JOURNAL OF MATHEMATICAL ANALYSIS AND APPLICATIONS **204,** 786–812 (1996)
ARTICLE NO. 0468

Bifurcation Analysis of a Chemostat Model with a Distributed Delay*

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Received August 7, 1995

A chemostat model of a single species feeding on a limiting nutrient supplied at a constant rate is proposed. The model incorporates a general nutrient uptake function and a distributed delay. The delay indicates that the growth of the species depends on the past concentration of nutrient. Using the average time delay as a bifurcation parameter, it is proven that the model undergoes a sequence of Hopf bifurcations. Stability criteria for the bifurcating periodic solutions are derived. It is also found that the periodic solutions become unstable if the dilution rate is increased. Computer simulations illustrate the results.

1. INTRODUCTION

The chemostat is an important laboratory apparatus used to culture microorganisms. It is of both ecological and mathematical interest since it is one of the few places where the mathematics is tractable, the parameters are measurable, and the experiments are reasonable. For recent development and mathematical analysis on chemostat models, we refer to the book by Smith and Waltman [35].

* Research supported by the Natural Sciences and Engineering Research Council of Canada.

0022-247X/96 $18.00

It is well known that time delays in ecological systems can have a considerable influence on the qualitative behavior of these systems. Some non-stationary phenomena, such as instabilities and periodic fluctuations, can be explained by incorporating time delays in model systems (see Cooke and Grossman [6], Cushing [11], Hale and Lunel [20], MacDonald [29], May [31], and the references cited there). Discrete delay was first included in a chemostat model by Finn and Wilson [14] in order to model sustained oscillations that they observed in a yeast population in a chemostat. Caperon [4], who observed oscillatory transients in experimental populations, incorporated both discrete delay and distributed delay in chemostat models. Thingstad and Langeland [37] discussed in detail the stability analysis and numerical solutions of one of Caperon's models. Bush and Cook [3] also studied a model of growth of one organism in the chemostat with a discrete delay in the intrinsic growth rate of the microorganism. For other early work, see for example, Cunningham and Maas [8], Cunningham and Nisbet [9], and MacDonald [28]. We also refer to a survey paper by MacDonald [30] regarding time delays in chemostat models.

Recently, Freedman *et al*. [15] extended the model of Bush and Cook to a competition model with two microorganisms competing for the substrate. They provided a careful analysis of the bifurcation of a planar periodic orbit involving only the substrate and one population to a three-dimensional periodic orbit involving the substrate and both competitor populations. Freedman *et al*. [16] also considered another delayed chemostat model. For this model, recently Ellermeyer [12], Hsu *et al*. [22], and Zhao [41] investigated the global asymptotic behavior of solutions, such as convergence and persistence of one of the competitors. Global asymptotic behavior of this model and a more general chemostat model with discrete delays was studied by Wolkowicz and Xia [40]. For other related models, we refer to Beretta *et al*. [2], Freedman and Xu [17] and Ruan [34].

It has been found that "continuously distributed" delay models are more realistic (see Caswell [5]) and "continuously distributed" delays are more accurate than instantaneous time lags (see Caperon [4]). In this paper, we incorporate a distributed delay in a chemostat-type model of a single species feeding on a limiting nutrient supplied at a constant rate. The distributed delay is included since it is assumed that the growth of the species depends on the past concentration of nutrient. A general function is also used to describe the nutrient uptake. For both strong and weak kernels, using the average time delay as a bifurcation parameter, we prove that Hopf bifurcation occurs, i.e., a family of periodic solutions bifurcates from the equilibrium when the bifurcation parameter passes through a critical value.

In general, as pointed out by Cushing [10], it is quite difficult to determine the stability of bifurcating periodic solutions for delay systems (and even for ordinary differential equations). However, there are a number of papers dealing with the stability of bifurcating periodic solutions for delay systems. We refer to Kazarinoff *et al*. [24], Huang *et al*. [23], and the reference cited therein for discrete delay models and Beretta *et al*. [1], Farkas [13], Gopalsamy and Aggarwala [19], and Stépán [36] for models involving distributed delays. In the case of our model with the weak kernel, by using the algorithm in Hassard *et al*. [21], we derive criteria to determine the stability of the bifurcating periodic solutions. Computer simulations illustrate the results.

Morita [33] investigated the destabilization of periodic solutions arising in delay−diffusion equations. He showed that the stability regions of the bifurcation parameter depends on other factors such as the diffusion constant and the shape of the domain. One of his results indicates that the periodic solution becomes unstable near the bifurcation point if the diffusion coefficient is varied. See also Lin and Kahn [27] and Memory [32] for related results. Following the idea and the procedure of Morita [33], we find that for this chemostat model with a distributed delay, when one of the parameters (washout rate) is varied the bifurcating periodic solution loses its stability. The numerical simulation verifies our analysis.

The paper is organized as follows. The model is described in Section 2. In Section 3, we study the existence of bifurcating periodic solutions. The stability analysis is carried out in Section 4. In Section 5, we study the destabilization of the bifurcating periodic solutions. A numerical example is given in Section 6. Finally, a discussion is presented in Section 7.

2. THE MODEL

Let $S(t)$ and $x(t)$ denote the concentration of the nutrient and the populations of microorganisms at time t. Our model is described by the integrodifferential equations

$$\begin{aligned} \frac{dS}{dt} &= \big(S^0 - S(t)\big)D - ax(t)p(S(t)), \\ \frac{dx}{dt} &= x(t)\left[-D_1 + \int_{-\infty}^{t} F(t-\tau)p(S(\tau))\,d\tau\right], \end{aligned} \tag{2.1}$$

where all of the parameters are nonnegative. S^0 denotes the input concentration of nutrient. D is referred to as the dilution rate and D_1 denotes the sum of the dilution rate and the death rate of the population of microorganisms. The function $p(S)$ describes the species specific growth rate. The nutrient uptake rate is assumed to be proportional to the growth rate with constant of proportionality a, and so $1/a$ is referred to as the growth yield constant. We assume throughout that $p(S)$ satisfies the following assumptions:

$$p(0) = 0, \qquad p'(S) > 0, \qquad \text{and} \qquad \lim_{S \to \infty} p(S) = m < \infty. \tag{2.2}$$

For example, these hypotheses are satisfied by the Michaelis–Menten (Holling type II) function

$$p(S) = \frac{mS}{k + S} \qquad (m > 0, k > 0), \tag{2.3}$$

where m denotes the maximal growth rate of the species and k is called the half-saturation constant.

The distributed delay term in system (2.1) models the situation that where the past history of consumption is important, but nutrient consumed either very recently or a long time ago has an insignificant effect on the growth of the organism. The weight function $F(s)$ is a nonnegative bounded function defined on $[0, \infty)$ which describes the influence of nutrient experience on future growth of the organism. It is assumed in this model that the presence of the distributed time delay does not affect the equilibrium values, so we normalize the kernel so that

$$\int_0^\infty F(s)\, ds = 1. \tag{2.4}$$

As in MacDonald [29], we define the average time lag as

$$T = \int_0^\infty sF(s)\, ds. \tag{2.5}$$

In particular, the weak kernel

$$F(s) = \alpha e^{-\alpha s}, \qquad \alpha > 0 \tag{2.6}$$

and the strong kernel

$$F(s) = \alpha^2 s e^{-\alpha s}, \qquad \alpha > 0 \tag{2.7}$$

are often used (see Cushing [11]). The average time lags for the weak and strong kernels are

$$T = \frac{1}{\alpha} \tag{2.8}$$

and

$$T = \frac{2}{\alpha}, \tag{2.9}$$

respectively.

We consider system (2.1) under the initial value conditions

$$S(s) = \phi(s) > 0, \qquad -\infty < s \le 0, \qquad x(0) = x_0 > 0, \tag{2.10}$$

where $\phi(s)$ is a continuous function on $(-\infty, 0]$.

Note that $E_0 = (S^0, 0)$ is always an equilibrium for system (2.1). There is an interior equilibrium $E^* = (S^*, x^*)$ with

$$S^* = p^{-1}(D_1), \qquad x^* = \frac{D(S^0 - S^*)}{aD_1} \tag{2.11}$$

provided $S^* < S^0$ and $\lim_{S \to \infty} p(S) > D_1$.

