# DIVERGENCE CRITERION FOR GENERIC PLANAR SYSTEMS[*]

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**Abstract.** The divergence criterion has been shown to be helpful in distinguishing between sub- and supercritical Hopf bifurcations, but its applicability is limited to systems whose divergence is sign definite. A step-by-step computational procedure which allows one to extend the applicability of the divergence criterion is derived by altering the system to an equivalent one with sign definite divergence. The procedure is based on multiplying the original vector field by a positive quadratic function in a neighborhood of the bifurcating rest point. This procedure is then applied to several examples of planar systems that exhibit the Hopf bifurcation. Specifically, it is demonstrated that only supercritical bifurcations occur in a system modeling specific immune responses with handling time. It is also shown that the FitzHugh–Nagumo equations and the chemostat equations with substrate inhibition and linear yield coefficient may exhibit both sub- and supercritical Hopf bifurcations. In both cases, simple analytic criteria for determining the criticality of the bifurcation are presented.

**1. Introduction.** The bifurcation of a rest point for a system of ordinary differential equations to a periodic solution has been an intriguing area of research for the past half-century. The early work of Hopf [10] is usually referenced as the beginning point of research in this area, and this type of bifurcation bears his name.[1] The theory has been developed very extensively since. Several textbooks cover the subject, including those of Marsden and McCracken [14], Hassard, Kazarinoff, and Wan [8], Chow and Hale [4], and Kuznetsov [13]. The general subject of bifurcations has been developed to a sophisticated level, and it is now a proper part of nonlinear functional analysis.

Bifurcations are important in physical and biological systems because they represent the points at which the dynamics of the system undergoes a qualitative change. In terms of the parameters of the model system, the bifurcation points can frequently be expressed as thresholds. In many instances, experiments can be designed to detect such thresholds to test a particular model and/or theory. We refer the reader to [11] for an expository article on bifurcations in mathematical biology.

Many population models are described by planar dynamical systems, and simply detecting the existence of a Hopf bifurcation is not difficult. However, determining the direction of bifurcation, whether the bifurcation is subcritical or supercritical (i.e., determining the *criticality* of the bifurcation), is a more delicate problem, as the calculations in the above cited textbooks show. The subcritical bifurcations are especially important in biological systems because they show the existence of (often

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[1]Depending on the source, the Hopf bifurcation may be also referred to as the Andronov–Hopf bifurcation.

unexpected) periodic solutions and multiple periodic solutions in dissipative systems [19, 9, 16].

In previous work [16], a planar bifurcation theorem which determined the criticality of bifurcation was established using the divergence criterion. In particular, it was shown that a subcritical Hopf bifurcation produces at least two limit cycles in a planar, dissipative system. The applicability of the theorem was restricted to systems whose divergence was of one sign (except for a set of measure zero) in a neighborhood of the bifurcation point. In this work, we develop a general approach for determining the criticality of Hopf bifurcations in planar dynamical systems. We show that, for a generic system, one can multiply the vector field by a positive quadratic function and obtain a system whose divergence is sign definite near the bifurcating rest point. Since the resulting system has the same set of trajectories as the original system, the divergence criterion will determine the criticality of the bifurcation. This approach makes Theorem 2.1 in [16] applicable to a wide class of problems.

The divergence criterion is a generalization of the Dulac criterion. This criterion was used by Hofbauer and So [9] to determine the criticality of the Hopf bifurcation for a class of predator-prey equations, and was later generalized by Pilyugin and Waltman [16]. See also [17] for an earlier planar bifurcation theorem in this direction, and see Wolkowicz [19] and Zhu, Campbell, and Wolkowicz [20] for bifurcation analysis of predator-prey systems using the Lyapunov coefficient method. The change in the vector field simplifies the calculations and often renders them amenable to direct computation or to symbolic algebraic processors such as Mathematica [18] or Maple [7]. Sometimes, the simplification can be truly significant. In [16], the use of the divergence criterion resulted in the correction of mistakes found in a series of papers [1, 5, 6] that used the Lyapunov coefficient criterion.

This paper is organized as follows. We describe the construction of the quadratic function in section 2 and formulate the criterion for determining the criticality of the Hopf bifurcation. In section 3, we illustrate the procedure using two important biological problems. In section 4, we introduce a nonlinear rescaling of the vector field, which further simplifies the divergence criterion for a specific set of planar systems including the chemostat (also known as a bio-reactor or a CSTR), and study the Hopf bifurcation in the chemostat with variable yield and substrate inhibition. We conclude with a discussion section.

