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# A MATHEMATICAL MODEL OF THE CHEMOSTAT WITH PERIODIC WASHOUT RATE*

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**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

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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

$$S'(t)=(S^0-S(t))D(t)-\left(\frac{m_1}{y_1}\right)\frac{S(t)x_1(t)}{a_1+S(t)}-\left(\frac{m_2}{y_2}\right)\frac{S(t)x_2(t)}{a_2+S(t)},$$

$$x_i'(t)=x_i(t)\left(\frac{m_iS(t)}{a_i+S(t)}-D(t)\right),\qquad i=1,2,$$

$$x_i(0)=x_{i0}\geqq 0,\qquad S(0)=S_0\geqq 0.$$

$S^0$ 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 $S^0y_1$ and $x_2$ in units of $S^0y_2$. 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

$$S'(t)=(1-S(t))D(t)-\frac{m_1S(t)x_1(t)}{a_1+S(t)}-\frac{m_2S(t)x_2(t)}{a_2+S(t)},$$

$$x_i'(t)=x_i(t)\left(\frac{m_iS(t)}{a_i+S(t)}-D(t)\right),\qquad i=1,2, \tag{2.1}$$

$$x_i(0)=x_{i0}\geqq 0,\qquad S(0)=S_0\geqq 0,$$

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 $\omega$.

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* $\Omega$ *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* $t\to\infty$, *i.e. the system is dissipative. In fact,* $\lim_{t\to\infty}(S(t)+x_1(t)+x_2(t))=1$, *and the rate of convergence is exponential.*

(iii) *There is a constant* $\eta>0$ *such that* $\underline{\lim}_{t\to\infty} S(t)\geqq\eta$ *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

$$z(t)=1+(z_0-1)\exp\int_0^t -D(s)\,ds. \tag{2.2}$$

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

(iii) In fact

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

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

and $\eta_0$ 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 $S'(t_n)\to 0$ as $n\to\infty$. But then

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

a contradiction.

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

*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, $\omega$-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 $\lambda_i$ to be $a_i/(m_i-1)$, $(m_i\neq 1)$, $i=1,2$. In the autonomous case, the relative values of the $\lambda_i$ 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*

$$\frac{m_i}{a_i+1}\leqq 1,\qquad i=1,2.$$

*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, $\lim_{t\to\infty}x_1(t)=\lim_{t\to\infty}x_2(t)=0$ 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 $t\geqq 0$, we have

$$\frac{x_i'(t)}{x_i(t)}=\frac{m_iS(t)}{a_i+S(t)}-D(t). \tag{2.3}$$

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

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

Letting $m\to\infty$, we find $\overline{\lim}_{t\to\infty}x_i(t)>0$, contrary to supposition. This proves the first part of the lemma. For the second part let $1-m_1/(a_i+1)=2\varepsilon_i>0$. Since $\overline{\lim}_{t\to\infty}S(t)\leqq 1$, we have $m_iS(t)/(a_i+S(t))\leqq m_i/(a_i+1)+\varepsilon_i$ for $t\geqq t_i$, say, and so $x_i'(t)/x_i(t)\leqq 1-\varepsilon_i-D(t)$, for $t\geqq t_i$. Upon integrating both sides of this inequality, it then follows that $\lim_{t\to\infty}x_i(t)=0$, 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* $\lambda_1<\lambda_2<1$, $m_1\geqq m_2$. *Then for all solutions of* (2.1) *with positive initial conditions, we have* $x_2(t)\to 0$ *as* $t\to\infty$. *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 $\xi(m_2S/(a_2+S)-1)-(m_1S/(a_1+S)-1)<$

$-\eta_1 < 0$ 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

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

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 $\lambda_2 \leqq 1$, 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 $S \to \infty$ in the inequality $m_1 S/(a_1 + S) > m_2 S/(a_2 + S)$, we also have $m_1 \geqq m_2$; so Lemma 2.4 shows that $\lim_{t\to\infty} x_2(t) = 0$. 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