3. EXISTENCE OF HOPF BIFURCATIONS

In this section we study the existence of bifurcating periodic solutions. Let

$$u_1 = S - S^*, \qquad u_2 = x - x^*. \tag{3.1}$$

System (2.1) can be written

$$\begin{aligned}
\frac{du_1}{dt} &= ax^* p(S^*) - Du_1 - a(u_2 + x^*) p(u_1 + S^*), \\
\frac{du_2}{dt} &= (u_2 + x^*)\left[-D_1 + \int_{-\infty}^{t} F(t - \tau) p\big(u_1(\tau) + S^*\big)\, d\tau\right],
\end{aligned}$$

or

$$\frac{du}{dt} = Lu(t) + \int_{-\infty}^{0} K(\tau) u(t + \tau)\, d\tau + H(u), \tag{3.2}$$

where

$$L = \begin{pmatrix} -D - ax^* p'(S^*) & -ap(S^*) \\ 0 & 0 \end{pmatrix}, \tag{3.3}$$

$$K(\tau) = \begin{pmatrix} 0 & 0 \\ x^* p'(S^*) F(-\tau) & 0 \end{pmatrix}, \tag{3.4}$$

$$H(u) = \begin{pmatrix} -ap'(S^*) u_1 u_2 \\ p'(S^*) u_2 \int_{-\infty}^{0} F(-\tau) u_1(t + \tau)\, d\tau \end{pmatrix} + H.O.T. \tag{3.5}$$

The characteristic equation of the linearized system is

$$\begin{aligned} D(\lambda) &= \det\left[\lambda I - L - \int_{-\infty}^{0} e^{\lambda\tau} K(\tau)\, d\tau\right] \\ &= \lambda^2 + [D + ax^* p'(S^*)]\lambda + aD_1 x^* p'(S^*) \int_{-\infty}^{0} e^{\lambda\tau} F(-\tau)\, d\tau. \end{aligned} \tag{3.6}$$

If $F(s)$ is a weak kernel, i.e., $F(s) = \alpha e^{-as}$, $\alpha > 0$, then (3.6) becomes a third-order algebraic equation:

$$\lambda^3 + [\alpha + D + ax^* p'(S^*)]\lambda^2 + \alpha[D + ax^* p'(S^*)]\lambda + \alpha a D_1 x^* p'(S^*) = 0.$$

Define

$$\begin{aligned} b_1 &= b_1(\alpha) = \alpha + D + ax^* p'(S^*) > 0, \\ b_2 &= b_2(\alpha) = \alpha[D + ax^* p'(S^*)] > 0, \\ b_3 &= b_3(\alpha) = \alpha a D_1 x^* p'(S^*) > 0. \end{aligned}$$

Then the characteristic equation takes the form

$$\lambda^3 + b_1\lambda^2 + b_2\lambda + b_3 = 0. \tag{3.7}$$

Let $\psi_1 : (0, \infty) \to R$ be a continuously differentiable function defined by

$$\psi_1(\alpha) = b_1(\alpha) b_2(\alpha) - b_3(\alpha). \tag{3.8}$$

The Routh–Hurwitz criterion implies that the equilibrium (S^*, x^*) is locally asymptotically stable if $\psi_1(\alpha) > 0$. If

$$\alpha_0 = \frac{aD_1 x^* p'(S^*)}{D + ax^* p'(S^*)} - [D + ax^* p'(S^*)], \tag{3.9}$$

then $\psi_1(\alpha_0) = 0$, and the characteristic equation has a pair of purely imaginary roots $\lambda_{1,2} = \pm\omega_0 i$, where $\omega_0 = \sqrt{b_2(\alpha_0)}$ and a real root $\lambda_3 = -b_1(\alpha_0) < 0$.

After some calculations, it follows that

$$\frac{d}{d\alpha}[\operatorname{Re}\lambda_1]_{\alpha_0} = -\frac{1}{4(b_1^2 + b_2)} \left.\frac{d\psi_1}{d\alpha}\right|_{\alpha_0}, \tag{3.10}$$

where

$$\left.\frac{d\psi_1}{d\alpha}\right|_{\alpha_0} = aD_1 x^* p'(S^*) - [D + ax^* p'(S^*)]^2.$$

The above analysis can be summarized as follows:

THEOREM 3.1. *If $\psi_1(\alpha) > 0$, then the equilibrium (S^*, x^*) of system (2.1) is locally asymptotically stable. If $aD_1 x^* p'(S^*) - [D + ax^* p'(S^*)]^2 \neq 0$, then as α passes through the critical value α_0, there is a Hopf bifurcation at the equilibrium (S^*, x^*).*

If $F(s)$ is a strong kernel, i.e., $F(s) = \alpha^2 s e^{-\alpha s}$, $\alpha > 0$, then the characteristic equation is

$$\lambda^2 + [D + ax^* p'(S^*)]\lambda + aD_1 x^* p'(S^*) \frac{\alpha^2}{(\alpha + \lambda)^2} = 0.$$

Define

$$\begin{aligned}
c_1 &= c_1(\alpha) = 2\alpha + D + ax^* p'(S^*) > 0,\\
c_2 &= c_2(\alpha) = \alpha^2 + 2\alpha[D + ax^* p'(S^*)] > 0,\\
c_3 &= c_3(\alpha) = \alpha^2[D + ax^* p'(S^*)] > 0,\\
c_4 &= c_4(\alpha) = \alpha^2 aD_1 x^* p'(S^*) > 0.
\end{aligned}$$

Then the characteristic equation can be rewritten

$$\lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4 = 0. \tag{3.11}$$

Define

$$\psi_2(\alpha) = c_1(\alpha)c_3(\alpha)\, d_3(\alpha) - c_3(\alpha)^2 - c_1(\alpha)^2 c_4(\alpha). \tag{3.12}$$

The Routh–Hurwitz criterion implies that the equilibrium (S^*, x^*) of system (2.1) is locally asymptotically stable if $\psi_2(\alpha) > 0$.

Let λ_i $(i = 1, 2, 3, 4)$ be the roots of the characteristic equation (3.11). Then we have

$$\begin{aligned}
\lambda_1 + \lambda_2 + \lambda_3 + \lambda_4 &= -c_1,\\
\lambda_1\lambda_2 + \lambda_1\lambda_3 + \lambda_1\lambda_4 + \lambda_2\lambda_3 + \lambda_2\lambda_4 + \lambda_3\lambda_4 &= c_2,\\
\lambda_1\lambda_2\lambda_3 + \lambda_1\lambda_3\lambda_4 + \lambda_2\lambda_3\lambda_4 + \lambda_1\lambda_2\lambda_4 &= -c_3,\\
\lambda_1\lambda_2\lambda_3\lambda_4 &= c_4.
\end{aligned} \tag{3.13}$$

If there exists $\alpha_0 \in R$ such that $\psi_2(\alpha_0) = 0$, then by the Routh–Hurwitz criterion at least one root, say λ_1, has real part equal to zero. From the fourth equation of (3.13) it follows that $\operatorname{Im} \lambda_1 = \omega_0 \neq 0$, and hence there is another root, say λ_2, such that $\lambda_2 = \bar{\lambda}_1$. Since $\psi_2(\alpha)$ is a continuous function of its roots, λ_1 and λ_2 are complex conjugate for α in an open interval including α_0. Therefore, the equations in (3.13) have the following form at α_0:

$$\begin{aligned} \lambda_3 + \lambda_4 &= -c_1, \\ \omega_0^2 + \lambda_3\lambda_4 &= c_2, \\ \omega_0^2(\lambda_3 + \lambda_4) &= -c_3, \\ \omega_0^2\lambda_3\lambda_4 &= c_4. \end{aligned} \tag{3.14}$$

If λ_3 and λ_4 are complex conjugate, from the first equation of (3.14) it follows that $2\,\mathrm{Re}\,\lambda_3 = -c_1 < 0$. If λ_3 and λ_4 are real, from the first and fourth equations of (3.14) it follows that $\lambda_3 < 0$ and $\lambda_4 < 0$. Also, after some calculations it follows that

$$\frac{d}{d\alpha}[\mathrm{Re}\,\lambda_1]_{\alpha_0} = -\frac{c_1}{2\left[c_1^2c_4 + (c_1c_2 - 2c_3)^2\right]}\frac{d\psi_2}{d\alpha}\bigg|_{\alpha_0}.$$

Thus, we have the following result.

