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DYNAMICS OF COMPETITION IN THE UNSTIRRED CHEMOSTAT

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1. Introduction. The chemostat is a piece of laboratory apparatus which plays an important role in microbiology [**5, 2, 25, 29, 30**]. It is used as a model of a simple lake, in the commercial production of microorganisms and as a model for waste water treatment. The Monod model of competition between microbial populations for a single growth-limiting nutrient in the chemostat occupies a central position in microbial ecology. It is a model which has mathematical tractability and experimental confirmation.

The basic chemostat consists of three vessels. The first vessel, the feed bottle, contains all of the needed nutrients for growth in abundance except one which is limiting. The nutrient is pumped at a constant rate into the second, called the culture vessel or bio-reactor. The culture vessel, whose volume is constant, contains microorganisms which compete for the nutrient. The contents of the culture vessel are pumped, at the same constant rate, into the third vessel, called the overflow vessel. It is assumed that the culture vessel is well mixed and that all other relevant variables (temperature, pH, etc.) are constant. The basic equations (for two competitors x_1 and x_2 and nutrient S) are [**29**]

$$\begin{aligned}
&S' = (S^{(0)} - S)D - \frac{m_1 S x_1}{a_1 + S} - \frac{m_2 S x_2}{a_2 + S}\\
&x_1' = x_1\left(\frac{m_1 S}{a_1 + S} - D\right), \qquad x_2' = x_2\left(\frac{m_2 S}{a_2 + S} - D\right)\\
&S(0) \geq 0, \qquad x_i(0) \geq 0
\end{aligned}$$

$S^{(0)}$ is the input nutrient concentration, D is called the dilution or washout rate, m_i and a_i, $i = 1, 2$, are properties of the organism.

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The principle result is that competitive exclusion occurs; only one population survives.

In [**27**] and [**9**] a model for the unstirred chemostat was proposed. It took the form

$$\begin{aligned} S_t &= dS_{xx} - \frac{m_1 S u}{a_1 + S} - \frac{m_2 S_v}{a_2 + S} \\ u_t &= du_{xx} + \frac{m_1 S u}{a_1 + S} \qquad 0 < x < 1 \\ v_t &= dv_{xx} + \frac{m_2 S v}{a_2 + S}, \end{aligned}$$

with boundary conditions

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

where $r > 0$, and initial conditions

$$\begin{aligned} S(0,x) &= S_0(x) \geq 0 \\ u(0,x) &= u_0(x) \geq 0 \\ v(0,x) &= v_0(x) \geq 0. \end{aligned}$$

The boundary conditions were derived in [**9**] where the constants were interpreted in terms of the parameters of the well-mixed chemostat model. The steady state solutions of the equations above and their stability properties were determined in [**27**] and [**9**]. The principal result of [**9**] was persistence: that coexistence of both populations was possible. However, no information concerning the behavior of the coexisting solutions was given in [**9**]. Convergence of solutions to single-population steady states was established in [**10**], assuming that no positive steady state exists.

In this paper we consider a more general model, and we attempt to secure information about the asymptotic behavior of the coexistence solutions. The theory of monotone dynamical systems is used to provide conditions for a generic solution to converge to a positive, stable, steady state solution which may depend on the initial data. If the positive steady state is unique, then it is globally asymptotically stable. If not, then there exist two ordered positive steady state solutions each of which is the omega limit set of a monotone heteroclinic orbit whose alpha limit set is a single-population steady state, that is, a steady state for which exactly one population, u or v, is nonzero. Every solution is attracted to the order interval determined by the two distinguished positive steady states and an open and dense set of initial data generate solutions which converge to a stable positive steady state belonging to the order interval.

2. Preliminaries. We consider

$$\begin{aligned} &S_t = dS_{xx} - uf_1(S) - vf_2(S) \\ &u_t = du_{xx} + uf_1(S), \qquad v_t = dv_{xx} + vf_2(S) \end{aligned} \tag{2.1}$$

with boundary conditions

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

where $r > 0$, and initial conditions

$$\begin{aligned} S(0,x) &= S_0(x) \geq 0 \\ u(0,x) &= u_0(x) \geq 0 \\ v(0,x) &= v_0(x) \geq 0. \end{aligned} \tag{2.3}$$

The growth functions f_i will be assumed to satisfy:

(i) $f : \mathbf{R}_+ \to \mathbf{R}_+$ and $f(0) = 0$;

(ii) f is twice continuously differentiable and $f'(S) > 0$.

The Monod function, $f(S) = mS/(a + S)$ considered in [9], is a particular example of such an f.

We view (2.1)–(2.3) as a semi-dynamical system on $C_+^3 \equiv C_+ \times C_+ \times C_+$, where C_+ is the cone of nonnegative functions in the Banach space

C of continuous functions on $[0,1]$ with the usual supremum norm, $|\bullet|$. If $\psi_i \in C$ then we write $\psi_2 \geq \psi_1 (\psi_2 > \psi_1)$ whenever $\psi_2(x) \geq \psi_1(x)$ $(\psi_2(x) > \psi_1(x))$ for $0 \leq x \leq 1$. The order interval $[\psi_1, \psi_2]$ is defined by

$$[\psi_1, \psi_2] = \{\psi \in C : \psi_1 \leq \psi \leq \psi_2\}.$$

As noted in [9], for the system (2.1)–(2.3), there exists $\alpha > 0$ such that

$$|S(t,\bullet) + u(t,\bullet) + v(t,\bullet) - \phi| = O(e^{-\alpha t})$$

as $t \to \infty$, where $\phi = \phi(x) = S^{(0)}(((1+r)/r) - x)$. Therefore, it is necessary to first study the dynamics of (2.1)–(2.3) restricted to the invariant exponentially attracting set given by $S + u + v = \phi$. On this set, (2.1)–(2.3) reduces to

$$\begin{aligned} u_t &= du_{xx} + f_1(\phi - u - v)u \\ v_t &= dv_{xx} + f_2(\phi - u - v)v \end{aligned} \tag{2.4}$$

together with boundary and initial data taken from (2.2) and (2.3). Equation (2.4) is biologically relevant in the region

$$\Omega = \{(u,v) \in C_+ \times C_+ : u \geq 0, v \geq 0, u + v \leq \phi\}.$$

In particular, we assume that the initial data $(u_0, v_0) \in \Omega$.

