

## Periodic Traveling Waves in Integro-differential Equations for Nonlocal Dispersal\*

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**Abstract.** Periodic traveling waves (wavetrains) have been extensively studied for reaction-diffusion equations. One important motivation for this work has been the identification of periodic traveling wave patterns in spatiotemporal data sets in ecology. However, for many ecological populations, diffusion is no more than a rough phenomenological representation of dispersal, and spatial convolution with a dispersal kernel is more realistic. This paper concerns periodic traveling wave solutions of differential equations with nonlocal dispersal terms, and with local dynamics of lambda-omega form. These kinetics include the normal form near a standard supercritical Hopf bifurcation and are therefore significant for a wide range of applications. For general dispersal kernels, an explicit family of periodic traveling wave solutions is derived, as well as the condition for waves to be stable to perturbations of arbitrarily small wavenumber. Three specific kernels are then considered in detail: Laplace, Gaussian, and top hat. For Laplace and Gaussian kernels, it is shown that stability to perturbations of arbitrarily small wavenumber implies stability, a result that also applies for reaction-diffusion equations with lambda-omega kinetics. However, for the top hat kernel it is shown that periodic traveling waves may be stable to perturbations with small wavenumber but not to those with larger wavenumber. The wave family for the top hat kernel also shows significant qualitative differences from those for the Laplace and Gaussian kernels, and for reaction-diffusion equations with the same kinetics.

**Key words.** wavetrain, dispersal kernel, lambda-omega, nonlocal, ecology, traveling wave

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**1. Introduction.** Many natural populations exhibit long-term oscillations in abundance. Historic data on such cyclic populations is restricted to time series, most famously the data from the Hudson Bay Trading Company on Canadian lynx populations in the 19th century [1]. Over the last two decades there has been a pronounced increase in *spatiotemporal* field studies for cyclic populations, with a parallel development of new spatiotemporal statistical methods [2, 3, 4]. In many cases, this has shown that the oscillations are not uniform in space, but instead are organized into a periodic traveling wave (PTW). This is particularly well documented for voles [5, 6, 7] and moths [8, 9, 10]; a fuller list of examples is given in Table 1 of [11].

PTW (wavetrain) solutions of reaction-diffusion equations have been studied since the 1970s because of their relevance to spiral waves and target patterns in oscillatory chemical reactions [12]. The discovery of their ecological importance in the 1990s was paralleled by renewed mathematical interest, and the literature on PTWs in reaction-diffusion models for interacting populations is now extensive (see [13, 14, 15] for recent examples). However, for

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many ecological populations, diffusion is no more than a rough phenomenological representation of dispersal, and spatial convolution with a dispersal kernel is more realistic. Dispersal kernels were first proposed in the 1970s [16, 17] and have been widely used since the late 1990s. They reflect the importance of rare long-distance dispersal events, and can be directly related to empirical data. There is now a wide range of methods for estimating dispersal kernels, including mark-recapture (e.g., [18]), tracking of dispersing individuals (e.g., [19]), and, for plants, genotyping of individual seedlings to determine the source plant (e.g., [20]). Using such methods, dispersal kernels have been estimated for many plants and animals; see Table 15.1 of [21] for a comprehensive list.

There is a significant literature on PTW solutions of reaction-diffusion models with nonlocal terms in the kinetics. This includes work on models with nonlocal delays [22, 23, 24, 25] and recent work by Merchant and Nagata on predator-prey models with nonlocal prey competition [26, 27]. Also Lutscher [28] has studied PTWs in integrodifferential equation models for populations in heterogeneous landscapes, but here the wave periodicity simply reflects the periodic dependence of parameters on space. However, there has been almost no previous work on PTW solutions of autonomous differential equation models in which dispersal is represented by an integral term—in marked contrast to the very large literature on PTWs in standard reaction-diffusion equations. The relevant work that I am aware of comes from the physics literature and involves brief discussions of plane wave solutions of the complex Ginzburg–Landau equation with nonlocal coupling [29, 30]. This paper is a first step in a detailed study of PTWs in models with nonlocal dispersal.

An important contribution to the study of PTWs in reaction-diffusion equations was the introduction by Kopell and Howard [12] of “ $\lambda$ - $\omega$ ” systems:

$$(1.1) \quad \partial u / \partial t = \partial^2 u / \partial x^2 + \lambda(r)u - \omega(r)v, \quad \partial v / \partial t = \partial^2 v / \partial x^2 + \omega(r)u + \lambda(r)v$$

( $r = \sqrt{u^2 + v^2}$ ). Here  $\lambda(0) > 0$  and  $\lambda(\cdot)$  is a strictly decreasing function with a simple zero. For the case of

$$(1.2) \quad \lambda(r) = \lambda_0 - \lambda_1 r^2, \quad \omega(r) = \omega_0 + \omega_1 r^2,$$

where  $\lambda_0, \lambda_1 > 0$ , equations (1.1) are simply the complex Ginzburg–Landau equation with a real diffusion coefficient [31, 32], and they have a special significance as the normal form of a reaction-diffusion system with scalar diffusion close to a standard supercritical Hopf bifurcation. For example, Appendix A of [33] presents a derivation of  $\lambda_0, \lambda_1, \omega_0$ , and  $\omega_1$  as functions of ecological parameters for the classic Rosenzweig–MacArthur [34] model for predator-prey systems. Such a direct link is an important motivation for the study of (1.1), which has the great advantage of being analytically tractable. In particular the PTW family can be written down explicitly:  $u = R \cos[\omega(R)t \pm \lambda(R)^{1/2}x]$ ,  $v = R \sin[\omega(R)t \pm \lambda(R)^{1/2}x]$ . Here  $R$  is a parameter that can take any positive value such that  $\lambda(R) \geq 0$ . The existence of a one-parameter family of PTWs is a general feature of oscillatory reaction-diffusion equations [12]. However, only some members of the family are stable, and this is a very important issue because the loss of stability (as a parameter is varied) can herald the onset of spatiotemporal chaos [35]. Here and throughout this paper I use the term (in)stability to mean spectral (in)stability. For (1.1) the stability condition can be found exactly [12]:

$$(1.3) \quad R\lambda'(R) + 4\lambda(R) [1 + \omega'(R)^2/\lambda'(R)^2] \leq 0.$$