THEOREM 3.2. *If $\psi_2(\alpha) > 0$, then the equilibrium (S^*, x^*) of system* (2.1) *is locally asymptotically stable. If there exists $\alpha_0 \in R$ such that $\psi_2(\alpha_0) = 0$ and $(d\psi_2/d\alpha)|_{\alpha_0} \neq 0$, then as α passes through α_0, a Hopf bifurcation occurs at (S^*, x^*).*

4. STABILITY OF BIFURCATING PERIODIC SOLUTIONS

In this section, we study the stability of the bifurcating periodic solutions. We suppose that the kernel is a weak kernel, i.e., $F(s) = \alpha e^{-\alpha s}$, $\alpha > 0$. The case of the strong kernel can be discussed similarly.

We first transform system (3.2) into an operator equation of the form

$$\frac{du_t}{dt} = Au_t + Fu_t, \tag{4.1}$$

where $u = col(u_1, u_2)$, $u_t = u(t+\theta)$, $\theta \in (-\infty, 0]$, and the operators A and F are defined as

$$A\phi(\theta) = \begin{cases} \dfrac{d\phi(\theta)}{d\theta}, & -\infty < \theta < 0 \\ L\phi(0) + \int_{-\infty}^0 K(\tau)\phi(\tau)\,d\tau, & \theta = 0, \end{cases} \tag{4.2}$$

$$F\phi(\theta) = \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & -\infty < \theta < 0 \\ \begin{pmatrix} -ap'(S^*)\phi_1(0)\phi_2(0) \\ p'(S^*)\phi_2(0)\int_{-\infty}^0 \alpha e^{\alpha\tau}\phi_1(\tau)\,d\tau \end{pmatrix}, & \theta = 0, \end{cases} \tag{4.3}$$

where L and K are defined as in (3.3) and (3.4).

Note that the operator A depends on the bifurcation parameter α. By Theorem 3.1, a Hopf bifurcation occurs when α passes through α_0. Set

$$\mu = \alpha - \alpha_0 .$$

Then the Hopf bifurcation occurs when $\mu = 0$.

The adjoint operator A^* of A is defined as

$$A^*\psi(\delta) = \begin{cases} -\dfrac{d\psi(\delta)}{d\delta}, & 0 < \delta < \infty \\ L^T\psi(0) + \int_{-\infty}^{0} K^T(\tau)\psi(-\tau)\,d\tau, & \delta = 0, \end{cases}$$

where L^T and K^T are the transposes of the matrices L and K, respectively. Note that A and A^* can have complex eigenvectors. It is therefore suitable to assume that $\phi, \psi: [0, \infty) \to C^2$. Define the bilinear form:

$$\langle \psi, \phi \rangle = \bar{\psi}^T(0)\phi(0) - \int_{-\infty}^{0}\int_{0}^{\theta} \bar{\psi}^T(\xi - \theta)K(\theta)\phi(\xi)\,d\xi\,d\theta .$$

To determine the Poincaré normal form of the operator A, we need to calculate the eigenvector q of A belonging to the eigenvalue $i\omega_0$ and the eigenvector q^* of A^* belonging to the eigenvalue $-i\omega_0$. We find that

$$q(\theta) = \begin{pmatrix} 1 \\ B \end{pmatrix} e^{i\omega_0\theta}, \qquad -\infty < \theta \le 0,$$

where

$$B = -\frac{x^* p'(S^*)\alpha(\omega_0 + i\alpha)}{\omega_0(\alpha^2 + \omega_0^2)}$$

and

$$q^*(\delta) = E\begin{pmatrix} 1 \\ C \end{pmatrix} e^{i\omega_0\delta}, \qquad 0 \le \delta < \infty,$$

where

$$C = \frac{\alpha[D + ax^*p'(S^*)] - \omega_0^2 - i\omega_0[\alpha + D + ax^*p'(S^*)]}{x^*p'(S^*)\alpha},$$

$$\bar{E} = \frac{1}{1 + B\bar{C} + \dfrac{\bar{C}x^*p'(S^*)\alpha}{(\alpha + i\omega_0)^2}} .$$

We compute that

$$\langle q^*, q \rangle = 1, \qquad \langle q^*, \bar{q} \rangle = 0 .$$

Using the same notation as Hassard *et al*. [21], we first construct the coordinates to describe the centre manifold $\mathscr{C}_0$ at $\mu = 0$ ($\alpha = \alpha_0$). Let

$$z(t) = \langle q^*, u_t \rangle, \qquad w(t,\theta) = u_t - 2\operatorname{Re}\{z(t)q(\theta)\}. \tag{4.4}$$

On the centre manifold $\mathscr{C}_0, w(t,\theta) = w(z(t), \bar{z}(t), \theta)$, where

$$w(z,\bar{z},\theta) = w_{20}(\theta)\frac{z^2}{2} + w_{11}(\theta)z\bar{z} + w_{02}(\theta)\frac{\bar{z}^2}{2} + w_{30}\frac{z^3}{6} + \cdots. \tag{4.5}$$

z and $\bar{z}$ are local coordinates for the centre manifold $\mathscr{C}_0$ in the direction of q^* and $\overline{q^*}$. Note that w is real if u_t is real. We consider only real solutions.

For solution $u_t \in \mathscr{C}_0$ of (4.1), since $\mu = 0$.

$$\begin{aligned}\dot{z}(t) &= i\omega_0 z(t) + \langle q^*(\theta), F(w + 2\operatorname{Re}\{z(t)q(\theta)\})\rangle \\ &= i\omega_0 z(t) + [\overline{q^*}(0)]^T F(w(z,\bar{z},0) + 2\operatorname{Re}\{z(t)q(0)\}).\end{aligned}$$

We rewrite this as

$$\dot{z} = i\omega_0 z(t) + g(z,\bar{z}), \tag{4.6}$$

where

$$g(z,\bar{z}) = [\overline{q^*}(0)]^T F(w(z,\bar{z},0) + 2\operatorname{Re}\{z(t)q(0)\}). \tag{4.7}$$

Using (4.1) and (4.5), we have

$$\begin{aligned}\dot{w} &= \dot{u}_t - \dot{z}q - \dot{\bar{z}}\bar{q} \\ &= Aw - 2\operatorname{Re}\{\langle q^*(\theta), F(w + 2\operatorname{Re}\{z(t)q(\theta)\})\rangle q(\theta)\} \\ &\quad + F(w + 2\operatorname{Re}\{z(t)q(\theta)\}) \\ &= Aw - 2\operatorname{Re}\{g(z,\bar{z})q(\theta)\} + F(w + 2\operatorname{Re}\{z(t)q(\theta)\}),\end{aligned}$$

which can also be rewritten as

$$\dot{w} = Aw + H(z,\bar{z},\theta), \tag{4.8}$$

where

$$H(z,\bar{z},\theta) = -2\operatorname{Re}\{g(z,\bar{z})q(\theta)\} + F(w + 2\operatorname{Re}\{z(t)q(\theta)\}). \tag{4.9}$$

We expand the function $g(z,\bar{z})$ on the centre manifold $\mathscr{C}_0$ in powers of z and $\bar{z}$:

$$g(z,\bar{z}) = g_{20}\frac{z^2}{2} + g_{11}z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2} + \cdots. \tag{4.10}$$

The coefficients of (4.10) can be determined by comparing (4.10) with (4.7) where w is replaced by its expansion (4.5). In order to determine the coefficients $w_{ij}(\theta)$ of the expansion (4.5), we expand the function $H(z, \bar{z}, \theta)$ in powers of z and $\bar{z}$ on the manifold $\mathscr{C}_0$:

$$H(z, \bar{z}, \theta) = H_{20}(\theta)\frac{z^2}{2} + H_{11}(\theta) z\bar{z} + H_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots. \quad (4.11)$$