Let

$$D(A_0) = \{w \in C^2([0,1], \mathbf{R}) : w_x(0) = 0, w_x(1) + rw(1) = 0\}$$

and

$$A_0 w = dw_{xx}, \qquad w \in D(A_0).$$

Then using Stewart [28], A_0 is closed in C and generates an analytic semigroup $\{U_0(t)\}$ on C. Define the analytic semigroup $U(t)$ on $C_+ \times C_+$ by $U(t) = (U_0(t), U_0(t))$ and let $F : \Omega \to C_+ \times C_+$ be defined by

$$F(u,v) = (uf_1(\phi - u - v), vf_2(\phi - u - v)).$$

By a solution of (2.4), we mean a continuous function $w = (u,v)$: $[0, \sigma) \to \Omega$ satisfying

$$w(t) = U(t)w(0) + \int_0^t U(t-s)F(w(s))ds \tag{2.5}$$

for $0 < t < \sigma$. We remark that if such a solution exists, then [**14**, Theorem 3.1] as F is locally Lipschitz and $\{U(t)\}$ is analytic, it follows that $w(t)$ is continuously differentiable on $(0, \sigma)$, $w(t) \in D(A) \equiv D(A_0) \times D(A_0)$ for such t and

$$w'(t) = Aw(t) + F(w(t)), \qquad 0 < t < \sigma,$$

where $A = A_0 \times A_0$ is the generator of $\{U(t)\}$. Since $w(t)$ is differentiable in $C \times C$ and belongs to $D(A)$, it follows immediately that $w(t,x) = (w(t))(x) = (u(t,x), v(t,x))$ is a classical solution of (2.4) for $(t,x) \in (0,\sigma) \times (0,1)$.

Our first result says that (1.4) generates a smooth dynamical system on Ω.

Proposition 2.1. *For each $w_0 \in \Omega$ there is a unique solution $w : [0, \infty) \to \Omega$ of (2.5). The family of maps $T = \{T(t)\}$, defined by*

$$T(t)w_0 = w(t),$$

satisfies the usual properties of a (nonlinear) semiflow on Ω. Furthermore, $T(t)w$ is continuously differentiable in $w \in \Omega$ and $T(t)$ is completely continuous for each $t > 0$.

Proof. The existence of a unique globally defined solution in Ω follows from [**14**, Theorem 5.1]. We provide some details. Observe that F is Lipschitz continuous on Ω. Elementary maximum principle arguments imply that $U(t)\Omega \subset \Omega$ for $t > 0$. The remaining hypothesis to check is

$$\lim_{h \to 0+} h^{-1} d(w + hF(w), \Omega) = 0, \qquad w \in \Omega,$$

where $d(w, \Omega)$ is the distance of w to Ω. Actually, it suffices to establish that the limit inferior vanishes (see [14, exercise 12]). As

$$w + hF(w) = (u(1 + hf_1(\phi - u - v)), v(1 + hf_2(\phi - u - v))),$$

where $w = (u,v)$, it follows that $w + hF(w) \geq 0$ for $h > 0$ and consequently

$$\begin{aligned} d(w + hF(w), \Omega) &= d(u(1 + hf_1(\phi - u - v)) \\ &\qquad + v(1 + hf_2(\phi - u - v)), [0, \phi]) \\ &= |[u(1 + hf_1(\phi - u - v)) \\ &\qquad + v(1 + hf_2(\phi - u - v)) - \phi]_+| \end{aligned}$$

where $[0,\phi]$ is the order interval $\{\psi \in C : 0 \leq \psi \leq \phi\}$ and $[\psi]_+(x) = \max\{\psi(x), 0\}$, is the positive part of ψ. See [15, Lemma 2.1] for the last equality. Set

$$z_n = [u(1 + n^{-1} f_1(\phi - u - v)) + v(1 + n^{-1} f_2(\phi - u - v)) - \phi]_+.$$

For each $h = 1/n$ let x_n be a point where $z(x_n) = |z_n|$. By compactness, we may as well assume that $x_n \to x_0$ as $n \to \infty$. Let M be so large that $uf_1(\phi - u - v) + vf_2(\phi - u - v) \leq M$ for all $(u,v) \in \Omega$. If $u(x_0) + v(x_0) < \phi(x_0)$ then there exists N such that

$$\phi(x_n) - u(x_n) - v(x_n) > m \equiv (\phi(x_0) - u(x_0) - v(x_0))/2$$

for $n \geq N$. It follows that

$$u + v - \phi + (uf_1(\phi - u - v) + vf_2(\phi - u - v))/n < -m + M/n \leq 0$$

when evaluated at $x = x_n$, for all large n. Consequently, $z_n(x_n) = 0$ and therefore, $\lim_{n\to\infty} n|z_n| = 0$. We are done in this case. If $u(x_0) + v(x_0) = \phi(x_0)$ then

$$\begin{aligned} z_n(x_n) \leq n^{-1}(u(x_n) f_1(\phi(x_n) - u(x_n) - v(x_n)) \\ + v(x_n) f_2(\phi(x_n) - u(x_n) - v(x_n))) \end{aligned}$$

so

$$\begin{aligned} \lim_{n\to\infty} n|z_n| \leq \lim_{n\to\infty} u(x_n) f_1(\phi(x_n) - u(x_n) - v(x_n)) \\ + v(x_n) f_2(\phi(x_n) - u(x_n) - v(x_n)) = 0 \end{aligned}$$

since $\phi(x_n) - u(x_n) - v(x_n) \to 0$ as $n \to \infty$.

The fact that T is continuously differentiable follows from [**18**, Theorem 4.1]. The complete continuity of $T(t)$ is standard [**14**, Theorem 5.2]. □

3. An order property.

In this section we show that the reduced system (2.4) defines a monotone system with respect to a certain partial order. The partial order introduced reflects the competitive properties of the system and is crucial for determining the existence of limits for some orbits.

We introduce a partial order on $C_+ \times C_+$ as follows. Let $w_i = (u_i, v_i)$, $i = 1, 2$, be two points of $C_+ \times C_+$. Define $w_1 \leq_K w_2$ ($w_1 <_K w_2$) if and only $u_1 \leq u_2$ ($u_1 < u_2$) and $v_1 \geq v_2$ ($v_1 > v_2$). Let $[w_1, w_2]_K = \{w \in C_+ \times C_+ : w_1 \leq_K w \leq_K w_2\}$.

Proposition 3.1. *$T(t)$ has the following properties:*

(1) *If $(u_0, v_0) \in \Omega$ satisfies $u_0 \neq 0$ ($v_0 \neq 0$), then $T(t)(u_0, v_0) = (u(t), v(t))$ satisfies $u(t) > 0$ ($v(t) > 0$) for $t > 0$.*

(2) *If w_0 and w_1 belong to the interior of Ω and satisfy $w_0 \leq_K w_1$, $w_0 \neq w_1$, then*

$$T(t)w_0 <_K T(t)w_1$$

for $t > 0$.

