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SLOW PASSAGE THROUGH A HOPF BIFURCATION: FROM OSCILLATORY TO STEADY STATE SOLUTIONS*

LISA HOLDEN†‡ AND THOMAS ERNEUX†

Abstract. This paper investigates the slow passage through a supercritical Hopf bifurcation from a branch of slowly varying periodic solutions to a branch of slowly varying steady states. This analysis is motivated by a recent numerical study of bursting oscillations in an enzymatic system. It was found that the transition from oscillations to steady states is delayed even if the rate of change of the control parameter is extremely small.

The delay due to the slow passage is characterized by determining the amplitude of the oscillations at the bifurcation point. Defining ε as the rate of change of the bifurcation parameter, it is shown that the amplitude is an $O(\varepsilon^{1/4})$ quantity as $\varepsilon \to 0$.

In addition, a particular class of equations leading to relaxation oscillations is considered. It is assumed that frequency ω of the oscillations at the Hopf bifurcation can be controlled using a second parameter distinct from the bifurcation parameter. It is then shown that the amplitude of the oscillations at the Hopf bifurcation point increases like $\varepsilon^{1/4}\omega^{-1}$ as $\omega \to 0$, ε small but fixed.

Finally, this paper concentrates on a specific model of bursting oscillations appearing in an enzymatic system, and the theory is applied.

Key words. delayed bifurcation, bursting oscillations, singular perturbations

AMS(MOS) subject classifications. 34C15, 34E15, 58F14, 58F21

1. Introduction. In many problems that are modeled mathematically as bifurcation problems, the control parameter varies naturally with time or is deliberately varied by the experimenter. Slow catalyst deactivation due to poisoning is a serious problem in industrial chemical reactors. It may constrain their performances or lead to unexpected jump transitions [12]. On the contrary, quick transitions are desirable for optically bistable devices and are forced by increasing or decreasing a key parameter [13]. It is particularly interesting to determine the solution of these problems in the limit of small rates of change of the bifurcation parameter. A general observation for a large variety of bifurcation and limit-point problems is that the bifurcation or jump transition does not occur at the bifurcation or limit point, but is delayed [14]. For some bifurcation problems such as Hopf bifurcations, this delay is an $O(1)$ quantity even if the rate of change of the control parameter is small. This delay property motivates the study of a wide variety of bifurcation problems with time-dependent control parameters.

In this paper, we formulate a theory for a slow passage through a supercritical Hopf bifurcation. Previous studies have analyzed the slow passage through a Hopf bifurcation from a stable steady state to a stable time-periodic solution [1]-[5]. The reverse transition, namely, the transition from an oscillatory solution to a steady state, has never been investigated. Our interest for this transition is motivated by a recent numerical study of bursting oscillations in an enzymatic system [10] shown in Fig. 1, § 4. This study suggests that the reverse Hopf transition is delayed even if the rate of change is chosen to be extremely small. In addition to bursting oscillations, the problem appears in experimental studies of oscillatory chemical reactions as they slowly approach thermodynamic equilibrium. Furthermore, the reverse Hopf transition is important if the control parameter

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† Department of Engineering Sciences and Applied Mathematics, Northwestern University, Evanston, Illinois 60208.

‡ Present address, Department of Mathematics, Kalamazoo College, Kalamazoo, Michigan 49007.

periodically passes through a Hopf bifurcation. A dynamical hysteresis for the amplitude versus the bifurcation parameter is possible because the response near the bifurcation point is different for the forward and backward transitions.

Our theoretical analysis of the reverse Hopf bifurcation transition involves two parts. First, we consider the slow passage through a regular Hopf bifurcation for a general class of ordinary differential equations (ODEs). Second, we examine the case of a low-frequency Hopf bifurcation, a situation that occurs in many problems exhibiting relaxation oscillations.

In the regular case, we characterize the transition by determining the amplitude of the oscillations at or near the Hopf bifurcation point. If ε is defined as the dimensionless rate of change, this amplitude is proportional to an $O(\varepsilon^{1/4})$ quantity.

In the special case of a Hopf bifurcation characterized by a low frequency, we analyze a particular class of ODEs and show that the amplitude of the oscillations at the Hopf bifurcation point may become more dramatic.

The paper is organized as follows. Section 2 investigates the slow passage through a regular Hopf bifurcation using the method of matched asymptotic expansions. Of particular interest is the limit of weak nonlinear damping. In § 3 we analyze the case of a slow passage through a low-frequency Hopf bifurcation. We apply our results in § 4 by considering a model for bursting oscillations in an enzymatic system. In § 5 we discuss possible limitations of our results.

2. Slow passage through a regular Hopf bifurcation. We consider the general system of equations

$$\frac{d\mathbf{u}}{dt} = \mathbf{F}(\mathbf{u}, \lambda(\varepsilon t)), \tag{2.1}$$

where $\mathbf{u} = \operatorname{col}(u_1, u_2, \ldots, u_n)$ and $\mathbf{F} = \operatorname{col}(F_1, F_2, \ldots, F_n)$ are n-dimensional vectors ($n \geqq 2$). $\lambda(\varepsilon t)$ is a slowly decreasing bifurcation parameter given by

$$\lambda(\varepsilon t) = \lambda_i - \varepsilon t, \qquad 0 < \varepsilon \ll 1. \tag{2.2}$$

If $\varepsilon = 0$ and $\lambda > \lambda_H$, where λ_H corresponds to a Hopf bifurcation point, we assume that (2.1) admits a branch of stable $2\pi/\sigma(\lambda)$-periodic solutions given by

$$\mathbf{u} = \mathbf{v}(t, \lambda). \tag{2.3}$$

We consider the case when $\lambda_i \gg \lambda_H$ and investigate (2.1) and (2.2) with the initial conditions $\mathbf{u} = \mathbf{v}(0, \lambda_i)$. Our main objective is to describe the transition near the Hopf bifurcation. To this end, we determine a particular inner problem that is motivated by the behavior of the outer solution near $\lambda = \lambda_H$.