The argument of F is

$$w + zq(\theta) + \overline{zq}(\theta) = \begin{pmatrix} w^{(1)}(\theta) + ze^{i\omega_0\theta} + \bar{z}e^{-iw_0\theta} \\ w^{(2)}(\theta) + zBe^{i\omega_0\theta} + \bar{z}\overline{B}e^{-i\omega_0\theta} \end{pmatrix}.$$

Thus

$$F(w + 2\operatorname{Re}\{z(t)q(\theta)\}) = \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & -\infty < \theta < 0 \\ \begin{pmatrix} f_0^1 \\ f_0^2 \end{pmatrix}, & \theta = 0, \end{cases}$$

where

$$f_0^1 = -ap'(S^*)\big(w^{(1)}(0) + z + \bar{z}\big)\big(w^{(2)}(0) + zB + \bar{z}\overline{B}\big),$$

$$f_0^2 = x^* p'(S^*)\big(w^{(2)}(0) + zB + \bar{z}\overline{B}\big)\bigg\{\int_{-\infty}^0 w^{(1)}(s)\,\alpha e^{\alpha s}\,ds + \frac{\alpha}{\alpha^2 + \omega_0^2}\big[(\alpha - i\omega_0)z + (\alpha + i\omega_0)\bar{z}\big]\bigg\}.$$

By (4.7), it follows that

$$g(z, \bar{z}) = \overline{E} f_0^1(z, \bar{z}) + \overline{E}\,\overline{C} f_0^2(z, \bar{z}).$$

Therefore,

$$H(z, \bar{z}, \theta) = -2\operatorname{Re}\Big\{\Big[\overline{E} f_0^1(z, \bar{z}) + \overline{E}\,\overline{C} f_0^2(z, \bar{z})\Big] q(\theta)\Big\} + \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & -\infty < \theta < 0 \\ \begin{pmatrix} f_0^1(z, \bar{z}) \\ f_0^2(z, \bar{z}) \end{pmatrix}, & \theta = 0. \end{cases}$$

Since

$$\left[\frac{\partial^2 f_0^2(z,\bar z)}{\partial z^2}\right]_{z=\bar z=0} = -2ap'(S^*)B,$$
$$\left[\frac{\partial^2 f_0^2(z,\bar z)}{\partial z^2}\right]_{z=\bar z=0} = \frac{2x^* p'(S^*)B\alpha(\alpha - i\omega_0)}{\alpha^2+\omega_0^2},$$

if we define

$$G = Bp'(S^*)\left(a - \frac{\bar C x^*\alpha(\alpha - i\omega_0)}{\alpha^2+\omega_0^2}\right),$$
$$G_1 = Bp'(S^*)\left(a - \frac{C x^*\alpha(\alpha - i\omega_0)}{\alpha^2+\omega_0^2}\right),$$

by (4.9), we obtain

$$\begin{aligned} H_{20} &= \left[\frac{\partial^2 H(z,\bar z,\theta)}{\partial z^2}\right]_{z=\bar z=0} \\ &= 2\bar E G q(\theta) + 2EG_1\bar q(\theta) \\ &\quad + \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & -\infty < \theta < 0 \\ 2\begin{pmatrix} -ap'(S^*)B \\ \dfrac{x^* p'(S^*)B\alpha(\alpha - i\omega_0)}{\alpha^2+\omega_0^2} \end{pmatrix}, & \theta = 0. \end{cases} \end{aligned} \tag{4.12}$$

Similarly, since

$$\left[\frac{\partial^2 f_0^1(z,\bar z)}{\partial z\,\partial \bar z}\right]_{z=\bar z=0} = \left[\frac{\partial^2 \bar f_0^1(z,\bar z)}{\partial z\,\partial \bar z}\right]_{z=\bar z=0} = -2ap'(S^*)\,\mathrm{Re}\,B,$$
$$\left[\frac{\partial^2 f_0^2(z,\bar z)}{\partial z\,\partial \bar z}\right]_{z=\bar z=0} = \left[\frac{\partial^2 \bar f_0^2(z,\bar z)}{\partial z\,\partial \bar z}\right]_{z=\bar z=0} = 0,$$

we obtain

$$H_{11} = \left[\frac{\partial^2 H(z, \bar{z}, \theta)}{\partial z \, \partial \bar{z}} \right]_{z=\bar{z}=0}$$

$$= 2ap'(S^*)\operatorname{Re} B\left[\overline{E}q(\theta) + E\overline{q}(\theta) \right]$$

$$+ \begin{cases} \begin{pmatrix} 0 \\ 0 \end{pmatrix}, & -\infty < \theta < 0 \\ 2\begin{pmatrix} -ap'(S^*)\operatorname{Re} B \\ 0 \end{pmatrix}, & \theta = 0. \end{cases} \tag{4.13}$$

On the other hand, on the centre manifold $\mathscr{C}_0$ near the origin,

$$\dot{w}(z, \bar{z}) = w_z \dot{z} + w_{\bar{z}} \dot{\bar{z}}. \tag{4.14}$$

Using the expansion (4.5) to replace w_z and $w_{\bar{z}}$ and Eq. (4.6) to replace $\dot{z}$ and $\dot{\bar{z}}$, we obtain a second expression for $\dot{w}$. By comparison of this result with (4.8), we can derive equations for the coefficients $w_{ij}(\theta)$. These are

$$(2i\omega_0 I - A)w_{20}(\theta) = H_{20}(\theta), \tag{4.15}$$

$$-Aw_{11}(\theta) = H_{11}(\theta) \tag{4.16}$$

and $w_{02} = \overline{w}_{02}$. Define

$$w_{20}(\theta) = \begin{pmatrix} w_{20}^{(1)}(\theta) \\ w_{20}^{(2)}(\theta) \end{pmatrix}, \qquad -\infty < \theta < 0.$$

By substituting (4.2) and (4.12) into (4.15), when $-\infty < \theta < 0$, it follows that

$$\begin{pmatrix} 2i\omega_0 - \dfrac{d}{d\theta} & 0 \\ 0 & 2i\omega_0 - \dfrac{d}{d\theta} \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(\theta) \\ w_{20}^{(2)}(\theta) \end{pmatrix}$$

$$= \begin{pmatrix} 2\overline{E}Ge^{i\omega_0\theta} + 2EG_1 e^{-i\omega_0\theta} \\ 2B\overline{E}Ge^{i\omega_0\theta} + 2\overline{B}EG_1 e^{-i\omega_0\theta} \end{pmatrix}. \tag{4.17}$$

When $\theta = 0$, we obtain

$$\begin{pmatrix} 2i\omega_0 + [D + ax^* p'(S^*)] & ap(S^*) \\ 0 & 2i\omega_0 \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(0) \\ w_{20}^{(2)}(0) \end{pmatrix}$$

$$- \int_{-\infty}^{0} \begin{pmatrix} 0 & 0 \\ x^* p'(S^*)\alpha e^{\alpha s} & 0 \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(s) \\ w_{20}^{(2)}(s) \end{pmatrix} ds = \begin{pmatrix} H_{20}^{(1)}(0) \\ H_{20}^{(2)}(0) \end{pmatrix}. \tag{4.18}$$

In order to obtain a continuous solution $w(\theta)$ on $(-\infty, 0]$, we consider the above equations associated with the boundary condition

$$\lim_{\theta \to 0^-} \begin{pmatrix} w_{20}^{(1)}(\theta) \\ w_{20}^{(2)}(\theta) \end{pmatrix} = \begin{pmatrix} w_{20}^{(1)}(0) \\ w_{20}^{(2)}(0) \end{pmatrix}. \tag{4.19}$$

The general solution of (4.17) is

$$\begin{pmatrix} w_{20}^{(1)}(\theta) \\ w_{20}^{(2)}(\theta) \end{pmatrix} = \begin{pmatrix} k_0 \\ l_0 \end{pmatrix} e^{2i\omega_0\theta} + \begin{pmatrix} k_1 \\ l_1 \end{pmatrix} e^{i\omega_0\theta} + \begin{pmatrix} k_2 \\ l_2 \end{pmatrix} e^{-i\omega_0\theta}, \tag{4.20}$$

where

$$k_1 = -\frac{2\bar{E}G}{\omega_0} i, \qquad k_2 = -\frac{2EG_1}{3\omega_0};$$

$$l_1 = k_1 B, \qquad l_2 = k_2 \bar{B},$$

and l_0 and k_0 are determined by (4.19), i.e.,

$$k_0 = w_{20}^{(1)}(0) - (k_1 + k_2), \qquad l_0 = w_{20}^{(2)}(0) - (l_1 + l_2).$$