**2. Divergence criterion for generic systems.** Consider a planar dynamical system

$$(1) \qquad\qquad x' = f(x, y), \qquad y' = g(x, y),$$

where $f$ and $g$ are sufficiently smooth, and assume that $(0, 0)$ is a center, that is, $f^0 = g^0 = 0$, $f_x^0 + g_y^0 = 0$, and $f_x^0 g_y^0 - f_y^0 g_x^0 > 0$, where we adopt the notation $F^0 = F(0, 0)$. Necessarily, $f_y^0 g_x^0 < 0$. We remark that all of the subsequent calculations and conclusions will remain valid if $(0, 0)$ is replaced by $(x^0, y^0)$ and all derivatives are computed at $(x^0, y^0)$.

The *divergence criterion* states that if the divergence of the vector field of (1) is negative (positive) almost everywhere in some neighborhood of $(0, 0)$, then $(0, 0)$ is a stable (unstable) spiral point. In our earlier work [16], we showed that the Hopf bifurcation is supercritical (subcritical) if the bifurcating rest point is a stable (unstable) spiral point. Therefore, we demonstrated that the criticality of the bifurcation can be determined from the stability of the bifurcating rest point. In this paper, we use

the divergence criterion to distinguish between stable and unstable spiral points or, equivalently, between super- and subcritical Hopf bifurcations.

The divergence criterion may not apply directly to the original system (1), because the divergence of its vector field may not be sign definite near the origin. In this section, we show that for a generic vector field (1), one can choose a quadratic function $a(x, y)$ so that $a(0,0) = 1$ and the divergence of $(af, ag)$ given by

$$(2) \qquad \phi(x, y) = (af)_x + (ag)_y = a(f_x + g_y) + a_x f + a_y g$$

is sign definite in some neighborhood of $(0,0)$. Since $a(x, y)$ is necessarily positive in some neighborhood of $(0,0)$, the trajectories of (1) coincide with the trajectories of

$$(3) \qquad x' = a(x, y)f(x, y), \qquad y' = a(x, y)g(x, y)$$

near $(0,0)$. Consequently, systems (1) and (3) have the same orbital structure in a neighborhood of $(0,0)$.

We begin by formally expanding $\phi$, using the Taylor polynomial of second order

$$(4) \qquad \phi = \phi^0 + \phi_x^0 x + \phi_y^0 y + \frac{1}{2}\left(\phi_{xx}^0 x^2 + 2\phi_{xy}^0 xy + \phi_{yy}^0 y^2\right) + H.O.T.,$$

where $H.O.T.$ denotes higher order terms. Evaluating (2) at $(0,0)$, we find that $\phi^0 = 0$. Differentiating (2) yields

$$(5) \qquad \phi_x = a(f_{xx} + g_{yx}) + a_x(f_x + g_y) + a_{xx}f + a_x f_x + a_{yx}g + a_y g_x,$$

$$(6) \qquad \phi_y = a(f_{xy} + g_{yy}) + a_y(f_x + g_y) + a_{xy}f + a_x f_y + a_{yy}g + a_y g_y.$$

Setting $a(0,0) = 1$, it follows that

$$(7) \qquad \phi_x^0 = (f_{xx}^0 + g_{yx}^0) + a_x^0 f_x^0 + a_y^0 g_x^0, \quad \phi_y^0 = (f_{xy}^0 + g_{yy}^0) + a_x^0 f_y^0 + a_y^0 g_y^0.$$

Since $f_x^0 g_y^0 - f_y^0 g_x^0 > 0$, equations (7) uniquely define $a_x^0$ and $a_y^0$. Our primary interest is, of course, to eliminate the first order terms in (4). Thus we set $\phi_x^0 = \phi_y^0 = 0$ in (7) and solve for $a_x^0$ and $a_y^0$ to obtain

$$(8) \qquad a_x^0 = \frac{(f_{xx}^0 + g_{yx}^0)g_y^0 - (f_{xy}^0 + g_{yy}^0)g_x^0}{f_y^0 g_x^0 - f_x^0 g_y^0},$$

$$(9) \qquad a_y^0 = \frac{-(f_{xx}^0 + g_{yx}^0)f_y^0 + (f_{xy}^0 + g_{yy}^0)f_x^0}{f_y^0 g_x^0 - f_x^0 g_y^0}.$$

Subsequent differentiation of (5) and (6) yields

$$\phi_{xx} = a_x(f_{xx} + g_{yx}) + a(f_{xxx} + g_{yxx}) + a_{xx}(2f_x + g_y) + a_x(2f_{xx} + g_{yx})$$
$$+ a_{yx}g_x + a_y g_{xx} + a_{xxx}f + a_{xx}f_x + a_{yxx}g + a_{yx}g_x,$$

$$\phi_{xy} = a_y(f_{xx} + g_{yx}) + a(f_{xxy} + g_{yxy}) + a_{xy}(2f_x + g_y) + a_x(2f_{xy} + g_{yy})$$
$$+ a_{yy}g_x + a_y g_{xy} + a_{xxy}f + a_{xx}f_y + a_{yxy}g + a_{yx}g_y,$$

$$\phi_{yy} = a_y(f_{xy} + g_{yy}) + a(f_{xyy} + g_{yyy}) + a_{yy}(f_x + 2g_y) + a_y(f_{xy} + 2g_{yy})$$
$$+ a_{xy}f_y + a_x f_{yy} + a_{xyy}f + a_{xy}f_y + a_{yyy}g + a_{yy}g_y.$$

