J. Math. Biol. (1994) 32: 617–632

Journal of Mathematical Biology

Oscillatory reaction-diffusion equations on rings

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Received 16 February 1993; received in revised form 3 September 1993

Abstract. We study the behavior of traveling waves in $\lambda-\omega$ systems on both homogeneous and inhomogeneous rings. The stability regions in parameter space of $\lambda-\omega$ waves were previously known [15, 19]; the results are extended here. We show the existence of Hopf bifurcations of traveling waves and the stability of the limit cycles born at the Hopf bifurcation for some parameter ranges. Using a Lindstedt-type perturbation scheme, we formally construct periodic solutions of the $\lambda-\omega$ system near a Hopf bifurcation and show that the periodic solutions superimposed on the original traveling wave have the effect of altering its overall frequency and amplitude. We also study the $\lambda-\omega$ system on an annulus of *variable width*, which does not possess reflection symmetry about any axis. We formally construct traveling waves on this variable-width annulus by a perturbation scheme, and find that perturbing the width of the annulus alters the amplitude and frequency of traveling waves on the domain by a small (order ε^2) amount. For typical parameter values, we find that the speed, frequency, and stability are unaffected by the direction of travel of the wave on the annulus, despite the rotationally asymmetric inhomogeneity. This indicates that the $\lambda-\omega$ system on a variable-width domain cannot account for directional preferences of traveling waves in biological systems.

Key words: Oscillators – Bifurcations – Reaction-diffusion equations – Spatial heterogeneity

1 Introduction

We will study a particularly simple reaction-diffusion system, called the $\lambda-\omega$ system. It is the simplest useful form of a limit cycle oscillator with diffusion, and can be obtained as the limit of a string (or array) of coupled limit-cycle oscillators,

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as their size and spacing go to zero. It arises as the normal form of an oscillatory reaction-diffusion system near a Hopf bifurcation in the dynamics.

The $\lambda-\omega$ system is written

$$u_t=\lambda(r^2)u-\omega(r^2)v+Du_{xx} \tag{1}$$

$$v_t=\omega(r^2)u+\lambda(r^2)v+Dv_{xx} \tag{2}$$

where $x\epsilon R\backslash 2\pi Z$, $r^2=u^2+v^2$ and $\lambda'(r^2)<0$, $\omega'(r^2)\neq 0$ $\forall r^2>0$. The conversion to polar coordinates $u=r\cos\theta$, $v=r\sin\theta$ gives

$$r_t=\lambda r-Dr(\theta_x)^2+Dr_{xx} \tag{3}$$

$$\theta_t=\omega+D\theta_{xx}+2\frac{D}{r}r_x\theta_x\,. \tag{4}$$

(We will in general stay away from the equilibrium $r=0$, since it is of little interest to study a wave of zero amplitude.) In the absence of diffusion, i.e. when $D=0$, the ordinary differential (u, v) equations are a normal form appropriate to a Hopf bifurcation. If $\lambda(r_0)=0$, the amplitude of the stable $D=0$ limit cycle is r_0, and the frequency $\omega(r_0)$. Note the distinction between the spatially independent case, $D=0$, and the $D>0$ case which the rest of this paper examines. Here we speak of a *local* Hopf bifurcation, and in Sect. 2 we will speak of a *spatial* Hopf bifurcation. There exists a 1-parameter family of traveling wave solutions [15]

$$r=\alpha \tag{5}$$

$$\theta=\omega(\alpha)t-z\sqrt{\frac{\lambda(\alpha)}{D}}\,x+\theta_0 \tag{6}$$

where $z=\pm 1$ indicates the direction of travel, and θ_0 is arbitrary. The periodic boundary conditions force integer values of $\sqrt{\lambda(\alpha)/D}$, so we will define $k\equiv\sqrt{\lambda(\alpha)/D}$, $k\epsilon Z^+$.

Note that only a finite number of wavenumbers k can appear. If $k^2D=\lambda(\alpha)$, and $\lambda(r^2)$ is positive and decreasing through zero, with a maximum value at $r=0$, we require $\lambda(\alpha)\geqq 0$, and $\lambda(\alpha)\leqq\lambda(0)$. Thus only a finite number of integers k can satisfy $0\leqq k^2D=\lambda(\alpha)\leqq\lambda(0)$. For $\lambda(0)$ chosen small enough, there are no nonzero wavenumbers which can appear on the ring. Another interpretation is that in such circumstances, the ring is too small to hold a full wavelength.

Traveling waves in $\lambda-\omega$ equations were first studied by Kopell and Howard (1973) [15], who showed existence and criteria for stability of plane wave solutions of the system. Slow-time variations of these plane waves were studied by Howard and Kopell (1977) [8]. Cohen, Neu, and Rosales (1978) [2] showed the existence of spiral solutions to $\lambda-\omega$ systems, under specific conditions, and Duffy, Britton, and Murray (1980) [4] and Greenberg (1978) [5] generalized the results. Kopell and Howard (1981) [14] showed existence of target patterns and spiral waves for $\omega'<0$ and $-\omega'\ll 1$. Kopell (1980) [12] demonstrated horseshoes, and therefore chaos, and (1981) [13] examined the core of target patterns in connection with $\lambda-\omega$ systems. Hagan (1982) [6] examined multi-armed spiral waves of $\lambda-\omega$ systems and found that only one-armed spirals are stable. For an excellent overview, see [19].

Kopell and Howard [15] examined *linear* stability of $\lambda-\omega$ equations. In Sect. 2 we will review their results, and carry the analysis further, to examine *nonlinear* aspects of stability.

In Sect. 2, we will demonstrate the existence of Hopf bifurcations for traveling waves in the $\lambda-\omega$ equations, and examine the periodic solutions which are born at the Hopf bifurcation. For specific parameter values, the stability of these periodic solutions is determined. In Sect. 3, we will describe traveling $\lambda-\omega$ waves on a ring which has a small, nonuniform width. We make the conjecture that a nonuniform width of the ring could lead to waves propagating stably in one direction, but not in the other. We show that this conjecture is false, under typical conditions. Extensive use is made, throughout the analysis, of computer algebra (Macsyma), wherever calculations are sufficiently complicated.