To find $w_{20}^{(1)}(0)$ and $w_{20}^{(2)}(0)$, we substitute (4.20) into Eq. (4.18) to obtain

$$\begin{pmatrix} 2i\omega_0 + [D + ax^* p'(S^*)] & ap(S^*) \\ -\dfrac{2x^* p'(S^*)\alpha(\alpha - 2i\omega_0)}{\alpha^2 + 4\omega_0^2} & 2i\omega_0 \end{pmatrix} \begin{pmatrix} w_{20}^{(1)}(0) \\ w_{20}^{(2)}(0) \end{pmatrix} = \begin{pmatrix} c_{20}^{(1)} \\ c_{20}^{(2)} \end{pmatrix}, \tag{4.21}$$

where

$$c_{20}^{(1)} = H_{20}^{(1)},$$

$$c_{20}^{(2)} = H_{20}^{(2)} + i\frac{2x^* p'(S^*)\alpha}{\omega_0} \times \left\{ \frac{\left(B\bar{E}G + \frac{1}{3}\bar{B}EG_1\right)(\alpha - 2i\omega_0)}{\alpha^2 + 4\omega_0^2} - \frac{B\bar{E}G(\alpha - i\omega_0) + \frac{1}{3}\bar{B}EG_1(\alpha + i\omega_0)}{\alpha^2 + \omega_0^2} \right\}.$$

Define

$$\Delta = 2i\omega_0[2i\omega_0 + D + ax^* p'(S^*)] + \frac{aD_1 x^* p'(S^*)\alpha(\alpha - 2i\omega_0)}{\alpha^2 + 4\omega_0^2}.$$

Then we find that

$$w_{20}^{(1)}(0) = \frac{2i\omega_0 c_{20}^{(1)} - ap(S^*)c_{20}^{(2)}}{\Delta},$$

$$w_{20}^{(2)}(0) = \frac{\left[2i\omega_0 + D + ax^*p'(S^*)\right]c_{20}^{(2)} + \dfrac{2x^*p'(S^*)\alpha(\alpha - 2i\omega_0)}{\alpha^2 + 4\omega_0^2}c_{20}^{(1)}}{\Delta}.$$

Similarly, by Eq. (4.18),

$$\begin{pmatrix} w_{11}^{(1)}(0) \\ w_{11}^{(2)}(0) \end{pmatrix} = \begin{pmatrix} p_0 \\ q_0 \end{pmatrix} + \begin{pmatrix} p_1 \\ q_1 \end{pmatrix} e^{i\omega_0\theta} + \begin{pmatrix} p_2 \\ q_2 \end{pmatrix} e^{-i\omega_0\theta}, \qquad (4.22)$$

where

$$p_1 = \frac{2ap'(S^*)(\operatorname{Re} B)\overline{E}}{\omega_0}i, \qquad q_1 = p_1 B,$$

$$p_2 = \bar{p}_1, \qquad q_2 = p_2\overline{B},$$

$$p_0 = w_{11}^{(1)}(0) - (p_1 + p_2), \qquad q_0 = w_{11}^{(2)}(0) - (q_1 + q_2).$$

To find $w_{11}^{(1)}(0)$ and $w_{11}^{(2)}(0)$, we substitute (4.22) into (4.16) to obtain

$$\begin{pmatrix} D + ax^*p'(S^*) & ap(S^*) \\ -x^*p'(S^*) & 0 \end{pmatrix} \begin{pmatrix} w_{11}^{(1)}(0) \\ w_{11}^{(2)}(0) \end{pmatrix}$$

$$= \begin{pmatrix} H_{11}^{(1)}(0) \\ H_{11}^{(2)}(0) - x^*p'(S^*)\left[(p_1 + p_2) + p_1\alpha\dfrac{\alpha - i\omega_0}{\alpha^2 + \omega_0^2} + p_2\alpha\dfrac{\alpha + i\omega_0}{\alpha^2 + \omega_0^2}\right] \end{pmatrix}$$

$$= \begin{pmatrix} H_{11}^{(1)}(0) \\ H_{11}^{(2)}(0) + \dfrac{2aD_1\alpha x^*p'(S^*)(\operatorname{Re} B)}{\omega_0} \times\left[\dfrac{\alpha - i\omega_0}{\alpha^2 + \omega_0^2}Ei - \dfrac{\alpha + i\omega_0}{\alpha^2 + \omega_0^2}\overline{E}i - \dfrac{1}{\alpha}(\overline{E}i - Ei)\right] \end{pmatrix}$$

$$= \begin{pmatrix} c_{11}^{(1)} \\ c_{11}^{(2)} \end{pmatrix},$$

where

$$c_{11}^{(1)} = H_{11}^{(1)}(0),$$

$$c_{11}^{(2)} = H_{11}^{(2)}(0) + \frac{4aD_1 \alpha x^* p'(S^*)(\operatorname{Re} B)}{\omega_0}\left[\frac{\operatorname{Im}\left(\overline{E}(\alpha - i\omega_0)\right)}{\alpha^2 + \omega_0^2} + \frac{\operatorname{Im} E}{\alpha}\right].$$

Solving for $w_{11}^{(1)}(0)$ and $w_{11}^{(2)}(0)$, it follows that

$$w_{11}^{(1)}(0) = -\frac{c_{11}^{(1)}}{x^* p'(S^*)},$$

$$w_{11}^{(2)}(0) = \frac{[D + ax^* p'(S^*)]c_{11}^{(2)} + x^* p'(S^*)c_{11}^{(1)}}{aD_1 x^* p'(S^*)}$$

Now we consider $F(w(z, \bar{z}, 0) + 2\operatorname{Re}\{z(t)q(0)\})$. Since

$$\begin{aligned} w(z, \bar{z}, 0) &+ 2\operatorname{Re}\{z(t)q(0)\} \\ &= w_{20}(0)\frac{z^2}{2} + w_{11}(0)z\bar{z} + w_{02}(0)\frac{\bar{z}^2}{2} + \cdots + 2\operatorname{Re}\{z(t)q(0)\} \\ &= \begin{pmatrix} w_{20}^{(1)}(0) \\ w_{20}^{(2)}(0) \end{pmatrix}\frac{z^2}{2} + \begin{pmatrix} w_{11}^{(1)}(0) \\ w_{11}^{(2)}(0) \end{pmatrix} z\bar{z} + \begin{pmatrix} w_{02}^{(1)}(0) \\ w_{02}^{(2)}(0) \end{pmatrix}\frac{\bar{z}^2}{2} \\ &\quad + \cdots + 2\operatorname{Re}\{z(t)q(0)\}, \end{aligned}$$

we find

$$\begin{aligned} f_0^1 = -ap'(S^*)&\left[w_{20}^{(1)}(0)\frac{z^2}{2} + w_{11}^{(1)}(0)z\bar{z} + w_{02}^{(1)}(0)\frac{\bar{z}^2}{2} + (z + \bar{z})\right] \\ &\left[w_{20}^{(2)}(0)\frac{z^2}{2} + w_{11}^{(2)}(0)z\bar{z} + w_{02}^{(2)}(0)\frac{\bar{z}^2}{2} + (zB + \bar{z}\overline{B})\right], \end{aligned}$$

$$\begin{aligned} f_0^2 = x^* p'(S^*)&\left[w_{20}^{(2)}(0)\frac{z^2}{2} + w_{11}^{(2)}(0)z\bar{z} + w_{02}^{(2)}(0)\frac{\bar{z}^2}{2} + (zB + \bar{z}\overline{B})\right] \\ &\left[\tilde{w}_{20}^{(1)}(0)\frac{z^2}{2} + \tilde{w}_{11}^{(1)}(0)z\bar{z} + \tilde{w}_{02}^{(1)}(0)\frac{\bar{z}^2}{2}\right. \\ &\left.\quad + \frac{\alpha}{\alpha^2 + \omega_0^2}(z(\alpha - i\omega_0) + \bar{z}(\alpha + i\omega_0))\right], \end{aligned}$$

