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COMPETITION IN THE UNSTIRRED CHEMOSTAT WITH PERIODIC INPUT AND WASHOUT*

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Abstract. The model of an unstirred chemostat is generalized to that of a chemostat with time-dependent input/washout rates. The novelty of the new model is that time periodicity appears in the boundary conditions. The asymptotic dynamics of the competition between two microbial populations is determined in terms of the corresponding period map, which is shown to preserve the standard competitive ordering. It is shown that the dynamics of competition is similar to that of a chemostat with constant boundary conditions. Simple criteria for coexistence versus competitive exclusion are presented.

Key words. microbial competition, chemostat, time-periodic boundary conditions, monotone dynamical system

AMS subject classifications. 92D25, 34C35, 35K57

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1. Introduction.

The chemostat represents a basic model of an open system in microbial ecology. In its simplest form, it consists of three vessels. The first, called the feed bottle, contains medium with all of the nutrients needed for growth in surplus except one, which hereafter is simply called the nutrient. The contents of the feed bottle are pumped at a constant rate into the second vessel, called the culture vessel or bioreactor. The culture vessel is charged with one or more populations of microorganisms. The contents of the culture vessel are pumped into the remaining vessel, called the overflow vessel, at a constant rate, keeping the volume of the reactor constant. The organisms compete for the nutrient in a purely exploitative manner. Basic assumptions include that the vessel is well mixed and that all other parameters (pH, temperature, etc.) are strictly controlled. The flow rate is assumed to be sufficient to preclude wall growth or the accumulation of metabolic products.

Let $S(t)$ denote the concentration of the nutrient in the culture vessel and $x_i(t)$, $i = 1, 2$, denote the concentration of the competitors. Let S^0 denote the concentration of the input nutrient and let D denote the dilution rate (flow rate/volume). If growth is assumed to be proportional to consumption then the basic equations take the form

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

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

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

The parameters γ_i, $i = 1, 2$, are yield constants. A typical choice for the f_i's is $f_i(S) = \frac{m_i S}{a_i + S}$.

This model is the starting point for many models of open systems. The literature spans biology, mathematics, chemical engineering, and physiology. Several such

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models and a large number of references can be found in [21]. A general survey of microbial competition can be found in [4].

The use of the unstirred chemostat removes the well-mixed hypothesis from the model. This model lets the contents diffuse through the culture vessel. This model has been developed in a sequence of papers [10, 12, 22, 24]. One space variable is sufficient to capture the basic consequences of spatial dependence (although multidimensional models were considered in [22]). The model corresponding to the basic chemostat on $[0, 1]$ takes the form

$$\begin{aligned} S_t &= dS_{xx} - f_1(S)\frac{u}{\gamma_1} - f_2(S)\frac{v}{\gamma_2}, \qquad 0 < x < 1 \ , \\ u_t &= du_{xx} + f_1(S)u, \qquad 0 < x < 1 \ , \\ v_t &= dv_{xx} + f_2(S)v, \qquad 0 < x < 1 \ . \end{aligned}$$

It is convenient to rescale u to $\frac{u}{\gamma_1}$ and v to $\frac{v}{\gamma_2}$ in order to reduce the number of parameters. This makes these variables nondimensional. One could also scale S to be nondimensional (say, by dividing by the maximum of the input concentration), but this doesn't alter the number of parameters so we will not do it. The scaled system takes the form

$$\begin{aligned} S_t &= dS_{xx} - f_1(S)u - f_2(S)v, \qquad 0 < x < 1 \ , \\ u_t &= du_{xx} + f_1(S)u, \qquad 0 < x < 1 \ , \\ v_t &= dv_{xx} + f_2(S)v, \qquad 0 < x < 1 \ . \end{aligned}$$

The boundary conditions at the left endpoint $x = 0$ can be written as

$$\begin{gathered} S_x(t, 0) = -S^0, \\ u_x(t, 0) = 0 \ , \qquad v_x(t, 0) = 0. \end{gathered}$$

The boundary conditions at $x = 1$ take the form

$$\begin{aligned} S_x(t, 1) + rS(t, 1) &= 0, \\ u_x(t, 1) + ru(t, 1) &= 0, \\ v_x(t, 1) + rv(t, 1) &= 0. \end{aligned}$$

The initial conditions for this system of partial differential equations are formulated as

$$S(0, x) = S_0(x) \ , \qquad u(0, x) = u_0(x) \ , \qquad v(0, x) = v_0(x)$$

with $0 \le x \le 1$, where all three functions S_0, u_0, and v_0 are nonnegative. See [21, Chapter 10] or any of the papers cited above for details.

One of the modifications of the basic well-mixed chemostat was to introduce periodic time dependence in the nutrient concentration and/or the flow rate to account for seasonal or daily changes. The theory was developed in a sequence of papers [2, 6, 9, 19, 25]. This paper makes the corresponding modification for the spatially dependent chemostat described above by replacing the constant nutrient input concentration and the flow rate by time-dependent functions.

2. The model. The equations remain the same as those above, but changes occur in the boundary conditions where the nutrient may be brought into the vessel at a periodic rate and the pump may operate so as to provide a periodic removal rate. The model takes the form

$$
\begin{aligned}
S_t &= dS_{xx} - f_1(S)u - f_2(S)v, \qquad 0 < x < 1, \\
u_t &= du_{xx} + f_1(S)u, \qquad 0 < x < 1, \\
v_t &= dv_{xx} + f_2(S)v, \qquad 0 < x < 1,
\end{aligned} \tag{2.1}
$$

$$
\begin{aligned}
&S_x(t,0) = -S^0(t), \\
&u_x(t,0) = 0, \qquad v_x(t,0) = 0, \\
&S_x(t,1) + r(t)S(t,1) = 0, \\
&u_x(t,1) + r(t)u(t,1) = 0, \\
&v_x(t,1) + r(t)v(t,1) = 0,
\end{aligned} \tag{2.2}
$$

with, of course, corresponding nonnegative initial conditions

$$
S(0,x) = S_0(x), \qquad u(0,x) = u_0(x), \qquad v(0,x) = v_0(x). \tag{2.3}
$$

There is no need to restrict the analysis to the Monod model for the functions $f_i(S)$. $f_i(S)$, $i = 1,2$, are assumed to be C^1 with $f_i'(S) > 0$, $f_i(0) = 0$, and with a finite limit as $S \to \infty$. The functions $S^0(t)$ and $r(t)$ are assumed to be C^1, ω-periodic, and positive on $[0,\omega]$. Although the restriction that $S^0(t)$ and $r(t)$ have a common period is strong, it does allow either one to be constant. If $r(t)$ is constant and $S^0(t)$ is periodic, the problem can be handled in a much simpler fashion than the analysis presented here. Thus the main emphasis is on $r(t)$ being periodic.

The assumption of strict positivity for $S^0(t)$ and $r(t)$ is rather technical, and we will use it to construct a certain pair of strict sub- and supersolutions in Lemma 3.2 needed for further analysis.

The approach to the problem will be through the period map and the theory of monotone dynamical systems. The novelty of the equations is that the periodicity appears in the boundary conditions. The equations will be manipulated to achieve a "limiting" system of two equations. The period mapping for the resulting system will generate a semidynamical system on the product of two Banach spaces with a competitive order. This is exactly the problem that has been considered in abstract form in [8] and [11]. Once it has been established that the period mapping is well defined (a problem is that the domain changes with time), then the machinery of the general case applies.

3. Reduction to a simpler system. In this section, it will be shown that the analysis requires the study of the dynamics of a related system with only two equations. To begin the study, we investigate the dynamics of the following problem:

$$
\phi_t = d\phi_{xx}, \tag{3.1}
$$

$$
\phi_x(t,0) = -S^0(t) \qquad \text{and} \qquad \phi_x(t,1) + r(t)\phi(t,1) = 0. \tag{3.2}
$$

It will be shown that there exists an ω-periodic positive solution of (3.1)–(3.2) which attracts every other positive solution at an exponential rate. To show the existence of such a solution, a theorem of Hess [7] is used which requires the existence of sub- and supersolutions.