Proof. Assertion (1) is essentially contained in the Lemma of Martin, [**13**], where it is proved that either $u \equiv 0$ or $u > 0$ for $t > 0$ and similarly for v. Assertion (2) is a well-known consequence of the fact that the partial derivative of $f_1(\phi - u - v)u$ ($f_2(\phi - u - v)v$) with respect to v (u) is negative in Ω. See, e.g., [**17**] or [**19**]. □

By continuity of the semiflow and Proposition 3.1 (2) it follows that $T(t)w_0 \leq_K T(t)w_1$ for $t \geq 0$ whenever $w_0 \leq_K w_1$. Thus T is a monotone semiflow with respect to the partial order $\leq_K$ on Ω. As a consequence, (2.4) has no nontrivial attracting periodic orbits (see [**7**, p. 30]). The theory of monotone dynamical systems (see, e.g., [**7**, **24**]) suggests that most solutions of (2.4) will converge to equilibrium. At least in one case we show this to be the case (see Theorem 5.2).

4. The boundary equilibria. Equilibrium solutions (also called steady states and rest points) of (2.4) are solutions of the boundary value problem

$$\begin{aligned} 0 &= du_{xx} + f_1(\phi - u - v)u, \\ 0 &= dv_{xx} + f_2(\phi - u - v)v \\ u_x(0) &= v_x(0) = 0 \qquad 0 < x < 1 \\ u_x(1) + ru(1) &= v_x(1) + rv(1) = 0. \end{aligned} \tag{4.1}$$

We begin by considering the boundary equilibria, that is, the equilibria (u, v) for which at least one of u or v vanishes identically on $[0, 1]$.

There are three types of equilibrium solutions on the boundary of Ω, $E_0 = (0,0)$, $E_1 = (\hat{u}, 0)$ and $E_2 = (0, \tilde{v})$. As shown below, there is exactly one of each type. The stability and nature of the attracting set of each equilibrium depend on parameters of the system. For the well-stirred chemostat model, the crucial parameter (the "lambda value") could be expressed directly in terms of parameters of the equation. Here it will be expressed in terms of the largest eigenvalue of a boundary value problem whose constituent parts come from the original equation.

Denote by λ_1, the largest eigenvalue of

$$\lambda u = du_{xx} + f_1(\phi)u$$
$$u_x(0) = 0, \qquad u_x(1) + ru(1) = 0,$$

and let μ_1 be the largest eigenvalue of

$$\mu v = dv_{xx} + f_2(\phi)v$$
$$v_x(0) = 0, \qquad v_x(1) + rv(1) = 0.$$

The following proposition was established in [**27**] and [**9**] for f_i that are of the Monod type.

Proposition 4.1. *If* $\lambda_1 < 0$ *then*

$$\lim_{t\to\infty} T(t)(u,0) = E_0 \equiv (0,0)$$

for all $(u, 0) \in \Omega$. *If* $\lambda_1 > 0$ *then there exists a unique nontrivial equilibrium* $E_1 \equiv (\hat{u}, 0)$ *and* $\hat{u} > 0$. *In this case*

$$\lim_{t\to\infty} T(t)(u,0) = E_1$$

for all $(u, 0) \in \Omega$ *with* $u \neq 0$. *If* $\mu_1 < 0$ *then*

$$\lim_{t\to\infty} T(t)(0,v) = E_0$$

for all $(0, v) \in \Omega$. *If* $\mu_1 > 0$ *then there exists a unique nontrivial equilibrium* $E_2 = (0, \tilde{v})$ *and* $\tilde{v} > 0$. *In this case*

$$\lim_{t\to\infty} T(t)(0,v) = E_2$$

for all $(0, v) \in \Omega$ *with* $v \neq 0$. *Finally, if* $(u, v) \in \Omega$ *is an equilibrium of* (2.4) *distinct from* E_i, $i = 0, 1, 2$, *then* $u > 0$ *and* $v > 0$.

Proof. As noted above, the result was proved in [**27**] and [**9**] in the case that the f_i are of Monod type. The proofs given in these references extend to the current situation. We comment on the uniqueness of the equilibrium $E_1 = (\hat{u}, 0)$. The boundary value problem for $\hat{u}$ can be recast as a fixed point equation $u = KF(u)$ where K is a strongly positive compact linear operator on $C([0,1])$ (the inverse of the differential operator $-du_{xx} + \alpha^2 u$, together with the boundary conditions) and F is a strictly increasing Nemytskii operator (from the nonlinear term $u[\alpha^2 + f_1(\phi - u)]$ where α is suitably large). It can then be shown that $T = K \circ F$ is an increasing concave operator so uniqueness follows from [**11**, Theorem 6.3]. See [**23**, Proposition 1.1] for a similar argument. □

The content of the preceding lemma is that the problem is interesting only if $\lambda_1 > 0$ and $\mu_1 > 0$. Indeed, if $(u, v) \in \Omega$, then $(0, v) \leq_K (u, v) \leq_K (u, 0)$. Let $(0, \bar{v}(t)) \equiv T(t)(0, v)$, $(u(t), v(t)) \equiv T(t)(u, v)$ and $(\bar{u}(t), 0) \equiv T(t)(u, 0)$. Then, by monotonicity of T we have

$$(0, \bar{v}(t)) \leq_K (u(t), v(t)) \leq_K (\bar{u}(t), 0).$$

As a consequence of Proposition 4.1, if $\lambda_1 < 0$, then $\bar{u}(t) \to 0$ as $t \to \infty$, implying that $u(t) \to 0$ as $t \to \infty$. Similarly, if $\mu_1 < 0$, then Proposition 4.1 implies $\bar{v}(t) \to 0$ as $t \to \infty$ so $v(t) \to 0$ as $t \to \infty$. In particular, if $\lambda_1 < 0$ and $\mu_1 < 0$ then $(u(t), v(t)) \to (0, 0)$ as $t \to \infty$. Since our focus in this paper is on the possibility for coexistence, only the case $\lambda_1 > 0$, $\mu_1 > 0$ is of interest.

The next proposition examines the stability of E_0 under this condition.

Proposition 4.2. *If* $\lambda_1 > 0$ *and* $\mu_1 > 0$ *then there exists a neighborhood* V *of* E_0 *in* Ω *such that for each* $w \in V$, $w \neq E_0$, *there is a* $\tau = \tau(w) > 0$ *for which*

$$T(\tau)w \in \partial V.$$

In other words, E_0 *is a repeller in* Ω.