In Sect. 3, we will study $\lambda-\omega$ waves on an inhomogeneous ring, to determine whether we can construct an inhomogeneous ring which will stably support waves in one direction only. This question is motivated by an interesting biological phenomenon. Twining plants exhibit a regular oscillatory motion of their stems, in the direction of twining [3]. This direction of twining is constant within a given species, and is unaffected by external factors. A possible explanation for the handedness of the oscillations is that there is an anatomical asymmetry in the plants which causes a behavioral asymmetry. Lubkin [16, 17] modeled the behavior, called circumnutation, by a system of reaction-diffusion equations on a ring, where the reaction term may be oscillatory or excitable. In this paper, we address the case of the oscillatory reaction term, near a Hopf bifurcation.

2 Spatially uniform ring

In this section, we will investigate nonlinear aspects of the stability of traveling waves of the system (3, 4), including Hopf bifurcations, their criticality, and the stability of the limit cycles born at the bifurcations.

Joseph and Sattinger (1972) [10] used a perturbation scheme, very similar to the one we will use, for the Navier-Stokes equations, and proved the convergence of the perturbation series on those equations. Auchmuty and Nicolis (1976) [1] applied the techniques of [10] to the Brusselator, with periodic boundary conditions.

Stability of the traveling waves (5, 6) of our $\lambda-\omega$ system may be investigated by adding a small perturbation (p, q) to our traveling wave solution (5, 6). We set

$$r=\alpha+\mu p(x, t, \mu) \tag{7}$$

$$\theta=\omega(\alpha)t-zkx+\theta_0+\mu q(x, t, \mu) \tag{8}$$

in (3, 4), to obtain nonlinear equations in p and q:

$$\frac{\partial p}{\partial t}=\frac{1}{2}\left(\left(p\left(4Dk\mu\frac{\partial q}{\partial x}z-2D\mu^2\left(\frac{\partial q}{\partial x}\right)^2+2\alpha\lambda'(\alpha)\right)+4\alpha Dk\frac{\partial q}{\partial x}z-2\alpha D\mu\left(\frac{\partial q}{\partial x}\right)^2\right.\right.$$
$$\left.\left.+2D\frac{\partial^2 p}{\partial x^2}+\lambda''(\alpha)\mu^2p^3+(\alpha\lambda''(\alpha)+2\lambda'(\alpha))\,\mu p^2\right)\right) \tag{9}$$

$$\frac{\partial q}{\partial t}=\frac{1}{2\mu p+2\alpha}\left(-4Dk\frac{\partial p}{\partial x}z+p^2(\alpha\mu\omega''(\alpha)+2\mu\omega'(\alpha))+\mu^2p^3\omega''(\alpha)\right.$$
$$\left.+p\left(2\alpha\omega'(\alpha)+2D\mu\frac{\partial^2 q}{\partial x^2}\right)+2\alpha D\frac{\partial^2 q}{\partial x^2}+4D\mu\frac{\partial p}{\partial x}\frac{\partial q}{\partial x}\right) \tag{10}$$

where we assume that λ and ω are quadratic, i.e.

$$\lambda(r^2)=\gamma-r^2, \qquad \omega(r^2)=\delta+\eta r^2 . \tag{11}$$

We will use η, the "twist", as a stretched parameter in the perturbation scheme. Let us write (9, 10) in operator form,

$$L\begin{pmatrix}p\\q\end{pmatrix}=NL\begin{pmatrix}p\\q\end{pmatrix} \tag{12}$$

where L is linear and NL is strictly nonlinear. We will seek periodic solutions to (9, 10), whose parameters lie on the boundary between stable and unstable regions of parameter space.

Let $\tau=st$. We assume a series for p and q,

$$\begin{aligned} p&=p_0+\mu p_1+\mu^2 p_2+O(\mu^3)\\ q&=q_0+\mu q_1+\mu^2 q_2+O(\mu^3) \end{aligned} \tag{13}$$

where $\mu \ll 1$. We stretch s and η:

$$s=s_0+\mu s_1+\mu^2 s_2+O(\mu^3) \tag{14}$$

$$\eta=\eta_0+\mu\eta_1+\mu^2\eta_2+O(\mu^3) \tag{15}$$

giving, for the $O(1)$ term,

$$L\begin{pmatrix}p_0\\q_0\end{pmatrix}=0 \tag{16}$$

for the $O(\mu)$ term,

$$L\begin{pmatrix}p_1\\q_1\end{pmatrix}+F_1(p_0,q_0;s_1,\eta_1)=0 \tag{17}$$

for the $O(\mu^2)$ term,

$$L\begin{pmatrix}p_2\\q_2\end{pmatrix}+F_2(p_0,q_0,p_1,q_1;s_1,s_2,\eta_1,\eta_2)=0 \tag{18}$$

et cetera, where

$$L=\begin{pmatrix} s_0\dfrac{\partial}{\partial\tau}-D\dfrac{\partial^2}{\partial x^2}-\alpha\lambda'(\alpha) & -2\alpha Dkz\dfrac{\partial}{\partial x}\\ \dfrac{2Dkz}{\alpha}\dfrac{\partial}{\partial x}-\omega'(\alpha) & s_0\dfrac{\partial}{\partial\tau}-D\dfrac{\partial^2}{\partial x^2} \end{pmatrix} \tag{19}$$

and where the F_i terms are given in the appendix.