In this paper I will study the equivalent of (1.1) for nonlocal dispersal:

$$(1.4) \quad \begin{aligned} \partial u / \partial t &= \int_{y=-\infty}^{y=+\infty} K(x-y)u(y)dy + \lambda(r)u - \omega(r)v, \\ \partial v / \partial t &= \int_{y=-\infty}^{y=+\infty} K(x-y)v(y)dy + \omega(r)u + \lambda(r)v \end{aligned}$$

(as above  $r = \sqrt{u^2 + v^2}$ ). Again, when  $\lambda(\cdot)$  and  $\omega(\cdot)$  are given by (1.2) these equations are the normal form close to a standard supercritical Hopf bifurcation for any model with scalar nonlocal dispersal [29, 36]. Consequently, results for (1.4) are significant for any ecological model with low amplitude populations cycles and with dispersal terms that are nonlocal with the same dispersal coefficient for each population.

Any dispersal kernel  $K(y)$  must be  $\geq 0$  for all  $y$  and must satisfy  $\int_{-\infty}^{+\infty} K(y) dy = 1$  so that the dispersal term conserves population. For most of the paper (sections 2 and 3) I will restrict attention to kernels that are “thin-tailed,” i.e., exponentially bounded, meaning that there exist  $\delta > 0$  and  $L > 0$  for which  $K(s) < \exp(-\delta|s|)$  for  $|s| > L$ . There is a significant literature on “fat-tailed” kernels, especially in the context of invasion fronts (e.g., [37, 38, 39]). Such kernels are of clear ecological relevance [21, 40], and in section 4 I consider PTWs for one example, the Cauchy kernel. In keeping with the symmetry of positive and negative  $x$  directions in (1.1), I will further assume that  $K(\cdot)$  is an even function; asymmetric kernels correspond to biased dispersal, such as occurs in populations living in rivers [41].

In section 2 I present results on wave existence and stability for general kernels. I derive an explicit family of PTW solutions, but my results on wave stability are only partial. In sections 3.2 and 3.3 I consider the special cases of the Laplace and Gaussian kernels, with  $\lambda(\cdot)$  and  $\omega(\cdot)$  given by (1.2). The main results of the paper are explicit conditions for wave stability in these cases. As part of my derivation, I show that for these two kernels, waves are stable if they are stable to perturbations with sufficiently small wavenumber. This result also applies for (1.1), and was fundamental to Kopell and Howard’s [12] derivation of the stability condition (1.3). In section 3.4 I show that this result is not generally true for the integrodifferential equations (1.4) by considering the example of the top hat kernel, again with  $\lambda(\cdot)$  and  $\omega(\cdot)$  given by (1.2). The PTW family for this kernel also has major qualitative differences from that for (1.1), (1.2).

Before proceeding, I introduce notation that I will use throughout the paper:

$$(1.5) \quad \mathcal{C}_n = \int_{s=-\infty}^{s=+\infty} s^n K(s) \cos(\alpha s) ds, \quad \mathcal{S}_n = \int_{s=-\infty}^{s=+\infty} s^n K(s) \sin(\alpha s) ds.$$

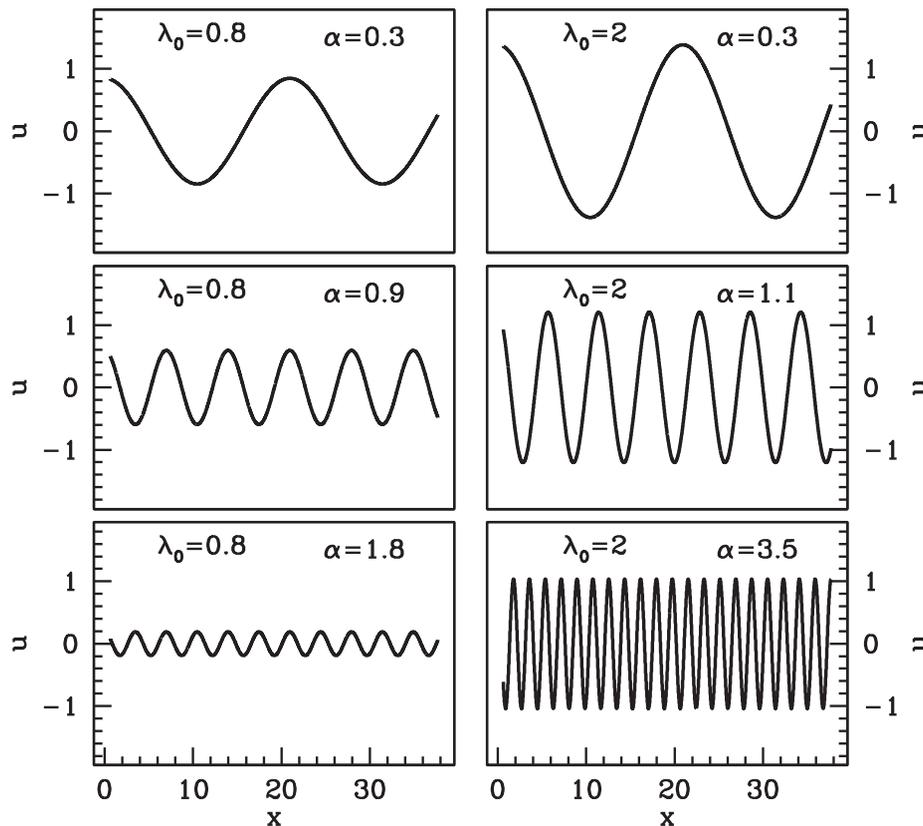
**2. Periodic traveling wave family.** In this section I will derive an explicit form for a family of PTW solutions of (1.4) and make some preliminary remarks concerning wave stability. Following standard practice for (1.1), I begin by rewriting (1.4) in terms of polar coordinates in the  $u$ - $v$  plane,  $r$ , and  $\theta = \tan^{-1}(v/u)$ :