Proof. Since $\lambda_1 > 0$ and $\mu_1 > 0$, there exists $h > 0$ such that the largest eigenvalues $\lambda = m$ and $\mu = n$ of

$$\lambda u = du_{xx} + f_1(\phi(1-h))u$$
$$u_x(0) = 0, \qquad u_x(1) + ru(1) = 0$$

and

$$\mu v = dv_{xx} + f_2(\phi(1-h))v$$
$$v_x(0) = 0, \qquad v_x(1) + rv(1) = 0$$

are positive. Let $\bar{u} > 0$ and $\bar{v} > 0$ be the corresponding eigenfunctions and set

$$U = \{(u,v) \in \Omega : u + v < h\phi\}.$$

If $(u,v) \in U$ then $f_i(\phi - u - v) \geq f_i(\phi(1-h))$, $i = 1,2$. Consequently, if $(u,v) \in U$ then so long as $T(t)(u,v) \in U$, one has that

$$u_t \geq du_{xx} + f_1(\phi(1-h))u, \qquad v_t \geq dv_{xx} + f_2(\phi(1-h))v.$$

By Proposition 3.1, we may as well assume that either $u(0) > 0$ or $v(0) > 0$ or both. Then there exists $s > 0$ such that either $u(0) > s\bar{u}$ or $v(0) > s\bar{v}$ or both. Suppose the former holds. As $U(t,x) = e^{mt}s\bar{u}$ satisfies the differential equality corresponding to the differential inequality for u above and it satisfies the boundary conditions, a standard differential inequality argument [**26**, Theorem 10.1] implies that $u(t,x) \geq U(t,x)$ so long as $(u(t),v(t))$ remains in the closure of U. Clearly, this inequality cannot hold for all $t \geq 0$ and so the Proposition is proved. □

The stability properties of E_1 are determined by the eigenvalue problem associated with the variational equation of (2.4) about E_1. It is given by:

$$\begin{aligned} \lambda p &= dp_{xx} + [f_1(\phi - \hat{u}) - f_1'(\phi - \hat{u})\hat{u}]p - f_1'(\phi - \hat{u})\hat{u}q \\ \lambda q &= dq_{xx} + f_2(\phi - \hat{u})q \end{aligned} \tag{4.2}$$

with boundary conditions as in (4.1). The next result summarizes the local stability properties of E_1.

Proposition 4.3. *Let $\lambda_1 > 0$. Then E_1 is locally asymptotically stable (unstable) if the largest eigenvalue $\lambda = \Lambda_1$ of*

$$(4.3)\qquad \begin{aligned} \lambda q &= dq_{xx} + f_2(\phi - \hat{u})q \\ q_x(0) = 0, &\qquad q_x(1) + rq(1) = 0 \end{aligned}$$

is negative (positive). The corresponding eigenfunction $q_1 > 0$. If $\Lambda_1 \geq 0$, then it is an eigenvalue of (4.2) and a corresponding eigenfunction is (p_1, q_1) where p_1 is the unique solution of

$$(4.4)\qquad \begin{aligned} &\Lambda_1 p = dp_{xx} + [f_1(\phi - \hat{u}) - f_1'(\phi - \hat{u})\hat{u}]p - f_1'(\phi - \hat{u})\hat{u}q_1, \\ &p_x(0) = 0, \qquad p_x(1) + rp(1) = 0. \end{aligned}$$

Moreover, $p_1 < 0$. If $\Lambda_1 \geq 0$ then $\mu_1 > 0$. An analogous result holds for E_2. If $\mu_1 > 0$ then E_2 is locally asymptotically stable (unstable) if the largest eigenvalue, $\lambda = \Lambda_2$, of

$$\begin{aligned} \lambda p &= dp_{xx} + f_1(\phi - \tilde{v})p \\ p_x(0) = 0, &\qquad p_x(1) + rp(1) = 0 \end{aligned}$$

is negative (positive). The corresponding eigenfunction $p_2 > 0$ and if $\Lambda_2 > 0$ then the boundary value problem analogous to (4.4) has a unique solution q_2 and $q_2 < 0$. If $\Lambda_2 \geq 0$ then $\lambda_1 > 0$.

Proof. The validity of the principle of linearized stability is established in [**18**, Theorem 4.2]. The linearization of (2.4) about E_1 leads immediately to the eigenvalue problem (4.2) (see [**27**, **9**]). The stability assertion of the Proposition was established in [**9**]. We show that (4.4) has a unique solution which is negative when $\Lambda_1 \geq 0$. For simplicity of notation set $b = f_1'(\phi - \hat{u})\hat{u}$ and $a = f_1(\phi - \hat{u})$ and note that $a > 0$, $b > 0$. Choose a positive number s such that $s - a \geq 0$ and $s - b - \Lambda_1 > 0$. Then (4.4) takes the form

$$-bq_1 = Lp - (s - b - \Lambda_1)p,$$

together with the boundary conditions, where $Lp = -dp_{xx} + (s - a)p$. Denote by $\bar{\lambda}(m)$, the smallest eigenvalue of $Lp = \lambda mp$ where $m(x) > 0$ is continuous and the boundary conditions are the usual ones. By [**1**, Theorem 4.5],

$$\bar{\lambda}(s - b - \Lambda_1) > \bar{\lambda}(s).$$

Since $L\hat{u} = 1s\hat{u}$ and $\hat{u}$ satisfies the boundary conditions, it follows that $\bar{\lambda}(s) = 1$ and that $\hat{u}$ is the corresponding eigenfunction, therefore $\bar{\lambda}(s - b - \Lambda_1) > 1$. Then, by [**1**, Theorem 4.4], the nonhomogeneous boundary value problem (4.4), reformulated above, has exactly one solution p_1 and it is negative since $-bq_1 < 0$.

The inequality $f_2(\phi - \hat{u}) < f_2(\phi)$ together with Theorem 15, Chapter 1 of [**21**], implies that $\mu_1 > \Lambda_1$. This completes the proof. □

It is worth stressing that E_2 exists ($\mu_1 > 0$) whenever E_1 is unstable in the linear approximation ($\Lambda_1 > 0$). Similarly, E_1 exists if E_2 is unstable in the linear approximation.

5. Principal theorems. In this section we develop a technique (suggested by the work of Matano and of Poláčik) for establishing the existence of a heteroclinic orbit whose alpha limit is E_1 and whose omega limit set is either a positive equilibrium or E_2. The proof makes use of ideas in [**16**] and [**20**] but does not follow from any of their results since $T(t)$ is not strongly monotone in $\Omega \cap [E_2, E_1]_K$.