We will see that for investigation of the nature of the Hopf bifurcation (supercritical or subcritical), we need only look at terms of (p, q) up to $O(\mu^2)$. We seek periodic solutions of (p_0, q_0), (p_1, q_1), (p_2, q_2), etc. sequentially. The existence of periodic (separable) solutions of (p_1, q_1), (p_2, q_2) requires, by the Fredholm Alternative [11], that the (p_1, q_1) and (p_2, q_2) equations, (17) and (18), satisfy the compatibility condition

$$\langle F_1, \xi\rangle=0 \tag{20}$$

$$\langle F_2, \xi\rangle=0 \tag{21}$$

for all ξ in the null space of L^*, the adjoint of L, where we use the $L^2([0, 2\pi) \times (0, (2\pi/|s_0|))$ inner product,

$$\langle a, b\rangle = \frac{1}{2\pi}\int_0^{2\pi}\left(\frac{|s_0|}{2\pi}\int_0^{\frac{2\pi}{|s_0|}} a \cdot \bar{b}\, dt\right) dx . \tag{22}$$

We may assume a solution to (16) of the form

$$\begin{pmatrix} p \\ q \end{pmatrix} = e^{st}\begin{pmatrix} a_1 \sin nx + a_2 \cos nx \\ a_3 \sin nx + a_4 \cos nx \end{pmatrix} \tag{23}$$

for $n > 0$. Individual Fourier modes decouple, due to the linearity of (19), and the periodic boundary conditions. Substituting (23) into (16), and seeking nontrivial periodic solutions, gives the characteristic equation for the eigenvalues s:

$$\begin{aligned} &s^4 + s^3(4Dn^2 - 2\alpha\lambda') + s^2(2Dn^2(D(3n^2 - 4k^2) - 3\alpha\lambda') + \alpha^2\lambda'^2) \\ &+ s(2Dn^2(Dn^2 - \alpha\lambda' - 4Dk^2)(2Dn^2 - \alpha\lambda')) \\ &+ D^2n^2(4\alpha^2k^2\omega'^2 + n^2(Dn^2 - \alpha\lambda' - 4Dk^2)^2) = 0 \end{aligned} \tag{24}$$

which has solutions

$$s = \frac{\alpha\lambda'}{2} - Dn^2 \pm \frac{1}{2\sqrt{2}}\sqrt{X + \sqrt{Y}} \pm \frac{1}{2\sqrt{2}}\sqrt{X - \sqrt{Y}} \tag{25}$$

where

$$X = 16D^2k^2n^2 + \alpha^2\lambda'^2 \tag{26}$$

$$Y = (8\alpha Dkn\omega')^2 + X^2 . \tag{27}$$

If we assume $\omega' \neq 0$ and $\lambda' < 0$, then $\sqrt{Y} > X$ always, and s is of the form

$$s = \text{real negative} \pm \text{real positive} \pm \text{pure imaginary} . \tag{28}$$

Note $s = 0$ *only* when $n = 0$ or when $\omega' = 0$, which we shall not consider. The $n = 0$ case corresponds to a uniform phase shift, due solely to the $O(2)$ symmetry of the ring. The criterion for s for having zero real part (i.e. the location in parameter space of the bifurcation) is

$$k^2 = \frac{(Dn^2 - \alpha\lambda')}{4D\left(1 + \dfrac{\alpha^2\omega'^2}{(2Dn^2 - \alpha\lambda')^2}\right)} . \tag{29}$$

The right hand-side of the above is monotonic (strictly increasing) in n^2, and therefore one-to-one in n^2. This leads us to the following conclusions:

(*I*) Asymptotic stability to perturbations of all wavenumbers is not possible, since the zero wavenumber is always neutrally stable – it corresponds to a uniform phase shift in q. It simply reflects the $O(2)$ symmetry of the unperturbed system. So when we look for the stability criterion, we must look for decay in all nodes except for the zero mode. Stability to all perturbations of wavenumber $n>0$ requires that

$$k^2 < \frac{(Dn^2 - \alpha\lambda')}{4D\left(1 + \frac{\alpha^2\omega'^2}{(2Dn^2 - \alpha\lambda')^2}\right)} \tag{30}$$

be satisfied when $n^2 = 1$.

(*II*) In the infinite-dimensional linear system, (9, 10), there are at most two eigenvalues on the imaginary axis (plus the zero root), since when Re $s = 0$, (29) gives k^2 as a 1:1 function of n^2. The other eigenvalues are bounded away from the real axis. See Fig. 1.

We now have almost the complete proof of

Theorem 2.1 (Hopf Bifurcation) *The stability equations* (9, 10) *exhibit Hopf bifurcations in their time-behavior at the loci* (*HB*) *in parameter space*

$$k^2 = \frac{(Dn^2 - \alpha\lambda')}{4D\left(1 + \frac{\alpha^2\omega'^2}{(2Dn^2 - \alpha\lambda')^2}\right)}. \tag{31}$$

If λ and ω are quadratic, then the Hopf bifurcation has no nontrivial degeneracies.

The remainder of the proof, dealing with the transversality requirements of a Hopf bifurcation (nondegeneracy), is given in [16]. Now, a nondegenerate Hopf bifurcation is either supercritical or subcritical. Determining which requires examining the nonlinear terms of the governing equations, i.e. finding the higher-order terms in the Lindstedt series, (17, 18). We examine the $n=1$ wave, because

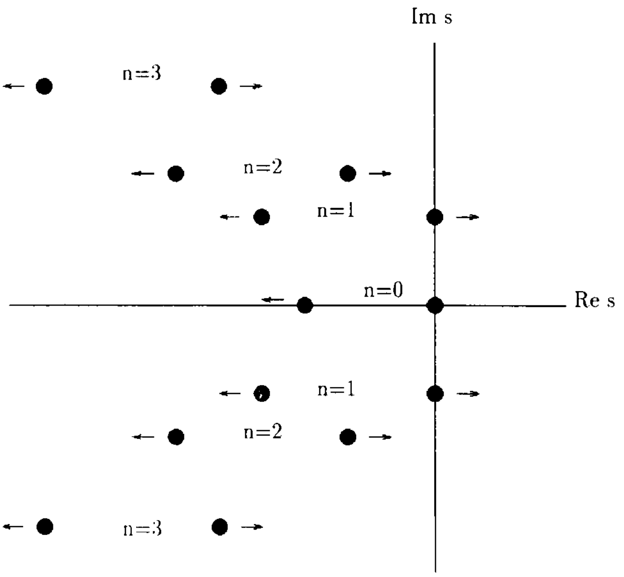

Fig. 1. Eigenvalues of the linear (p, q) system, at the Hopf bifurcation for $n=1$. Arrows indicate the direction eigenvalues move as α decreases

$n=1$ is the first unstable wavenumber. Other wavenumbers may be studied by the same methods.