Remark 3.1. For all $A, d > 0$ there exists a function $f : [0, +\infty) \to \mathbb{R}^+$ such that for all $t \in [0, +\infty)$:

$$0 < f(t) \le A \qquad \text{and} \qquad 0 < f'(t) \le 2df(t)\ .$$

Proof. Consider $y(t) = \frac{At}{t+1}$; then $0 < y(t) \le A$ and $0 < y'(t)$ for all $t \in [0, +\infty)$. Moreover, if $t \ge 1$, $y(t) \ge \frac{A}{2}$. In addition, when $t \ge 1/\sqrt{d} - 1$, $y'(t) \le dA$. So, if $t_0 = \max(1, 1/\sqrt{d} - 1)$, then for $t \ge t_0 : \ y'(t) \le 2dy(t)$. Define $f(t) = y(t + t_0)$ for $t \in [0, +\infty)$. ◻

LEMMA 3.2. *There exists a positive stable* ω*-periodic solution of* (3.1)–(3.2), *and all positive solutions converge to it.*

Proof. The existence of a positive stable periodic solution will follow from [7, Theorem 22.3] if there exists a properly ordered pair of positive strict sub- and supersolutions for (3.1)–(3.2). Let $\underline{S} = \inf_{[0,\omega]} S^0(t)$, $\overline{S} = \sup_{[0,\omega]} S^0(t)$, $\underline{r} = \inf_{[0,\omega]} r(t)$, and $\overline{r} = \sup_{[0,\omega]} r(t)$. Also define $S_* = \frac{1}{2}\underline{S}$, $S^* = 2\overline{S}$, and similarly $r_* = \frac{1}{2}\underline{r}$, $r^* = 2\overline{r}$. By construction, all four constants are strictly positive, so that $0 < 4S_* \le S^*$, and $0 < 4r_* \le r^*$. Finally, let $0 < A = \frac{S_*}{4+r^*}$.

By Remark 3.1 there exists a strictly increasing positive function $f(t)$, such that $0 < f(t) \le A$ and $0 < f'(t) \le 2\ d\ f(t)$ for $t \ge 0$.

We begin by constructing a strict subsolution. Define $\underline{\phi}$ as

$$\underline{\phi}(t,x) = f(t)\left(\frac{1}{2} - x\right)^2 + S_*\left(\frac{1+r^*}{r^*} - x\right), \qquad x \in [0,1], \qquad t \ge 0.$$

By construction, $\underline{\phi}$ satisfies the following inequalities:

(i) $\underline{\phi}_t = f'(t)(\frac{1}{2} - x)^2 \le \frac{1}{4}f'(t) \le 2df(t) = d\underline{\phi}_{xx},\ x \in (0,1),\ t \ge 0;$

(ii) $\underline{\phi}_x(t,0) = -f(t) - S_* \ge -\frac{5}{4}S_* \ge -\underline{S} \ge -S^0(t),\ t \ge 0;$

(iii) $\underline{\phi}_x(t,1) + r(t)\underline{\phi}(t,1) \le f(t) - S_* + \overline{r}(\frac{f(t)}{4} + \frac{S_*}{r^*}) \le f(t)(1 + \frac{r^*}{4}) - \frac{S_*}{2} \le -\frac{S_*}{4} \le 0,\ t \ge 0.$

It is also clear that since $f(t)$ is a strictly increasing function of t, so is $\underline{\phi}$. Therefore, $\underline{\phi}$ is a strict subsolution of (3.1)–(3.2).

Similarly, we construct a strict supersolution. Define $\overline{\phi}$ as

$$\overline{\phi}(t,x) = -f(t)\left(\frac{1}{2} - x\right)^2 + S^*\left(\frac{1+r_*}{r_*} - x\right), \qquad x \in [0,1], \qquad t \ge 0.$$

Then by construction, $\overline{\phi}$ satisfies the following inequalities:

(ia) $\overline{\phi}_t = -f'(t)(\frac{1}{2} - x)^2 \ge -\frac{1}{4}f'(t) \ge -2df(t) = d\underline{\phi}_{xx},\ x \in (0,1),\ t \ge 0;$

(iia) $\overline{\phi}_x(t,0) = f(t) - S^* \le \frac{1}{4}S_* - S^* \le -\overline{S} \le -S^0(t),\ t \ge 0;$

(iiia) $\overline{\phi}_x(t,1) + r(t)\overline{\phi}(t,1) \ge -f(t) - S^* + \underline{r}(-\frac{f(t)}{4} + \frac{S^*}{r_*}) \ge -f(t)(1 + \frac{r^*}{4}) + S^* \ge \frac{3}{4}S^* \ge 0.$

Since $\overline{\phi}$ is a strictly decreasing function of t, it is a strict supersolution of (3.1)–(3.2).

The pair of functions $\overline{\phi}$ and $\underline{\phi}$ is ordered because

$$\overline{\phi} - \underline{\phi} = -\,2f(t)\left(\frac{1}{2} - x\right)^2 + S^*\left(\frac{1+r_*}{r_*} - x\right) - S_*\left(\frac{1+r^*}{r^*} - x\right),\ \ x \in [0,1],\ t \ge 0,$$

$$\overline{\phi} - \underline{\phi} = -\frac{1}{2}f(t) + \frac{S^*}{r_*} - \frac{S_*}{r^*} + (S^* - S_*)(1-x)$$
$$\geq -\frac{1}{2}f(t) + \frac{S^*}{r_*} - \frac{S_*}{r^*} \geq \frac{S_*}{r^*} > 0$$

for $x \in [0,1], t \geq 0$, and since $\underline{\phi} \geq S_*/r^* > 0$, the functions $\underline{\phi}$ and $\overline{\phi}$ form an ordered pair of positive strict sub- and supersolutions of (3.1)–(3.2).

Thus, there exists a positive stable ω-periodic solution $\phi(t,x)$ of (3.1)–(3.2). The convergence result will follow from Lemma 3.3 below. ∎

Let $w(t,x) = \phi(t,x) - (S(t,x) + u(t,x) + v(t,x))$, so that $S(t,x) = \phi(t,x) - w(t,x) - u(t,x) - v(t,x)$. Adding the equations, initial conditions, and boundary conditions in (2.1)–(2.3), we can rewrite the system in terms of w, u, and v:

$$\begin{aligned} w_t &= dw_{xx}, \\ u_t &= du_{xx} + uf_1(\phi - w - u - v), \\ v_t &= dv_{xx} + vf_2(\phi - w - u - v), \end{aligned} \tag{3.3}$$

with the boundary conditions

$$\begin{aligned} w_x(t,0) &= 0, \qquad w_x(t,1) + r(t)w(t,1) = 0, \\ u_x(t,0) &= 0, \qquad u_x(t,1) + r(t)u(t,1) = 0, \\ v_x(t,0) &= 0, \qquad v_x(t,1) + r(t)v(t,1) = 0, \end{aligned} \tag{3.4}$$

and the initial conditions

$$\begin{aligned} w(0,x) &= \phi(0,x) - (S_0(x) + u_0(x) + v_0(x)), \\ u(x,0) &= u_0(x), \\ v(x,0) &= v_0(x). \end{aligned} \tag{3.5}$$

The advantage of writing the system in this form is that the first equation is uncoupled from the other two, and its asymptotic behavior can be studied independently. The uncoupled problem is

$$\begin{aligned} &w_t = dw_{xx}, \\ &w_x(t,0) = 0, \qquad w_x(t,1) + r(t)w(t,1) = 0. \end{aligned} \tag{3.6}$$

Moreover, the difference between the periodic solution whose existence was shown in Lemma 3.2 and any other solution of (3.1)–(3.2) also satisfies (3.6).

The system (3.3)–(3.5) is equivalent to the original system (2.1)–(2.3) by means of the inverse transformation $S(t,x) = \phi(t,x) - w(t,x) - u(t,x) - v(t,x)$. Therefore, any conclusion about the asymptotic dynamics of (3.3)–(3.5) can be immediately translated to the system written in the original coordinates, that is, the system (2.1)–(2.3).

The following lemma represents an important step in reducing the original system (2.1)–(2.3) to a monotone system and concludes the proof of Lemma 3.2.

LEMMA 3.3. *For any nonnegative solution $w(t,x)$ of* (3.6) *there exists $\alpha > 0$, such that $|w(t,x)| = O(e^{-\alpha t})$ as $t \to \infty$.*

Proof. The proof will be by the standard comparison technique for parabolic equations; see, for example, [23, Theorem 10.1]. The theorem applies to two nonnegative functions w_1 and w_2, such that $w_1(0,x) = w_2(0,x)$,

$$(w_i)_t = d(w_i)_{xx}, \qquad i = 1, 2,$$

and

$$(w_1)_x(t,0) \le (w_2)_x(t,0),$$

$$w_1(t,1) + r(t)(w_1)_x(t,1) \ge w_2(t,1) + r(t)(w_2)_x(t,1)$$

for $t \ge 0$. It concludes that $w_1(t,x) \ge w_2(t,x)$ for $t \ge 0$ and $x \in [0,1]$.