Theorem 5.1. *Suppose that*

$$\lambda_1 > 0 \quad \textit{and} \quad \Lambda_1 > 0. \tag{5.1}$$

Then one of the following hold:

(1) *There exists a monotone heteroclinic orbit connecting E_1 to E_2. That is, there exists*

$$W : (-\infty, \infty) \to \Omega$$

satisfying

$$T(t)W(s) = W(t + s) \tag{5.2}$$

for $t \geq 0$ and $s \in \mathbf{R}$,

$$E_2 <_K W(t_2) <_K W(t_1) <_K E_1, \tag{5.3}$$

if $t_1 < t_2$, and

$$W(t) \to E_2, \qquad t \to \infty \tag{5.4}$$

$$W(t) \to E_1, \qquad t \to -\infty. \tag{5.5}$$

Furthermore,

$$T(t)w \to E_2, \qquad t \to \infty$$

for every $w = (u, v) \in \Omega$ *for which*

$$E_2 \leq_K w \leq_K E_1$$

and $v \neq 0$.

(2) *There exists an equilibrium* $E_* = (u^*, v^*)$ *satisfying* $u^* > 0$, $v^* > 0$ *and* $E_2 <_K E_* <_K E_1$, *and a monotone heteroclinic orbit connecting* E_1 *to* E_*. *That is, there exists* $W : (-\infty, \infty) \to \Omega$ *satisfying* (5.2), (5.3), (5.4) *and* (5.5) *except that* E_2 *is replaced by* E_*. *Furthermore,*

$$T(t)w \to E_*, \qquad t \to \infty$$

for every $w = (u, v) \in \Omega$ *for which*

$$E_* \leq_K w \leq_K E_1$$

and $v \neq 0$.

Proof. Let $u_h = hp_1 + \hat{u}$ and $v_h = hq_1$ for $h > 0$. Then $(u_h, v_h) \in \Omega$ and satisfies the boundary conditions for all small h. Furthermore, $(u, v) = (u_h, v_h)$ satisfies

$$\begin{aligned}
du_{xx} &+ f_1(\phi - u - v)u \\
&= hd(p_1)_{xx} + d\hat{u}_{xx} + f_1(\phi - \hat{u} - h(p_1 + q_1))(\hat{u} + hp_1) \\
&= h[\Lambda_1 p_1 + f_1'(\phi - \hat{u})\hat{u}(p_1 + q_1) - f_1(\phi - \hat{u})p_1] \\
&\quad - f_1(\phi - \hat{u})\hat{u} + f_1(\phi - \hat{u} - h(p_1 + q_1))(\hat{u} + hp_1) \\
&= h\{p_1(\Lambda_1 + f_1(\phi - \hat{u} - h(p_1 + q_1)) - f_1(\phi - \hat{u})) \\
&\qquad + \hat{u}h^{-1}[f_1(\phi - \hat{u} - h(p_1 + q_1)) - f_1(\phi - \hat{u}) \\
&\qquad\qquad + hf_1'(\phi - \hat{u})(p_1 + q_1)]\}.
\end{aligned}$$

The terms inside the outer brackets tend to $\Lambda_1 p_1 < 0$ as h tends to zero so it follows that

$$d(u_h)_{xx} + f_1(\phi - u_h - v_h)u_h < 0$$

for small positive h. Similarly, v_h satisfies

$$\begin{aligned} d(v_h)_{xx}+f_2(\phi-u_h-v_h)v_h &= h[d(q_1)_{xx}+f_2(\phi-\hat{u}-h(q_1+p_1))q_1] \\ &= hq_1[\Lambda_1-f_2(\phi-\hat{u})+f_2(\phi-\hat{u}-h(p_1+q))] \\ &> 0 \end{aligned}$$

for small positive h since $\Lambda_1 > 0$ and $q_1 > 0$. Fix $h_0 > 0$ such that both inequalities hold for $0 < h \leq h_0$. Standard comparison arguments [**17**, Lemma 3.2, **15**, Theorem 2.3] imply that if $w_h = (u_h, v_h)$ then

$$E_2 <_K T(t)w_h <_K w_h <_K E_1.$$

By strong monotonicity (Proposition 3.1 (2)),

$$E_2 <_K T(t_2)w_h <_K T(t_1)w_h <_K w_h <_K E_1$$

whenever $0 < t_1 < t_2$ and $0 < h \leq h_0$. Consequently, [**7, 16**], the positive orbit through w_h converges to an equilibrium solution:

$$E_h = \lim_{t\to\infty} T(t)w_h.$$

Clearly,

$$E_2 \leq_K E_h \leq_K w_h = E_1 + h(p_1, q_1) <_K E_1.$$

Also, if $0 < h_1 < h_2 \leq h_0$ then $w_{h_2} <_K w_{h_1}$ so $T(t)w_{h_2} <_K T(t)w_{h_1}$ which implies that $E_{h_2} \leq_K E_{h_1}$. Fix h satisfying $0 < h < h_0$. Since $E_h <_K E_1 + h(p_1, q_1)$, we can choose $k > 0$ such that $h + k \leq h_0$, $E_h \leq_K E_1 + (h+k)(p_1, q_1) = w_{h+k}$ and such that k is maximal with these properties. Then, by monotonicity, $E_h = T(t)E_h \leq_K T(t)w_{h+k}$ which implies that $E_h \leq_K E_{h+k}$. But then $E_h = E_{h+k}$ since the reverse inequality was noted above. Therefore, $E_h = E_{h+k} <_K E_1 + (h+k)(p_1, q_1)$ and, by the maximality of k, it follows that $h + k = h_0$. Consequently, $E_h = E_{h_0}$, and since h was arbitrary, this equality holds for all $h \leq h_0$.

Set $E_* = E_{h_0}$. It may be the case that $E_* = E_2$. If $w = (u, v) \in \Omega$ satisfies $E_* \leq_K w \leq_K E_1$ and $v \neq 0$ then, by Proposition 3.1, we may find $h \in (0, h_0]$ such that $E_* \leq_K T(1)w \leq_K w_h$ and monotonicity implies that $E_* \leq_K T(t+1)w \leq_K T(t)w_h$ for $t \geq 0$. Therefore, as $T(t)w_h \to E_*$ as $t \to \infty$, the same holds for $T(t)w$.