Assuming that the functions $f$ and $g$ are sufficiently smooth, the mixed derivatives are independent of the order of differentiation. Therefore, evaluating the above expression at the center $(0,0)$ yields

$$(10) \qquad \phi_{xx}^0 = Q^{xx} + 2f_x^0 a_{xx}^0 + 2g_x^0 a_{xy}^0,$$

$$(11) \qquad \phi_{xy}^0 = Q^{xy} + f_y^0 a_{xx}^0 + g_x^0 a_{yy}^0,$$

$$(12) \qquad \phi_{yy}^0 = Q^{yy} + 2f_y^0 a_{xy}^0 + 2g_y^0 a_{yy}^0,$$

where

$$Q^{xx} = (f_{xxx}^0 + g_{yxx}^0) + a_x^0(3f_{xx}^0 + 2g_{xy}^0) + a_y^0 g_{xx}^0,$$

$$Q^{xy} = (f_{xxy}^0 + g_{yxy}^0) + a_x^0(2f_{xy}^0 + g_{yy}^0) + a_y^0(f_{xx}^0 + 2g_{xy}^0),$$

$$Q^{yy} = (f_{xyy}^0 + g_{yyy}^0) + a_x^0 f_{yy}^0 + a_y^0(2f_{xy}^0 + 3g_{yy}^0).$$

Thus far, the linear terms in (4) have been eliminated by choosing appropriate values for $a_x^0$ and $a_y^0$. In what follows, we seek to choose the values $a_{xx}^0$, $a_{xy}^0$, and $a_{yy}^0$ so as to make the second order terms in (4) sign definite. The second order terms in (4) are sign definite whenever the discriminant

$$\mathcal{D} = \phi_{xx}^0 \phi_{yy}^0 - (\phi_{xy}^0)^2$$

is positive. We set

$$(13) \qquad a_{xx}^0 = -\frac{1}{2}\frac{Q^{xy}}{f_y^0}, \qquad a_{yy}^0 = -\frac{1}{2}\frac{Q^{xy}}{g_x^0},$$

because such a choice yields $\phi_{xy}^0 = 0$. The discriminant then can be written as

$$\mathcal{D} = \left(Q^{xx} - \frac{Q^{xy}f_x^0}{f_y^0} + 2g_x^0 a_{xy}^0\right)\left(Q^{yy} - \frac{Q^{xy}g_y^0}{g_x^0} + 2f_y^0 a_{xy}^0\right) = (\beta_1 + \alpha_1 z)(\beta_2 + \alpha_2 z),$$

(14)

where $z = a_{xy}^0$, $\beta_1 = Q^{xx} - (Q^{xy}f_x^0/f_y^0)$, $\beta_2 = Q^{yy} - (Q^{xy}g_y^0/g_x^0)$, $\alpha_1 = 2g_x^0$, and $\alpha_2 = 2f_y^0$. Since the product $\alpha_1\alpha_2 = 4g_x^0 f_y^0 < 0$, the discriminant $\mathcal{D}$ is positive for any $z$ located strictly between the roots $z_1 = -\beta_1/\alpha_1$ and $z_2 = -\beta_2/\alpha_2$. For generic functions $f$ and $g$, $z_1 \neq z_2$. Thus we choose

$$(15) \qquad z^* = -\frac{1}{2}\left(\frac{\beta_1}{\alpha_1} + \frac{\beta_2}{\alpha_2}\right) = -\frac{1}{2}\frac{Q^{xx}f_y^0 + Q^{yy}g_x^0}{2g_x^0 f_y^0}$$

and set $a_{xy}^0 = z^*$.

At this point, we have determined all coefficients of the quadratic function

$$(16) \qquad a(x,y) = 1 + a_x^0 x + a_y^0 y + \frac{1}{2}(a_{xx}^0 x^2 + 2a_{xy}^0 xy + a_{yy}^0 y^2).$$

Finally, we transform the original vector field $(f, g)$ into a vector field $(af, ag)$ with sign definite divergence $\phi$ near the origin. The divergence $\phi$ is positive (negative) if $\phi^0_{xx}$ is positive (negative). Substituting (13) and (15) into (10), we find that

$$(17) \qquad\qquad \phi^0_{xx} = \frac{1}{2}\left(Q^{xx} - Q^{yy}\frac{g^0_x}{f^0_y}\right) - Q^{xy}\frac{f^0_x}{f^0_y}.$$

For a given planar system that undergoes a Hopf bifurcation, we evaluate appropriate partial derivatives of its vector field at the bifurcation point and compute the quantity (17). The Hopf bifurcation is supercritical (subcritical) if (17) is negative (positive).