In this setting, let $w_1 = \hat{w}$ and $w_2 = w$, where $\hat{w}$ solves

$$\hat{w}_t = d\hat{w}_{xx},$$

$$\hat{w}_x(t,0) = \hat{w}_x(t,1) + \underline{r}\hat{w}(t,1) = 0,$$

and where $\underline{r} = \inf_{[0,\omega]} r(t)$. Then, since

$$\hat{w}_x(t,1) + r(t)\hat{w}(t,1) \ge \hat{w}_x(t,1) + \underline{r}\hat{w}(t,1) = 0 = w_x(t,1) + r(t)w(t,1),$$

it follows that $\hat{w}(t,x) \ge w(t,x)$ for $t \ge 0$ and $x \in [0,1]$.

It has been shown in [12] that there exists $\alpha > 0$, such that

$$|\hat{w}(t,x)| = O(e^{-\alpha t}) \text{ as } t \to +\infty,$$

and this holds for any solution of (3.6) with a nonnegative initial condition. Therefore,

$$|w(t,x)| \le |\hat{w}(t,x)| = O(e^{-\alpha t}) \text{ as } t \to +\infty.$$

Thus any solution $w(t,x)$ tends to the zero function at an exponential rate. ∎

This has a biologically important interpretation. The distribution of the total biomass $S + u + v$ approaches some periodic distribution ϕ independently of the initial conditions. In terms of the system (3.3)–(3.5) this means that the set $w = 0$ is an invariant set which attracts the solutions at an exponential rate. Therefore, it is necessary to first study the behavior of solutions of (3.3)–(3.5) on this exponentially attracting set.

Setting $w(t,x) = 0$, or equivalently, $S(t,x) + u(t,x) + v(t,x) = \phi(t,x)$ reduces the full system to the following periodic-parabolic system:

$$u_t = du_{xx} + uf_1(\phi - u - v),$$

$$v_t = dv_{xx} + vf_2(\phi - u - v),$$

together with corresponding boundary conditions, and initial conditions inherited from (3.3)–(3.5). This system is called the *limiting system*, and since S must be a nonnegative quantity, the biologically relevant region for the limiting system is the set $\{u \ge 0,\ v \ge 0,\ S = \phi - u - v \ge 0\}$.

4. The limiting system. In this section we set up the period map for the limiting system obtained at the end of the last section:

$$u_t = du_{xx} + uf_1(\phi - u - v), \tag{4.1}$$

$$v_t = dv_{xx} + vf_2(\phi - u - v),$$

with the boundary conditions

$$u_x(t,0) = v_x(t,0) = 0,$$

$$u_x(t,1) + r(t)u(t,1) = v_x(t,1) + r(t)v(t,1) = 0, \tag{4.2}$$

where $\phi(t,x)$ is a smooth, positive, and ω-periodic function.

In this and the following sections we need some standard notions of order. Let X_i be ordered Banach spaces with positive cones X_i^+ for $i = 1, 2$. Assume that $\mathrm{Int}X_i^+ \neq \emptyset$. If $x_i, y_i \in X_i$, we say that $x_i \leq y_i$ (x_i is less than or equal to y_i) if $y_i - x_i \in X_i^+$, $x_i < y_i$ (x_i is strictly less than y_i) if $x_i \leq y_i$ and $x_i \neq y_i$, and $x_i << y_i$ (x_i is strongly less than y_i) if $y_i - x_i \in \mathrm{Int}X_i^+$.

Let X be an ordered Banach space with order $\leq$. Given two points $a, b \in X$, the *closed order interval* $[a, b]$ and the *open order interval* (a, b) are defined as follows:

$$[a, b] = \{c \in X | a \leq c \leq b\}, \qquad (a, b) = \{c \in X | a << c << b\}.$$

On the space $X = X_1 \times X_2$, define the *competitive ordering* as the ordering generated by the cone $K = X_1^+ \times (-X_2^+)$. In particular, if $x_1, x_2 \in X_1$ and $y_1, y_2 \in X_2$, we say that

$$(x_1, y_1) \leq_K (x_2, y_2) \text{ if } x_1 \leq x_2,\ y_1 \geq y_2,$$

$$(x_1, y_1) <_K (x_2, y_2) \text{ if } (x_1, y_1) \leq_K (x_2, y_2), (x_1, y_1) \neq (x_2, y_2),$$

and

$$(x_1, y_1)\ <<_K (x_2, y_2) \text{ if } x_1 << x_2,\ y_1 >> y_2.$$

An example of such an ordering is the Banach space $X = C^0(I) \times C^0(I)$ of pairs of continuous functions defined over the common interval I. The order cone C^+ in $C^0(I)$ is the cone of nonnegative functions on I, defining the natural order on the space of continuous functions. The corresponding competitive order cone K in the product space is defined as $K = C^+ \times (-C^+) = C^+ \times C^-$. It is evident that K has a nonempty interior in X, so all three order relationships are well defined.

A mapping $T : X \to X$ is called *K-monotone* (*K-order preserving*) if

$$x_1 \leq_K x_2 \text{ implies } T(x_1) \leq_K T(x_2) \text{ for all } x_1, x_2 \in X.$$

T is called *strictly K-monotone* (*strictly K-order preserving*) if

$$x_1 <_K x_2 \text{ implies } T(x_1) <_K T(x_2)$$

and *strongly K-monotone* (*strongly K-order preserving*) if

$$x_1 <_K x_2 \text{ implies } T(x_1)\ <<_K T(x_2).$$

It will always be clear from the context which ordering is used in each particular situation, or for each particular space. We will omit the K-subscript when speaking of either an ordering of real numbers or the natural ordering in C^0.

THEOREM 4.1. *Consider the system* (4.1)–(4.2). *Let*

$$\Omega = \{(u,v) \in C_+ \times C_+ : \; u(x) \geq 0, \; v(x) \geq 0, \; u(x)+v(x) \leq \phi(x,0) \\ \text{for all } x \in [0,1]\}.$$

For every pair $(u_0, v_0) \in \Omega$, *there exists a unique nonnegative solution* (u,v) *of* (4.1)–(4.2) *which exists at least for* $0 \leq t \leq \omega$. $(u(t), v(t))$ *becomes a classical solution for* $t > 0$. *Moreover*, $u(t,x) + v(t,x) \leq \phi(t,x)$ *for any* $0 \leq t \leq \omega$ *and* $x \in [0,1]$. *In particular*, *the period map*

$$P(u_0, v_0) = (u(\omega), v(\omega))$$

maps Ω *into* Ω *and is Fréchet differentiable*, *compact*, *strictly* K*-order preserving in* Ω, *and strongly* K*-order preserving in* Int Ω.

The first lemma is necessary in the proof of existence and to set up the dynamics. It is a special case of results in [17] and [26], formulated for our purposes. (See also [14] and [16].) We provide some of the details to guide the reader.

LEMMA 4.2. *Consider the time-dependent differential operator* $A(t)$*:*

$$A(t)u = du_{xx} + a(t,x)u_x + b(t,x)u, \qquad t > 0, \qquad x \in (0,1), \tag{4.3}$$

where the functions $a(t,x)$ *and* $b(t,x)$ *are continuously differentiable in both* t *and* x *and* ω*-periodic in* t. *If the domain of* $A(t)$ *is time independent*,

$$D = D(A(t)) = \{u \in C^2([0,1], \mathbb{R}) : u_x(t,0) = u_x(t,1) = 0\},$$

then for each $t \geq 0$, $A(t)$ *is closed in* C *and generates an analytic semigroup* $U_t(s)$ *on* C. *Moreover, there exists a unique evolution operator* $U(t,s)$ *associated with* (4.3), *such that*

(1) $\|U(t,s)\| \leq K$ *for* $0 \leq s \leq t \leq \omega$.

(2) *For* $0 \leq s < t \leq \omega$, $U(t,s) : C \to D$, $U(t,s)$ *is Fréchet differentiable in* C, *and*

$$\frac{\partial}{\partial t} U(t,s) = A(t)U(t,s), \qquad 0 \leq s < t \leq \omega.$$

(3) *For every* $u \in C$, $u(x) \geq 0$, *and* $u(x) \not\equiv 0$ *on* $[0,1]$, $U(t,s)u(x) > 0$ *for* $x \in [0,1]$ *and* $0 \leq s < t \leq \omega$.

Proof. The operator $A(t)$ is uniformly strongly elliptic for $t \in [0,\omega]$, since its principal part is a time-independent one-dimensional Laplace operator. In addition, the domain $[0,1]$ has a two-point boundary which can be thought of as infinitely regular of class C^∞. Also, since the domain $[0,1]$ is compact (and thus bounded), the completion of D in the C-norm is the space $C[0,1]$.

Theorem 2 of [26] states that for every $t \in [0,\omega]$, the operator $A(t)$ generates an analytic semigroup in the space $C[0,1]$ with the corresponding supremum norm. We denote this semigroup by $U_t(s)$, $s \geq 0$, $0 \leq t \leq \omega$.