Set $M = \{w_h : 0 \leq h \leq h_0\}$ and denote by $\mathcal{O}$

$$\omega(M) = \bigcap_{s \geq 0} \text{Closure}\left(\bigcup_{t \geq s} T(t)M \right)$$

the omega limit set of the set M. It exists, is nonempty, compact, invariant, connected and contains both E_1 and E_*. The existence follows from the compactness of $T(t)$ and the fact that the bounded set Ω is positively invariant. That $\omega(M)$ contains E_1 and E_* is obvious and the remaining properties of $\omega(M)$ are standard [6, Lemma 3.2.1, **12**, Theorem 2.1]. Indeed, since the order interval $M \subset [E_*, E_1]$ and the latter is positively invariant, it follows that $\omega(M) \subset [E_*, E_1]$. E_0 cannot belong to $\omega(M)$ by Proposition 4.2 since it is a repeller. Finally [**12**, Lemma 2.1], it is well known that for each $x \in \omega(M)$ there exists a negative orbit through x in $\omega(M)$, that is, there exists a map $X : (-\infty, 0] \to \omega(M)$ satisfying $X(0) = x$ and $T(t)X(s) = X(t+s)$ for $t \geq 0$, $s \leq 0$ such that $t + s \leq 0$.

We claim that $\omega(M) \subset P$ where $P = \{w \in \Omega : T(t)w \leq_K w, t \geq 0\}$ is the set of "supersolutions" of $T(t)$. In fact, $M \subset P$ and P is closed and positively invariant by the monotonicity of $T(t)$. It follows immediately from the definition of $\omega(M)$ that it is contained in P and therefore consists of supersolutions.

Since $\omega(M)$ is connected, we may choose $x \in \omega(M)$ distinct from E_1 and E_*. Then $E_* \leq_K x \leq_K E_1$ and x is not an equilibrium since the only equilibria in $[E_*, E_1]_K$ are E_1, E_* and possibly E_0 if $E_* = E_2$. Consequently, $T(t)x \leq_K x$ for $t > 0$ and equality does not hold. Let $X(t)$ be a negative orbit through x in $\omega(M)$ and extend $X(t)$ for $t \geq 0$ by defining it to be $T(t)x$ for $t > 0$. If $t_1 < t_2$ then $X(t_2) = T(t_2 - t_1)X(t_1) \leq_K X(t_1)$ since $X(t_1)$ is a supersolution. Therefore, X is monotone decreasing with respect to the ordering $\leq_K$. Now, if $x = (u, 0)$ then $X(t) = (U(t), 0)$ where $U(t) \to E_1$ as $t \to \infty$ must hold by Proposition 4.1 and $U(t) \to E_0$ as $t \to -\infty$ must hold by monotonicity and compactness. The latter implies the contradiction that E_0 belongs to $\omega(M)$. We conclude that $x = (u, v)$ with $v \neq 0$. But then by Proposition 3.1, it follows that $X(t) > 0$ for all t and that X is strictly decreasing; that is, $X(t_2) <_K X(t_1)$ whenever $t_1 < t_2$. Therefore, $E_* <_K X(t) <_K E_1$ and both limits $\lim_{t \to \pm\infty} X(t)$ exist and are equilibria. It is easy to see, by comparison with $T(t)w_h$ for

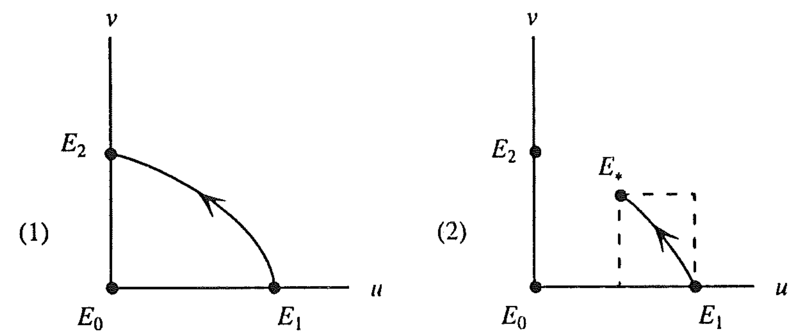

FIGURE 5.1. The two cases of Theorem 5.1. The box in (2) represents part of the region of attraction of E_*.

some h that the positive limit must be E_*. The only possibility for the negative limit is E_1. Therefore, we have established the existence of a heteroclinic orbit as asserted. □

Figure 5.1 illustrates the two cases of Theorem 5.1.

Obviously, a symmetric result holds if it is assumed that $\Lambda_2 > 0$.

Theorem 5.2. *Let* $\lambda_1 > 0$, $\mu_1 > 0$, *hold and suppose that*

$$\Lambda_1 > 0, \qquad \Lambda_2 > 0. \tag{5.6}$$

Then there exist equilibria E_* *and* E_{**}, *possibly identical, satisfying*

$$E_2 <_K E_{**} \leq_K E_* <_K E_1.$$

There exists a monotone heteroclinic orbit connecting E_1 *to* E_*. *That is, the conclusions of* (2) *of Theorem* 5.1 *hold. Similarly, there exists a monotone heteroclinic orbit connecting* E_2 *and* E_{**} *and* E_{**} *attracts all points* $w = (u, v)$ *satisfying* $E_2 \leq_K w \leq_K E_{**}$ *for which* $u \neq 0$. *The omega limit set of every point* $w = (u, v) \in \Omega$ *for which* $u \neq 0$ *and* $v \neq 0$ *is contained in* $[E_{**}, E_*]_K$. *Furthermore, there is an open dense set of* $w \in \Omega$ *such that* $T(t)w$ *converges to a stable equilibrium belonging to* $[E_{**}, E_*]_K$. *If* $E_{**} = E_*$, *then*

$$T(t)w \to E_*, \qquad t \to \infty$$

for all $w = (u, v) \in \Omega$ *for which* $u \neq 0$ *and* $v \neq 0$.