$$(2.1) \quad \begin{aligned} \frac{\partial r}{\partial t} &= \int_{y=-\infty}^{y=+\infty} K(y-x)r(y) \cos[\theta(y) - \theta(x)] dy + r\lambda(r) - r, \\ \frac{\partial \theta}{\partial t} &= \int_{y=-\infty}^{y=+\infty} K(y-x) \frac{r(y)}{r(x)} \sin[\theta(y) - \theta(x)] dy + \omega(r). \end{aligned}$$

Motivated by the form of PTW solutions of (1.1), I look for solutions of (2.1) with the form  $r = R$ ,  $\theta = \alpha x + \beta t$ , where  $R \geq 0$ ,  $\alpha \geq 0$ , and  $\beta$  are constants, giving

$$(2.2) \quad \lambda(R) = 1 - C_0, \quad \omega(R) = \beta.$$

Note that (2.2) is only valid for even kernels  $K(\cdot)$ . Figure 1 shows various examples of such PTW solutions, when  $K(\cdot)$  is the Laplace kernel (defined in (3.1) below).



**Figure 1.** Examples of PTW solutions of (1.4) for the Laplace kernel (3.1) with  $a = 1$ , plotted as a function of space  $x$ . The functions  $\lambda(\cdot)$  and  $\omega(\cdot)$  are given by (1.2) with  $\lambda_1 = 1$ ; the values of  $\lambda_0$  and  $\alpha$  are as shown in the figure. Note that the values of  $\omega_0$  and  $\omega_1$  do not affect the PTW as a function of space. The left- and right-hand columns illustrate wave families for  $\lambda(0) < 1$  and  $\lambda(0) > 1$ , respectively. In both cases, waves for small  $\alpha$  have large wavelength and high amplitude, approaching a spatially homogeneous oscillation as  $\alpha \rightarrow 0^+$ . When  $\lambda(0) < 1$ , the wave amplitude is zero at a finite value of  $\alpha$ , which is 2 for the value of  $\lambda_0$  used in the left-hand column of the figure. In contrast when  $\lambda(0) > 1$  there is no upper bound on the values of  $\alpha$  giving waves, and the wavelength  $\rightarrow 0$  with the amplitude remaining nonzero as  $\alpha \rightarrow \infty$ .

Since  $\lambda(\cdot)$  is strictly decreasing, (2.2) has a (unique) solution for  $R$  and  $\beta$  if and only if  $C_0 \in [1 - \lambda(0), 1]$ . Intuitive understanding of this is helped by considering the cases  $\alpha = 0$  and

$\alpha \rightarrow \infty$ . My assumptions of nonnegativity and exponential boundedness for  $K$  imply that

$$\begin{aligned} 0 \leq 1 - \mathcal{C}_0 &= \int_{s=-\infty}^{s=\infty} K(s)[1 - \cos(\alpha s)] ds \\ &\leq \int_{s=-L}^{s=L} K(s)[1 - \cos(\alpha s)] ds + 2 \int_{s=L}^{s=\infty} e^{-\delta s} [1 - \cos(\alpha s)] ds \\ &= \int_{s=-L}^{s=L} K(s)[1 - \cos(\alpha s)] ds + 2e^{-\delta L} \left( \frac{1}{\delta} + \frac{\alpha \sin(\alpha L) - \delta \cos(\alpha L)}{\alpha^2 + \delta^2} \right), \end{aligned}$$

which  $\rightarrow 0$  as  $\alpha \rightarrow 0^+$ . Therefore  $\mathcal{C}_0 \rightarrow 1$  as  $\alpha \rightarrow 0^+$ , implying  $\lambda(R) \rightarrow 0$ . Therefore for sufficiently small positive  $\alpha$  there is a PTW solution, which approaches the spatially uniform oscillations in the population kinetics as  $\alpha \rightarrow 0^+$ . This is illustrated by the top row of panels in Figure 1.

Rewriting the integral in the definition of  $\mathcal{C}_0$  using the integration variable  $s\alpha$  shows immediately that  $\mathcal{C}_0 \rightarrow 0$  as  $\alpha \rightarrow \infty$ . Moreover  $\mathcal{C}_0$  is a continuous function of  $\alpha$ . Therefore if  $\lambda(0) < 1$ , there must be at least one  $\alpha > 0$  for which  $\mathcal{C}_0 = 1 - \lambda(0)$ , implying that  $R = 0$ . This is illustrated by the left-hand column of panels in Figure 1. The top hat kernel discussed in section 3.4 provides an example for which there are multiple  $\alpha$  values for which  $R = 0$ . A zero amplitude endpoint of a PTW family is a standard feature for (1.1), corresponding to a Hopf bifurcation in the traveling wave ODEs. In fact, branches of PTW solutions of reaction-diffusion equations must end either at such a Hopf bifurcation point, or at infinity, or at a homoclinic solution of the traveling wave ODEs. However, for (1.4) there is an additional possibility. If  $\lambda(0) > 1$ , then there are PTW solutions for all sufficiently large values of  $\alpha$ , and as  $\alpha \rightarrow \infty$  the PTWs approach a singularity in which the speed and spatial period of the waves  $\rightarrow 0$ , with their amplitude remaining finite and nonzero. This is illustrated by the right-hand column of panels in Figure 1. The limiting (singular) PTW form is not differentiable, which would not be permitted for reaction-diffusion equations, but is allowable for (1.4) provided that the wave speed  $\rightarrow 0$ .