where

$$
\begin{aligned}
\tilde{w}_{20}^{(1)}(0) &= \int_{-\infty}^{0} \alpha e^{\alpha s} w_{20}^{(1)}(s)\, ds \\
&= \int_{-\infty}^{0} \alpha e^{\alpha s}\Big[k_1 e^{i\omega_0 s} + k_2 e^{-i\omega_0 s} + \big(w_{20}^{(1)}(0) - (k_1 + k_2)\big) e^{2i\omega_0 s}\Big]\, ds \\
&= \alpha \Bigg[k_1 \frac{\alpha - i\omega_0}{\alpha^2 + \omega_0^2} + k_2 \frac{\alpha + i\omega_0}{\alpha^2 + \omega_0^2} \\
&\qquad + \big(w_{20}^{(1)}(0) - (k_1 + k_2)\big) \frac{\alpha - 2i\omega_0}{\alpha^2 + 4\omega_0^2} \Bigg], \\
\tilde{w}_{11}^{(1)}(0) &= \int_{-\infty}^{0} \alpha e^{\alpha s} w_{11}^{(1)}(s)\, ds \\
&= \int_{-\infty}^{0} \alpha e^{\alpha s}\big[p_1 e^{i\omega_0 s} + p_2 e^{-i\omega_0 s} + w_{11}^{(1)}(0) - (p_1 + p_2)\big]\, ds \\
&= \frac{\alpha}{\alpha^2 + \omega_0^2}\big[p_1(\alpha - i\omega_0) + p_2(\alpha + i\omega_0)\big] + w_{11}^{(1)}(0) - (p_1 + p_2), \\
\tilde{w}_{02}^{(1)}(0) &= \int_{-\infty}^{0} \alpha e^{\alpha s} w_{02}^{(1)}(s)\, ds.
\end{aligned}
$$

Thus,

$$
\begin{aligned}
g(z, \bar{z}) &= \big[\overline{q^*}(0)\big]^T F\big(w(z, \bar{z}, 0) + 2\,\mathrm{Re}\{z(t) q(0)\}\big) \\
&= (\bar{E}, \bar{E}\bar{C}) \begin{pmatrix} f_0^1 \\ f_0^2 \end{pmatrix} \\
&= \bar{E}\big(f_0^1 + \bar{C} f_0^2\big).
\end{aligned}
\tag{4.23}
$$

Comparison of the coefficients of (4.10) and (4.23) yields

$$
\begin{aligned}
g_{20} &= -2\bar{E}G, \\
g_{11} &= -2\bar{E} a p'(S^*)\,\mathrm{Re}\, B, \\
g_{02} &= 2p'(S^*)\bar{E}\bar{B}\left[-a + \frac{\bar{C} x^* \alpha(\alpha + i\omega_0)}{\alpha^2 + \omega_0^2} \right],
\end{aligned}
$$

$$g_{21} = 2\bar{E}p'(S^*)\left\{-a\left[\frac{\bar{B}w_{20}^{(1)}(0)}{2} + \frac{w_{20}^{(2)}(0)}{2} + w_{11}^{(1)}(0)B + w_{11}^{(2)}(0)\right]\right.$$

$$+x^*\bar{C}\left[\frac{\bar{B}\tilde{w}_{20}^{(1)}(0)}{2} + \frac{w_{20}^{(2)}(0)}{2}\frac{\alpha(\alpha + i\omega_0)}{\alpha^2 + \omega_0^2}\right.$$

$$\left.\left.+w_{11}^{(2)}(0)\frac{\alpha(\alpha - i\omega_0)}{\alpha^2 + \omega_0^2} + B\tilde{w}_{11}^{(1)}(0)\right]\right\}.$$

Therefore, we can compute the following parameters:

$$c_1(0) = \frac{i}{2\omega_0}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{g_{21}}{2},$$

$$\mu_2 = -\frac{\operatorname{Re} c_1(0)}{\operatorname{Re} \lambda_1'(\alpha_0)},$$

$$\tau_2 = -\frac{\operatorname{Im} c_1(0) + \mu_2 \operatorname{Im} \lambda_1'(\alpha_0)}{\omega_0},$$

$$\beta_2 = 2\operatorname{Re} c_1(0),$$

$$T = \frac{2\pi}{\omega_0}\left(1 + \tau_2\varepsilon^2 + O(\varepsilon^4)\right), \qquad \varepsilon^2 = \frac{\alpha - \alpha_0}{\mu_2} + O(\alpha - \alpha_0)^2.$$

We obtain

$$c_1(0) = i\frac{2\bar{E}^2p'(S^*)}{\omega_0}\left[a(\operatorname{Re} B)G - a^2p'(S^*)(\operatorname{Re} B)^2\right.$$

$$\left.-\frac{1}{3}p'(S^*)\bar{B}^2\left(-a + ax^*\bar{C}\frac{\alpha(\alpha + i\omega_0)}{\alpha^2 + \omega_0^2}\right)^2\right]$$

$$+\bar{E}p'(S^*)\left\{-a\left[\frac{\bar{B}w_{20}^{(1)}(0)}{2} + \frac{w_{20}^{(2)}(0)}{2} + w_{11}^{(1)}(0)B + w_{11}^{(2)}(0)\right]\right.$$

$$+x^*\bar{C}\left[\frac{\bar{B}\tilde{w}_{20}^{(1)}(0)}{2} + \frac{w_{20}^{(2)}(0)}{2}\frac{\alpha(\alpha + i\omega_0)}{\alpha^2 + \omega_0^2}\right.$$

$$\left.\left.+w_{11}^{(2)}(0)\frac{\alpha(\alpha - i\omega_0)}{\alpha_2 + \omega_0^2} + B\tilde{w}_{11}^{(1)}(0)\right]\right\}.$$

Now we can state the main result of this section.

THEOREM 4.1. *The direction of the Hopf bifurcation described in Theorem* 3.1 *is determined by the sign of* μ_2: *if* $\mu_2 > 0$ (< 0), *then the bifurcating periodic solutions exist for* $\alpha > \alpha_0$ $(\alpha < \alpha_0)$. *The periodic solutions are stable* (*unstable*) *if* $\beta_2 < 0$ (> 0). *The period of the bifurcating periodic solutions of system* (2.1) *increases* (*decreases*) *if* $\tau_2 > 0$ (< 0).

5. DESTABILIZATION OF THE PERIODIC SOLUTIONS

By Theorem 3.1, under certain assumptions system (2.1) has a periodic solution bifurcating from the equilibrium $E^* = (S^*, x^*)$ when α passes through a critical value α_0. Let ε be a measure of the amplitude of the periodic solution $p(t; \varepsilon)$, $\varepsilon = \max_t \| p(t; \varepsilon) \|$. According to Hassard *et al.* [21], there is an open interval $(0, \varepsilon_1)$ such that for any $\mu = \alpha - \alpha_0$ in the interval

$$J_1 = \left\{ \mu \,|\, 0 < \frac{\mu}{\mu_2} < \frac{\mu(\varepsilon_1)}{\mu_2} \right\},$$

there is a unique $\varepsilon \in (0, \varepsilon_1)$ for which $\mu(\varepsilon) = \mu$. For $\mu \in J_1$, the period $T(\mu)$ and the Floquet characteristic exponent $\beta(\mu)$ of the periodic solution $p(t; \varepsilon)$ are

$$T(\mu) = \frac{2\pi}{\omega_0}\left(1 + T_2 \varepsilon^2 + O(\varepsilon^4)\right), \tag{5.1}$$

$$\beta(\mu) = \beta_2 \varepsilon^2 + O(\varepsilon^4), \tag{5.2}$$

where

$$\mu(\varepsilon) = \mu_2 \varepsilon^2 + O(\varepsilon^4), \tag{5.3}$$

$$\omega(\varepsilon) = \omega_0 + \omega_2 \varepsilon^2 + O(\varepsilon^4), \tag{5.4}$$

$$\varepsilon^2 = \frac{\mu}{\mu_2} + O(\mu_2). \tag{5.5}$$

By Theorem 4.1, if $\beta_2 < 0$, then the periodic solution $p(t; \varepsilon)$ is stable. In order to study the change of stability of $p(t; \varepsilon)$ as D is varied, we write the linearized system of (3.2) around $p(t; \varepsilon)$ as

$$\frac{dz}{dt} = -Ez(t) + f_u(\mu(\varepsilon), p_t(\cdot; \varepsilon)) z_t, \tag{5.6}$$

where

$$E = \begin{pmatrix} D & 0 \\ 0 & 0 \end{pmatrix}. \tag{5.7}$$

Define

$$\int_{\infty}^{0} d\eta[\tau]\phi(-\tau) = (L - E)\phi(0) + \int_{\infty}^{0} K(\tau)\phi(\tau)\,d\tau,$$

where L and K are defined as in (3.3) and (3.4), and E is defined by (5.7). Define two vectors ζ_0 and ζ_0^* by

$$\left(i\omega_0 - \int_{\infty}^{0} e^{i\omega_0\theta}[d\eta(\theta)]\right)\zeta_0 = 0 \tag{5.8}$$

and

$$\left(-i\omega_0 - \int_{\infty}^{0} e^{-i\omega_0\theta}[d\eta(\theta)]^T\right)\zeta_0^* = 0. \tag{5.9}$$