It is straightforward to find solutions (p_0, q_0, p^*, q^*) to the linear equation (16), and to the adjoint equation

$$\begin{pmatrix} \overline{s_0}-D\dfrac{\partial^2}{\partial x^2}-\alpha\lambda'(\alpha) & -\dfrac{2Dkz}{\alpha}\dfrac{\partial}{\partial x}-\omega'(\alpha) \\ 2\alpha Dkz\dfrac{\partial}{\partial x} & \overline{s_0}-D\dfrac{\partial^2}{\partial x^2} \end{pmatrix}\begin{pmatrix} p^* \\ q^* \end{pmatrix}=0\,. \tag{32}$$

This also gives us the first-order frequency s_0 and twist η_0 terms. Proceeding to the solution of the (p_1, q_1) equations (17), by use of the Fredholm Alternative (20), we find that the order μ corrections to the frequency s_1 and twist η_1 are zero. This is common, but not universal, in systems with a Hopf bifurcations. Proceeding to order μ^2, and applying the Fredholm Alternative to the (p_2, q_2) equations (18), using the already computed solutions for $(p_0, q_0; s_0, \eta_0)$, $(p_1, q_1; s_1, \eta_1)$, (p^*, q^*), we obtain nonzero values for the frequency and twist corrections s_2 and η_2. Because of the intricacy of the computation, and the finite computational power available, it was not feasible to find solutions in general form. We picked arbitrary parameter values,

$$D=1,\ k=1; \qquad \lambda(r^2)=\gamma-r^2,\ \omega(r^2)=\delta+\eta r^2; \qquad \gamma=3,\ \eta_0=\tfrac{3}{4} \tag{33}$$

where δ is left general, because it does not affect stability; for these, we found that

$$\eta_2=\frac{1025}{92}\left(\frac{1}{2}c_1^2+\left(2c_2+\frac{5}{\sqrt{2}}c_1\right)^2\right) \tag{34}$$

by exact (symbolic) computation, where c_1 and c_2 measure the amplitudes of the (p_0, q_0) eigenvectors. Since $\eta=\eta_0+\mu\eta_1+\mu^2\eta_2+\cdots=\eta_0+\mu^2\eta_2+\cdots$ and $\eta_2>0$, we see that for these particular parameter values, periodic (p, q) soutions of order μ^2 exist only for $\eta>\eta_0$. In the region of parameter space where $\eta>\eta_0$, the origin is unstable. Thus, within the $n=1$ subspace of the center manifold of the system, the limit cycle which is born at the $n=1$ Hopf bifurcation is *stable* for these parameters values, and the Hopf bifurcation is supercritical [18]. The implications for *global* stability are subtle, however, and are addressed in the Discussion. We also find that $s_2 \neq 0$, i.e. there is a nonzero correction to the frequency and twist, but the corrections only appear at order μ^2.

3 Spatially inhomogeneous ring

Twining plants exhibit a more or less strict chirality of their spatiotemporal oscillations (circumnutation); for example, bean (*Phaseolus vulgaris*) stems only oscillate right-handed to their direction of elongation. We note [16, 17] that the primary ion of circumnutation, potassium, is concentrated in an irregular ring in the cross-section of a circumnutating stem, and model the associated ion-water transport processes as a reaction-diffusion system with an as yet *unknown* reaction term of excitatory or oscillatory behavior. In the oscillatory case, we choose the $\lambda-\omega$ system as a particularly simple case to examine on the irregular ring geometry. We ask whether an annular domain with a nonuniform cross-section can be constructed that will stably support traveling waves in one direction but not in the other. For simplicity, we model the 2-dimensional annulus as a one-dimensional ring. We approximate a 2-dimensional diffusion operator by a one-dimensional operator, by assuming the 2-dimensional domain is thin.

Consider a thin strip of width $A(x)$, on which a substance of concentration c may diffuse. If we partition the strip into elements of width Δx, indexing on i, and define s_i to be the quantity of diffusable substance in element i, then the discrete diffusion approximation is

$$\frac{ds_i}{dt}=\frac{D}{\Delta x}\left[A_{i+}(c_{i+1}-c_i)-A_{i-}(c_i-c_{i-1})\right] \tag{35}$$

where $A_{i\pm}$ is the width between elements, and D is the diffusion coefficient. We may rewrite this as

$$\frac{ds_i}{dt}=D\Delta x\Delta\left[\frac{A(\Delta c/\Delta x)}{\Delta x}\right] \tag{36}$$

and, noting that $c=s/(A\Delta x)$ and taking the limit as Δx goes to zero, we obtain

$$\frac{\partial c}{\partial t}=\frac{D}{A(x)}\frac{\partial}{\partial x}\left(A(x)\frac{\partial c}{\partial x}\right) \tag{37}$$

the quasilinear diffusion equation, where we assume the cross-sectional area $A(x)>0$ and $A(x)\in C^1$. If there is also a reaction term, we obtain the modified reaction-diffusion equation,

$$\frac{\partial c}{\partial t}=f(c)+\frac{D}{A(x)}\frac{\partial}{\partial x}\left(A(x)\frac{\partial c}{\partial x}\right). \tag{38}$$