For partial differential equations, families of PTWs typically subdivide into solutions that are stable and unstable as solutions of the original model equations. Wave stability is a key issue in applications where a given set of boundary and initial conditions selects a particular member of the PTW family [42, 43]. As parameters are varied, the selected PTW can lose stability, often heralding the onset of spatiotemporal chaos [35, 44, 45]. Following Kopell and Howard’s [12] work on (1.1), I will begin my investigation of stability by determining the conditions for PTW solutions of (1.4) to be “Eckhaus stable,” i.e., stable to perturbations of sufficiently small wavenumber. This is clearly a necessary but not sufficient condition for stability; however, the condition is relatively easy to obtain since it requires only Taylor series expansion of the eigenvalue for small wavenumbers. In the remainder of this section I will derive a condition for Eckhaus stability. The investigation of whether Eckhaus stability implies stability is much more difficult, and I will consider this only for particular dispersal kernels. Specifically, in sections 3.2 and 3.3 I will prove that Eckhaus stability implies stability for the specific cases of Laplace and Gaussian kernels, with  $\lambda(\cdot)$  and  $\omega(\cdot)$  given by (1.2).

Linearizing (2.1) about the PTW  $r = R, \theta = \alpha x + \omega(R)t$  and substituting  $(r - R, \theta -$

$\alpha x - \omega(R)t = (r_0, \theta_0)e^{i\xi x + \Lambda t}$  gives

$$(2.3) \quad \begin{aligned} [-\Lambda + \mathcal{I} + \lambda(R) - 1 + R\lambda'(R)] r_0 - iR\mathcal{J}\theta_0 &= 0, \\ [\omega'(R) + i\mathcal{J}/R] r_0 + [-\Lambda + \mathcal{I} + \lambda(R) - 1] \theta_0 &= 0, \end{aligned}$$

where

$$(2.4) \quad \mathcal{I} = \int_{s=-\infty}^{\infty} K(s) \cos(\xi s) \cos(\alpha s) ds, \quad \mathcal{J} = \int_{s=-\infty}^{\infty} K(s) \sin(\xi s) \sin(\alpha s) ds.$$

Note that (2.3) depends on the kernel  $K(\cdot)$  being even. The condition for nontrivial solutions is therefore a quadratic in the eigenvalue  $\Lambda$ , whose solutions are

$$(2.5) \quad \Lambda_{\pm} = \mathcal{I} + \lambda(R) - 1 + \frac{1}{2}R\lambda'(R) \pm \left\{ \frac{1}{4}R^2\lambda'(R)^2 + \mathcal{J}^2 - iR\omega'(R)\mathcal{J} \right\}^{1/2}.$$

This formula simplifies considerably when  $\xi = 0$  and in the limit as  $\xi \rightarrow \infty$ . In the latter case, the Riemann–Lebesgue lemma implies that  $\mathcal{I} = \mathcal{J} = 0$ , so that  $\Lambda_- = \lambda(R) - 1 + R\lambda'(R)$  and  $\Lambda_+ = \lambda(R) - 1$ . When the wavenumber  $\xi = 0$ ,  $\Lambda_- = R\lambda'(R) < 0$  and  $\Lambda_+ = 0$ . The zero eigenvalue reflects the neutral stability of the PTW to translations. The PTW will be Eckhaus stable if and only if  $\text{Re } \Lambda_+ < 0$  for  $|\xi|$  sufficiently small but nonzero. Expanding (2.5) in a Taylor series in  $\xi$  gives (after much algebraic manipulation)

$$\text{Re } \Lambda_+ = - \left[ \frac{1}{2}\mathcal{C}_2 + \frac{(\omega'(R)^2 + \lambda'(R)^2)\mathcal{S}_1^2}{R\lambda'(R)^3} \right] \xi^2 + O(\xi^4).$$

This implies the first part of the following.

**Theorem 2.1.** (i) *The PTW  $r = R$ ,  $\theta = \alpha x + \omega(R)t$  is stable to perturbations with sufficiently small wavenumber  $\Leftrightarrow$*

$$(2.6) \quad \frac{1}{2}R\lambda'(R)\mathcal{C}_2 + \mathcal{S}_1^2 \left[ 1 + (\omega'(R)/\lambda'(R))^2 \right] < 0.$$

(ii) *If  $\lambda(0) \leq 1$ , then PTWs with sufficiently small  $R$  are unstable.*

(iii) *PTWs with sufficiently small  $\alpha$  are stable.*

Note that the condition  $\lambda(0) \leq 1$  in (ii) is exactly the condition that the PTW family includes the trivial wave  $R = 0$ , either for a finite  $\alpha$  ( $\lambda(0) < 1$ ) or as the limiting form as  $\alpha \rightarrow \infty$  ( $\lambda(0) = 1$ ). Intuitively (ii) corresponds to the inheritance of instability from the equilibrium point  $u = v = 0$ , while (iii) corresponds to the inheritance of stability from the spatially homogeneous oscillation  $u = \cos \omega(0)t$ ,  $v = \sin \omega(0)t$ . Note that condition (2.6) is very similar to condition (1.3) for PTW stability in (1.1). However, no formal link between the conditions is possible because there is no form of the kernel for which (1.4) reverts to (1.1). A special case of (2.6) was derived previously by García-Morales, Hölzel, and Krischer [30] as a prelude to a study of complex spatiotemporal patterns in the nonlocal complex Ginzburg–Landau equation.