Unfortunately, for a generic system, expression (17) may become too complicated for symbolic applications. In this case, our method will have no advantage over the standard normal form computation. However, our approach can, sometimes, have a clear advantage over the standard method. To illustrate this, we treat several examples in subsequent sections. Expression (17) will be greatly simplified if the divergence of the vector field essentially involves only one of the state space variables $x$ or $y$. It is therefore helpful to introduce a preliminary change of variables to achieve this, whenever possible. A specific change of variables that applies to chemostats is discussed in section 4.

**3. Applications.** In this section, we apply the change of vector fields to two examples in biological literature and determine the criticality of bifurcation. Before beginning, we note two changes from the usual presentation of bifurcation results.

- It is possible, and the theory is usually presented this way, to change variables so that the bifurcating rest point is always at the origin. Such a change, however, complicates the calculations for a specific problem, and we do not make it. The reader should be cautioned that, as parameters vary, the coordinates of the rest point vary.
- The traditional approach is to fix all of the parameters except one (usually designated as the bifurcation parameter) and let that parameter determine the bifurcation. We choose instead to present a *bifurcation locus*, which is defined as a hypersurface in the parameter space on which the bifurcation occurs. We have two reasons for doing this. First of all, biological problems frequently have many parameters, and it would be artificial to select a single one unless there is a specific experiment which can vary it. Secondly, our technique for determining the criticality of bifurcation depends only on the stability of the rest point at the critical parameter value(s). This implies that any parametric path crossing the bifurcation locus will produce a bifurcation whose criticality is determined exclusively by its crossing point on the bifurcation locus. In particular, any two parametric paths crossing the bifurcation locus via the same point will produce Hopf bifurcations of the same criticality. Of course, one has to ascertain that a bifurcation does indeed occur, that is, that the rest point does change its stability along the parametric path. On the other hand, our result does not require that the parametric path be strictly transverse to the bifurcation locus or, equivalently, that the pair of complex eigenvalues cross the imaginary axis with nonzero velocity. For more details, we refer the reader to the proof of the original Theorem 2.1 in [16].

For any crossing point on the bifurcation locus, the linearization of a planar system has purely imaginary eigenvalues. Such a rest point for the nonlinear system can be a stable or an unstable spiral, or a center, the choice being determined by the

nonlinear terms. Our quadratic factor determines whether the rest point is a stable spiral or an unstable spiral, depending on the sign of the (sign specific) divergence. It is also possible that the quadratic terms in (4) vanish, in which case our technique does not apply. If this is the case, then the rest point could still be a center or a spiral determined by nonlinear terms of higher order (and hence such a case would be nongeneric).

In the next two subsections, we study the criticality of Hopf bifurcations in two biological problems, where we can add to results already in the literature. These examples also illustrate the ease with which the technique can be applied to biological problems.

**3.1. Specific immune responses with handling time.** In this section, we apply the general divergence criterion to the model of specific immunity studied by Pilyugin and Antia in [15]. The authors reported the existence of Hopf bifurcation in the system

$$(18) \qquad x' = rx - \frac{hx}{k+x}y,$$

$$(19) \qquad y' = a + \left( \frac{\rho x}{k+x} - d \right) y,$$

where $r$, $h$, $k$, $a$, $\rho$, $d$ are positive parameters. Here $x$ and $y$ are dimensionless variables that represent the abundance of parasite (i.e., the number of infected cells) and the magnitude of the specific (cytotoxic) immune response, respectively. In this model, both the proliferation rate of immune cells $\frac{\rho x}{k+x}$ and the killing rate of infected cells $\frac{hx}{k+x}$ saturate as the number of infected cells $x$ becomes large. The quantities $r$, $a$, and $d$ represent the (per capita) rate of parasite replication, the input of immune cells from an external source, and the (per capita) death rate of immune cells, respectively. We restrict the bifurcation analysis to the biologically relevant case $x, y > 0$.

To simplify computations, we multiply the vector field of (18)–(19) by a positive function $k + x$ and consider the new system of the form

$$(20) \qquad x' = rx(k+x) - hxy = f(x,y), \quad x(0) > 0,$$

$$(21) \qquad y' = a(k+x) + (\rho x - d(k+x))y = g(x,y), \quad y(0) > 0.$$

Since $k + x > 0$, the phase portraits of (18)–(19) and (20)–(21) are identical.