When the reaction term is the $\lambda-\omega$ oscillator of Sects. 1 and 2, we have an inhomogeneous $\lambda-\omega$ system,

$$u_t=\lambda u-\omega v+\frac{1}{A(x)}D(Au_x)_x \tag{39}$$

$$v_t=\omega u+\lambda v+\frac{1}{A(x)}D(Av_x)_x\,. \tag{40}$$

It is assumed that $A(x)$ is 2π-periodic, positive everywhere, and sufficiently differentiable, i.e. $A(x)\in C^1_+(S^1)$. The conversion to polar coordinates $u=r\cos\theta$, $v=r\sin\theta$ gives

$$r_t=\lambda r-Dr(\theta_x)^2+Dr_{xx}+\frac{A_x}{A}Dr_x \tag{41}$$

$$\theta_t=\omega+D\theta_{xx}+2\frac{D}{r}r_x\theta_x+\frac{A_x}{A}D\theta_x\,. \tag{42}$$

Assuming small variations in $A(x)$, we write

$$\varepsilon B(x)\equiv\frac{A_x}{A} \tag{43}$$

or

$$A(x)=e^{\varepsilon\int^x B(\xi)d\xi} \tag{44}$$

where $\varepsilon \ll 1$ and $B(\xi)$ is 2π-periodic. That is, A can be thought of as the exponential of a periodic function which C^∞-small. We will use ε as a perturbation parameter.

When $\varepsilon = 0$, traveling wave solutions

$$r = \alpha \tag{45}$$

$$\theta = \omega(\alpha)t - z\sqrt{\frac{\lambda(\alpha)}{D}}\,x + \theta_0 \tag{46}$$

are found, as in Sect. 2. When $\varepsilon \neq 0$, we write

$$r = \alpha + \varepsilon\rho(x, t; \varepsilon) \tag{47}$$

$$\theta = \omega(\alpha)t - zkx + \theta_0 + \varepsilon\phi(x, t; \varepsilon)\,. \tag{48}$$

Writing

$$\lambda(r) = \lambda(\alpha) + \lambda'(\alpha)(r-\alpha) + \frac{\lambda''(\alpha)}{2}(r-\alpha)^2 + \cdots \tag{49}$$

$$\omega(r) = \omega(\alpha) + \omega'(\alpha)(r-\alpha) + \frac{\omega''(\alpha)}{2}(r-\alpha)^2 + \cdots \tag{50}$$

and neglecting higher-order terms of λ and ω, we obtain nonlinear equations for ρ and ϕ

$$\rho_t = 2\alpha Dkz\phi_x + D\rho_{xx} + \alpha\lambda'\rho + \varepsilon\left(2Dkz\rho\phi_x + DB(x)\rho_x + \left(\frac{\alpha\lambda''}{2} + \lambda'\right)\rho^2 - \alpha D\phi_x^2\right)$$
$$+\varepsilon^2\left(\frac{\lambda''}{2}\rho^3 - D\rho\phi_x^2\right) + O(\varepsilon^3) \tag{51}$$

$$\phi_t = \frac{1}{\alpha + \varepsilon\rho}\Bigg[-2Dkz\rho_x - \alpha DkzB(x) + \alpha\omega'\rho + \alpha D\phi_{xx}$$
$$+\varepsilon\left(-DkzB(x)\rho + \left(\frac{\alpha\omega''}{2} + \omega'\right)\rho^2 + 2D\rho_x\phi_x + D\rho\phi_{xx} + \alpha DB(x)\phi_x\right)$$
$$+\varepsilon^2\left(\frac{\omega''}{2}\rho^3 + DB(x)\rho\phi_x\right)\Bigg] + O(\varepsilon^3)\,. \tag{52}$$

If λ and ω are quadratic, these equations are exact, as we shall assume in the analysis to follow.

Since we have assumed the asymmetric domain of the reaction-diffusion system is "close" to the symmetric domain, i.e. it is scaled by a small parameter $\varepsilon \ll 1$, we can write the effect of the inhomogeneity as a perturbation series in ε,

$$\rho = \rho_0 + \varepsilon\rho_1 + \varepsilon^2\rho_2 + \cdots \tag{53}$$

$$\phi = \phi_0 + \varepsilon\phi_1 + \varepsilon^2\phi_2 + \cdots\,. \tag{54}$$

Substituting (53, 54) into (51, 52), and collecting like coefficients of ε, gives us a set of linear equations

$$L\begin{pmatrix}\rho_0\\ \phi_0\end{pmatrix}=\begin{pmatrix}0\\ -DkzB(x)\end{pmatrix} \tag{55}$$

$$L\begin{pmatrix}\rho_1\\ \phi_1\end{pmatrix}=\begin{pmatrix}G_1(\rho_0,\phi_0)\\ G_2(\rho_0,\phi_0)\end{pmatrix} \tag{56}$$

$$L\begin{pmatrix}\rho_2\\ \phi_2\end{pmatrix}=\begin{pmatrix}G_3(\rho_0,\phi_0,\rho_1,\phi_1)\\ G_4(\rho_0,\phi_0,\rho_1,\phi_1)\end{pmatrix} \tag{57}$$

where G_i are complicated nonlinear functions of their variables, comparable in complexity to (85–88) [16]. These give the successive corrections to the amplitude and phase of the wave due to the inhomogeneity.

Since we are specifically considering waves on a ring, we can write $B(x)$ in Fourier series. Note that there will be no constant term[1] in the Fourier series for B, since the average value of B around the ring is

$$\frac{1}{2\pi}\int_0^{2\pi} B(x)dx=\frac{1}{2\pi\varepsilon}\int_0^{2\pi}\frac{dA/dx}{A}dx=\frac{1}{2\pi\varepsilon}\int_{A(0)}^{A(2\pi)}\frac{dA}{A}=0\,. \tag{58}$$