*Proof of (ii), (iii).* Substituting  $R = 0$  into (2.6) immediately implies instability, and (ii) follows by continuity. For (iii), one cannot use (2.6) since this can only provide a necessary

condition for stability. Instead I return to (2.5). For  $\alpha = 0$ , (1.5) and (2.2) imply that  $\lambda(R) = 0$ , and substituting  $\alpha = 0$  into (2.5) gives two real eigenvalues with

$$\Lambda_- \leq \Lambda_+ = -1 + \int_{s=-\infty}^{s=\infty} K(s) \cos(\xi s) ds.$$

Now

$$(2.7) \quad \left| \int_{s=-\infty}^{s=\infty} K(s) \cos(\xi s) ds \right| \leq \int_{s=-\infty}^{s=\infty} K(s) |\cos(\xi s)| ds \leq \int_{s=-\infty}^{s=\infty} K(s) ds = 1.$$

Moreover for any given  $\xi \neq 0$ ,  $|\cos(\xi s)| < 1$  except at a discrete set of  $s$  values, implying that the second inequality in (2.7) is strict unless  $\xi = 0$ . Therefore the PTW is stable when  $\alpha = 0$ , and (iii) follows by continuity. ■

### 3. Three examples of periodic traveling wave families.

**3.1. Introduction to the three examples.** Having established some general results on the existence and stability of PTWs, I will now present a more detailed study for three particular cases. I consider the following three kernels:

$$(3.1) \quad \text{Laplace kernel: } K(s) = (1/2a) \exp(-|s|/a).$$

$$(3.2) \quad \text{Gaussian kernel: } K(s) = (1/a\sqrt{\pi}) \exp(-s^2/a^2).$$

$$(3.3) \quad \text{Top hat kernel: } K(s) = (1/2a) \text{ if } |s| < a, \quad 0 \text{ otherwise.}$$

The first two examples are chosen because they are probably the most widely used kernels in ecological and epidemiological models (e.g., [41, 46, 47]). The top hat kernel is included primarily for mathematical reasons: it provides an example for which the PTW family differs significantly from that for (1.1). In each case I will consider only  $\lambda(\cdot)$  and  $\omega(\cdot)$  with the form (1.2). This is by far the most important example of  $\lambda$ - $\omega$  kinetics, being the normal form close to a standard supercritical Hopf bifurcation.

Before proceeding, it may be helpful to make a comment concerning the possibility of rescaling (1.4), (1.2) to remove parameters in (1.2). The parameter  $\omega_0$  only affects the frequency of the temporal oscillations in  $u$  and  $v$ , and it can be removed via the substitution  $u_{new} + iv_{new} = (u + iv)e^{-i\omega_0 t}$ , which is known as a “gauge transformation” in the physics literature. The parameter  $\lambda_1$  can also be removed via the substitutions  $u_{new} = \lambda_1^{1/2} u$ ,  $v_{new} = \lambda_1^{1/2} v$ ,  $\omega_{1,new} = \lambda_1 \omega_1$ . However, the parameters  $\lambda_0$  and  $\omega_1$  cannot be removed via rescaling. This contrasts with the situation for (1.1), (1.2), for which  $\lambda_0$  can also be removed by rescaling the spatial coordinate: this is not possible for (1.4), (1.2). Therefore the study of PTWs for (1.4), (1.2) involves a parameter space of higher dimensionality than for (1.1), (1.2). In the following analysis I will retain all four of the parameters in (1.2) to emphasize the generality of my results.

I conclude this subsection by proving a result that I will use for both the Laplace and Gaussian kernels.

**Lemma 3.1.** *When  $\lambda(\cdot)$  and  $\omega(\cdot)$  have the form (1.2), the PTW  $r = R$ ,  $\theta = \alpha x + \omega(R)t$  is stable as a solution of (1.4) if the following conditions hold:*

- (i)  $\mathcal{I}$  is a decreasing function of  $\xi > 0$ .
- (ii)  $(C_0 - \mathcal{I})/\mathcal{J}^2$  is an increasing function of  $\xi > 0$ .
- (iii) Condition (2.6) holds.

Here  $\mathcal{I}$  and  $\mathcal{J}$  are defined in (2.4) and  $C_0$  is defined in (1.5).

Note that conditions (i)–(iii) are sufficient for stability, but not necessary.

*Proof.* Suppose that (i)–(iii) hold. Since the kernel  $K(\cdot)$  is exponentially bounded, it is straightforward to expand  $\mathcal{I}$  and  $\mathcal{J}$  in Taylor series for small  $\xi$ :

$$\mathcal{I} = C_0 - \frac{1}{2}C_2\xi^2 + O(\xi^4), \quad \mathcal{J} = \mathcal{S}_1\xi + O(\xi^3).$$

Therefore as  $\xi \rightarrow 0^+$

$$\frac{C_0 - \mathcal{I}}{\mathcal{J}^2} \rightarrow \frac{C_2}{2\mathcal{S}_1^2} > \frac{1}{2\lambda_1 R^2} \left(1 + \frac{\omega_1^2}{\lambda_1^2}\right)$$

using (iii). Therefore (ii)  $\Rightarrow$

$$(3.4) \quad \frac{C_0 - \mathcal{I}}{\mathcal{J}^2} > \frac{1}{2\lambda_1 R^2} \left(1 + \frac{\omega_1^2}{\lambda_1^2}\right)$$

for all  $\xi > 0$ . I now define

$$(3.5) \quad \widehat{\mathcal{I}} = (\mathcal{I} + \lambda_0 - 1)/(\lambda_1 R^2) \quad \text{and} \quad \widehat{\mathcal{J}} = \mathcal{J}/(\lambda_1 R^2);$$

recall that  $\lambda_1 R^2 = C_0 + \lambda_0 - 1$ . Then

$$(3.6) \quad \frac{1 - \widehat{\mathcal{I}}}{\widehat{\mathcal{J}}^2} = \lambda_1 R^2 (C_0 - \mathcal{I})/\mathcal{J}^2 > \frac{1}{2} \left(1 + \frac{\omega_1^2}{\lambda_1^2}\right)$$

using (3.4). Also (i)  $\Rightarrow \mathcal{I} \leq \mathcal{I}|_{\xi=0} = C_0$  for all  $\xi > 0$ ,  $\Rightarrow \widehat{\mathcal{I}} \leq (C_0 + \lambda_0 - 1)/(\lambda_1 R^2) = 1$ , using (2.2). Together these imply