The bifurcating rest point of (20)–(21) has coordinates

$$(22) \qquad x^0 = \frac{rdk - ah}{r(\rho - d)} > 0, \quad y^0 = \frac{kr\rho - ah}{h(\rho - d)} > 0.$$

We compute the partial derivatives of $f$ and $g$ to find

$$f_x = rk + 2rx - hy, \quad f_y = -hx, \quad f_{xx} = 2r, \quad f_{xy} = -h, \quad f_{yy} = 0,$$

$$g_x = a + (\rho - d)y, \quad g_y = (\rho - d)x - dk, \quad g_{xy} = \rho - d, \quad g_{xx} = g_{yy} = 0.$$

Consequently,

$$f_x^0 = rx^0, \quad f_y^0 = -hx^0, \quad f_{xx}^0 = 2r, \quad f_{xy}^0 = -h, \quad f_{yy}^0 = 0,$$

$$g_x^0 = \frac{kr\rho}{h}, \quad g_y^0 = -\frac{ah}{r}, \quad g_{xy}^0 = \rho - d, \quad g_{xx}^0 = g_{yy}^0 = 0.$$

The bifurcating rest point must necessarily satisfy $0 = f_x^0 + g_y^0 = rx^0 - \frac{ah}{r}$, and thus

$$x^0 = \frac{ah}{r^2}.$$

Equating this value with that of (22), we find that the bifurcation locus is a subset of the hypersurface

(23) $$d(r^2 k + ah) = ah(\rho + r).$$

The determinant of the variational matrix is given by

$$\det(J) = -rx^0 \frac{ah}{r} + hx^0 \frac{kr\rho}{h} = x^0(kr\rho - ah).$$

A necessary condition for the Hopf bifurcation is that $\det(J) > 0$. Since $x^0 > 0$, it follows that $kr\rho - ah > 0$, and inequalities (22) further imply that $\rho - d > 0$ and $rdk - ah > 0$. Since $\rho - d > 0$ and $rdk - ah > 0$ together imply $kr\rho - ah > 0$, the bifurcation locus can be described as the subset of (23) restricted by two inequalities

(24) $$rdk - ah > 0, \quad \rho - d > 0.$$

Using (8)–(9), we compute

(25) $$a_x^0 = \frac{kr\rho - \frac{ah}{r}(2r + (\rho - d))}{\frac{ah}{r^2}(ah - kr\rho)}, \quad a_y^0 = \frac{(r + (\rho - d))h}{ah - kr\rho}.$$

The quantities $Q^{**}$ are

$$Q^{xx} = a_x^0(6r + 2(\rho - d)), \quad Q^{xy} = -2ha_x^0 + a_y^0(2r + 2(\rho - d)), \quad Q^{yy} = -2ha_y^0.$$

Therefore,

$$\phi_{xx}^0 = a_x^0(r + (\rho - d)) + a_y^0 \left( h + \frac{2r}{h}(r + (\rho - d)) \right),$$

which can be simplified to

(26) $$\phi_{xx}^0 = -\frac{(r + (\rho - d))^2}{k(r + \rho)}.$$

Clearly, $\phi_{xx}^0 < 0$. Since the divergence of the rescaled vector field is negative definite at any point on the bifurcation locus, the bifurcation is always supercritical.

**3.2. Diffusionless FitzHugh–Nagumo equations.** Several numerical examples of supercritical and subcritical Hopf bifurcations were presented by Kostova, Ravindran, and Schonbek [12] in the context of the classical FitzHugh–Nagumo equations. They derived a complicated expression to determine the criticality of the Hopf bifurcation using the normal form calculation. In this section, we use the divergence criterion to derive a simple analytic criterion to determine the criticality of the Hopf bifurcation.

The FitzHugh–Nagumo equations for a single neuron are

(27) $$x' = F(x) - y + I = f(x, y),$$

(28) $$y' = \quad x - wy \quad = g(x, y),$$

where $F(x) = \varepsilon x(1-x)(x-\lambda)$ and $\varepsilon > 0$, $0 < \lambda < 1$, $w > 0$, and $I$ are parameters. The variable $x$ represents the membrane potential, $y$ is the recovery variable that represents a negative feedback, and $I$ is the membrane current.

Computing the partial derivatives of $f$ and $g$, we find that

$$f_x = F'(x), \quad f_y = -1, \quad f_{xx} = F''(x), \quad f_{xy} = f_{yy} = 0,$$

$$g_x = 1, \quad g_y = -w, \quad g_{xy} = g_{xx} = g_{yy} = 0.$$

Consequently, at any rest point $(x^0, y^0)$, we have

$$f_x^0 = F'(x^0), \quad f_y^0 = -1, \quad f_{xx}^0 = F''(x^0), \quad f_{xy}^0 = f_{yy}^0 = 0,$$

$$g_x^0 = 1, \quad g_y^0 = -w, \quad g_{xy}^0 = g_{xx}^0 = g_{yy}^0 = 0.$$

The bifurcation locus consists of rest points $(x^0, y^0)$ such that $f_x^0 + g_y^0 = 0$ and $f_x^0 g_y^0 - f_y^0 g_x^0 > 0$. The former condition implies that $F'(x^0) = w$. The latter condition then implies that $1 - w^2 > 0$. Hence the bifurcation locus is the set of rest points $(x^0, y^0)$ such that

$$(29) \qquad f^0 = g^0 = 0, \quad F'(x^0) = w, \quad w^2 < 1.$$

Since $F'(x) = \varepsilon(-3x^2 + 2(1+\lambda)x - \lambda)$, the second condition in (29) implies that $x^0$ must satisfy the quadratic equation

$$3(x^0)^2 - 2(1+\lambda)x^0 + \lambda + \frac{w}{\varepsilon} = 0$$

or, equivalently,

$$(30) \qquad x_{1,2}^0 = \frac{(1+\lambda) \pm \sqrt{(1+\lambda)^2 - 3(\lambda + \frac{w}{\varepsilon})}}{3}.$$