Proof. Theorem 5.1 and its symmetric analog for E_2 imply the existence of E_* and E_{**} satisfying $E_2 <_K E_{**} \leq_K E_* <_K E_1$. Also, E_* attracts all points $w = (u, v)$ satisfying $E_* \leq_K w \leq_K E_1$ and $v \neq 0$; E_{**} attracts all points $w = (u, v)$ satisfying $E_2 \leq_K w \leq_K E_{**}$ and $u \neq 0$. If $w = (u, v) \in \Omega$, then $(0, v) \leq_K w \leq_K (u, 0)$ and monotonicity implies that $T(t)(0, v) \leq_K T(t)w \leq_K T(t)(u, 0)$ for all $t \geq 0$. As $T(t)(0, v)$ converges to E_2 (or to E_0 if $v = 0$) and $T(t)(u, 0)$ converges to E_1 (or to E_0 if $u = 0$), it follows that the omega limit set of w is contained in $[E_2, E_1]_K \cap \Omega$. Furthermore, if $w \in [E_2, E_1]_K$ and $u \neq 0$ and $v \neq 0$, then the omega limit set of w is contained in $[E_{**}, E_*]_K$. Indeed, by Proposition 3.1, we may as well assume that $u > 0$ and $v > 0$ and therefore $E_2 + h(p_2, q_2) \leq_K w \leq_K E_1 + h(p_1, q_1)$ holds for some $h > 0$. As $T(t)(E_i + h(p_i, q_i))$ converge to E_{**} if $i = 2$ and E_* if $i = 1$, the claim follows by a comparison argument. Finally, if an omega limit point of w belongs to $[E_{**}, E_*]_k$ then it follows that $E_2 <_K T(t)w <_K E_1$ for some $t > 0$ and therefore the entire omega limit set must belong to $[E_{**}, E_*]_K$.

Suppose that w satisfies $u \neq 0$ and $v \neq 0$ and let ω denote its omega limit set. If $z = (x, y) \in \omega$ satisfies $x \neq 0$ and $y \neq 0$ then invariance of ω implies that $x > 0$, $y > 0$ and $E_2 <_K z <_K E_1$. The omega limit set of z must belong to $[E_{**}, E_*]_K$ since $z \in [E_1, E_2]_K$ and it must also belong to ω. But then, as observed above, $\omega \subset [E_{**}, E_*]_K$. Therefore, $\omega \subset [E_{**}, E_*]_K$ if ω contains a point $z = (x, y)$ with $x \neq 0$ and $y \neq 0$.

If every point $z = (x, y) \in \omega$ satisfies either $x = 0$ or $y = 0$, then, since E_0 does not belong to ω and by connectedness and invariance of ω, it follows that either $\omega = E_1$ or $\omega = E_2$. Assume that the former holds (the argument in the other case is similar). We have that $u(t) + v(t) \to \hat{u}$ as $t \to \infty$. Fix $s > 0$ so small that the largest eigenvalue, $\lambda = c$, of

$$\begin{gathered}\lambda q = dq_{xx} + f_2(\phi - \hat{u} - s)q \\ q_x(0) = 0, \qquad q_x(1) + rq(1) = 0\end{gathered}$$

is positive. Denote by $\bar{v}$ the corresponding positive eigenfunction. There exists $t_0 > 0$ such that for all $t \geq t_0$, we have $f_2(\phi - u - v) \geq f_2(\phi - \hat{u} - s)$. Let $\delta > 0$ be such that $v(t_0) \geq \delta\bar{v}$. Then, for $t \geq t_0$

$$v_t \geq dv_{xx} + f_2(\phi - \hat{u} - s)v, \qquad v(t_0) \geq \delta\bar{v}$$

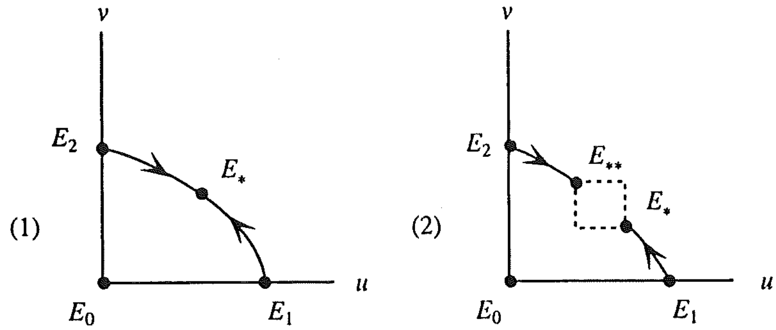

FIGURE 5.2. (1) The case that $E_* = E_{**}$; (2) The case that they are distinct. The box represents the attracting order interval $[E_{**}, E_*]_K$.

so [**22, 26**, Theorem 10.1] by comparison

$$v(t) \geq \delta \bar{v} e^{c(t-t_0)}, \qquad t \geq t_0.$$

This contradicts the boundedness of the solution $w(t)$ and we conclude that $\omega = E_1$ is impossible. We have shown that $\omega \subset [E_{**}, E_*]_K$.

Theorem 2 in [**24**] establishes the convergence to a stable equilibrium for an open and dense subset of Ω. $\square$

Figure 5.2 illustrates two cases of Theorem 5.2.

A positive equilibrium of (2.4) is an equilibrium $w = (u, v)$ for which $u > 0$ and $v > 0$. It is a challenging problem to find all positive solutions of (4.1) and it remains an open problem to provide sufficient conditions for the uniqueness of a positive equilibrium ($E_{**} = E_*$) under the hypotheses of Theorem 5.2. This same issue is unresolved in the case of the Lotka-Volterra system with constant coefficients and diffusion. See [**3**] and [**4**].

Because of the monotonicity properties of (2.4), the stability of a positive equilibrium (u, v) is determined by a single simple eigenvalue of the eigenvalue problem

(5.7)

$$\begin{aligned}\lambda U &= dU_{xx} + [f_1(\phi - u - v) - f_1'(\phi - u - v)u]U - f_1'(\phi - u - v)uV\\ \lambda V &= dV_{xx} - f_2'(\phi - u - v)vU + [f_2(\phi - u - v) - f_2'(\phi - u - v)v]V\end{aligned}$$

where U and V must satisfy the same boundary conditions as u and v (see (2.2)). A standard application of the Krein-Rutman Theorem, as in [1, Chapter 1, Section 3], implies that (5.7) has a unique real eigenvalue, $\lambda = \Lambda_w$, which is strictly larger than the real part of all other eigenvalues and is simple and that there exists a corresponding eigenfunction W satisfying $0 <_K W$. The positive equilibrium (u, v) is asymptotically stable (unstable) if $\Lambda_w < 0$ ($\Lambda_w > 0$).

Just as we constructed a monotone heteroclinic orbit emanating from E_1 in case $\Lambda_1 > 0$, a similar construction works at a positive equilibrium w provided $\Lambda_w > 0$. Indeed, two monotone heteroclinic orbits may be constructed, one which is monotone increasing and connects w to a larger equilibrium (possibly E_1), and another which is monotone decreasing and connects w to a smaller equilibrium (possibly E_2). These orbits are constructed using the line segments $w \pm hW$ where $0 < h \leq h_0$, $0 <_K W$ is the principle eigenfunction of (5.7) and $h_0 > 0$ is sufficiently small.