$$(3.7) \quad \begin{aligned} (2 - \widehat{\mathcal{I}})^2 \left[ \frac{(3 - \widehat{\mathcal{I}})(1 - \widehat{\mathcal{I}})}{\widehat{\mathcal{J}}^2} - 1 \right] &> \omega_1^2/\lambda_1^2 \\ &\Rightarrow (\omega_1^2/\lambda_1^2)\widehat{\mathcal{J}}^2 < (2 - \widehat{\mathcal{I}})^2 \left[ (2 - \widehat{\mathcal{I}})^2 - (1 + \widehat{\mathcal{J}}^2) \right] \\ &\Rightarrow 4(\omega_1^2/\lambda_1^2)\widehat{\mathcal{J}}^2 + (1 + \widehat{\mathcal{J}}^2)^2 < \left[ 2(2 - \widehat{\mathcal{I}})^2 - (1 + \widehat{\mathcal{J}}^2) \right]^2 \\ &= \left[ \widehat{\mathcal{I}}^2 - \widehat{\mathcal{J}}^2 + (1 - \widehat{\mathcal{I}})(7 - \widehat{\mathcal{I}}) \right]^2. \end{aligned}$$

Now (3.6)  $\Rightarrow (1 - \widehat{\mathcal{I}})/\widehat{\mathcal{J}}^2 > \frac{1}{2}$ . Also  $7 - \widehat{\mathcal{I}} \geq 6$ . Therefore

$$\begin{aligned} \frac{(7 - \widehat{\mathcal{I}})(1 - \widehat{\mathcal{I}}) + \widehat{\mathcal{I}}^2}{\widehat{\mathcal{J}}^2} &\geq \frac{(7 - \widehat{\mathcal{I}})(1 - \widehat{\mathcal{I}})}{\widehat{\mathcal{J}}^2} > 3 \\ &\Rightarrow \widehat{\mathcal{I}}^2 - \widehat{\mathcal{J}}^2 + (1 - \widehat{\mathcal{I}})(7 - \widehat{\mathcal{I}}) > 2\widehat{\mathcal{J}}^2 \geq 0. \end{aligned}$$

Therefore the inequality in (3.7) is preserved when taking the square root of both sides, giving

$$(3.8) \quad (2 - \widehat{\mathcal{I}})^2 \geq \frac{1}{2} \left[ 1 + \widehat{\mathcal{J}}^2 + \sqrt{4(\omega_1/\lambda_1)^2 \widehat{\mathcal{J}}^2 + (1 + \widehat{\mathcal{J}}^2)^2} \right].$$

Since  $\widehat{\mathcal{I}} \leq 1$ , the inequality in (3.8) is also preserved when taking the square root of both sides. Undoing the substitutions (3.5) and using the identity  $\text{Re}(p + iq)^{1/2} = [\frac{1}{2}(\sqrt{p^2 + q^2} + p)]^{1/2}$ , this implies  $\text{Re } \Lambda_+ < 0$  for all  $\xi > 0$ . Since  $\text{Re } \Lambda_- \leq \text{Re } \Lambda_+$  with both being even functions of  $\xi$ , it follows that the PTW is stable. ■

**3.2. Periodic traveling waves for the Laplace kernel with (1.2).** For the Laplace kernel (3.1) with (1.2), (2.2) gives  $\lambda_0 - \lambda_1 R^2 = a^2 \alpha^2 / (1 + a^2 \alpha^2)$ . Therefore the PTW amplitude  $R$  is a strictly decreasing function of  $\alpha$ . As always, the case  $\alpha = 0$  corresponds to the spatially homogeneous oscillations of the population kinetics ( $R = \sqrt{\lambda_0/\lambda_1}$ ). If  $\lambda_0 < 1$ , then the wave family terminates at  $\alpha = \alpha_L^* \equiv [\lambda_0/(1 - \lambda_0)]^{1/2}/a$  when the wave amplitude  $R = 0$ . If  $\lambda_0 \geq 1$ , then there are PTWs for all values of  $\alpha$ , and the speed and spatial period of the wave  $\rightarrow 0$  as the end of the wave family is approached. These two cases are illustrated in the two columns of Figure 1.

The condition (2.6) for Eckhaus stability is easily calculated as

$$(3.9) \quad H_L(\alpha) \equiv \left( \frac{1}{a^2 \alpha^2} - 3 \right) [1 + (\lambda_0 - 1)(1 + a^2 \alpha^2)] > 2 \left( 1 + \frac{\omega_1^2}{\lambda_1^2} \right).$$