2.1. Outer solution. We apply the method of multiple scales for slowly varying and strongly nonlinear oscillators [6, p. 264], [11] and introduce a new fast time ξ and a slow time τ defined by

$$\xi = \varepsilon^{-1}\theta(\tau) + \psi(\tau) \quad \text{and} \quad \tau = \varepsilon t. \tag{2.4}$$

$\theta'(\tau) = \omega(\tau)$ and $\psi(\tau)$ are referred to as the slowly varying frequency and the slowly varying phase, respectively. The function $\omega(\tau)$ is determined by requiring that the leading-order approximation of the solution is periodic in ξ with a period that does not depend on ξ. The value of the constant period is arbitrary and we choose 2π. We now seek a solution of (2.1) and (2.2) of the form

$$\mathbf{u}(\xi, \tau, \varepsilon) = \mathbf{u}_0(\xi, \tau) + \varepsilon\mathbf{u}_1(\xi, \tau) + \ldots, \tag{2.5}$$

where the coefficients $\mathbf{u}_0, \mathbf{u}_1, \ldots$, are bounded, 2π-periodic functions of ξ. After substituting (2.5) into (2.1) and using (2.4), we find the following problems for $\mathbf{u}_0$ and $\mathbf{u}_1$:

$$\omega \mathbf{u}_{0\xi} - \mathbf{F}(\mathbf{u}_0, \lambda(\tau)) = 0, \qquad \mathbf{u}_0(0,0) = \mathbf{v}(0, \lambda_i), \tag{2.6}$$

$$\omega \mathbf{u}_{1\xi} - \mathbf{F}_u(\mathbf{u}_0, \lambda(\tau))u_1 = -\mathbf{u}_{0\tau} - \psi' u_{0\xi}, \qquad \mathbf{u}_1(0,0) = 0. \tag{2.7}$$

Here, the matrix $\mathbf{F}_u(\mathbf{u}_0, \lambda(\tau))$ is the derivative of $\mathbf{F}(\mathbf{u}, \lambda)$ with respect to $\mathbf{u}$. If $\omega = \sigma(\lambda)$, (2.6) is equivalent to (2.1), and its solution is given by the limit cycle solution with a slowly decreasing bifurcation parameter $\lambda(\tau)$

$$\mathbf{u}_0(\xi, \tau) = \mathbf{u}_0(\xi, \lambda(\tau)) = \mathbf{v}(t, \lambda(\tau)). \tag{2.8}$$

Next, we consider (2.7). Because the homogeneous problem has a periodic solution given by $\mathbf{u}_1 = \mathbf{u}_{0\xi}$, we apply a solvability condition. Using the fact that $\mathbf{u}_{0\tau} = -\mathbf{u}_{0\lambda}$, this condition leads to an equation for the phase shift ψ

$$\psi'(\tau) = G(\lambda(\tau)) = \int_0^{2\pi} (\mathbf{u}_{0\lambda}, \mathbf{w})\, d\xi \left[\int_0^{2\pi} (\mathbf{v}_\xi, \mathbf{w})\, d\xi\right]^{-1}, \tag{2.9}$$

where $(\mathbf{a}, \mathbf{b})$ represents the usual scalar product of vectors $\mathbf{a}$ and $\mathbf{b}$, and where $\mathbf{w}(\xi, \lambda)$ is defined as the 2π-periodic solution of the adjoint linear problem.

It is not necessary to solve the initial value problem to find the behavior of the outer solution near the bifurcation point. As we demonstrate, the expansion of the solution given by (2.5) becomes nonuniform as λ approaches the bifurcation point $\lambda = \lambda_H$. This occurs at a critical time $t = t_H$ defined by

$$t_H = \varepsilon^{-1}(\lambda_i - \lambda_H). \tag{2.10}$$

As $t \to t_H^-$ (or, equivalently, as $\lambda - \lambda_H = -\varepsilon(t - t_H) \to 0^+$), $\mathbf{u}_0$ and $\mathbf{u}_1$ are harmonic functions of ξ and have the limits

$$\mathbf{u}_0 \to \mathbf{v}_H + [-\varepsilon(t - t_H)]^{1/2}(\mathbf{p}e^{i\xi} + \text{c.c.}), \tag{2.11}$$

$$\mathbf{u}_1 \to [-\varepsilon(t - t_H)]^{-3/2}(\mathbf{p}_1 e^{i\xi} + \text{c.c.}), \tag{2.12}$$

where $(\mathbf{v}, \lambda) = (\mathbf{v}_H, \lambda_H)$ is the Hopf bifurcation point, and $\mathbf{p}$ and $\mathbf{p}_1$ are two constant vectors. Equation (2.11) follows from the expansion of the periodic solution $\mathbf{v}(t, \lambda)$ near $\lambda = \lambda_H$. Equation (2.12) is found from an analysis of (2.7) as $\lambda \to \lambda_H$, using (2.11). Expansion (2.5) becomes invalid as $t \to t_H$ because $|\mathbf{u}_1| \to \infty$ as $t \to t_H$. Substituting (2.11) and (2.12) into (2.5), we find that (2.5) is nonuniform as soon as

$$-\varepsilon(t - t_H) = O(\varepsilon^{1/2}). \tag{2.13}$$

Using (2.13), we also note from (2.5), (2.11), and (2.12) that

$$\mathbf{u} - \mathbf{v}_H = O(\varepsilon^{1/4}). \tag{2.14}$$

Moreover, the limiting form of (2.9) with (2.13) gives

$$\psi'(\tau) \to [-\varepsilon(t - t_H)]^{-1}C = O(\varepsilon^{-1/2}), \tag{2.15}$$

where C is a constant. It suggests that the appropriate slow time for the transition is given by $s = \varepsilon^{1/2}(t - t_H) = O(1)$ (instead of $\tau = \varepsilon(t - t_H)$).