Using (8)–(9), we compute

$$(31) \qquad a_x^0 = \frac{wF''(x^0)}{1-w^2}, \quad a_y^0 = -\frac{F''(x^0)}{1-w^2}.$$

The quantities $Q^{**}$ are

$$Q^{xx} = F'''(x^0) + \frac{3w(F''(x^0))^2}{1-w^2} = -6\varepsilon + \frac{3w(F''(x^0))^2}{1-w^2},$$

$$Q^{xy} = -\frac{(F''(x^0))^2}{1-w^2}, \quad Q^{yy} = 0.$$

Therefore,

$$\phi_{xx}^0 = \frac{1}{2}\left(-6\varepsilon + \frac{3w(F''(x^0))^2}{1-w^2}\right) + \frac{(F''(x^0))^2}{1-w^2}\frac{F'(x^0)}{-1},$$

which can be further simplified to

$$(32) \qquad \phi_{xx}^0 = \frac{1}{2}\left(-6\varepsilon + \frac{w(F''(x^0))^2}{1-w^2}\right).$$

Substituting $F''(x^0) = 2\varepsilon(1 + \lambda - 3x^0)$ into (32), we rewrite the quantity $\phi_{xx}^0$ as

$$\phi_{xx}^0 = \varepsilon\left(-3 + \frac{2\varepsilon w(1 + \lambda - 3x^0)^2}{1 - w^2}\right). \tag{33}$$

Using (30), we can rewrite the quantity $(1 + \lambda - 3x^0)^2$ as

$$(1 + \lambda - 3x^0)^2 = (1 + \lambda)^2 - 3\left(\lambda + \frac{w}{\varepsilon}\right).$$

Substituting this expression into (33), we finally obtain

$$\phi_{xx}^0 = \frac{\varepsilon}{1 - w^2}\left(2\varepsilon w(1 - \lambda + \lambda^2) - 3(1 + w^2)\right). \tag{34}$$

The multiplier $\frac{\varepsilon}{1-w^2}$ is positive due to (29). Consequently, $\phi_{xx}^0$ has the same sign as the quantity $2\varepsilon w(1 - \lambda + \lambda^2) - 3(1 + w^2)$. The Hopf bifurcation in the FitzHugh–Nagumo equations is subcritical if $\phi_{xx}^0 > 0$, that is, if it occurs on the part of the bifurcation locus where

$$\varepsilon > \frac{3(1 + w^2)}{2w(1 - \lambda + \lambda^2)},$$

and supercritical if it occurs on the part of the bifurcation locus where the reversed strict inequality holds.

In [12], two numerical examples were presented: a Figure 2 with $\varepsilon = 14.0$, $w = 0.38$, $\lambda = 0.1$ and a Figure 3 with $\varepsilon = 14.0$, $w = 0.06$, $\lambda = 0.5$. In the former case,

$$\varepsilon = 14.0 > \frac{3(1 + 0.38^2)}{2 \cdot 0.38(1 - 0.1 + 0.1^2)} = 4.964,$$

and the bifurcation is subcritical. In the latter case,

$$\varepsilon = 14.0 < \frac{3(1 + 0.06^2)}{2 \cdot 0.06(1 - 0.5 + 0.5^2)} = 33.453,$$

and the bifurcation(s) are supercritical.

**4. Rescaling for chemostat equations.** The method presented in this section for rescaling the vector field is a generalization of the technique used by Hofbauer and So [9]. Specifically, we consider the system

$$x' = f(x) - q_1(y)g(x), \quad y' = q_2(y)h(x), \tag{35}$$

where $f, g, h, q_i$ are sufficiently smooth and such that positive solutions of (35) remain positive. Also, suppose that $g(x) > 0$ and $q_2(y) > 0$ for $x, y > 0$. We multiply the vector field (35) by a positive function $Q(y)/g(x)$ to obtain a new system

$$x' = Q(y)f(x)/g(x) - q_1(y)Q(y) = Q(y)G(x) - q_1(y)Q(y), \tag{36}$$

$$y' = Q(y)q_2(y)h(x)/g(x) = Q(y)q_2(y)H(x), \tag{37}$$

where $(Qq_2)' = \beta Q$ and $\beta$ is a real number to be determined later. The explicit expression for $Q(y)$ is

$$Q(y) = \frac{\exp\left(\beta \int \frac{dy}{q_2(y)}\right)}{q_2(y)} > 0.$$

Any positive rest point $(x^0, y^0)$ of (36)–(37) must satisfy $H(x^0) = 0$. The divergence of the new vector field (36)–(37) is given by

$$(38) \qquad D(x, y) = Q(y)G'(x) + (Q(y)q_2(y))'H(x) = Q(y)\big(G'(x) + \beta H(x)\big).$$