After adopting new variables

$$s = \omega(\varepsilon)t, w(s) = z\left(\frac{s}{\omega}\right) = z(t),$$

system (5.6) can be written as

$$\omega(\varepsilon)\frac{d}{ds}w(s) = -Ew(s) + f_u\big(\mu(\varepsilon), y_{s,\,\omega(\varepsilon)}(\cdot;\varepsilon)\big)w_{s,w(\varepsilon)}, \tag{5.10}$$

where

$$y(s,\varepsilon) = p\left(\frac{s}{\omega(\varepsilon)};\varepsilon\right),$$

$$w_{s,\,\omega(\varepsilon)}(\theta) = w(s + \omega(\varepsilon)\theta), \qquad \infty < \theta \le 0.$$

Let

$$E = \varepsilon^2 E_2 \qquad \left(i.e., D = \varepsilon^2 D_2\right) \tag{5.11}$$

for some matrix E_2 (for some constant D_2). Now Eq. (5.10) has the same form as the one that appears in Morita [33]. Applying the results in [33] it follows that for $D = \varepsilon^2 D_2$, the exponents of (5.10) have the form

$$\gamma = \gamma(\varepsilon, D_2) = \gamma_2(D_2)\varepsilon^2 + \hat{\gamma}(\varepsilon, D_2)\varepsilon^2, \qquad \hat{\gamma}(0,\cdot) = 0, \tag{5.12}$$

where $\gamma_2 = \gamma_2(D_2)$ satisfies

$$\begin{aligned}\gamma_2^2 + 2\,\mathrm{Re}\{(E_2\zeta_0, \zeta_0^*) - B_1\}\gamma_2 + |(E_2\zeta_0, \zeta_0^*)|^2 \\ - 2\,\mathrm{Re}\{\overline{B}_1(E_2\zeta_0, \zeta_0^*)\} = 0,\end{aligned} \tag{5.13}$$

and

$$B_1 = i\omega_2 - \mu_2 \mathrm{Re}\frac{d\lambda}{d\mu}(0), \tag{5.14}$$

where μ_2 and ω_2 are defined in (5.3) and (5.4). ζ_0 and ζ_0^* are defined by (5.8) and (5.9).

Thus we have the following result.

THEOREM 5.1. *Under the hypotheses of Theorems* 3.1 *and* 4.1, *if* $D = \varepsilon^2 D_2$ *and Eq.* (5.13) *has a positive root* γ_2, *then there exists an* $\bar{\varepsilon} > 0$ *such that for each* $\varepsilon \in (0, \bar{\varepsilon})$, $\mu = \mu(\varepsilon)$ *the periodic solution in system* (2.1) *is unstable*.

6. AN EXAMPLE

Consider system (2.1) where $p(S)$ takes the Michaelis–Menten form and $F(s)$ is the weak kernel. In particular, consider the following system:

$$\begin{aligned} \frac{dS}{dt} &= 0.08(3.66 - S(t)) - 4.25x(t)\frac{S(t)}{5.85 + S(t)}, \\ \frac{dx}{dt} &= x(t)\left[-0.66 + 3.45\int_{-\infty}^{t} \alpha e^{-\alpha(t-\tau)}\frac{S(\tau)}{5.85 + S(\tau)}\,d\tau\right]. \end{aligned} \tag{6.1}$$

By theorem 3.1, we can determine that

$$\alpha_0 = 0.1903, \qquad \omega_0 = 0.2098. \tag{6.2}$$

The positive equilibrium is

$$E^* = (1.3839, 0.2240). \tag{6.3}$$

By the results in Section 4, it follows that

$$\mu_2 = -13.2535, \qquad \beta_2 = -1.3174, \qquad \tau_2 = 8.3164. \tag{6.4}$$

These calculations prove that the equilibrium E^* is stable when $\alpha > \alpha_0$ as is illustrated by the computer simulations (Figs. 1 and 2, $\alpha = 0.4645$). When α passes through the critical value $\alpha_0 = 0.1903$, E^* loses its stability and a Hopf bifurcation occurs; i.e., a family of periodic solutions bifurcate from E^*. The individual periodic orbits are stable since $\beta_2 < 0$. Choosing $\alpha = 0.1813$, as predicted by the theory, Fig. 3 shows that there is an orbitally stable limit cycle. Since $\mu_2 < 0$, the bifurcating periodic solutions exist at least for values of α slightly less than the critical value. Recall that in (2.8), the average time delay is defined by $T = 1/\alpha$. Note that T increases when α decreases. For a slightly smaller value of α, $\alpha = 0.1723$, the orbitally stable periodic solution persists and is plotted in Fig. 4. The period is approximately 35 (Fig. 5). Since $\tau_2 > 0$, the period of the periodic solutions increases as α decreases.

From Theorem 5.1, the periodic solution loses its stability if the dilution rate D is varied. As we increase D from 0.08 to 0.14, the periodic solution in Fig. 4 becomes unstable and the equilibrium E^* regains its stability (Fig. 6).

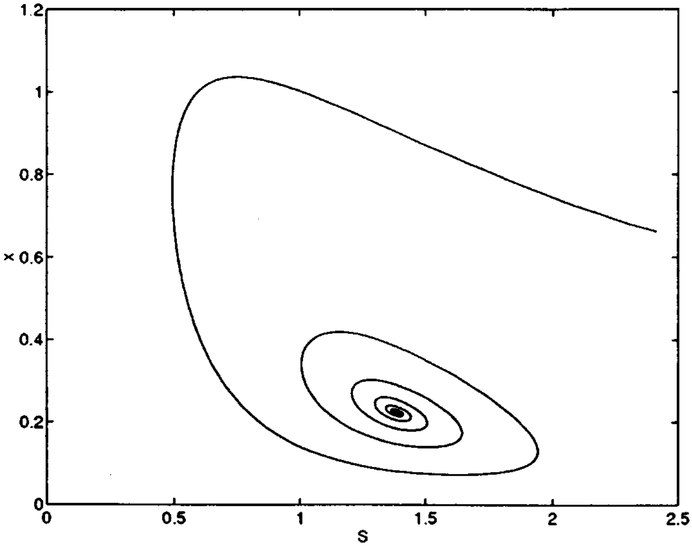

FIG. 1. The equilibrium $E^* = (1.3839, 0.2240)$ of system (5.1) is asymptotically stable when $\alpha > \alpha_0$. Here $\alpha = 0.4645$.

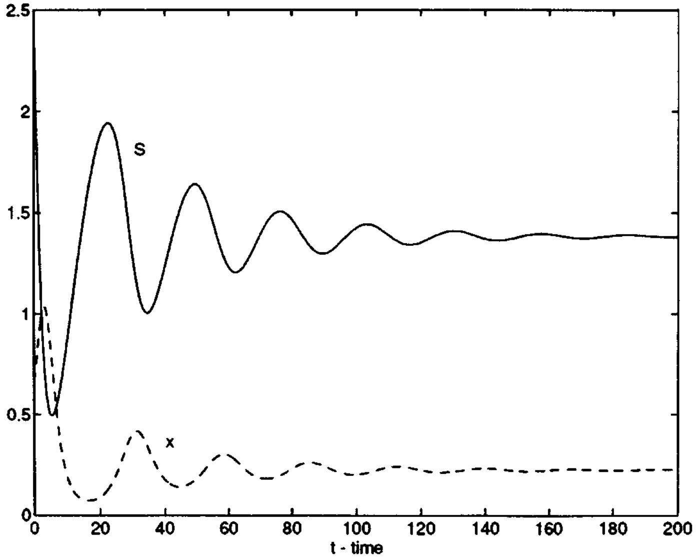

FIG. 2. The trajectories of S and x with respect to time when $\alpha = 0.4645$.

