannot occur since the eigenvalue μ^* is unique. We may exclude the possibilities (i), (ii) and (iii) as follows:

If $m_2 = 0$, the second equation in (3.1) is $x_2' = -D(t)x_2$, which has only the zero solution as a periodic solution. Hence there is no positive solution of (3.1) for $m_2 = 0$ and (i) is impossible. It also follows that to rule out (ii), we only have to consider $m_2 \geq 0$. Near to the bifurcation point, positive periodic solutions of (3.1) will satisfy $\max(x_1(t) + x_2(t)) < 1$. Since Σ is a continuum, if (ii) occurs there exists $\bar{m}_2 > 0$ such that with $m_2 = \bar{m}_2$, (3.1) has a positive periodic solution with $\max(x_1(t) + x_2(t)) = 1$, i.e. there exists t_0 such that

$$x_1(t_0) + x_2(t_0) = 1, \quad x_1'(t_0) + x_2'(t_0) = 0.$$

But (3.1) gives $x'_1(t_0) + x'_2(t_0) = -D(t_0) < 0$. This contradiction shows that (ii) cannot occur.

If m_2 is sufficiently large, we shall have $\lambda_2 < \lambda_1$ and $m_2 > m_1$, in which case Lemma 2.4 applies with the roles of x_1 and x_2 interchanged, and $x_1(t) \rightarrow 0$ as $t \rightarrow \infty$. Hence (3.1) has no positive periodic solution. It follows that (iii) cannot occur.

Therefore, the only alternative that can occur is (iv). Note that the continuum of positive periodic solutions cannot connect with the solution $(0, 0)$ of (3.1) since $(0, 0)$ is a repeller (uniformly on compact sets of m_2 -values) for (3.1). Hence the continuum must connect $(\phi_1, 0)$ with $(0, \phi_2)$. Note also that we cannot rule out the possibility that $\bar{m}_2 = \mu^*$ and that there is a whole tube of periodic solutions connecting $(\phi_1, 0)$ with $(0, \phi_2)$ when $m_2 = \mu^*$. Finally we must show that $S = 1 - x_1 - x_2$ is a positive function. The first equation in (2.1) shows that $S'(t) > 0$ whenever $S(t) = 0$. It follows (since S is periodic) that $S(t)$ is either positive for all t or is negative for all t . Suppose that $S(t)$ were negative for all t . If $S(t) \rightarrow -a_i$ as $t \rightarrow \tau$, then $S'(t) \rightarrow \infty$ as $t \rightarrow \tau$. It follows that $S(t) + a_i$ is of one sign for all t . If we had $S(t) + a_i < 0$ for all t , this together with the negativity of $S(t)$, implies that $x'_i(t) \geq x_i(t)(m_i - D(t))$ for all t , which would yield $x_i(t) \rightarrow \infty$ as $t \rightarrow \infty$, since $m_i = \langle D \rangle = m_i - 1 > 0$. This contradiction shows that $S(t) + a_i > 0$ for all t , for $i = 1, 2$. But this, together with $S(t) < 0$ for all t , implies that $x'_i(t) < 0$ for all t , which contradicts the periodicity of $x_i(t)$, $i = 1, 2$. So we finally conclude that $S(t) > 0$ for all t , and the proof of the theorem is complete.

4. Stable coexistence. By obtaining a Lyapunov-Schmidt expansion near the bifurcation point, one may give stability criteria for the positive periodic solutions given by Theorem 3.1. We follow the exposition due to Cushing [3], [5], and refer to these papers for the details for the following development. Assuming that f_1 and f_2 are twice continuously differentiable with respect to x_1, x_2 , we may write

$$\begin{aligned}
 x_1(t) &= \phi_1(t) + x_{11}(t)\varepsilon + x_{12}(t)\varepsilon^2 + o(\varepsilon^2), \\
 x_2(t) &= x_{12}(t)\varepsilon + x_{22}(t)\varepsilon^2 + o(\varepsilon^2), \\
 \mu &= \mu^* + \mu_1\varepsilon + o(\varepsilon).
 \end{aligned}
 \tag{4.1}$$

Using the notation of Theorem 3.1, except that we write $f_2 = f_2(t, x_1, x_2, \mu)$ to indicate its dependence on the bifurcation parameter μ , we define

$$Y(t) = \exp \int_0^t \{f_1(s, \phi_1(s), 0) + \phi_1(s)f_{11}(s, \phi_1(s), 0)\} ds.$$

Since $f_{11} < 0$, $Y(\omega) = \exp \int_0^\omega \phi_1(s)f_{11}(s, \phi_1(s), 0) ds < 1$; and so if $G(t, s)$ is defined by

$$G(t, s) = \begin{cases} Y(t)(1 - Y(\omega))^{-1} / Y(s), & 0 \leq s \leq t \leq \omega, \\ Y(t + \omega)(1 - Y(\omega))^{-1} / Y(s), & 0 \leq t < s < \omega, \end{cases}$$

then $G(t, s) > 0$. $G(t, s)$ is just the Green's function associated with (3.4).