In our next result, we address the stability of the equilibria in Theorems 5.1 and 5.2.

Proposition 5.3. (1) *Let the hypotheses of Theorem* 5.1 *hold. If alternative* (1) *of Theorem* 5.1 *holds then* $\Lambda_2 \leq 0$; *if alternative* (2) *holds then* $\Lambda_* \equiv \Lambda_{E_*} \leq 0$. *If* $\Lambda_2 < 0$, *alternative* (2) *holds and* $\Lambda_* < 0$, *then there exists an equilibrium* w *satisfying* $E_2 <_K w <_K E_*$ *and* $\Lambda_w \geq 0$.

(2) *Let the hypotheses of Theorem* 5.2 *hold. Then* $\Lambda_* \leq 0$ *and* $\Lambda_{**} \equiv \Lambda_{E_{**}} \leq 0$. *If these equilibria are distinct and* $\Lambda_* < 0$ *and* $\Lambda_{**} < 0$ *then there exists an equilibrium* w *satisfying* $E_{**} <_K w <_K E_*$ *and* $\Lambda_w \geq 0$.

Proof. If the hypotheses of Theorem 5.1 hold and alternative (1) holds and $\Lambda_2 > 0$ then we may argue exactly as in the proof of Theorem 5.1 for the case of E_1, that E_2 is unstable from above (i.e., for the semiflow restricted to $\{w : E_2 \leq_K w\}$). As it is obvious from alternative (1) of Theorem 5.1 and standard comparison arguments that E_2 is stable from above, we conclude that $\Lambda_2 \leq 0$.

Suppose that alternative (2) of Theorem 5.1 holds. If $\Lambda_* > 0$ and $0 <_K W_*$ is the corresponding eigenfunction of (5.7) where $w = E_*$

then we may argue exactly as in Theorem 5.1 for the case of E_1, that for small positive h, $T(t)(E_* + hW)$ converges to E_1. But this would contradict (2) of Theorem 5.1. We conclude that $\Lambda_* \leq 0$.

Suppose that (2) of Theorem 5.1 holds and $\Lambda_2 < 0$ and $\Lambda_* < 0$. The arguments used in the proof of [**16**, Lemma 3.1] can be used to prove the existence of an equilibrium w_0 satisfying $E_2 <_K w_0 <_K E_*$. If $\Lambda_{w_0} \geq 0$ then we are done; if $\Lambda_{w_0} < 0$ then the same argument gives an equilibrium w_1 satisfying $w_0 <_K w_1 <_K E_*$. Again, if $\Lambda_{w_1} \geq 0$ we are done while if $\Lambda_{w_1} < 0$ then we find another equilibrium w_2 satisfying $w_1 <_K w_2 <_K E_*$. Either eventually this process yields an equilibrium w_k satisfying $\Lambda_{w_k} \leq 0$ or we may construct a sequence $\{w_n\}$ satisfying $E_2 <_K w_n <_K w_{n+1} <_K E_*$. Since the sequence is monotone and precompact, $w_n \to w$ as $n \to \infty$ where w is an equilibrium necessarily satisfying $\Lambda_w = 0$. In either case, we can find an equilibrium $w \in [E_2, E_*]_K$ satisfying $\Lambda_w \geq 0$.

Suppose that the hypotheses of Theorem 5.2 hold. From above, we know that $\Lambda_* \leq 0$ and a similar argument establishes that $\Lambda_{**} \leq 0$. If both inequalities are strict then we argue as above to obtain an equilibrium w as asserted. This completes our proof. □

Remark 1. Consider the case that $E_{**} \neq E_*$ and make the generic assumption that $\Lambda_* < 0$ and $\Lambda_{**} < 0$. By Proposition 5.3, there exists an equilibrium w satisfying $E_{**} <_K w <_K E_*$ for which $\Lambda_w \geq 0$. Let's make the generic assumption that strict inequality holds, that is, that w is unstable. In this case, we may argue exactly as in the proof of Theorem 5.1 where we constructed a monotone heteroclinic orbit emanating from E_1, that there exist two monotone heteroclinic orbits $U_i : (-\infty, +\infty) \to \Omega$, $i = 1, 2$, and two equilibria w_1 and w_2 satisfying $\Lambda_{w_i} \leq 0$ and

$$E_{**} \leq_K w_1 <_K U_1(t_2) <_K U_1(t_1) <_K w <_K U_2(t_1) \\ <_K U_2(t_2) <_K w_2 \leq_K E_*$$

whenever $t_1 < t_2$ and

$$\begin{aligned} U_i(t) &\to w, & t &\to -\infty \\ U_i(t) &\to w_i, & t &\to \infty. \end{aligned}$$

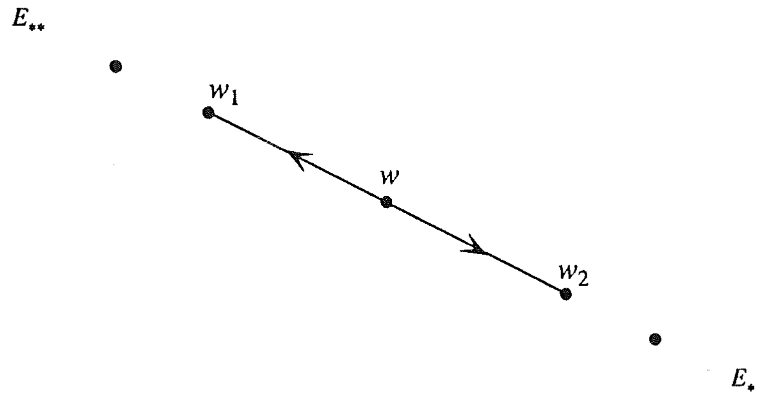

FIGURE 5.3. The monotone heteroclinic orbits of Remark 1. Of course $w_2 = E_*$ or $w_1 = E_{**}$ are possible.

Figure 5.3 illustrates the equilibria and the heteroclinic connections. Clearly, this process can be continued provided the equilibria w_i are nondegenerate.

Remark 2: If both $\Lambda_i < 0$ for $i = 1, 2$ so that E_1 and E_2 are asymptotically stable, then it can be shown that there is an equilibrium w satisfying $E_2 <_K w <_K E_1$ and $\Lambda_w \geq 0$. A proof of this can be given using degree theory and is technical since one must account for the unstable equilibrium E_0. A proof in the finite dimensional case, which can be extended to include the present case, is given in [**25**, Proposition E.2, Appendix E]. For a proof in the case of an infinite dimensional discrete model of competition, see [8].

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