The general solution of the linear equation (55) will have a complementary part and a particular part. The complementary part has been found in Sect. 2, for p and q. We seek particular solutions which are dependent on x only, since the inhomogeneity B is dependent only on x. Let us therefore write $\rho_0=\rho_0(x)$ and $\phi_0=\phi_0(x)$, and

$$B(x)=\sum_{n=1}^{\infty}(b_n\cos nx+c_n\sin nx) \tag{59}$$

$$\rho_0(x)=\sum_{n=1}^{\infty}(r_n\cos nx+s_n\sin nx) \tag{60}$$

$$\phi_0(x)=\sum_{n=1}^{\infty}(f_n\cos nx+g_n\sin nx)+\Phi_0 \tag{61}$$

where Φ_0 is an arbitrary phase shift. Substitutions of (59, 60, 61) into (51, 52) gives the coefficients

$$r_n=\frac{-2k^2D^2\alpha n}{\alpha\lambda'(\alpha)-Dn^2}\,\frac{Wc_n-Zb_n}{W^2+Z^2} \tag{62}$$

$$s_n=\frac{2k^2D^2\alpha n}{\alpha\lambda'(\alpha)-Dn^2}\,\frac{(Wb_n+Zc_n)}{W^2+Z^2} \tag{63}$$

[1] If we were to include a constant term in the Fourier expansion for B, e.g. for another application, there would be a time-stretching solution ($\rho_0=0$, $\phi_0=-Dkzb_0t$) of (55) added on to the particular solution

$$f_n = \frac{zkD(Wb_n + Zc_n)}{W^2 + Z^2} \tag{64}$$

$$g_n = \frac{zkD(Wc_n - Zb_n)}{W^2 + Z^2} \tag{65}$$

for $n = 1, 2, 3, \ldots,$ where

$$W = -Dn^2\left(\frac{4k^2D}{\alpha\lambda'(\alpha) - Dn^2} + 1\right) \tag{66}$$

$$Z = \frac{2\omega'(\alpha)zkD\alpha n}{\alpha\lambda'(\alpha) - Dn^2}\,. \tag{67}$$

Observe that $r_n^2 + s_n^2$ is independent of z, i.e. the amplitude of each mode of the perturbation ρ_0 is independent of z, the direction of travel. Observe, also, that $f_n^2 + g_n^2$, the overall phase shift of each mode of ϕ_0, is independent of z.

For the higher order terms, (ρ_1, ϕ_1), etc., finding explicit solutions for an infinite Fourier series becomes impossible, since it involves the multiplication of infinite series. We therefore found explicit solutions for the *truncated* Fourier series,

$$B(x) = v_1 \sin x + v_2 \sin 2x + v_3 \cos 2x \tag{68}$$

which is the simplest possible $B(x)$ which is capable of breaking the reflection symmetry of the ring geometry. We expect that the truncated series exhibits the same behavior as the full series, since the corrections (r_n, s_n, f_n, g_n) converge very quickly, as n^{-4}.

When we compute the solutions (ρ_1, ϕ_1), (ρ_2, ϕ_2), we find that

$$\begin{pmatrix} r \\ \theta \end{pmatrix} = \begin{pmatrix} \alpha \\ \omega(\alpha)t - zkx + \theta_0 \end{pmatrix} + \varepsilon H_1(x) + \varepsilon^2\left[\begin{pmatrix} a_1 \\ h_1 t \end{pmatrix} + H_2(x)\right] + O(\varepsilon^3) \tag{69}$$

where a_1 and h_1 are constants which depend on the parameters, and where H_i are spatially periodic functions whose space-averages are zero. We see from (69) that the heterogeneity affects the solutions of r and θ to first order in *local* spatial dependence only, but that at the next higher order, there is an additional *global* effect on the overall frequency and average amplitude of wave solutions.

For all nonzero v_1, v_2, and v_3, we find, for our chosen parameter values (33),

$$a_1 = -\frac{1575v_1^2 + 1332(v_2^2 + v_3^2)}{7400} \tag{70}$$

$$h_1 = \frac{675\sqrt{2}v_1^2 + 222\sqrt{2}(v_2^2 + v_3^2)}{7400} \tag{71}$$

so that $a_1 < 0$ and $h_1 > 0$ for all nonzero v_1, v_2, v_3. That is, perturbing the width of the domain of our $\lambda - \omega$ system reduces the average amplitude of a traveling wave of a given wavenumber, and increases its frequency, at order ε^2.

It is interesting to compare these results with the experimental fluid convection results of Hartung et al. (1990) [7], who found drift in convection rolls in an annular convection channel whose height was modulated by an asymmetric sinusoidal function. They found that the drift rate of the convection rolls was proportional to the amplitude of the modulation, and to the amount of asymmetry in its shape. That is, if the width of their channel domain for convection was $A=A_0+\varepsilon\sin x$, they found the drift frequency of convection rolls to be proportional to ε. In our system,

$$A(x)=e^{\varepsilon\int^x B(\xi)d\xi}\sim 1+\varepsilon\int^x B(\xi)d\xi+\cdots \tag{72}$$

but we first find a change in frequency – equivalent to a drift frequency – at order ε^2, i.e. the term $\varepsilon^2 h_1 t$ of the series for ϕ (69). There is no order-ε effect of the spatial modulation on the frequency of our traveling waves, whereas there is an order-ε effect in the convection experiments [7].

We have seen that putting our $\lambda-\omega$ wave on a waveguide of sorts can change the local amplitude and phase by a small amount ($O(\varepsilon)$), and can change the overall frequency by a small amount ($O(\varepsilon^2)$). Is there a change in *stability* of the waves associated with the waveguide? To our modifications of the traveling wave, (ρ, ϕ), let us add a small perturbation, (p, q), scaled with $\mu\ll 1$:

$$r=\alpha+\varepsilon\rho(x,t;\varepsilon)+\mu p(x,t;\varepsilon) \tag{73}$$

$$\theta=\omega(\alpha)t-zkx+\theta_0+\varepsilon\phi(x,t;\varepsilon)+\mu q(x,t;\varepsilon) \tag{74}$$

We have already written ρ and ϕ in a series (53), (54) in ε. We will also write p and q in a series in ε, and stretch the twist η of the original wave, and the frequency s of the perturbation (p, q) in the same way.

Looking at linear stability entails linearizing the (p, q) equations in μ. Note the heuristic difference between ε and μ: ε is a measure of the effect of the spatial heterogeneity, while μ is a measure of the size of a deviation from the pure traveling wave. Stability is scaled by μ, but stability can be affected by terms of order ε etc. Thus we look at linear stability by linearizing in μ, but we look at nonlinear effects of $B(x)$ by taking $O(\varepsilon)$ and higher terms.