The first order terms in ε in (4.1) are the solutions of a linear system, which may be solved explicitly as

$$\begin{aligned}
 x_{11}(t) &= \int_0^\omega G(t, s)\phi_1(s)f_{12}(s, \phi_1(s), 0) ds, \\
 x_{21}(t) &= \exp \int_0^t f_2(s, \phi_1(s), 0, \mu^*) ds.
 \end{aligned}
 \tag{4.2}$$

Since G is positive and f_{12} negative, we see that $x_{11}(t) < 0 < x_{21}(t)$ for all t . An

orthogonality condition reveals that

$$(4.3) \quad \mu_1 = -\langle f_{21}(t, \phi_1(t), 0, \mu^*)x_{21}(t) + f_{22}(t, \phi_1(t), 0, \mu^*)x_{22}(t) \rangle$$

and the stability of the bifurcating periodic solutions depends on the direction of bifurcation; they are stable if $\mu_1 > 0$, unstable if $\mu_1 < 0$ (see [5, Thm. 8]). Evaluating the partial derivatives, this leads to the condition that the bifurcating periodic solutions (near to the bifurcation value) are

$$(4.4) \quad \begin{aligned} &\text{stable, if } \left\langle \frac{x_{21}(t) + x_{22}(t)}{1 + a_2 - \phi_1(t)} \right\rangle > 0, \\ &\text{unstable, if } \left\langle \frac{x_{21}(t) + x_{22}(t)}{1 + a_2 - \phi_1(t)} \right\rangle < 0. \end{aligned}$$

(4.4) is not immediately helpful: first of all, because it requires knowledge of $\phi_1(t)$ before x_{21} , x_{22} and the mean values can be determined; secondly, because one cannot obtain any clue as to the direction of bifurcation when $D(t)$ is nearly constant (small amplitude about its mean value). For in the case of constant D , the bifurcation is nongeneric with a line of (constant) periodic solutions occurring when $m_2 = \mu^*$.

We have numerical evidence that at least in some instances, there is bifurcation to stable periodic solutions, and intend to pursue this question of stability in a future paper.

5. Discussion. We have seen that all solutions of (2.1) with positive initial conditions asymptotically approach the invariant triangle Δ as $t \rightarrow \infty$. In the case that the solution (S, x_1, x_2) of (2.1) restricted to Δ is locally (globally) exponentially asymptotically stable with respect to Δ , then it will be locally (globally) exponentially asymptotically stable for the full system (2.1). Such results were given in § 2 and § 3. Although we were unable to satisfactorily resolve the stability of the bifurcating periodic solutions obtained in § 3—this is a very hard problem for competitive systems even in the simplest cases [3]—we are able to utilize results of Hirsch [8] and Hale and Somolinos [8] to yield information about the possible asymptotic nature of solutions of (2.1).

Restricting (2.1) to Δ and eliminating S from the equation leads to the 2-dimensional dissipative competition equations (3.1). (Dissipative means that all solutions are asymptotically uniformly bounded.) As Hirsch has shown in the autonomous case of such systems, the dynamics are essentially trivial, in the sense that solutions approach equilibrium as $t \rightarrow \infty$. Extending this to periodic systems, Hale and Somolinos show that all solutions approach an ω -periodic solution as $t \rightarrow \infty$. They also show that when the system is analytic, as it is in the present case, there are a finite number of periodic solutions, except in the case that one of the periodic solutions in the boundary of Δ (i.e. $x_1 = \phi_1$, $x_2 = 0$ or $x_1 = 0$, $x_2 = \phi_2$) has a zero Floquet multiplier.

From the results of Hale and Somolinos it follows that (2.1) will possess an asymptotically stable periodic orbit provided that neither of the solutions $(\phi_1, 0)$ and $(0, \phi_2)$ has a zero Floquet multiplier. We anticipate, but cannot prove, that this is the case for almost all sets of parameter values.

There will be an asymptotically stable positive periodic orbit if $I_1 \cdot I_2 > 0$, where $I_j = \langle m_j(1 - \phi_j) / (1 + a_j - \phi_j) \rangle - 1$, $j = 1, 2$; see [7, p. 44].