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

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 $t \to \infty$, for some $\alpha < 0$. (Repeat the proof of Lemma 2.1, using (2.4) in place of (2.1).) Fix such a solution $(S_1(t), x_1(t))$. Then $x_1(t)$ solves an equation of the form

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

where $r(t) = O(e^{\alpha t})$ as $t \to \infty$ and depends on the choice of $x_1(t)$. For the moment rewrite (2.5) as

$$y' = F(t, y) + r(t) \tag{2.6}$$

which in turn is viewed as a perturbation of

$$z' = F(t, z). \tag{2.7}$$

Equation (2.7) has a unique positive $\omega$-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 $x_1(t)$, although (2.6) is not; in particular $x_1(t)$ converges exponentially to $\phi(t)$ as $t \to \infty$. Define $\psi(t) = 1 - \phi(t)$. Then $S_1(t)$

converges exponentially to $\psi(t)$ as $t\to\infty$. 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* $\omega$*-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 $\Omega$, the constant solution $E_0=(1,0,0)$ and the solutions

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

$E_0$ 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

$$\begin{pmatrix} -D(t)-\dfrac{m_1a_1\phi_1(t)}{(a_1+S_1(t))^2} & \dfrac{m_1S_1(t)}{a_1+S_1(t)} & \dfrac{-m_2S_1(t)}{a_2+S_1(t)} \\ \dfrac{m_1a_1\phi_1(t)}{(a_1+S_1(t))^2} & \dfrac{m_1S_1(t)}{a_1+S_1(t)}-D(t) & 0 \\ 0 & 0 & \dfrac{m_2S_1(t)}{a_2+S_1(t)}-D(t)\end{pmatrix} \tag{2.8}$$

with a similar expression for $E_2$.

Thus the Floquet exponent that determines local stability for $E_1$ is $I=\langle m_2S_1/(a_2+S_1)\rangle-1$, i.e. $E_1$ is exponentially locally asymptotically stable if $\langle m_2S_1/(a_2+S_1)\rangle<1$ and unstable if $\langle m_2S_1/(a_2+S_1)\rangle>1$.

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* $m_1\geqq m_2$. *Then all solutions of* (2.1) *with positive initial conditions satisfy* $S(t)\to S_1(t)$, $x_1(t)\to\phi_1(t)$, $x_2(t)\to 0$ *as* $t\to\infty$, *where* $S_1$, $\phi_1$ *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 imput. We prefer, however, to give the following alternative argument:

Consider two systems

$$x' = x \wedge F(t, x, y), \quad y' = y \wedge G(t, x, y), \quad x(0), y(0) \geqq 0, \tag{2.9}$$

$$x' = x \wedge F(t, x, 0), \qquad x(0) \geqq 0. \tag{2.10}$$

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 $u = (u_1, \cdots, u_r)$, $v = (v_1, \cdots, v_r)$, the notation $u \wedge v$ indicates the vector $(u_1 v_1, \cdots, u_r v_r)$. (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 $\omega$-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 $\mathscr{C}_n$, $\mathscr{C}_k$ of $\mathbf{R}^n$, $\mathbf{R}^k$. Note that the interior of $\mathscr{C}_n$, 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* $t \to \infty$.

(iii) *There is a solution* $\psi$ *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* $y(t) \to 0$ *as* $t \to \infty$.

*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 $T: \mathscr{C}_n \to \mathscr{C}_n$ 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 $\mathscr{C}_k$.