Let

$$r = \sup_{(t,x) \in [0,\omega] \times [0,1]} |b(t,x)|,$$

and let

$$B_k(t)u = du_{xx} + a(t,x)u_x + (k + b(t,x))u, \qquad t > 0, \qquad x \in (0,1),$$

or, $B_k(t) = A(t) + kI$. If $k > r$, then the coefficient $(k + b(t,x))$ is strictly positive on $[0,\omega] \times [0,1]$.

If $B_k(t)$ generates an evolution system $\overline{U}(t,s)$ with properties (1)–(3), then $A(t)$ generates the corresponding evolution system $U(t,s) = e^{-k(t-s)}\overline{U}(t,s)$ with the same properties, and vice versa. Indeed, for $0 \le s \le t \le \omega$,

$$\|U(t,s)\| \le \|e^{-k(t-s)}\overline{U}(t,s)\| \le e^{k\omega}\|\overline{U}(t,s)\|,$$

and if $\overline{U}(t,s)$ is Fréchet differentiable in C, then so is $U(t,s)$, and

$$\frac{\partial}{\partial t}U(t,s) - A(t)U(t,s) = e^{-k(t-s)}\frac{\partial}{\partial t}\overline{U}(t,s) - ke^{-k(t-s)}\overline{U}(t,s)$$

$$- (B_k(t) - kI)e^{-k(t-s)}\overline{U}(t,s) = e^{-k(t-s)}\left(\frac{\partial}{\partial t}\overline{U}(t,s) - B_k(t)\overline{U}(t,s)\right) = 0$$

because $B_k(t)$ generates $\overline{U}(t,s)$. The third property is satisfied automatically because U equals $\overline{U}$ multiplied by a strictly positive function. Therefore, it suffices to show that $B_k(t)$ generates $\overline{U}(t,s)$ with the required properties (1)–(3).

Observe that the domain of $A(t)$ is time independent. Since $A(t)$ is uniformly strongly elliptic for $t \in [0,\omega]$, one can repeat the steps in the proof of Lemma 6.1 of Pazy [17, p. 227] to show that there exists a sufficiently large constant $k > r$, such that the family of operators $\{B_k(t) = A(t) + kI,\ t \in [0,\omega]\}$ satisfies the following two conditions. First, the resolvent $R(\lambda : B_k(t))$ exists for all $\Re\,\lambda \le 0$, and there exists a constant $M > 0$, such that

$$\|R(\lambda\ :\ B_k(t))\| \le \frac{M}{|\lambda| + 1}$$

for all $\Re\,\lambda \le 0$ and $t \in [0,\omega]$. Second, there exists a constant $L > 0$, such that

$$\|(B_k(t) - B_k(s))B_k(\tau)^{-1}\| \le L|t - s|$$

for $s, t, \tau \in [0,\omega]$. Consequently, Theorem 6.1 of Pazy [17, p. 150] states that there exists a unique evolution system $\overline{U}(t,s)$ with the required properties (1)–(2) for the family of operators $\{B_k(t)\}$.

The third property of $\overline{U}(t,s)$ follows from the standard maximum principle for parabolic equations [7, Lemma 13.4]. Indeed, if $u(x) \ge 0$ and $u(x) \not\equiv 0$, then for $0 < t \le \omega$ the function $u(t,x) = \overline{U}(t,0)u_0(x)$ is the classical solution of

$$u_t = B_k(t)u = du_{xx} + a(t,x)u_x + (k + b(t,x))u, \qquad t > 0, \qquad x \in (0,1),$$

with the nonnegative initial condition u_0 which is not identically zero. Consequently, $u(t,x)$ is strictly positive because $k + b(t,x) > 0$ by our choice of k. Thus, $\overline{U}(t,s)$ satisfies the property (3), and so does $U(t,s)$. ∎

The next lemma establishes the existence results necessary to define the period map on $C[0,1] \times C[0,1]$.

LEMMA 4.3. *For each set of initial conditions* (u_0, v_0) *there exists a unique solution* (u, v) *of* (4.1)–(4.2). *If the initial condition consists of smooth functions satisfying the* *boundary conditions, then* (u, v) *is a classical solution of* (4.1)–(4.2) *for* $t \geq 0$. *If the initial condition consists of only continuous functions*, (u, v) *becomes classical for* $t > 0$. *All solutions exist at least for* $t \in [0, \omega]$.

Proof. Consider the following change of variables:

$$u(t, x) = e^{g(t,x)} \hat{u}(t, x),$$

$$v(t, x) = e^{g(t,x)} \hat{v}(t, x),$$

where $g(t, x) = -\frac{x^2}{2} r(t)$. It will be used to move between the problem with periodic boundary conditions and the form with Neumann conditions at the expense of a time-dependent operator.

After some computation the system takes the form

$$\hat{u}_t = A(t)\hat{u} + e^g \hat{u} f_1(\phi - e^g \hat{u} - e^g \hat{v}), \tag{4.4}$$

$$\hat{v}_t = A(t)\hat{v} + e^g \hat{v} f_2(\phi - e^g \hat{u} - e^g \hat{v}),$$

where

$$A(t)w = dw_{xx} - 2dxr(t)w_x + \left(x^2 r^2(t) - dr(t) - \frac{x^2}{2} r'(t) \right) w,$$

and the boundary conditions are zero Neumann conditions.

The operator $A(t)$ is of the type considered in Lemma 4.2 and generates a smooth evolution system $U_A(t, s)$ on $C[0, 1]$. Let $U(t, s) = (U_A(t, s), U_A(t, s))$, $\hat{w} = (\hat{u}, \hat{v})$, and

$$F(t, \hat{w}) = \Big(e^g \hat{u} f_1(\phi - e^g \hat{u} - e^g \hat{v}), e^g \hat{v} f_2(\phi - e^g \hat{u} - e^g \hat{v}) \Big).$$

It is clear that $F(t, \hat{w})$ is a smooth map $F : \mathbb{R} \times (C[0, 1])^2 \to (C[0, 1])^2$, which is ω-periodic in time. Given an initial condition $\hat{w}_0 \in (C[0, 1])^2$, the mild solution of (4.4) is defined to be a continuous vector function $\hat{w}(t)$, such that

$$\hat{w}(t) = U(t, 0)\hat{w}_0 + \int_0^t U(t, s) F(s, \hat{w}(s))\, ds, \;\; s \in [0, \omega + \sigma), \tag{4.5}$$

for some $\sigma > 0$. It is known (see, for instance, [17, Theorem 1.2, p. 184]) that this integral equation has a unique solution. Moreover, for $t > 0$, $\hat{w}(t)$ is a smooth vector function, and thus a classical solution of (4.4). In addition, if $\hat{w}_0$ is smooth, then $\hat{w}(t)$ is a classical solution for $t \geq 0$. The existence of solutions is guaranteed for all t up to $t = \omega$. Finally, by making the inverse change of variables, the vector function $w = (u, v) = (e^g \hat{u}, e^g \hat{v})$ becomes the solution of (4.1)–(4.2) with the required properties. ∎

Proof of Theorem 4.1. For any pair of nonnegative functions $w_0 = (u_0, v_0)$, let $\hat{w}_0 = (\hat{u}_0(x), \hat{v}_0(x)) = (e^{-g(0,x)} u_0(x), e^{-g(0,x)} v_0(x))$, and let $\hat{w}(t, x)$ be the solution of (4.4) satisfying the initial condition $\hat{w}(0, x) = (\hat{u}_0(x), \hat{v}_0(x))$, $x \in [0, 1]$. Then $w(t, x) = (e^g \hat{u}, e^g \hat{v})$ solves (4.1)–(4.2) with the corresponding initial condition $w_0(x)$.

It follows from Lemma 4.2, property (3), that if $u_0(x), v_0(x) \geq 0$, then both coordinates of $U(t, s)w_0$ are nonnegative for $0 \leq s \leq t \leq \omega$. If, in addition, $u_0 \not\equiv 0$ and $v_0 \not\equiv 0$, then the coordinates of $U(t, s)w_0$ are strictly positive for $0 \leq s < t \leq \omega$. If, moreover, $u(t, x) + v(t, x) \leq \phi(t, x)$ for all $0 \leq t \leq \omega$, then both nonlinearities f_1 and f_2 are nonnegative, and so are the solutions of the nonlinear system.

To complete the proof, it remains only to show that an arbitrary nonnegative solution of (4.1)–(4.2) such that $u(0,x)+v(0,x) \le \phi(0,x)$ satisfies $u(t,x)+v(t,x) \le \phi(t,x)$ for all $0 \le t \le \omega$ and $x \in [0,1]$.