2.2. Inner solution. We now analyze the slow passage through the bifurcation point $\lambda = \lambda_H$. To this end, we define the inner time variable as

$$T = t - t_H \tag{2.16}$$

and seek a solution of the form

$$\mathbf{u}(S, s, \rho) = \mathbf{v}_H + \rho \mathbf{u}_1(S, s) + \rho^2 \mathbf{u}_2(S, s) + \dots, \tag{2.17}$$

where ρ, S, and s are defined by

$$\rho = \varepsilon^{1/4}, \quad S = \omega T, \quad s = \rho^2 T. \tag{2.18}$$

The frequency ω is determined using the condition that $\mathbf{u}(S, s, \rho)$ is 2π-periodic in S. With S and s, the differential equations (2.1) can be rewritten as

$$\omega \mathbf{u}_S + \rho^2 \mathbf{u}_s = \mathbf{F}(\mathbf{u}, \lambda(s)), \qquad \mathbf{u}(S, s, \rho) = \mathbf{u}(S + 2\pi, s, \rho), \tag{2.19}$$

where the subscripts S and s denote partial derivatives. Using the definition of the slow time, we can reformulate $\lambda(\varepsilon t)$, given by (2.2), as

$$\lambda(s) = -\rho^2 s. \tag{2.20}$$

Introducing (2.17) and (2.20) into (2.19) leads to the usual sequence of problems for a Hopf bifurcation. The leading-order solution is given by

$$\mathbf{u}_1(S, s) = \alpha(s)\mathbf{p}e^{iS} + \text{c.c.}, \tag{2.21}$$

where the complex amplitude α is obtained from a solvability condition at $O(\rho^3)$ and satisfies the ODE

$$\frac{d\alpha}{ds} = -sa\alpha + A\alpha^2\bar{\alpha}. \tag{2.22}$$

In this equation a and A are complex coefficients. In terms of $\alpha = r \exp(i\theta)$, (2.22) is equivalent to the following equations for r and θ:

$$\frac{dr}{ds} = -sa_1 r + A_1 r^3, \tag{2.23}$$

and

$$\frac{d\theta}{ds} = -sa_2 + A_2 r^2. \tag{2.24}$$

In (2.23), $a_1 > 0$ because the basic solution is unstable if $\lambda > \lambda_H$ and $\varepsilon = 0$. $A_1 < 0$ because we assumed that the periodic solutions are stable if $\lambda > \lambda_H$ and $\varepsilon = 0$. Since the slow time evolution equation for r does not depend on θ, we can analyze the passage through the bifurcation point by studying this equation. This equation must be solved with a matching condition given by

$$r(s) \to (sa_1/A_1)^{1/2} \quad \text{as } s \to -\infty. \tag{2.25}$$

This condition implies that the slowly varying oscillations are matching the branch of periodic solutions $\mathbf{u} = \mathbf{v}(t, \lambda)$ as $(\lambda - \lambda_H)\rho^{-2} \to \infty$. This description of the slow passage through a Hopf bifurcation is similar but simpler than the slow passage through resonance, which requires the solution of both the r and θ equations [6, p. 236].

2.3. Weak damping. As we now show, the limit $A_1 \to 0$ is of particular physical interest. We introduce a new time variable defined as

$$\mu = sa_1^{1/2} \tag{2.26}$$

and rewrite (2.23) and (2.25) in terms of μ

$$\frac{dr}{d\mu} = -\mu r - Br^3, \qquad r(\mu) \to (-\mu/B)^{1/2} \quad \text{as } \mu \to -\infty, \tag{2.27}$$

where $B = -A_1/a_1^{1/2} > 0$. Equation (2.27) is a Bernoulli equation that has the solution

$$r(\mu) = \left[B\sqrt{\pi} \exp(\mu^2) + 2B \exp(\mu^2) \int_0^\mu \exp(-x^2)\, dx \right]^{-1/2}. \tag{2.28}$$

The limit $A_1 \to 0$ or $B \to 0$ corresponds to the limit of weak nonlinear damping. This situation appears for Hopf bifurcations to relaxation oscillations [7] or for low-frequency oscillator problems such as the CO_2 laser [8]. We consider the case when $\varepsilon \ll B \ll 1$ and assume that the amplitude equation (2.27) correctly describes the transition through the Hopf bifurcation (located at $\mu = 0$). To estimate how the amplitude changes at $\mu = 0$, we determine $r(0)$ from (2.30) and obtain

$$r(0) = B^{-1/2}\pi^{-1/4}. \tag{2.29}$$

Since $r(0) \to \infty$ as $B \to 0$, we conclude that weak nonlinear damping may lead to large amplitude oscillations at the bifurcation point.

Our analysis of the slow passage through the Hopf bifurcation indicates that the amplitude of the oscillations can be important at the Hopf bifurcation point. This suggests that we characterize the delay of the bifurcation transition by determining the amplitude of the oscillations rather than by determining the value of the bifurcation parameter where the oscillations cease to exist. In terms of the original variables, we have found that

$$\mathbf{u} - \mathbf{v}_H = O((\varepsilon B^{-2})^{1/4}) \tag{2.30}$$

at the bifurcation point $\lambda = \lambda_H$. In (2.30), ε is the rate of change of the bifurcation parameter and B characterizes the nonlinear damping. This result is valid in the limit $\varepsilon \to 0$, B fixed. We now propose a new asymptotic analysis, which is based on the limit $B \to 0$ and $\varepsilon = \varepsilon(B) \to 0$.

3. Slow passage through a low-frequency Hopf bifurcation. In this section, we consider a class of problems leading to relaxation oscillations that are modeled by equations of the form

$$\frac{dx}{dt} = f(x, y, \lambda, \delta) \quad \text{and} \quad \frac{dy}{dt} = \delta g(x, y, \lambda, \delta), \tag{3.1}$$

where $\delta \ll 1$ is a new small parameter. We assume that (3.1) has a Hopf bifurcation point defined by

$$(x\, y, \lambda) = (x_H(\delta), y_H(\delta), \lambda_H(\delta)) \tag{3.2}$$

and consider the case of a supercritical bifurcation. The basic assumptions on the Hopf bifurcation are described in [7]. In particular, if $\delta = 0$, $\lambda_H(0)$ satisfies the condition $f_x(x_H(0), y_H(0), \lambda_H(0)) = 0$ and corresponds to a double-zero eigenvalue of the linearized problem.