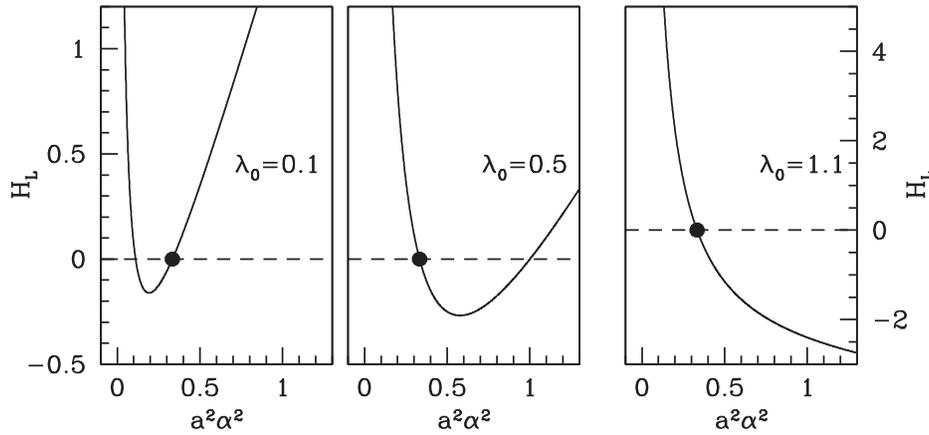
Figure 2 illustrates the form of  $H_L(\alpha)$  for different values of  $\lambda_0$ . For all  $\lambda_0 > 0$ ,  $H_L \rightarrow \infty$  as  $\alpha \rightarrow 0^+$ , and  $H_L(1/a\sqrt{3}) = 0$ . When  $\lambda_0 \geq 1$ ,  $H_L$  is a decreasing function of  $\alpha$ . For  $\lambda_0 \in (\frac{1}{4}, 1)$ ,  $H_L$  is decreasing on  $0 < \alpha < 1/(a\sqrt{3})$ , beyond which it has a local minimum, passing through zero again at  $\alpha = \alpha_L^*$  (defined above). The significance of  $\lambda_0 = \frac{1}{4}$  is that at this value  $\alpha_L^* = 1/(a\sqrt{3})$ , and  $H_L(\alpha)$  then has a double root (local minimum) at  $\alpha = \alpha_L^* = 1/(a\sqrt{3})$ . For  $\lambda_0 \in (0, \frac{1}{4})$ ,  $H_L$  is decreasing on  $0 < \alpha < \alpha_L^* < 1/(a\sqrt{3})$ . Recall that for  $\lambda_0 < 1$ ,  $\alpha_L^*$  is the value of  $\alpha$  at which  $R = 0$ , with  $\alpha < \alpha_L^*$  being a requirement for a PTW. Therefore for any given values of  $\lambda_0, \lambda_1, \omega_0, \omega_1$ , and  $a$  there is a unique value of  $\alpha \leq 1/(a\sqrt{3})$  above / below which PTWs are stable / unstable. In particular all waves with  $\alpha > 1/(a\sqrt{3})$  are unstable, irrespective of the values of  $\lambda_0, \lambda_1, \omega_0$ , and  $\omega_1$ .

I will now consider the stability of PTWs for the Laplace kernel. My key result is that waves that are stable to perturbations of sufficiently small wavenumber are in fact stable to perturbations of all wavenumbers. The following is a formal statement of this result.

**Theorem 3.2.** *When  $K(\cdot)$  is given by (3.1) and  $\lambda(\cdot)$  and  $\omega(\cdot)$  are given by (1.2), the PTW  $r = R, \theta = \alpha x + \omega(R)t$  is stable as a solution of (1.4) if and only if (3.9) holds.*

*Proof.* I will prove this result using Lemma 3.1. Since (3.9) is the condition (2.6) for Eckhaus stability, it is sufficient to prove that conditions (i) and (ii) of Lemma 3.1 hold whenever (3.9) holds. Evaluating the necessary integrals gives  $\mathcal{C}_0 = 1/(1 + a^2 \alpha^2)$  and

$$\mathcal{I} = \left[ \frac{\frac{1}{2}}{1 + a^2(\xi - \alpha)^2} + \frac{\frac{1}{2}}{1 + a^2(\xi + \alpha)^2} \right], \quad \mathcal{J} = \left[ \frac{\frac{1}{2}}{1 + a^2(\xi - \alpha)^2} - \frac{\frac{1}{2}}{1 + a^2(\xi + \alpha)^2} \right].$$



**Figure 2.** An illustration of the form of  $H_L(\alpha)$  for different values of  $\lambda_0$ . The qualitative form differs in the three cases  $\lambda_0 < \frac{1}{4}$ ,  $\lambda_0 \in (\frac{1}{4}, 1)$ , and  $\lambda_0 > 1$ . The solid dot indicates  $\alpha = 1/(a\sqrt{3})$ . The vertical axis limits for  $\lambda_0 = 0.5$  are the same as for  $\lambda_0 = 0.1$ . The key message of the figure is that  $H_L$  attains each positive value exactly once on  $(0, 1/a\sqrt{3})$ . This result also applies in the special cases  $\lambda_0 = \frac{1}{4}$  and  $\lambda_0 = 1$ . When  $\lambda_0 = \frac{1}{4}$ ,  $H_L$  has a double root at  $\alpha = 1/(a\sqrt{3})$ . The case  $\lambda_0 = 1$  differs from  $\lambda_0 > 1$  in that  $H_L \rightarrow -3$  in the former case and  $H_L \rightarrow -\infty$  in the latter as  $\alpha \rightarrow \infty$ . In both cases,  $H_L(\cdot)$  is strictly decreasing on  $(0, \infty)$ .

I consider first condition (i).

$$(3.10) \quad d\mathcal{I}/d\xi = \frac{2a^2\xi [(1 + a^2\alpha^2)(3a^2\alpha^2 - 1) - 2(1 + a^2\alpha^2)a^2\xi^2 - a^4\xi^4]}{(1 + a^2\xi^2 + a^2\alpha^2 - 2a^2\xi\alpha)^2 (1 + a^2\xi^2 + a^2\alpha^2 + 2a^2\xi\alpha)^2}.$$

My discussion of the form of  $H_L$  implies that  $\alpha \leq 1/(a\sqrt{3})$  whenever (3.9) holds. Hence  $d\mathcal{I}/d\xi < 0$  for all  $\xi > 0$ .