Let $\overline{f}(p) = \max(f_1(p), f_2(p))$ for $0 \le p \le \infty$ be the upper envelope of f_1 and f_2. It is clear that $\overline{f}$ is strictly monotone because both f_1 and f_2 are strictly monotone. Given a solution $(u(t,x), v(t,x))$ of (4.1)–(4.2) with $u(0,x)+v(0,x) \le \phi(0,x)$, let $z(t,x) = u(t,x)+v(t,x)$. In the region $0 \le z \le \phi$, z satisfies the following inequality:

$$z_t = dz_{xx} + uf_1(\phi - z) + vf_2(\phi - z) \le dz_{xx} + z\overline{f}(\phi - z),$$

and the corresponding boundary conditions $z_x(t,0) = z_x(t,1) + r(t)z(t,1) = 0$.

Let $\overline{F}(p) = M\overline{f}(\phi - p)$ for $0 \le p \le \phi$, where $M = \max_{x,t}\phi(t,x), x \in [0,1],\ t \in [0,\omega]$. Then obviously $pf_i(\phi - p) \le \overline{F}(p)$ for $p \le \phi$ and $i = 1,2$. Therefore,

$$z_t \le dz_{xx} + \overline{F}(z) = dz_{xx} + M\overline{f}(\phi - z).$$

Let $\tilde{z}$ be the solution of

$$\tilde{z}_t = d\tilde{z}_{xx} + \overline{F}(\tilde{z}), \tag{4.6}$$

with the boundary conditions

$$\tilde{z}_x(t,0) = -S^0(t),\ \tilde{z}_x(t,1) + r(t)\tilde{z}(t,1) = 0 \tag{4.7}$$

and the initial condition $\tilde{z}(0,x) = z(0,x),\ x \in [0,1]$. Equation (4.6) is monotone in $\tilde{z}$ because $\overline{F}(\tilde{z})$ is a strictly decreasing function of $\tilde{z}$. In addition, the function $\phi(t,x)$ is itself a solution of (4.6). Since $\tilde{z}$ and ϕ are ordered at $t=0$, that is, $\tilde{z}(0,x) = u(0,x)+v(0,x) \le \phi(0,x)$, then $\tilde{z}(t,x) \le \phi(t,x)$ for $0 \le t \le \omega$.

Finally, since for $0 \le t \le \omega$,

$$z_t - dz_{xx} - z\overline{f}(\phi - z) \le 0 = \tilde{z}_t - d\tilde{z}_{xx} - \tilde{z}\overline{f}(\phi - \tilde{z}),$$

$$z_x(t,0) = 0 \ge -S^0(t) = \tilde{z}_x(t,0),$$

$$z_x(t,1) + r(t)z(t,1) = \tilde{z}_x(t,1) + r(t)\tilde{z}_x(t,1) = 0,$$

and

$$z(0,x) = u(0,x) + v(0,x) = \tilde{z}(0,x),$$

we can use the comparison principle to conclude that $z(t,x) \le \tilde{z}(t,x)$ for $0 \le t \le \omega$ and, consequently, that $u(t,x)+v(t,x) = z(t,x) \le \phi(t,x)$ for $0 \le t \le \omega$.

In particular, we apply this inequality at $t = \omega$ to show that Ω is positively invariant with respect to the period map P associated with (4.1)–(4.2). P is Fréchet differentiable and compact on Ω because the nonlinearity F is smooth, and the evolution system U is compact and smooth.

It is easy to see that if $u(t,x)+v(t,x) \le \phi(t,x)$, then the partial derivatives $(uf_1(\phi - u - v)_v$ and $(vf_2(\phi - u - v))_u$ are nonpositive. Since the evolution system U is strictly positive (the property (3) in Lemma 4.2), the period map P is strictly K-order preserving in Ω. Moreover, since in Int Ω the corresponding partial derivatives are strictly negative, P is strongly K-order preserving in Int Ω. ∎

We intend to describe the dynamics of the limiting system (4.1)–(4.2) in terms of its period map. Theorem 4.1 guarantees that the period map

$$P : \Omega \to \Omega,\ \Omega = \{(u,v) \in C_+[0,1] \times C_+[0,1],\ u(x)+v(x) \le \phi(0,x),\ x \in [0,1]\},$$

is well defined and enjoys the following properties:

(P1) P is Fréchet differentiable and compact in C^0 topology.

(P2) P is strictly K-order preserving on Ω, and strongly K-order preserving in the interior Int Ω of Ω. K is the cone $C_+ \times C_-$ in the product Banach space $C \times C$.

(P3) The following sets are positively invariant under P: $\Omega \bigcap (0 \times C_+[0,1])$ and $\Omega \bigcap (C_+[0,1] \times 0)$. Indeed, since the solutions are unique, then $u_0(x) \equiv 0$ implies $u(t,x) = 0$ for all $t \geq 0$. The case $v_0(x) \equiv 0$ is similar.

(P4) Let P_u be the restriction of P on $\Omega \bigcap (C_+[0,1] \times 0)$, and let P_v be the restriction of P on $\Omega \bigcap (0 \times C_+[0,1])$. Both P_u and P_v are strictly monotone in the usual sense of continuous functions; that is, if $0 \leq u_1 < u_2$ then $0 \leq P_u(u_1) < P_u(u_2)$, and similarly if $0 \leq v_1 < v_2$, then $0 \leq P_v(v_1) < P_v(v_2)$.

5. Periodic solutions of the limiting system. The next step is to put the limiting system of the previous section into the form of the general competition theory [11, 8] in order to make use of the general machinery. The sets $u \equiv 0$ or $v \equiv 0$ are clearly invariant sets for the system (4.1)–(4.2) and correspond to single population growth. We need some elementary facts about the solution in these sets. If we set $u \equiv 0$, then the system (4.1)–(4.2) reduces to

$$v_t = dv_{xx} + f_2(\phi - v)v, \tag{5.1}$$

$$v_x(t,0) = v_x(t,1) + r(t)v(t,1) = 0,$$

$$v(0,x) = v_0(x) \geq 0.$$

The linearized equation about the zero solution of (5.1) becomes

$$w_t = dw_{xx} + f_2(\phi(t,x))w \ , \ w(0,x) = w_0(x). \tag{5.2}$$

Let $T_v = W_v(\omega, 0)$, where $W_v(t,\tau)$ is the evolution operator associated with (5.2). Since the boundary of $C_+ \times C_+$ is positively invariant under P, we can, without loss of generality, consider the restriction P_v of P to study the evolution of the population v alone. It is evident that P_v is differentiable at $v = 0$, and $P_v'(0) = T_v$.

Note that setting $v \equiv 0$ and considering the corresponding single population equation for u yields a similar linearized equation where f_1 is replaced with f_2, so that $P_u'(0) = T_u$.

LEMMA 5.1.

(a) *If the principal eigenvalue* λ *of* T_v *satisfies* $\lambda > 1$, *then the zero solution of* (5.1) *is linearly unstable*, *and there exists a unique positive periodic solution* $V = V(t,x)$ *of* (5.1) *which attracts all positive solutions of* (5.1).

(b) *If* $\lambda < 1$, *then the solution* $v(t) \equiv 0$ *is linearly stable* (*moreover*, *order stable*) *and attracts all positive solutions of* (5.1).

Proof. Obviously, if $\lambda > 1$, $v(t) \equiv 0$ is linearly unstable. Since the period map P_v is strictly monotone, the principal eigenfunction must be positive by the Krein–Rutman theorem [13]. Let ψ be this principal eigenfunction; then

$$P_v(\alpha\psi) = \lambda\alpha\psi + o(\alpha) >> \alpha\psi$$

for sufficiently small α, that is, $\alpha \in (0, \epsilon)$. Define $\{v_k\}$ as $v_k = P_v^k(\alpha\psi)$, $k = 0, 1, 2, \ldots$, for some $\alpha \in (0, \epsilon)$. In view of the preceding inequality this is a monotone increasing sequence $\{v_k, k \in 0, 1, 2, \ldots\}$ such that $v_0 >> 0$ and $P_v(v_{k-1}) = v_k >> v_{k-1}$. This sequence converges to a positive function v_∞ since the sequence v_k is bounded from above by the positive function

$$\overline{\phi}(x) = \sup_{t\in[0,\omega]} \phi(t,x).$$

The continuity of P_v implies that v_∞ is a fixed point of P_v: $P_v(v_\infty) = v_\infty$. Therefore, the corresponding solution $V(t,x)$ with the initial condition $V(0,x) = v_\infty(x)$ is a periodic solution of (5.1), and the vector function $(0, V(t,x))$ is a periodic solution of (4.1)–(4.2).

The uniqueness of $V(t,x) > 0$ is equivalent to the uniqueness of a positive fixed point of P_v. Therefore, it suffices to show that $v_\infty > 0$ is the only fixed point of P_v.