Our main objective is to show that the slow passage through the Hopf bifurcation depends on a small damping term proportional to δ. To this end, we determine the coefficients of the amplitude equation (2.23) in terms of partial derivatives of f and g. If $\lambda - \lambda_H = O(\delta)$, we know that the local approximation of the periodic solution for $\lambda - \lambda_H \to 0$ (δ small and fixed) matches the small δ expansion of the solution (amplitude small and fixed) [7]. It is mathematically more convenient to first determine the bifurcation equations in the limit $\delta \to 0$ and then consider the small amplitude limit of this equation.

Specifically, we assume the following range of values for $\lambda(0) = \lambda_i$:

$$\lambda_i - \lambda_H(0) = O(\delta) \tag{3.3}$$

and analyze the slow passage through the Hopf bifurcation. A particular problem is analyzed in § 4. To analyze the transition, we introduce the new time

$$s = \delta^{1/2}(t - t_H), \tag{3.4}$$

where t_H is defined by the condition $\lambda(\varepsilon t_H) = \lambda_H(0)$ and is given by

$$t_H = \varepsilon^{-1}(\lambda_i - \lambda_H(0)). \tag{3.5}$$

To analyze the solution in the vicinity of the bifurcation point, we reformulate the evolution equations so that the leading-order problem as $\delta \to 0$ does not depend on δ. To this end, we introduce the deviations u, v, and Λ defined as [7]

$$u(s) = \delta^{-1/2}(x - x_H(0)) = O(1), \tag{3.6}$$

$$v(s) = \delta^{-1}(y - y_H(0)) = O(1), \tag{3.7}$$

$$\Lambda(s) = \delta^{-1}(\lambda - \lambda_H(0)) = \delta^{-1}(-\varepsilon\delta^{-1/2}s). \tag{3.8}$$

(Note that the initial value of Λ is $\Lambda(s = -\delta^{1/2}t_H) = \delta^{-1}(\lambda_i - \lambda_H(0)) = O(1)$.) Using (3.4) and (3.6)–(3.8), we rewrite (3.1) in terms of u and v. Note that $f_x(x_H, y_H, \lambda_H(0), 0) = 0$. Expanding in Taylor series the right-hand sides of (3.1), we obtain the following equations for u and v:

$$\frac{du}{ds} = f_y v + \frac{1}{2} f_{xx} u^2 + f_\lambda \Lambda + f_\delta + \delta^{1/2}\bar{f}(u, v, \Lambda, \delta^{1/2}), \tag{3.9}$$

$$\frac{dv}{ds} = g_x u + \delta^{1/2}\bar{g}(u, v, \Lambda, \delta^{1/2}). \tag{3.10}$$

All partial derivatives are evaluated at the bifurcation point $(x, y, \lambda, \delta) = (x_H(0), y_H(0), \lambda_H(0), 0)$. The functions $\bar{f}$ and $\bar{g}$ have the following limits as $\delta \to 0$:

$$\bar{f} = f_{x\lambda}\Lambda u + f_{xy} uv + f_{x\delta} u + \tfrac{1}{6} f_{xxx} u^3 + O(\delta^{1/2}), \tag{3.11}$$

$$\bar{g} = g_y v + g_\lambda \Lambda + g_\delta + \tfrac{1}{2} g_{xx} u^2 + O(\delta^{1/2}). \tag{3.12}$$

We now consider the case of a slowly varying bifurcation parameter. We introduce a fast time S and a slow time σ defined by

$$S = qs \quad \text{and} \quad \sigma = \delta^{1/2} S. \tag{3.13}$$

$q = O(1)$ is defined in the Appendix, and its expression allows us to eliminate some of the coefficients in (3.9) and (3.10). From (3.8), we first rewrite $\Lambda(\sigma)$ as follows:

$$\Lambda(\sigma) = \delta^{-1}(-\varepsilon q^{-1}\delta^{-1}\sigma). \tag{3.14}$$

(Note that the initial value of Λ is $\Lambda(\sigma = -\delta q t_H) = \delta^{-1}(\lambda_i - \lambda_H(0)) = O(1)$.) We assume that the rate of change of $\Lambda = \Lambda(\sigma)$ is small and requires that

$$\varepsilon\delta^{-2} \ll 1. \tag{3.15}$$

We now analyze the limit $\delta \to 0$ of (3.9) and (3.10). The perturbation analysis is similar to the analysis given in [7]. By successive changes of variables described in the Appendix, (3.9) and (3.10) can be rewritten as

$$\frac{dX}{dS} = -Y, \qquad \frac{dY}{dS} = X(1+Y) + \delta^{1/2}H(X, Y, \Lambda, \delta^{1/2}), \tag{3.16}$$

where X and S are proportional to u and s, respectively. The definitions of X, S, and H are given in the Appendix. If $\delta = 0$, we note that (3.16) has a first integral given by

$$N = \tfrac{1}{2}X^2 + Y - \ln(1+Y). \tag{3.17}$$

Recall that the Hopf bifurcation is located at $\Lambda = 0$. We now analyze the slow transition through $\Lambda = 0$ by determining how N is changing as $\delta \to 0$. Taking the derivative of (3.17) with respect to S and using (3.16), we obtain an equation for N

$$\frac{dN}{dS} = \delta^{1/2}\frac{Y}{1+Y}H(X, Y, \Lambda, \delta^{1/2}). \tag{3.18}$$

We solve (3.16) and (3.18) by seeking a solution for X, Y, and N of the form

$$X(\psi, \sigma, \delta^{1/2}) = X_0(\psi, \sigma) + \delta^{1/2}X_1(\psi, \sigma) + \dots, \tag{3.19}$$

$$Y(\psi, \sigma, \delta^{1/2}) = Y_0(\psi, \sigma) + \delta^{1/2}Y_1(\psi, \sigma) + \dots, \tag{3.20}$$

$$N(\psi, \sigma, \delta^{1/2}) = N_0(\psi, \sigma) + \delta^{1/2}N_1(\psi, \sigma) + \dots, \tag{3.21}$$