We obtain a series of linear partial differential equations in (p_i, q_i), as before, but containing dependence on (ρ_i, ϕ_i):

$$L\begin{pmatrix}p_0\\ q_0\end{pmatrix}=0 \tag{75}$$

$$L\begin{pmatrix}p_1\\ q_1\end{pmatrix}=\begin{pmatrix}F_{1a}(p_0, q_0, \rho_0, \phi_0; \eta_1, s_1)\\ F_{1b}(p_0, q_0, \rho_0, \phi_0; \eta_1, s_1)\end{pmatrix} \tag{76}$$

$$L\begin{pmatrix}p_2\\ q_2\end{pmatrix}=\begin{pmatrix}F_{2a}(p_0, q_0, p_1, q_1, \rho_0, \phi_0, \rho_1, \phi_1; \eta_1, \eta_2, s_1, s_2)\\ F_{2b}(p_0, q_0, p_1, q_1, \rho_0, \phi_0, \rho_1, \phi_1; \eta_1, \eta_2, s_1, s_2)\end{pmatrix} \tag{77}$$

where F_i are complicated nonlinear functions of their variables [16], comparable in complexity to (85–88).

We seek periodic solutions (p, q), which lie on the stability boundary. By this method, we determine the deviation in the stability boundary which is caused by the inhomogeneity, as a series in ε. Determining the effect of the inhomogeneity $B(x)$ on the stability of waves altered by $B(x)$ entails finding the stretch in η and s in terms of ε which will keep solutions of the (p, q) equations on the stability boundary. It is the Fredholm compatibility condition on the right-hand-sides of (76) and (77) which will determine η_1, η_2, s_1, and s_2.

As in the homogeneous case, we find that

$$\eta_1=s_1=0 \tag{78}$$

meaning that any effect which the inhomogeneity $B(x)$ has on the stability of wave solutions only shows up at order ε^2. Recall, too, that the frequency and amplitude effects of $B(x)$ only showed up at order ε^2.

From the solutions which we compute for (p_1, q_1) and the solutions for $(\rho_0, \phi_0, \rho_1, \phi_1)$ computed above, and the result $\eta_1 = s_1 = 0$, we determine the compatibility condition on η_2 and s_2. Again, due to the great size of the computation compared to the computing resources available, we were only able to determine the corrections to the stability boundary for a specific set of parameter values, but for these (33), we find

$$\eta_2 = -\frac{85}{48} v_1^2 + \frac{7769}{32080} (v_2^2 + v_3^2) \tag{79}$$

$$s_2 = -s_0 \left[\frac{517}{148} v_1^2 + \frac{28687}{120300} (v_1^2 + v_2^2) \right] \tag{80}$$

with no dependence whatsoever on z, the direction of propagation of the wave.

We conclude from this that under typical conditions, *existence and stability of the perturbed $\lambda - \omega$ wave are unaffected by the direction of wave propagation*, despite the asymmetric inhomogeneity, at least to $O(\varepsilon^2)$.

We further find that there exist particular values of v_1, v_2, v_3 which give the cubic Hopf bifurcation coefficient $\eta_2 = 0$, i.e. on the stability boundary. This means that the stability of any limit cycle depends on the nature of the inhomogeneity. For the parameter values chosen [16], for v_2 and v_3 sufficiently large in comparison with v_1, $\eta_2 > 0$, the Hopf bifurcation is supercritical, and the limit cycle is stable. For v_2 and v_3 sufficiently small in comparison with v_1, $\eta_2 < 0$, the Hopf bifurcation is subcritical, and the limit cycle is unstable. The inhomogeneity $B(x)$ alters the stability, but irrespective of the direction of the wave.

4 Discussion

In Sect. 2, we investigated Hopf bifurcations in traveling waves of $\lambda - \omega$ systems. We showed that for specific parameter values, the limit cycles born at the Hopf bifurcation exist when the equilibrium is unstable, i.e. the bifurcation is supercritical. Whether or not this means that the limit cycles are stable is a somewhat subtle point. If the center manifold of this system were 2-dimensional, and we were confined to this 2-dimensional center manifold, we could say, without reservation, that the limit cycles born at the Hopf bifurcation are stable, if the equilibrium points they encircle are unstable. But the center manifold of the system is 3-dimensional; there are two dimensions in the $n = 1$ subspace[2], corresponding to pure imaginary eigenvalues, and one dimension corresponding to the $n = 0$ subspace, i.e. the zero eigenvalue. Within the $n = 1$ subspace of the center manifold, which is an invariant nonlinear 2-manifold tangent to the 2-dimensional eigenspace, the limit cycles are stable. But when we try to observe them numerically [16], we run into difficulty, because we cannot effectively select initial data on this subspace and because the synchronous ($k = 0$) wave is weakly attracting. That is, solutions do not stay near the $n = 1$ subspace for all time. We observe orbits near

[2] Note k is the wavenumber of the traveling wave, and n is the wavenumber of perturbations off it

the limit cycle for a limited amount of time; eventually they depart from the $n=1$ subspace in the direction of the $n=0$ subspace. Recall from Sect. 2 that the $n=0$ eigenvalue was zero. This means that any tendency in the $n=0$ direction is a strictly nonlinear phenomenon. However, confining ourselves to the $n=0$ subspace of the center manifold of (p, q) solutions leaves us, through order μ^2, with the same solutions at each order, $(p=0, q=c)$, corresponding to a uniform phase shift. So we do not observe, in the perturbation analysis, any attraction or repulsion in the $n=0$ direction, to the order we have carried the calculations, although we do observe this attraction numerically.

We obtained frequency and amplitude shifts of traveling waves of the $\lambda-\omega$ system under perturbation by small superimposed waves, which were called p and q, and also by the effect of spatial inhomogeneities, which were manifest in small changes to the original waves, and called ρ and ϕ. These frequency and amplitude shifts only appeared at second order ($O(\varepsilon^2)$ or $O(\mu^2)$), which is not uncommon for Hopf bifurcation problems.