We know that $P_v(0) = 0$, and P_v is strictly monotone away from zero. Moreover, P_v is *strongly sublinear* in the following sense: if $v > 0$ and $\eta \in (0,1)$, then $P_v(\eta v) >> \eta P_v(v)$ (see Smith [18] or Hess [7] for further references).

To see this, let $v > 0$ and $\eta \in (0,1)$. We use the equivalent integral equation

$$P_v(v) = U(\omega,0)v(0) + \int_0^\omega U(\omega,s)v(s)f_2(\phi - v(s))\ ds,$$

where $U(t,s)$ is the evolution system associated with the linear part of (5.1). The existence of $U(t,s)$ is guaranteed by Lemma 4.2. Now, since $f_2(\phi - v)$ is strictly decreasing in v for any strictly increasing function f_2, then, since $\eta v < v$ for $0 < v \le \phi$,

$$f_2(\phi - \eta v) > f_2(\phi - v) \quad \text{for all} \quad \eta \in (0,1).$$

Using the linearity of U, one has

$$\begin{aligned} P_v(\eta v) &= U(\omega,0)\eta v + \int_0^\omega U(\omega,s)\eta v(s) f_2(\phi - \eta v(s))\ ds \\ &> U(\omega,0)\eta v + \int_0^\omega U(\omega,s)\eta v(s) f_2(\phi - v(s))\ ds \\ &= \eta\Big(U(\omega,0)v + \int_0^\omega U(\omega,s)v(s)f_2(\phi - v(s))\ ds\Big) = \eta P_v(v). \end{aligned}$$

Thus, P_v is strongly sublinear: $P_v(\eta v) >> \eta P_v(v)$.

It is well known from Amann [1, Theorem 22.4] that P_v can have at most one positive fixed point v_∞. We apply Theorem 5.1, part (b) of Hess [7, p. 17], which states that if there exists a unique positive fixed point of a strongly sublinear map P_v, $v_\infty > 0$, in our case, then it attracts all positive points of C_+.

It remains to show that $V(t,x)$ attracts all positive solutions of (5.1). Let $W(t,x)$ be a positive solution of (5.1) with the initial condition $w_0(x) > 0$, and let $w_k(x) = W(k\omega, x)$ for $k = 0,1,2,\ldots$. Then by the definition of P_v, $w_k = P_v^k(w_0)$ for $k = 0,1,2,\ldots$. Now, since v_∞ attracts all positive points, $w_k \to v_\infty$ as $k \to \infty$.

We use the integral equation once again. Since both W and V are solutions of (5.1), then

$$W(t,x) = U(t,k\omega)W(k\omega,x) + \int_{k\omega}^t U(t,s)W(s,x)f_2(\phi - W(s,x))\,ds,$$

$$V(t,x) = U(t,k\omega)V(k\omega,x) + \int_{k\omega}^t U(t,s)V(s,x)f_2(\phi - V(s,x))\,ds$$

for $t \in [k\omega, (k+1)\omega]$, and $x \in [0,1]$.

Let $G(y) = yf_2(\phi - y)$ for $y \in [0, \phi]$. Since f_2 is at least C^1 smooth, there exists $L > 0$ such that

$$|G(y_1) - G(y_2)| \le L|y_1 - y_2|, \qquad y_1, y_2 \in [0, \phi].$$

Let $K = \sup \|U(t,s\|,\ 0 \le s \le t \le \omega$. Since $U(t,s)$ is ω-periodic, $\|U(t,s)\| \le K$ for $t \in [k\omega, (k+1)\omega]$. We subtract one equation from the other and pass to the norms to obtain

$$\begin{aligned} &|W(t,x) - V(t,x)| \\ &\le \|U(t,s)\||W(k\omega,x) - V(k\omega,x)| + \int_{k\omega}^{t} \|U(t,s)\||G(W(s,x)) - G(V(s,x))|\, ds \\ &\le \|U(t,s)\||W(k\omega,x) - V(k\omega,x)| + \int_{k\omega}^{t} \|U(t,s)\|L|W(s,x) - V(s,x)|\, ds \\ &\le K\|w_k - v_\infty\|_C + \int_{k\omega}^{t} KL|W(s,x) - V(s,x)|\, ds \end{aligned}$$

for $t \in [k\omega, (k+1)\omega]$, and $x \in [0,1]$. Using the Gronwall inequality we finally obtain

$$|W(t,x) - V(t,x)| \le Ke^{KL(t-k\omega)}\|w_k - v_\infty\|_C \le Ke^{KL\omega}\|w_k - v_\infty\|_C$$

for $t \in [k\omega, (k+1)\omega]$, and $x \in [0,1]$. As $k \to \infty$, $\|w_k - v_\infty\|_C \to 0$, and thus $\|W(t,\cdot) - V(t,\cdot)\|_C \to 0$. This shows that V attracts all positive solutions of (5.1) and completes the proof of part (a).

In what follows E_1 denotes v_∞, the positive stable fixed point of P_v, but we will also refer to it as the periodic solution $V(t,x)$ itself. E_0 denotes the zero solution $u = v = 0$ of both the limiting system (4.1)–(4.2) and single population equation (5.1), and the zero function as a trivial fixed point of the period map P (P_v or P_u, accordingly). The usage will be clear from the context.

Part (b). Since the period map P_v is monotone, the principal eigenfunction ψ must be positive by the Krein–Rutman theorem [13], so then

$$P_v(\alpha\psi) = \psi(\lambda\alpha + o(\alpha)) << \alpha\psi$$

for sufficiently small $\alpha \in (0, \epsilon)$. Consequently, there is a strictly decreasing sequence $\{w_k, k \in 0, 1, 2, \ldots\}$ such that $w_0 >> 0$ and $P_v(w_{k-1}) = w_k << w_{k-1}$. The fact that $\lambda < 1$ implies that the zero solution of (5.1) is locally order stable (further, linearly stable) and attracts all positive solutions locally (see part (a)). In fact, it attracts any positive solution of (5.1). Indeed, given $x >> 0$, $x \in \mathrm{dom}P$, there exists an $\alpha \in (0,1)$ such that $\alpha x < w_0$; then strong monotonicity and sublinearity of P imply that

$$\alpha P_v(x) << P_v(\alpha x) << P_v(w) << w,$$

so by induction we show that for all k,

$$x_k := P_v^k(x) << \alpha w_k = \alpha P_v^k(w).$$

Any C-space with C^0-norm and the order cone C_+ is a lattice, namely,

$$\text{for all } x, y \in C\ :\ \exists m = \inf(x,y), \qquad M = \sup(x,y),$$

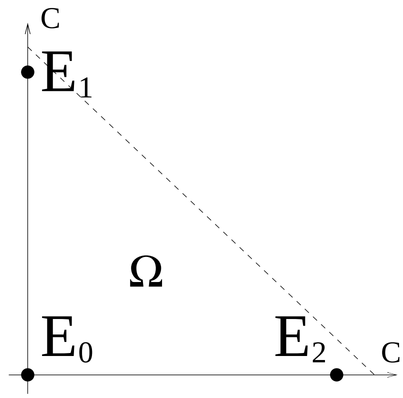


FIG. 5.1. *Location of E_0, E_1, and E_2 in $C_+ \times C_+$.*

so one can speak of the lim inf and lim sup of such sequences.

We then have $0 \leq \limsup P_v^k(x) \leq \frac{1}{\alpha} \limsup w_k = 0$; thus $P_v^k(x) \to 0$ as $k \to \infty$. Hence, 0 attracts all positive points under P_v. Finally, we employ the same continuity argument as in part (a) to conclude that the solution $v \equiv 0$ of (5.1) attracts all positive solutions. This completes the proof of part (b). □

Remark 5.2. We proceed similarly with the case when v is set equal to zero. We investigate the stability of E_0 under P_u, and find a possible unique positive periodic solution $U(t, x)$ which attracts all positive solutions. If $U(t, x)$ does not exist, E_0 is the only fixed point of P_u in C_+, and E_0 attracts all points of C_+ under P_u. If $U(t, x)$ does exist, we denote this solution and the corresponding fixed point of P_u by E_2.

There are biological interpretations of the existence of these rest points. If E_1 exists, then the v-population is capable of surviving in the chemostat without the competitive pressure. If E_1 does not exist, the v-population will go extinct independently of the presence of its competitor. A similar relationship holds for E_2 and the u-population.

In the next section we assume that both E_1 and E_2 exist to investigate whether it is possible for u and v to coexist. Figure 5.1 illustrates all three periodic solutions E_0, E_1, and E_2 and their locations in the product space $C_+ \times C_+$.

The period map developed in section 4 gives rise to a semidynamical system defined on $C_+ \times C_+$ [5], and Lemma 5.1 (and Remark 5.2) give precise information on the limit sets when one component of an initial condition is identically zero. The properties established exactly fit the theory developed in [11] (directly) or [8] (with some additional effort), and the theorems there describe the asymptotic behavior of the limiting system (4.1)–(4.2).