where $\psi = \delta^{-1/2}\theta(\sigma) + \Phi(\sigma)$ is redefined as the fast time of the oscillations. $\theta'(\sigma) = \omega(\sigma)$ and $\Phi(\sigma)$ are the slowly varying frequency and the slowly varying phase, respectively. We introduce (3.19)–(3.21) into (3.16) and (3.18) and use the chain rules $d/S = \omega(\sigma)\partial/\partial\psi + \delta^{1/2}[\partial/\partial\sigma + \Phi'(\sigma)\partial/\partial\psi]$. In first approximation, we obtain the following equations for X_0, Y_0, and N_0:

$$\omega X_{0\psi} = -Y_0, \qquad \omega Y_{0\psi} = X_0(1+Y_0), \quad \text{and} \quad \omega N_{0\psi} = 0, \tag{3.22}$$

where the subscript ψ means partial derivative with respect to ψ. From the equation for N_0, we conclude that

$$N_0 = N_0(\sigma) \tag{3.23}$$

is an unknown function of the slow time σ. Note that N_0 is related to X_0 and Y_0. Indeed, from (3.17), we have

$$N_0 = \tfrac{1}{2}X_0^2 + Y_0 - \ln(1+Y_0). \tag{3.24}$$

Since N_0 is unknown, we consider the $O(\delta^{1/2})$ problem for N_1 given by

$$\omega N_{1\psi} = -N_{0\sigma} - \Phi'(\sigma)N_{0\psi} + \frac{Y_0}{1+Y_0}H(X_0, Y_0, \Lambda, 0). \tag{3.25}$$

N_1 is a bounded periodic function of ψ if the right-hand side satisfies a solvability condition. This condition leads to the following ODE for $N_0(\sigma)$:

$$\frac{dN_0}{d\sigma} = \frac{1}{2\pi}\int_0^{2\pi}\frac{Y_0}{1+Y_0}H(X_0, Y_0, \Lambda, 0)\,d\psi. \tag{3.26}$$

We expect that this equation gives a valid description of the slow passage through the bifurcation point provided that N_0 is not too large. We do not analyze the validity of this equation for all $N_0 = O(1)$ because it depends on the function H. For example, N_0 may approach infinity as Λ approaches a critical value [7]. For small N_0, we can approximate the integral because X_0 and Y_0 approach harmonic functions. We then obtain an equation of the form

$$\frac{dN_0}{d\sigma} = (\Lambda - \Lambda_0)cN_0 + CN_0^2 + O(N_0^3), \tag{3.27}$$

where $\Lambda = \Lambda(\sigma)$, Λ_0 corresponds to the bifurcation point (i.e., $\lambda_H(\delta) = \lambda_H(0) + \delta\Lambda_0 + O(\delta^2)$), and c, C are constants. From our assumptions on the direction of the bifurcation, c and C are positive and negative, respectively. We now relate (3.27) to (2.23) and introduce the variables r and μ defined as

$$N_0(\varepsilon) = \tfrac{1}{2}\varepsilon^{1/2}r^2 \quad \text{and} \quad \mu = \mu_0 + \varepsilon^{1/2}b(t - t_H), \tag{3.28}$$

where $b = (cq/2)^{1/2}$. The scalings in (3.28) are motivated by the form of (2.23). From the definition of σ (see (3.4) and (3.13)) and the expression of $\Lambda(\sigma)$ (see (3.8) and (3.14)), we obtain the relations

$$\sigma = \delta q\varepsilon^{-1/2}b^{-1}(\mu - \mu_0) \quad \text{and} \quad \Lambda(\sigma) = -\delta^{-1}\varepsilon^{1/2}b^{-1}(\mu - \mu_0). \tag{3.29}$$

We can eliminate the term Λ_0 by specifying μ_0 as $\mu_0 = \Lambda_0 b\delta\varepsilon^{-1/2}$. Using (3.28) and (3.29), we rewrite (3.27) in terms of r and μ and find that

$$\frac{dr}{d\mu} = -\mu r - Br^3, \quad \text{where } B = -\frac{C\delta q}{4b}. \tag{3.30}$$

Equation (3.30) is now identical to (2.27), as we expected. However, we also find that the limit of weak nonlinear damping $B \to 0$ corresponds to the limit $\delta \to 0$, where δ is the physical parameter associated with the relaxation oscillations. Similarly to (2.32), we characterize the slow passage through the bifurcation point by determining the amplitude of the oscillations at the bifurcation point. From (2.31), we know that $r(0) = O(B^{-1/2}) = O(\delta^{-1/2})$. From (3.24) we have $N_0 \approx \frac{1}{2}(X_0^2 + Y_0^2)$ as $N_0 \to 0$, which implies that $X_0 = O(N_0^{1/2})$. Using the relation $N_0 = N_0(r)$ in (3.28) and the fact that $r(0) = O(\delta^{-1/2})$, we have

$$X_0 = O(N_0^{1/2}) = O(\varepsilon^{1/4}\delta^{-1/2}) = O(\varepsilon^{1/4}\omega^{-1}), \tag{3.31}$$

where $\omega = \omega(\delta)$ is defined as the frequency of the oscillations at the Hopf bifurcation point, which is an $O(\delta^{1/2})$ quantity as $\delta \to 0$ [7]. A specific application of our analysis is described in § 4.

4. Bursting oscillations. Bursting oscillations are defined as periodic oscillations consisting of clusters of spikes separated by periods of relative quiescence. They have been discovered in chemical and electrochemical systems and are modeled by coupled ODEs with "fast" and "slow" variables. The "fast" variables are rapidly oscillating, and the period slowly changes as the "slow" variables change. In [10], we consider a simple biochemical model for busting oscillations. It describes an enzymatic system that consists of two autocatalytic reactions coupled in series [9]. The kinetic equations involve the normalized concentration of a substrate α and two products β and γ. We have shown that the leading problem of our multiscale analysis requires the study of a slow passage through a Hopf bifurcation. This transition occurs from slowly varying oscillations to a slowly varying steady state. The simplified problem is formulated by equations

$$\frac{d\beta}{dt} = q_1\phi(A(\varepsilon T), \beta) - \eta(\beta, \gamma), \tag{4.1}$$

$$\frac{d\gamma}{dt} = q_2\eta(\beta, \gamma) - \bar{k}\gamma, \tag{4.2}$$

where A is proportional to α and is given by

$$A(\varepsilon t) = A_i - \varepsilon t. \tag{4.3}$$

The nonlinear functions $\phi(A, \beta)$ and $\eta(\beta, \gamma)$ are defined by

$$\phi(A, \beta) = \frac{A^2(1+\beta)^2}{1 + A^2(1+\beta)^2} \quad \text{and} \quad \eta(\beta, \gamma) = \frac{\beta(1+\gamma)^2}{L_2 + (1+\gamma)^2}. \tag{4.4}$$