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 $\Omega \subset \mathscr{C}_k$. Let $p \in \Omega$. Then the orbit of (2.9)′ through $p$ is also contained in $\Omega$. If $p \in \operatorname{int} \mathscr{C}_k$, then $T^n p \to p_0 = (\psi(0), 0)$, by (iii), and so $p_0 \in \Omega$. It now follows from (iv) that $\Omega = \{p_0\}$. Thus we have

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

If $p \in \partial \mathscr{C}_k$, the boundary of $\mathscr{C}_k$, 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 $\partial \mathscr{C}_k$. 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 $\mathscr{C}_n$ are invariant under $T$, it is easily seen that the stable and unstable manifolds of $q$ must lie in $\partial \mathscr{C}_n$. 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 $\Omega$ 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 $\mathscr{C}_k$, otherwise $\Omega$

would not be contained in $\mathscr{C}_k$. If $k=1$, this forces $q_1$ to lie in int $\mathscr{C}_k$ and so $\Omega \subset$ int $\mathscr{C}_k \neq \emptyset$, allowing us to complete the argument as before. If $k=2$, either $q_1 \in$ int $\mathscr{C}_k$ or $q_1 \in \partial \mathscr{C}_k$. 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 $q_2 \in \partial \mathscr{C}_k$. 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 $\partial \mathscr{C}_{k'}$ 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 $\partial \mathscr{C}_k$. As before, $\Omega$ must contain some point $q_3$ of the unstable manifold $W^u(q_2)$ of $q_2$, with $q_3 \neq q_2$, $q_3 \in \mathscr{C}_k$. Since $q_3$ cannot lie in $\partial \mathscr{C}_k$, it must be interior to $\mathscr{C}_k$. 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*

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

*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

$$\xi'(t) = A(t)\xi(t) + B(t)\eta(t) + r(t, \xi, \eta) \tag{2.11}$$

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

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

$$\xi'(t) = A(t)\xi(t) \tag{2.12}$$

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

Let $\varepsilon>0$ be given. Choose $\sigma=\sigma(\varepsilon)$ so that $|\xi|+|\eta|\leqq\sigma$ implies $|r(t,\xi,\eta)|\leqq \varepsilon(|\xi|+|\eta|)$. Let $\|B(t)\|\leqq C_1$ 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

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

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

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

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

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

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

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

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

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

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

Gronwall's inequality yields

$$z(t)\leqq\left(Cz(0)+\frac{(C_1+\varepsilon)M|\eta(0)|}{\beta-\alpha}\right)e^{C\varepsilon t},\qquad \text{i.e.}$$

$$(2.16)\qquad |\xi(t)|\leqq\left(C|\xi(0)|+\frac{(C_1+\varepsilon)M|\eta(0)|}{\beta-\alpha}\right)e^{(C\varepsilon-\alpha)t},$$

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

$$(2.17)\qquad |\eta(t)|\leqq M|\eta(0)|\,e^{-\beta t}\leqq M|\eta(0)|.$$

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

$$|\xi(t)|\leqq\left(C+\frac{(C_1+\alpha/C)M}{\beta-\alpha}\right)\delta\leqq\frac{\sigma}{2},$$

$$|\eta(t)|\leqq M\delta\leqq\frac{\sigma}{2},\quad \text{i.e.}$$

$|\xi(t)|+|\eta(t)|\leqq\sigma$. From this it follows that (2.16) and (2.17) are valid for all $t\geqq 0$ for all solutions $(\xi,\eta)$ with $|\xi(0)|+|\eta(0)|\leqq\delta$. 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

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

Consider also the system

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

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 $\phi_1$ as $t\to\infty$, 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 $y(t)\to 0$ 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

$$x'=x\left(\frac{m_1(1+y_1-y_2-x)}{1+a_1+y_1-y_2-x}-D(t)\right),$$

(2.20) $$y_1'=-D(t)y_1,$$

$$y_2'=y_2\left(\frac{m_2(1+y_1-y_2-x)}{1+a_2+y_1-y_2-x}-D(t)\right).$$

We also consider

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

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, $y_2\to 0$ 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 $y=(y_1,y_2)\to 0$ as $t\to\infty$ 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 $\omega$-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 $\omega$-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 $\Delta$: $S+x_1+x_2=1$; $S,x_1,x_2\geqq 0$. Eliminating $S$ from (2.1) restricted to $\Delta$, leads to the equations