REFERENCES

- [1] G. J. BUTLER AND H. I. FREEDMAN, *Periodic solutions of a predator-prey system with periodic coefficients*, Math. Biosci., 55 (1981), pp. 27-38.

- [2] W. A. COPPEL, *Stability and Asymptotic Behaviour in Differential Equations*, Heath, Boston, 1965.
- [3] J. M. CUSHING, *Two species competition in a periodic environment*, J. Math. Biol., 10 (1980), pp. 385-400.
- [4] ———, *Periodic time-dependent predator prey systems*, this Journal, 23 (1977), pp. 972-979.
- [5] ———, *Periodic Kolmogorov systems*, SIAM J. Math. Anal., 13 (1982), pp. 811-827.
- [6] A. G. FREDRICKSON AND G. STEPHANOPOULOS, *Microbial competition*, Science, 213 (1981), pp. 972-979.
- [7] J. K. HALE AND A. S. SOMOLINOS, *Competition for fluctuating nutrient*, J. Math. Biol., 18 (1983), pp. 255-280.
- [8] M. W. HIRSCH, *Systems of differential equations which are competitive or cooperative*, SIAM J. Math. Anal., 13 (1982), pp. 167-179.
- [9] S. B. HSU, *A competition model for a seasonally fluctuating nutrient*, J. Math. Biol., 9 (1980), pp. 115-132.
- [10] S. B. HSU, S. P. HUBBELL AND P. E. WALTMAN, *A mathematical theory for single-nutrient competition in continuous cultures of microorganisms*, this Journal, 32 (1977), pp. 366-383.
- [11] M. A. KRASNOSELSKII, *Topological Methods in the Theory of Nonlinear Integral Equations*, Macmillan, New York, 1964.
- [12] Z. NITECKI, *Differentiable Dynamics*, MIT Press, Cambridge, MA, 1971.
- [13] P. H. RABINOWITZ, *Some global results for nonlinear eigenvalue problems*, J. Functional Analysis, 7 (1971), pp. 487-513.
- [14] H. L. SMITH, *Competitive coexistence in an oscillating chemostat*, this Journal, 40 (1981), pp. 498-522.
- [15] G. STEPHANOPOULOS, A. G. FREDRICKSON AND R. ARIS, *The growth of competing microbial populations in a CSTR periodically varying inputs*, AIChE. J., 25 (1979), pp. 863-872.
- [16] H. VELDKAMP, *Ecological studies with the chemostat*, Adv. Microbial Ecology, 1 (1977), pp. 57-95.
- [17] P. WALTMAN, S. P. HUBBELL AND S. B. HSU, *Theoretical and experimental investigation of microbial competition in continuous culture*, in Modeling and Differential Equations in Biology, T. Burton, ed., Marcel Dekker, New York, 1980.

LINKED CITATIONS

- Page 1 of 1 -



You have printed the following article:

A Mathematical Model of the Chemostat with Periodic Washout Rate

G. J. Butler; S. B. Hsu; Paul Waltman

SIAM Journal on Applied Mathematics, Vol. 45, No. 3. (Jun., 1985), pp. 435-449.

Stable URL:

<http://links.jstor.org/sici?sici=0036-1399%28198506%2945%3A3%3C435%3AAMMOTC%3E2.0.CO%3B2-V>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

References

⁶ **Microbial Competition**

A. G. Fredrickson; Gregory Stephanopoulos

Science, New Series, Vol. 213, No. 4511. (Aug. 28, 1981), pp. 972-979.

Stable URL:

<http://links.jstor.org/sici?sici=0036-8075%2819810828%293%3A213%3A4511%3C972%3AMC%3E2.0.CO%3B2-S>

¹⁰ **A Mathematical Theory for Single-Nutrient Competition in Continuous Cultures of Micro-Organisms**

S. B. Hsu; S. Hubbell; P. Waltman

SIAM Journal on Applied Mathematics, Vol. 32, No. 2. (Mar., 1977), pp. 366-383.

Stable URL:

<http://links.jstor.org/sici?sici=0036-1399%28197703%2932%3A2%3C366%3AAMTFSC%3E2.0.CO%3B2-H>

¹⁴ **Competitive Coexistence in an Oscillating Chemostat**

Hal L. Smith

SIAM Journal on Applied Mathematics, Vol. 40, No. 3. (Jun., 1981), pp. 498-522.

Stable URL:

<http://links.jstor.org/sici?sici=0036-1399%28198106%2940%3A3%3C498%3ACCIAOC%3E2.0.CO%3B2-W>

NOTE: *The reference numbering from the original has been maintained in this citation list.*