In these equations, L_2 represents an allosteric constant; $\bar{k}$ is the dimensionless first-order rate constant for the removal of product β; q_1 and q_2 are constants arising from the normalization of the metabolite concentrations [9]. Typical values of these parameters are

$$q_1 = 50, \quad q_2 = 0.02, \quad L_2 = 10^2, \quad \bar{k} = 0.75, \quad A_i = 0.01, \quad \text{and} \quad \varepsilon = 10^{-6}. \tag{4.5}$$

Figure 1 shows the results of a numerical study of (4.1)–(4.4). If $\varepsilon = 0$, the variable A is constant and is considered as a bifurcation parameter. S and P denote the branch of steady states and the branch of periodic solutions and have been obtained using a continuation method (AUTO). Solid and broken lines correspond to stable and unstable solutions, respectively. If $\varepsilon \neq 0$, but is small, A is a slowly decreasing function of t, and we have represented the successive maxima of the oscillations of $\beta(t)$ as a function of A. As expected, the slowly varying maximum value of β follows the branch of periodic solutions except in the vicinity of the Hopf bifurcation point $A_H = 0.0038$. The oscillations disappear at a critical value of $A = A_c < A_H$, and the system then follows the branch of steady states.

An analysis of the steady-state solutions and the Hopf bifurcation of (4.1) and (4.2) with A constant indicates that $\beta = O(L_2 q_1)$ is large, $\gamma = O(1)$, and $A = O(L_2^{-1/2} q_1^{-1})$

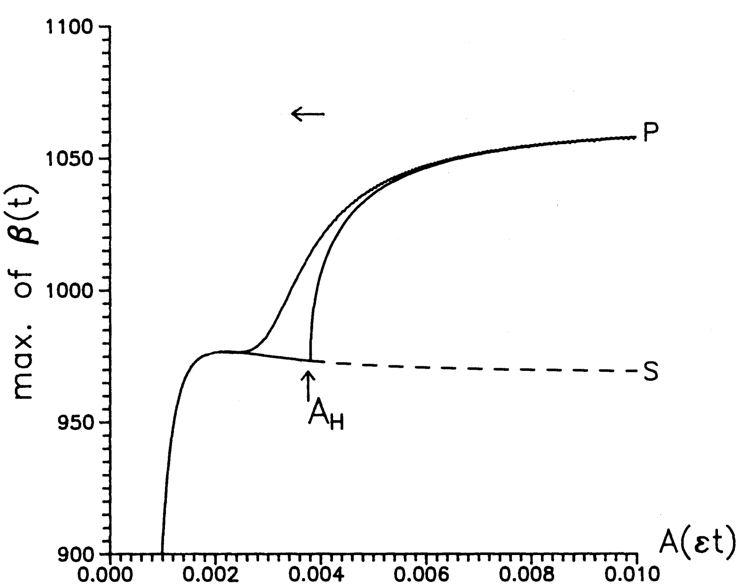

FIG. 1. *Slow passage through the Hopf bifurcation for the bursting model* (4.1)–(4.4). *The values of the parameters are* $q_1 = 50$, $q_2 = 0.02$, $L_2 = 10^2$, $\bar{k} = 0.75$, $A_i = 0.01$, and $\varepsilon = 10^{-6}$. *The figure represents the maximum of the oscillations as a function of the bifurcation parameter* A. S, P, *and* A_H *denote the branch of steady states, the branch of periodic solutions, and the static Hopf bifurcation point. Note the large deviation between the time-dependent solution and the branches of stable solutions near the bifurcation point.*

is small. This motivates the following change of variables [10]:

(4.6) $$A = L_2^{-1/2} q_1^{-1} \bar{A} \quad \text{and} \quad \beta = L_2 q_1 \bar{\beta}.$$

Substituting (4.6) into (4.1)–(4.3) and considering that $q_1 q_2 = 1$, we obtain the following simplified equations as $L_2 \to \infty$:

(4.7) $$L_2 \frac{d\bar{\beta}}{dt} = 1 - \bar{\beta}(1+\gamma)^2 - L_2^{-1}[(\bar{\beta}\bar{A})^{-2} - \bar{\beta}(1+\gamma)^4] + O(L_2^{-2}),$$

(4.8) $$\frac{d\gamma}{dt} = \bar{\beta}(1+\gamma)^2 - \bar{k}\gamma - L_2^{-1}\bar{\beta}(1+\gamma)^4 + O(L_2^{-2}),$$

where

(4.9) $$\bar{A}(t) = L_2^{1/2} q_1 (A_i - \varepsilon t).$$

The interesting region of values for $\bar{k}$ corresponds to $|\bar{k} - 1| = O(L_2^{-1})$, because $\bar{A}_H$ is then an $O(1)$ quantity. Substituting

(4.10) $$\bar{k} = (1 + L_2^{-1}\xi)$$

into (4.7) and (4.8) leads to equations

(4.11) $$L_2 \frac{d\bar{\beta}}{dt} = 1 - \bar{\beta}(1+\gamma)^2 - L_2^{-1}[(\bar{\beta}\bar{A})^{-2} - \bar{\beta}(1+\gamma)^4] + O(L_2^{-2}),$$

(4.12) $$\frac{d\gamma}{dt} = [\bar{\beta}(1+\gamma)^2 - (1 + L_2^{-1}\xi)\gamma] - L_2^{-1}\bar{\beta}(1+\gamma)^4 + O(L_2^{-2}).$$

These equations are of the form of (3.1) with

(4.13) $$x = \gamma \quad \text{and} \quad y = \bar{\beta}, \qquad \lambda = \bar{A} \quad \text{and} \quad \delta = L_2^{-1}.$$