(3.1) $$x_1'=x_1f_1(t,x_1,x_2),\qquad x_2'=x_2f_2(t,x_1,x_2)$$

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 $x_1'=x_1f_1(t,x_1,0)$, 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) $$\begin{aligned}\xi_1'&=\{f_1(t,\phi_1,0)+\phi_1f_{11}(t,\phi_1,0)\}\xi_1+\phi_1f_{12}(t,\phi_1,0)\xi_2+g_1(t,\xi_1,\xi_2),\\ \xi_2'&=f_2(t,\phi_1,0)\xi_2+g_2(t,\xi_1,\xi_2)\end{aligned}$$

where $g_i=g_i(t,\xi_1,\xi_2)=O(\xi_1^2+\xi_2^2)$ as $(\xi_1,\xi_2)\to(0,0)$, 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

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

Let $B$ denote the Banach space of continuous $\omega$-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*

$$y_1' = a_{11}y_1 + a_{12}y_2, \qquad y_2' = a_{22}y_2 \tag{3.4}$$

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

$$\xi_1' = a_{11}\xi_1 + a_{12}\xi_2 + h_1, \qquad \xi_2' = a_{22}\xi_2 + h_2 \tag{3.5}$$

*has a unique solution* $(\xi_1, \xi_2) \in B \times B$. *The operator* $L: (B\times B) \to (B \times B)$ *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* $L_1, L_2: B \to B$ *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

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

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 $\|(\xi_1, \xi_2)\| \to 0$.

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* $\mu^*$ *(reciprocal of a nonzero eigenvalue) of A, and will occur if* $\mu^*$ *has odd multiplicity. In this case, the bifurcation point corresponds to a continuous branch of eigenvectors of* $T_\mu$ *in a neighbourhood of the zero of X.*

LEMMA 3.5 [13]. *Let* $T_\mu$, *A, N, X be as above, and let* $\Sigma$ *be the closure of the set of all nontrivial solutions of* $T_\mu x=x$ *as* $\mu$ *ranges over* **R**. *If* $\mu^*$ *is a simple characteristic value of A, then* $\Sigma$ *contains two subcontinua* $\Sigma_\infty^+$, $\Sigma_\infty^-$ *whose only point in common for* $\mu$ *near* $\mu^*$ *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 $\mu^*$ is a characteristic value of $L^*$ iff the system

$$\xi_1'=a_{11}\xi_1+a_{12}\xi_2,\qquad \xi_2'=(\mu^*b(t)-D(t))\xi_2 \tag{3.7}$$

has a nontrivial $\omega$-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 $(\mu^*)^2L^*$ is one-dimensional. Lemma 3.3(c) may now be used to show that $\mu^*$ 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 $\mu^*$, 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 $\mu^*$, 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 $\omega$. 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

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

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

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

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

Consider $\mu^*$ 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 $\lambda^*$ is the value of $\lambda_2$ 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, $\lim_{a_2 \to \infty} \lambda_2^*(a_2) = \langle S_1 \rangle$, 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 $m_2 \to \hat{m}_2$.

(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 $\mu^*$ 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 $m_2 \geqq 0$. Near to the bifurcation point, positive periodic solutions of (3.1) will satisfy $\max(x_1(t)+x_2(t)) < 1$. Since $\Sigma$ 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

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

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 $x_1(t)\to 0$ as $t\to\infty$. 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 $S(t)\to -a_i$ as $t\to\tau$, then $S'(t)\to\infty$ as $t\to\tau$. 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 $x_i'(t)\geqq x_i(t)(m_i-D(t))$ for all $t$, which would yield $x_i(t)\to\infty$ as $t\to\infty$, 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 $\mu$, 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

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

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

The first order terms in $\varepsilon$ 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

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

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

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

(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 $\Delta$ as $t \to \infty$. In the case that the solution $(S, x_1, x_2)$ of (2.1) restricted to $\Delta$ is locally (globally) exponentially asymptotically stable with respect to $\Delta$, than 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 $\Delta$ 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 $t \to \infty$. Extending this to periodic systems, Hale and Somolinos show that all solutions approach an $\omega$-periodic solution as $t \to \infty$. 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 $\Delta$ (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.