Now suppose that $(x^0, y^0)$ is the bifurcating rest point, that is, that $D(x^0, y^0) = 0$. Since $Q(y^0) > 0$ and $H(x^0) = 0$, we necessarily have that

$$G'(x^0) + \beta H(x^0) = G'(x^0) = 0.$$

We choose $\beta = -G''(x^0)/H'(x^0)$, so that in a small neighborhood of $(x^0, y^0)$,

$$G'(x) + \beta H(x) = \frac{\delta}{2}(x - x^0)^2 + H.O.T.,$$

where

$$(39) \qquad \delta = G'''(x^0) - \frac{G''(x^0)}{H'(x^0)}H''(x^0) = H'(x^0)\left(\frac{G''}{H'}\right)'(x^0).$$

Since $Q(y) > 0$, the sign of $D(x, y)$ near $(x^0, y^0)$ is the same as the sign of $\delta$. Consequently, the application of the divergence criterion to systems of type (35) can be greatly simplified. For example, the predator-prey models analyzed in [2, 9, 19, 20] fall into this category. The criteria for the criticality of Hopf bifurcations obtained in these works can be directly compared to the expression (39). Various models of the chemostat are also of type (35). In the following subsection, we illustrate this simplified approach by treating a special case of the chemostat with substrate inhibition and a linear yield coefficient.

**4.1. Chemostats with substrate inhibition and linear yields.** In this section, we study the Hopf bifurcation in the model of a chemostat with linear yield coefficient which also features substrate inhibition of growth at higher substrate levels. For a general study of the chemostat with inhibition, constant yield, and several competitors, see Butler and Wolkowicz [3]. The original model presented in Agrawal et al. [1], takes the following form:

$$(40) \qquad\qquad x' = 1 - x - y\frac{\mu(x)}{1 + cx},$$

$$(41) \qquad\qquad y' = y(\mu(x) - 1),$$

where $x$ and $y$ denote the dimensionless substrate and biomass concentrations, and $\mu(x) = mx\exp(-x/K)$ is the microbial growth rate. The function $1 + cx$ represents the yield coefficient,[2] which is assumed to increase linearly with substrate concentration; thus $c > 0$.

Equations (40)–(41) are of the form (35) with

$$f(x) = 1 - x, \qquad g(x) = \frac{mx\exp(-x/K)}{1 + cx},$$

$$h(x) = mx\exp(-x/K) - 1, \qquad q_1(y) = q_2(y) = y.$$

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[2]The yield coefficient is defined as the ratio of the amount of substrate consumed to the amount of biomass produced at a steady state. There is strong biological evidence that the yield may increase with substrate concentration. For details, see [16] and the references therein.

Equations (40)–(41) admit up to two positive rest points. The $x$-coordinate of a positive rest point must satisfy $\mu(x) = 1$ with $0 < x < 1$. The function $\mu(x)$ has a maximum at $x = K$, and its maximal value is given by $\mu_{\max} = mKe^{-1}$. Consequently, if $mK > e$, then there exist two positive solutions of $\mu(x) = 1$, $x_1^0 < K < x_2^0$. It is easy to verify that the rest point with $x = x_2^0$ (if it is feasible, that is, if $x_2^0 < 1$) is always a saddle. Consequently, the Hopf bifurcation can occur only at the rest point $(x_1^0, y_1^0)$ with $0 < x_1^0 < \min(1, K)$ and $y_1^0 = (1 - x_1^0)(1 + cx_1^0)$. The bifurcation occurs when the trace of the variational matrix of (40)–(41) at $(x_1^0, y_1^0)$ equals zero:

$$-1 - y_1^0 \frac{d}{dx}\left(\frac{\mu(x)}{1 + cx}\right)(x_1^0) = 0.$$

Consequently, on the bifurcation locus, the value of $c$ is given by

$$(42) \qquad\qquad c = \frac{K - x_1^0 + (x_1^0)^2}{(x_1^0)^2(1 - K - x_1^0)}.$$

The bifurcation occurs in the feasible region if the value of $c$ given by (42) is positive, that is, if $x_1^0 < 1 - K$ and $0 < K < 1$.