From the linearized theory, we find that (4.11) and (4.12) admit a Hopf bifurcation point that has the following limit as $L_2 \to \infty$:

(4.14) $$\bar{\beta}_H \to \tfrac{1}{4}, \qquad \gamma_H \to 1, \quad \text{and} \quad \bar{A}_H \to \bar{A}_H(0) = 4(-\xi - 16)^{-1/2},$$

where $\xi < -16$ ($\xi = -25$ if $\bar{k} = 0.75$). We now investigate the limit $L_2 \to \infty$ and reformulate (4.11) and (4.12) in the form of (3.16). To this end, we first rewrite (4.11) and (4.12) in the form of (3.9) and (3.10) and then obtain (3.16) by using the change of variables described in the Appendix. Substituting

(4.15) $$\bar{\beta} = \tfrac{1}{4} + L_2^{-1} v, \qquad \gamma = 1 + L_2^{-1/2} u$$

into (4.11) and (4.12) leads to the following equations for u, v:

(4.16) $$\frac{du}{ds} = 4v + \frac{1}{4}u^2 - \xi - 4 + \delta^{1/2}[4uv - (\xi + 8)u] + O(\delta),$$

(4.17) $$\frac{dv}{ds} = -u + \delta^{1/2}\left[-4v - \frac{1}{4}u^2 - (4/\bar{A})^2 + 4\right] + O(\delta).$$

The new time variable s is defined by

(4.18) $$s = \delta^{1/2}(t - t_H),$$

where t_H is obtained from the condition $\bar{A}(\varepsilon t_H) = \bar{A}_H(0)$ and is given by

(4.19) $$t_H = \varepsilon^{-1}[A_i - L_2^{-1/2} q_1^{-1} \bar{A}_H(0)].$$

Equations (4.16) and (4.17) are of the form of (3.9) and (3.10). In (4.17), we did not expand the bifurcation parameter $\bar{A}$ for mathematical convenience. We next apply the analysis described in the Appendix and reformulate (4.16) and (4.17) in the form of (3.16). Inserting

$$X = u/4, \qquad Y = -dX/dS, \quad \text{and} \quad S = 2s \tag{4.20}$$

into (4.16) and (4.17), we obtain

$$\frac{dX}{dS} = -Y, \tag{4.21}$$

$$\begin{aligned}\frac{dY}{dS} &= X(1+Y) \\ &\quad + \delta^{1/2}\left[-4Y + \frac{1}{4}(\xi + (4/\bar{A})^2) + 4X^2 - 4Y^2 - 2X^2Y\right] + O(\delta).\end{aligned} \tag{4.22}$$

Using the definitions of $\bar{A}$, s, and S given by (4.9), (4.18), and (4.20), respectively, we rewrite $\bar{A}$ as a function of S

$$\bar{A}(S) = \bar{A}_H(0) - \tfrac{1}{2}L_2^{1/2}q_1\varepsilon\delta^{-1/2}S = \bar{A}_H(0) - \tfrac{1}{2}q_1\varepsilon\delta^{-1}S. \tag{4.23}$$

These equations have been analyzed numerically and the results are shown in Fig. 2. The values of the parameters are the same as in Fig. 1, except that $L_2 = 1000$. In Fig. 2, we represent the maximum of X as a function of $\bar{A}$. We also depict the branches of steady states and periodic solutions. The Hopf bifurcation is located at $\bar{A} = \bar{A}_H(0) \approx 1.33$. We have found that the periodic solutions are nearly harmonic functions of S for the entire range of values of $\bar{A}$ that are of interest. This suggests an approximation based on the limit $\bar{A} - \bar{A}_H \to 0$.

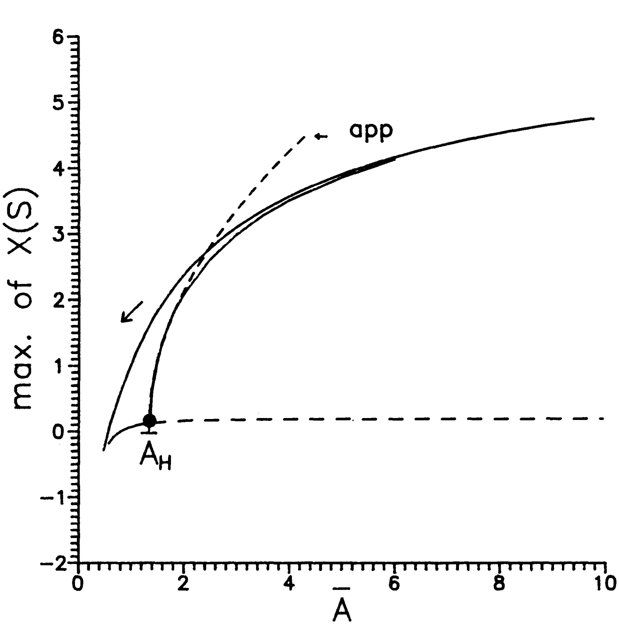

FIG. 2. *Slow passage through the Hopf bifurcation of* (4.22) *and* (4.23). *The values of the parameters are the same as in Fig.* 1 *except that* L_2 = 1000, *which is larger. The figure represents the maximum of the oscillations as a function of the scaled bifurcation parameter. The dotted line is the local approximation of the Hopf bifurcation curve and is obtained from the small amplitude limit of the* L_2 *large leading asymptotic result.*

To this end, we first determine the slow time evolution equation (3.26), which is based on the limit $\delta \to 0$. We then approximate this equation by investigating the limit of small amplitude solutions (which is based on the limit $N_0 \to 0$ and $\bar{A} - \bar{A}_H(0) = O(N_0)$). Applying the theory described in § 3, we obtain the amplitude equation

$$\frac{dN_0}{d\sigma} = \frac{1}{2\pi}\int_0^{2\pi} \frac{Y_0}{1+Y_0}\left[-4Y_0(1+Y_0) + \frac{1}{4}(\xi + (4/\bar{A})^2) + 6X_0^2\right] d\psi, \tag{4.24}$$

where $\sigma = \delta^{1/2}S$ is a slow time variable and $\bar{A}$ is rewritten in terms of σ as

$$\bar{A}(\sigma) = \bar{A}_H(0) - \tfrac{1}{2}q_1\varepsilon\delta^{-3/2}\sigma. \tag{4.25}$$