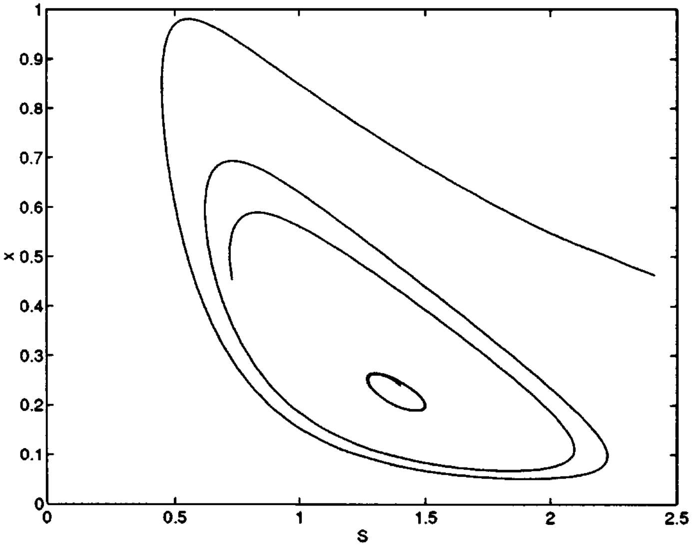

FIG. 3. With $\alpha = 0.1813$, there is an orbitally stable limit cycle attracting two trajectories. One trajectory has initial values inside the limit cycle and near the equilibrium; the other has initial values outside the limit cycle.

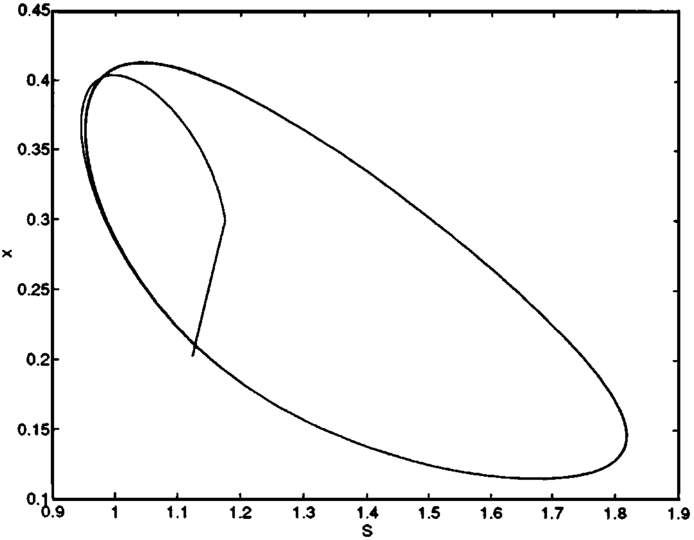

FIG. 4. The bifurcating periodic orbit persists for values of α slightly less than α_0. A stable periodic orbit is plotted with $\alpha = 0.1723$.

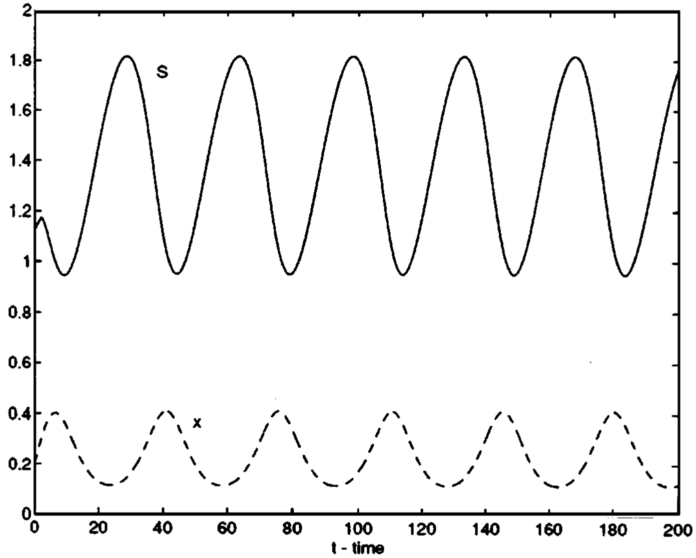

FIG. 5. The oscillations of S and x versus time when $\alpha = 0.1723$. The period is approximately 35.

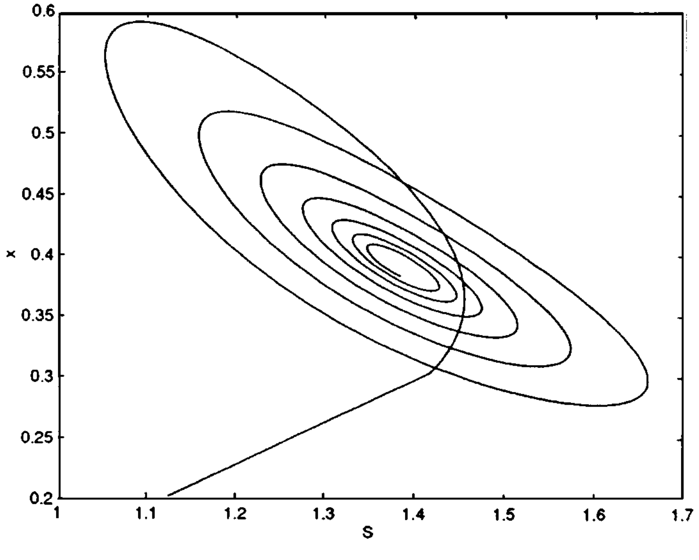

FIG. 6. The bifurcating periodic solution becomes unstable when $D = 0.14$ and the equilibrium regains its stability.

7. DISCUSSION

We have studied a chemostat model of a single species with a distributed delay. Using the average time delay as a bifurcation parameter, we have shown that a Hopf bifurcation occurs when this parameter passes through a critical value; i.e., a family of periodic orbits bifurcates from the positive equilibrium. The stability of the bifurcating periodic orbits is discussed. We have also studied the destabilization of the periodic solutions when the washout rate is varied.

If the kernel is a delta function of the form

$$F(s) = \delta(s - \tau), \qquad \tau > 0, \tag{7.1}$$

where τ is a constant, then system (2.1) reduces to the following model with a discrete delay τ:

$$\begin{aligned} \frac{dS}{dt} &= \left(S^0 - S(t)\right)D - ax(t)p(S(t)), \\ \frac{dx}{dt} &= x(t)\left[-D_1 + p(S(t - \tau))\right]. \end{aligned} \tag{7.2}$$

It has been shown by Freedman *et al.* [15] that there is a critical value of the discrete delay τ at which Hopf bifurcation occurs. Our Theorem 3.1 corresponds to one of their results.

If the kernel is a delta function of the form

$$F(s) = \delta(s), \tag{7.3}$$

then system (2.1) becomes the system of ordinary differential equations

$$\begin{aligned} \frac{dS}{dt} &= \left(S^0 - S(t)\right)D - ax(t)p(S(t)), \\ \frac{dx}{dt} &= x(t)\left[-D_1 + p(S(t))\right], \end{aligned} \tag{7.4}$$

which has been investigated by many authors. By constructing a Liapunov function (see Wolkowicz *et al.* [39]), it can be seen that if the positive equilibrium of (7.4) exists, it is globally asymptotically stable. Thus our result shows that delays can destabilize an otherwise stable equilibrium. This phenomenon has been observed by many authors in other settings (for example, see Cushing [11], Kuang [25], MacDonald [29]).

The stability of the bifurcating periodic orbits allows us to claim that for the delayed chemostat model, even if the positive equilibrium is not stable, all components may still coexist in an oscillatory mode.

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