To determine the criticality of the Hopf bifurcation, we computed the functions $G(x)$ and $H(x)$ as defined in (36)–(37) and found that

$$(43) \qquad\qquad G(x) = \frac{(1 - x)(1 + cx)\exp(x/K)}{mx},$$

$$(44) \qquad\qquad H(x) = \frac{(1 + cx)(mx - \exp(x/K))}{mx}.$$

Then we created a Mathematica [18] notebook to compute the quantity $\delta$ defined in (39), and found that

$$(45) \qquad \delta(x(m, K), K) = \frac{P_0(x) + KP_1(x) + K^2 P_2(x) + K^3 P_3(x) + K^4 P_4(x)}{K^2(K - x)(1 - x)(1 - K - x)x^3},$$

where $P_0(x) = 3(1 - x)^3 x^3$, $P_1(x) = 2x^2(1 - x)^2(x - 6)$, $P_2(x) = 2x(x - 1)(x^2 + x - 8)$, $P_3(x) = 2(5x^2 - 4x - 3)$, $P_4(x) = 2(3 - x)$, and $x_1^0 = x(m, K)$. The Hopf bifurcation in (40)–(41) is subcritical if $\delta > 0$ and supercritical if $\delta < 0$.

The existence of both sub- and supercritical Hopf bifurcations in (40)–(41) is illustrated in Figure 1. For $(K, m) \in A$, no rest point with $0 < x < 1$ exists. The curve between A and B is given by $m = e/K$. Region B $(\delta > 0)$ corresponds to subcritical bifurcations. The curve between B and C is the implicit plot of $\delta(x(m, K), K) = 0$. Region C $(\delta < 0)$ corresponds to supercritical bifurcations. The curve between C and D is the implicit plot of $x(m, K) = 1 - K$. For $(K, m) \in D$, no bifurcations with $c > 0$ occur. The region B terminates at $K = 0.413$, and the region C terminates at $K = 0.5$.

**5. Discussion.** We have developed a unifying approach for studying the Hopf bifurcation for generic planar systems, which stems from the divergence criterion. Specifically, we presented a step-by-step computational procedure which can be used to distinguish between sub- and supercritical bifurcations. This procedure can be easily programmed in any standard computer algebra system such as Maple [7] or Mathematica [18] so that all of the necessary computations can be automated. This work may serve as a good example of the analytic approach that involves computerized
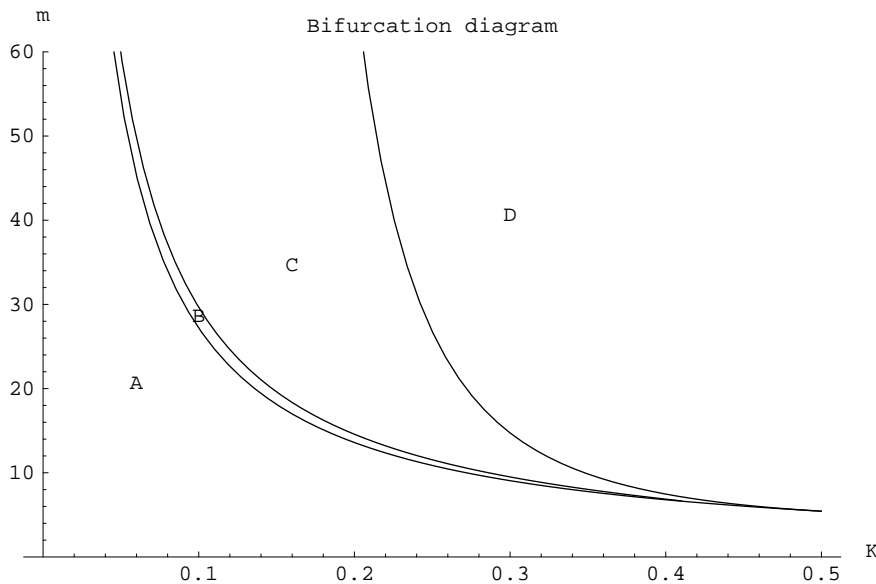
FIG. 1. *Existence and criticality of Hopf bifurcations in the $(K, m)$ plane.*

symbolic calculations. The technique is generic in the sense that it can be applied to a generic planar vector field.

We applied our procedure to several important biological systems and obtained new results on the criticality of Hopf bifurcation. Interestingly, we found that in several instances—for example, with diffusionless FitzHugh–Nagumo equations—we were able to perform all calculations by hand in a reasonable amount of time, which illustrated that our method may have an advantage over the calculation of the third Lyapunov coefficient and/or normal form calculation for the Hopf bifurcation. In particular, our method does not require such computational steps as

- changing coordinates to place the bifurcating rest point at the origin,
- finding eigenvalues and eigenvectors of the variational matrix,
- transforming the linear part of the vector field to the canonical form.

In certain examples, our method produces analytic expressions that are easier to simplify.

We have also presented a specific change of variables that works well with a whole class of planar systems including the equations of the chemostat. Performing this change of variables essentially eliminates one of the phase variables from the expression for divergence and thus greatly simplifies the analysis of Hopf bifurcation.

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