$X_0(\psi)$ and $Y_0(\psi)$ are functions of N_0 and satisfy (3.22) and (3.24). N_0 corresponds to the amplitude of the oscillations (from definition (3.24) and the fact that X_0 is maximum as $Y_0 = 0$, we find that max $(X_0) = (2N_0)^{1/2}$). We have used the fact that $4X_0^2 - 2X_0^2Y_0 = 6X_0^2 - 2X_0^2(1+Y_0)$ and that the last term gives a zero contribution to the integral [7]. Equation (4.24) describes the slow passage through the Hopf bifurcation for all values of ε, provided that

$$\varepsilon\delta^{-3/2}q_1 \ll 1. \tag{4.26}$$

We now investigate the limit $N_0 \to 0$ of (4.24). In first approximation, we find the simplified equation

$$\frac{dN_0}{d\sigma} = -\frac{1}{2}(\xi + 16)\bar{A}_H(0)^{-1}(\bar{A} - \bar{A}_H(0))N_0 - N_0^2, \tag{4.27}$$

where

$$\bar{A} - \bar{A}_H(0) = -\tfrac{1}{2}q_1\varepsilon\delta^{-3/2}\sigma = O(N_0). \tag{4.28}$$

Note from (4.27) that the local approximation of the branch of periodic solutions is given by

$$N_0 \approx -\tfrac{1}{2}(\xi + 16)\bar{A}_H(0)^{-1}(\bar{A} - \bar{A}_H(0)). \tag{4.29}$$

Since $X_M = (2N_0)^{1/2}$, (4.29) is equivalent to

$$X_M \approx [-(\xi + 16)\bar{A}_H(0)^{-1}]^{1/2}(\bar{A} - \bar{A}_H(0))^{1/2}. \tag{4.30}$$

The curve $X_M = X_M(\bar{A})$ is represented in Fig. 2 by the dotted line. It is in good agreement with the numerical branch until $X_M = 2$. It suggests that the amplitude equation (4.27) is a valid description of the time-dependent solution for $0 < X_M < 2$. We did not compare the time-dependent solution of (4.27) with the exact numerical result.

5. Discussion. We have investigated the slow passage through a Hopf bifurcation from a branch of slowly varying limit cycle oscillations to a branch of slowly varying steady states. Our analysis is motivated by recent numerical studies of bursting oscillations that indicated that the delay of the bifurcation transition cannot be ignored. If ε is defined as the rate of change of the bifurcation parameter, we have shown that the amplitude of the oscillations at the bifurcation point is an $O(\varepsilon^{1/4})$ quantity. This amplitude can be larger if the nonlinear damping of the oscillations is sufficiently weak. We have analyzed this case by studying a class of low-frequency Hopf bifurcation problems and applied our results to our bursting problem. If ω denotes the frequency of the oscillations at the Hopf point, we have found that the amplitude of the oscillations is then an $O(\varepsilon^{1/4}\omega^{-1})$ quantity as $\omega \to 0$.

Our analysis of the relaxation oscillators is motivated by a specific problem that exhibits low-frequency pulsating oscillations. The branch of periodic solutions is smooth, and the slow passage through the bifurcation point is also smooth because the rate of change of the bifurcation parameter is sufficiently small (see Fig. 2). As a result, a simple amplitude equation obtained from a local analysis provides a good description of the transition. In other problems exhibiting relaxation oscillations, such as the Fitzhugh–Nagumo equations, the smooth bifurcation curve is immediately followed by a quasi-vertical branch of periodic solutions even in the near vicinity of the bifurcation point [7]. We then expect to observe large amplitude oscillations even at the bifurcation point, and the local analysis for the reverse transition cannot be applied.

Appendix. Formulation of (3.16). In this Appendix, we describe the different changes of variables leading to (3.16). Our starting point is given by (3.9)–(3.12). We first introduce new variables A, C, and S defined as

$$A = (f_{xx}q^{-1})u, \qquad C = -(f_{xx}g_x^{-1})v, \quad \text{and} \quad S = qs, \tag{A1}$$

where $q = (-f_y g_x)^{1/2} (f_y g_x < 0)$. Equations (3.9)–(3.12) are then rewritten as

$$\frac{dA}{dS} = C + \frac{1}{2}A^2 + D\Lambda + E + \delta^{1/2}(LA + PAC + QA^3) + O(\delta), \tag{A2}$$

$$\frac{dC}{dS} = -A + \delta^{1/2}(F\Lambda + G + RC + WA^2) + O(\delta), \tag{A3}$$

where

$$\begin{aligned} &D = f_\lambda f_{xx}/q^2, \quad E = f_\delta f_{xx}/q^2, \quad L = (f_{x\lambda}\Lambda + f_{x\delta})/q, \\ &P = f_{xy}g_x/(f_{xx}q), \qquad Q = f_{xxx}q/(6f_{xx}^2), \\ &F = -g_\lambda f_{xx}/(qg_x), \qquad G = -g_\delta f_{xx}/(qg_x), \\ &R = g_y/q, \qquad W = -qg_{xx}/(2f_{xx}g_x). \end{aligned} \tag{A4}$$

Finally, we reformulate these equations in terms of

$$X = A \quad \text{and} \quad Y = -\frac{dA}{dS} \tag{A5}$$

and obtain

$$\frac{dX}{dS} = -Y, \qquad \frac{dY}{dS} = X(1+Y) + \delta^{1/2}H(X, Y, \Lambda, \delta^{1/2}), \tag{A6}$$

where $H(X, Y, \Lambda, \delta^{1/2})$ is given by

$$\begin{aligned} H(X, Y, \Lambda, \delta^{1/2}) = {} & (RD - F)\Lambda + RE - G + [L + R - P(D\Lambda + E)]Y \\ & + X^2(-W + P + \tfrac{1}{2}R) - PY^2 + X^2Y(3Q - \tfrac{1}{2}P) + O(\delta^{1/2}). \end{aligned} \tag{A7}$$

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