Let J denote the order interval $[E_1, E_2]_K$. By property (P2) of the period map and Lemma 5.1 (and its counterpart for P_u), the omega limit set of any orbit lies in this order interval. To see this, one just compares a solution with an initial condition in the cone with the corresponding solution with initial conditions with a coordinate identically zero. Theorem A of [11] yields directly (see also [3]) the following theorem.

THEOREM 5.3. *One of the following holds:*

(1) *P has a positive fixed point in J,*

(2) *$P^n(x) \to E_1$ as $n \to \infty$ for every $x = (u, v) \in J$ with $u \neq 0$, $v \neq 0$,*

(3) *$P^n(x) \to E_2$ as $n \to \infty$ for every $x \in J$ with $u \neq 0$, $v \neq 0$.*

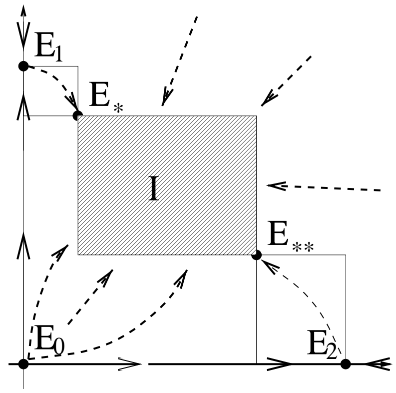


FIG. 5.2. *Dynamics of P with E_* and E_{**} present.*

If (2) *or* (3) *holds, and* $x \in C^+ \times C^+ \backslash J$ *satisfies* $u \neq 0$, $v \neq 0$, *then either* $P^n(x) \to E_1$ *as* $n \to \infty$ *or* $P^n(x) \to E_2$ *as* $n \to \infty$.

The situations (1), (2), and (3) in Theorem 5.3 can be distinguished by individual stability properties of E_1 and E_2. For instance, if E_1 is unstable, the outcome (2) obviously never occurs. Similarly, if E_2 is unstable, the outcome (3) also never occurs. Now, if both E_1 and E_2 are unstable or both E_1 and E_2 are stable, neither (2) nor (3) occurs, so there exists an additional fixed point of P in the interior of J (and the interior of Ω). Stability can be determined from the Krein–Rutman theorem. We state a version that is convenient in this application.

THEOREM 5.4 (Krein–Rutman). *Assume that* $P'(E_i)$, i=1, 2, *have positive spectral radii*, $r_1 > 0$ *and* $r_2 > 0$, *respectively*; *then*

(1) $r_1 = \lambda_v$ *is the principal eigenvalue of* $P'(E_1)$ *with some* K*-positive eigenfunction* (u_1, v_1), *and if* $\lambda_v > 1$, *then* $u_1 > 0$.

(2) $r_2 = \lambda_u$ *is the principal eigenvalue of* $P'(E_2)$ *with some* $(-K)$*-positive eigenfunction* (u_2, v_2), *and if* $\lambda_u > 1$, *then* $v_2 > 0$.

If there is no further fixed point of P in $\mathrm{Int}(J)$, an immediate consequence is that competitive exclusion results—one or both of the populations become extinct. If only one survives, the winner of the competition (the survivor) can be determined by local stability considerations.

THEOREM 5.5 (extinction). *If* $\lambda_v > 1$ *and there are no further fixed points of* P *in* Int J, *then* E_2 *attracts all points of the interior of* J. *If* $\lambda_u > 1$ *and there are no further fixed points of* P *in* Int J, *then* E_1 *attracts all points of the interior of* J.

THEOREM 5.6. *If there exists a fixed point in the interior of* J *and if* $\lambda_v > 1$, *then there exists a fixed point* E_* *which attracts the order interval* (E_1, E_*). *If there exists a fixed point in the interior of* J *and if* $\lambda_u > 1$, *then there exists a fixed point* E_{**} *which attracts the order interval* (E_{**}, E_2).

Proof. Using the eigenfunction (u_1, v_1) from Theorem 5.4 it is easy to argue that there exists a point $w = E_1 + h(u_1, v_1)$, for h arbitrarily small, such that $E_1 > w > T(w)$ (see, for example, the proof of Theorem 5.1 of [11], or [8]). The rest follows from monotonicity. □

Of course, both stability conditions can occur. In this case all orbits have their omega limit sets in the order interval $[E_*, E_{**}]$. This is illustrated in Figure 5.2. All of our numerical simulations produced $E_* = E_{**}$. The question of uniqueness of the interior fixed point remains open. The general theory would also allow both boundary rest points to be stable and thus guarantee an unstable interior rest point. We did not observe this in our simulations.

Since the system is monotone, it is a general theorem that almost all orbits converge to a fixed point. We remind the reader that a fixed point of the mapping P is a periodic solution of the limiting system of partial differential equations, (4.1)–(4.2).

6. Asymptotic behavior of the full system. It is now appropriate to interpret the results for the limiting system in terms of the original problem, (2.1)–(2.3). For instance, the trivial periodic solution of (4.1)–(4.2) with initial condition at E_0 corresponds to the limiting periodic distribution of (2.1)–(2.3), namely, $(S, u, v) = (\phi, 0, 0)$. The nontrivial "boundary" periodic solutions $(0, V(t, x))$ and $(U(t, x), 0)$ of (4.1)–(4.2) give rise to the corresponding periodic solutions of (2.1)–(2.3), namely, $(S, u, v) = (\phi - V, 0, V)$ and $(S, u, v) = (\phi - U, U, 0)$. More generally, all positive periodic solutions of the limiting system can be interpreted as solutions of (2.1)–(2.3) in the same fashion, $(\phi - U - V, U, V)$.

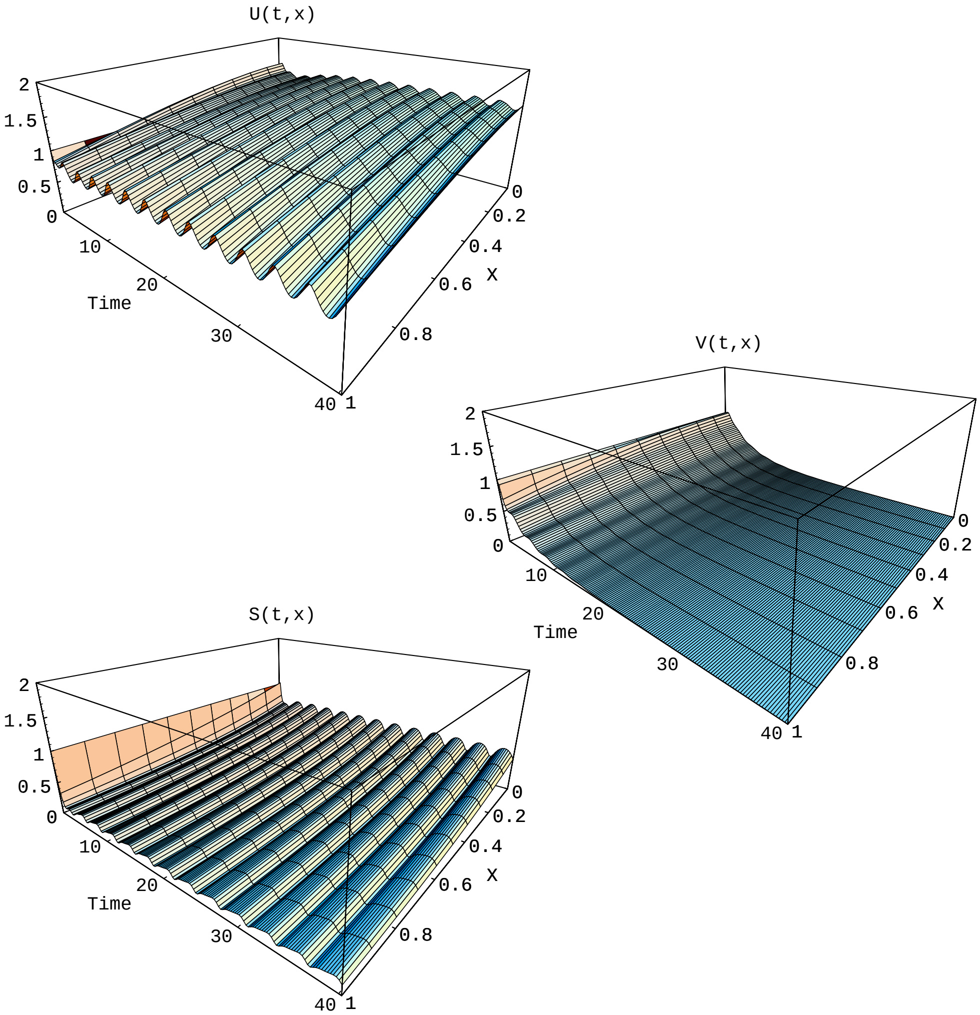
The convergence question is more interesting. In the case of competitive exclusion, all solutions of the limiting equations converge to a periodic solution. When there is an interior fixed point for the period map, then there are always two order intervals such that solutions for all initial conditions in these intervals converge. Outside of these order intervals, one knows only that all solutions come into an order interval (defined by the largest and smallest fixed point of the period map) and, from the general theory of monotone dynamical systems, that almost all initial conditions converge to a fixed point inside this order interval [20]. As noted above, our numerical experience was that the interior fixed point was stable and unique, so all solutions converged.