In an attempt to explain the observed directional preferences of twining plants [16, 17], we made the conjecture that there exists an irregular ring geometry which stably supports traveling waves of an excitable or oscillatory reaction-diffusion system in one direction only. The analysis of Sect. 3 indicates that for $\lambda-\omega$ systems, under fairly generic conditions, this unidirectionality of stability is *not* observed. We have not shown this lack of symmetry-breaking for general $\lambda-\omega$ systems, or for a specific system with a general inhomogeneity, but the arbitrariness of the parameters chosen for the case we did analyze suggests that unidirectionality of wave stability will not be found in $\lambda-\omega$ systems, for any perturbed ring geometry. We do *not* suggest that $\lambda-\omega$ waves on an inhomogeneous *infinite* domain (i.e. not on a ring) exhibit the same results. To the contrary, we expect that quite different results may hold on an infinite domain where $A(+\infty) \neq A(-\infty)$.

However, the implication that $\lambda-\omega$ systems on an inhomogeneous annular domain do not have waves which are unidirectionally stable should not be taken further to imply that *general* reaction-diffusion systems on an inhomogeneous annular domain cannot have waves which are unidirectionally stable. Other reaction-diffusion systems may have very different properties from oscillatory $(\lambda-\omega)$ reaction-diffusion systems. Future studies will involve spatial inhomogeneities similar to the ones of the present study, for *excitable* reaction-diffusion equations, building on Pauwelussen, Ikeda, and Mimura [9, 20, 21], who studied excitable and bistable reaction-diffusion equations associated with neural behavior. They found that waves could be blocked in one direction but not in the other by a step-function in $D(x)$, the spatially-dependent diffusion coefficient. Recently, Lubkin [17] found that traveling waves in an excitable FitzHugh–Nagumo system *can* be unidirectionally blocked by a periodic sawtooth inhomogeneity $A(x)$ on a ring. Thus, while the oscillatory $\lambda-\omega$ system is an inappropriate model for the directional preferences of twining plants, the excitable FitzHugh–Nagumo system is an appropriate model, which may indicate that the fundamental physiological nature of the plants' oscillations is excitable, rather than oscillatory.

5 Appendix: expansions

In Sect. 2 we expanded the nonlinear stability equations by Lindstedt's method. Upon substituting $\alpha=\sqrt{\gamma-Dk^2}$, and $\lambda(\alpha^2)=\gamma-\alpha^2$, $\omega(\alpha)=\delta+\eta\alpha^2$, those expansions become:

$$L\begin{pmatrix} p_0 \\ q_0 \end{pmatrix}=0 \tag{81}$$

for the $O(\mu)$ term,

$$L\begin{pmatrix} p_1 \\ q_1 \end{pmatrix}+F_1(p_0, q_0; s_1, \eta_1)=0 \tag{82}$$

for the $O(\mu^2)$ term,

$$L\begin{pmatrix} p_2 \\ q_2 \end{pmatrix}+F_2(p_0, q_0, p_1, q_1; s_1, s_2, \eta_1, \eta_2)=0 \tag{83}$$

et cetera, where

$$F_1=\begin{pmatrix} F_{11} \\ F_{12} \end{pmatrix}, \qquad F_2=\begin{pmatrix} F_{21} \\ F_{22} \end{pmatrix} \tag{84}$$

and

$$F_{11}=D((q_{0x})^2\sqrt{\gamma-Dk^2}-2zkp_0q_{0x})+3p_0^2\sqrt{\gamma-Dk^2}+s_1p_{0\tau} \tag{85}$$

$$\begin{aligned} F_{12}=&-(D(p_{0x}(-2q_{0x}\sqrt{\gamma-Dk^2}-2kp_0)+k^2(2\eta_1p_0\sqrt{\gamma-Dk^2}+\eta_0p_0^2)\\ &-k^2s_1q_{0\tau}-2\eta_1p_0\gamma\sqrt{\gamma-Dk^2}+s_1q_{0\tau}\gamma-\eta_0p_0^2\gamma)/(Dk^2-\gamma) \end{aligned} \tag{86}$$

$$\begin{aligned} F_{21}=&D(2q_{0x}q_{1x}\sqrt{\gamma-Dk^2}-2zk(p_0q_{1x}+p_1q_{0x})+p_0(q_{0x})^2)\\ &+6p_0p_1\sqrt{\gamma-Dk^2}+s_2p_{0\tau}+s_1p_{1\tau}+p_0^3 \end{aligned} \tag{87}$$

$$\begin{aligned} F_{22}=&-[D(k^2(-4\gamma^2p_0(\eta_2\sqrt{\gamma-Dk^2}+\eta_0p_1)-2\eta_1\gamma(2p_1\sqrt{\gamma-Dk^2}+p_0^2))\\ &+2p_{0x}(zk(p_1\gamma-p_0^2\sqrt{\gamma-Dk^2})+q_{1x}\gamma\sqrt{\gamma-Dk^2}-p_0q_{0x}\gamma)\\ &+2(\gamma-D^2k^2)p_{1x}(q_{0x}\sqrt{\gamma-Dk^2}+zkp_0)+(2k^2\gamma-D^2k^4)(s_2q_{0\tau}+s_1q_{1\tau}))\\ &+D^2k^2(2p_{0x}((p_0q_{0x}-q_{1x}\sqrt{\gamma-Dk^2})-zkp_1))+D^2k^4(\eta_1p_0^2)\\ &+2(D^2k^4+\gamma^2)(p_0(\eta_2\sqrt{\gamma-Dk^2}+\eta_0p_1)+\eta_1p_1\sqrt{\gamma-Dk^2})\\ &-s_2q_{0\tau}\gamma^2-s_1q_{1\tau}\gamma^2+(\gamma^2+D^2k^4)(\eta_1p_0^2)]/(\gamma-Dk^2)^2\,. \end{aligned} \tag{88}$$

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