Let (S_0, u_0, v_0) be initial conditions and let $S(t, x), u(t, x), v(t, x)$ denote the corresponding solution of (2.1)–(2.3). Suppose that the period map starting at (u_0, v_0) converges to a fixed point. Denote the corresponding periodic solution by $(U(t, x), V(t, x))$. Then it follows that

$$|S(t, x) - (\phi - U(t, x) - V(t, x))| + |u(t, x) - U(t, x)| + |v(t, x) - V(t, x)| \to 0.$$

Thus when the period map converges to a fixed point, the corresponding solution of (2.1)–(2.3) is asymptotic to a periodic solution.

7. Discussion. We have taken the basic unstirred chemostat model and let the input and "washout" rates be periodic functions. As a practical matter this would usually amount to varying the flow rate, but the results are general enough to allow for both. Conceptually, this might correspond to seasonal variations or diurnal variations in nature or to some periodic disturbance in the pump in a bioreactor. The papers cited in section 1 have developed the asymptotic behavior model for a well-mixed chemostat with periodic inputs or dilution rates. We have developed the corresponding theory here for the reaction diffusion model. In the case of the model for the well-mixed chemostat both the input nutrient concentration and the dilution rate appeared in the equation so the difficulties were those of moving from a dynamical system to a periodically forced system. In the reaction diffusion model the nutrient input and the removal appear in the boundary conditions causing technical difficulties. With the help of a transformation suggested by Professor Norman Dancer (see Acknowledgment) we are able to remove the periodicity from the boundary conditions to the operator with considerable increase in complexity. (This transformation probably has potential beyond our use in this problem.) Eventually, however, we were

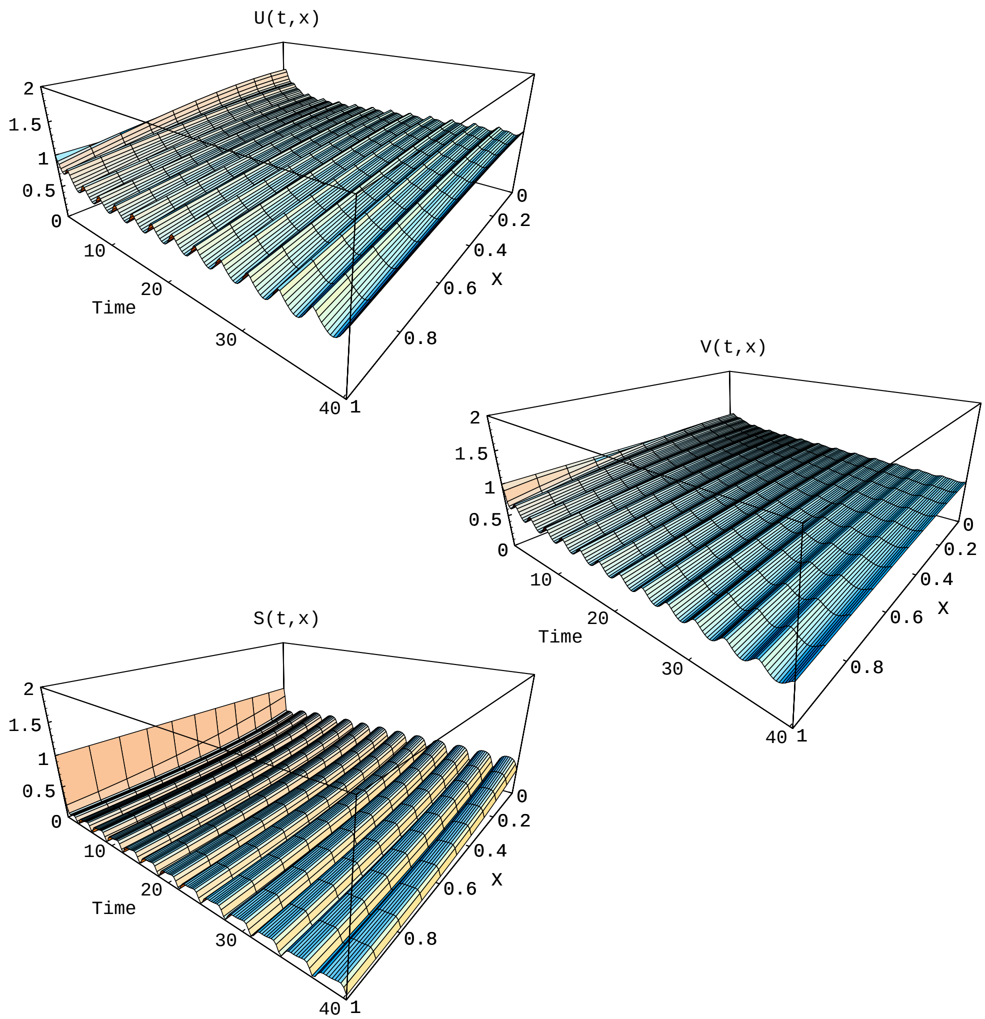


Parameters: $m_2 = 1$, $C_2 = 1$.
Common parameters: $d = 1.0$, $m_1 = 3.0$, $a_1 = 1.0$,
$a_2 = 1.0$, $A_1 = 0.1$, $C_1 = 1.0$, $A_2 = 0.3$, $B = 2.0$.
Initial conditions: $S(0, x) \equiv u(0, x) \equiv v(0, x) \equiv 1.0$.

Fig. 7.1. *Competitive exclusion.*

able to reduce the problem to one of a fixed point of the period map although now in an infinite-dimensional setting. The monotonicity of the map allowed one to make use of the theory of monotone dynamical systems, just as in the ordinary differential equations model. The choices between possible outcomes are dictated by the stability of the boundary rest points.

To illustrate the results we show two numerical examples. The simulations run from $t_0 = 0$ to $t_{\max} = 40.0$ relative time units. Since we are providing illustrations,



Parameters: $m_2 = 2.9$, $C_2 = 0.8$.
Common parameters: $d = 1.0$, $m_1 = 3.0$, $a_1 = 1.0$,
$a_2 = 1.0$, $A_1 = 0.1$, $C_1 = 1.0$, $A_2 = 0.3$, $B = 2.0$.
Initial conditions: $S(0, x) \equiv u(0, x) \equiv v(0, x) \equiv 1.0$.

FIG. 7.2. *Coexistence.*

the solutions and the graphs were obtained using *Mathematica* 3.0. More accuracy could likely be achieved with more sophisticated tools, but our goal is only to illustrate the solutions. We assume the Monod model with $f_i(S) = \frac{m_i S}{a_i + S}$, and choose $S^0(t) = C_1 + A_1 \sin(Bt)$ and $r(t) = C_2 + A_2 \sin(Bt)$.

Several parameters are common for all the simulations: the diffusion rate $d = 1.0$, and parameters $a_1 = 1.0$, $a_2 = 1.0$, $m_1 = 3.0$, $A_1 = 0.1$, $C_1 = 1.0$, $A_2 = 0.3$, and $B = 2.0$. The remaining parameters are varied in order to illustrate different outcomes of the competition.

The simulations presented below illustrate the following two major outcomes of the competition in the unstirred chemostat:

(1) competitive exclusion, the outcome when one competitor asymptotically reaches a positive periodic density distribution and the other competitor goes extinct, the nutrient density also reaching a positive periodic distribution (Figure 7.1);

(2) coexistence of the competing species, the outcome when both competitors reach positive periodic distributions (Figure 7.2).

In the situation presented in Figure 7.1, each competitor (U or V) is able to survive on its own without the other competitor present. Nevertheless, when both competitors are introduced to the chemostat simultaneously, the U species outcompetes the V species and drives it to extinction. If the environmental conditions become milder for the V species, that is, if m_2 is increased and the average washout rate C_2 is decreased, then V becomes able to survive the competition as shown in Figure 7.2.

Acknowledgment. The authors wish to acknowledge, with thanks, that Professor Norman Dancer suggested the change of variables used at the beginning of the proof of Lemma 4.3.

Note added in proof. The transformation used in the proof of Lemma 4.3 appears in greater generality in [27].

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