For condition (ii) of Lemma 3.1, a considerable amount of algebraic simplification yields

$$\frac{d}{d\xi} \left( \frac{C_0 - \mathcal{I}}{\mathcal{J}^2} \right) = \frac{\xi \left[ 3a^4\xi^4 + \frac{2}{3}\{4 + 5(1 - 3a^2\alpha^2)\}a^2\xi^2 + 7(a^2\alpha^2 - \frac{3}{7})^2 + \frac{12}{7} \right]}{2a^2(1 + a^2\alpha^2)},$$

which is  $> 0$  whenever  $\alpha < 1/(a\sqrt{3})$  and  $\xi > 0$ . ■

**3.3. Periodic traveling waves for the Gaussian kernel with (1.2).** For the Gaussian kernel (3.2) with (1.2), (2.2) gives  $\lambda_0 - \lambda_1 R^2 = 1 - \exp(-\alpha^2 a^2/4)$ . Therefore, as for the Laplace kernel, the PTW amplitude  $R$  is a strictly decreasing function of  $\alpha$  with  $\alpha = 0$  corresponding to the spatially homogeneous oscillations of the population kinetics ( $R = \sqrt{\lambda_0/\lambda_1}$ ). If  $\lambda_0 < 1$ , then the wave family terminates at  $\alpha = (2/a)[\log(1/(1 - \lambda_0))]^{1/2}$  when  $R = 0$ , while if  $\lambda_0 \geq 1$ , it extends to  $\alpha = \infty$ , with the speed and spatial period of the wave  $\rightarrow 0$  as the endpoint is approached.

In the remainder of this subsection, I will prove that for this example Eckhaus stability implies stability.

**Theorem 3.3.** When  $K(\cdot)$  is given by (3.2) and  $\lambda(\cdot)$  and  $\omega(\cdot)$  are given by (1.2), the PTW

$r = R$ ,  $\theta = \alpha x + \omega(R)t$  is stable as a solution of (1.4) if and only if

$$(3.11) \quad [1 + (\lambda_0 - 1) \exp(\alpha^2 a^2/4)] \cdot [2/(\alpha^2 a^2) - 1] > 1 + \omega_1^2/\lambda_1^2.$$

Note that when  $\alpha$  is such that a PTW exists,  $1 + (\lambda_0 - 1) \exp(\alpha^2 a^2/4) \geq 0$ , and hence the left-hand side of (3.11) is positive if and only if  $\alpha < \sqrt{2}/a$ . Moreover the left-hand side of (3.11) is strictly decreasing for  $\alpha \in (0, \sqrt{2}/a)$ . Therefore the theorem implies that there is a unique value  $\alpha_G^{\text{stab}} \in (0, \sqrt{2}/a)$  such that PTWs are stable if and only if  $\alpha < \alpha_G^{\text{stab}}$ .

When proving the theorem I will use the following lemma.

**Lemma 3.4.**  $\cosh \vartheta < 125/8 \Rightarrow \cosh \vartheta < (1 + \vartheta^2/6)^3$ .

The condition  $\cosh \vartheta \leq 125/8$  affords a straightforward proof and is sufficient for my purposes, but it is unnecessarily strict: numerical calculations indicate that  $\cosh \vartheta < (1 + \vartheta^2/6)^3$  holds for  $\vartheta$  between 0 and about 8.2, while  $\cosh^{-1}(125/8) \approx 3.4$ .

*Proof.* Without loss of generality, I assume  $\vartheta \geq 0$ . Then

$$\cosh \vartheta < 125/8 \Rightarrow 5 \sinh \vartheta (\cosh \vartheta)^{2/3} - 2 \sinh \vartheta \cosh \vartheta > 0.$$

Integrating from zero gives  $3(\cosh \vartheta)^{5/3} - (\cosh \vartheta)^2 - 2 > 0$ . Dividing this inequality through by  $9(\cosh \vartheta)^{5/3}$  and then integrating from zero gives  $\frac{1}{3}\vartheta > \frac{1}{3}(\cosh \vartheta)^{-2/3} \sinh \vartheta$ . Integrating again from zero gives  $1 + \vartheta^2/6 > (\cosh \vartheta)^{1/3}$ . ■

*Proof of Theorem 3.3.* I will prove this result using Lemma 3.1. Inequality (3.11) is simply the condition (2.6) for Eckhaus stability. Therefore the theorem will follow from a proof that conditions (i) and (ii) of Lemma 3.1 hold whenever (3.11) holds. Evaluating the necessary integrals gives  $\mathcal{C}_0 = \exp(-a^2 \alpha^2/4)$  and

$$\mathcal{I} = e^{-a^2 \alpha^2/4} e^{-a^2 \xi^2/4} \cosh(\frac{1}{2} a^2 \alpha \xi), \quad \mathcal{J} = e^{-a^2 \alpha^2/4} e^{-a^2 \xi^2/4} \sinh(\frac{1}{2} a^2 \alpha \xi).$$

The proof of this theorem is considerably more difficult than that of Theorem 3.2 because of the mixture of exponential and hyperbolic functions in these expressions—the corresponding expressions for the Laplace kernel were algebraic.

*Stage 1: Condition (i) holds.*

$$d\mathcal{I}/d\xi = \frac{1}{2} a^2 \mathcal{I} [\alpha \tanh(\frac{1}{2} a^2 \xi \alpha) - \xi] \leq \frac{1}{2} a^2 \mathcal{I} [\frac{1}{2} a^2 \xi \alpha^2 - \xi]$$

since  $\mathcal{I} > 0$ . But (3.11) implies that  $a^2 \alpha^2 < 2$ , so that condition (i) of Lemma 3.1 holds.

*Stage 2: Condition (ii) holds if  $\mathcal{G} > 0$ .* Proving that condition (ii) holds is more difficult and involves some delicate inequalities. Since

$$(\mathcal{C}_0 - \mathcal{I})/\mathcal{J}^2 = e^{a^2 \alpha^2/4} e^{a^2 \xi^2/4} \mathcal{F}, \quad \text{where } \mathcal{F} = [e^{a^2 \xi^2/4} - \cosh(\frac{1}{2} a^2 \xi \alpha)] / \sinh^2(\frac{1}{2} a^2 \xi \alpha),$$

it is sufficient to prove that  $\mathcal{F}$  is an increasing function of  $\xi$  on  $\xi > 0$ . Now  $d\mathcal{F}/d\xi = \frac{1}{2} a^2 \mathcal{G} / \sinh^3(\frac{1}{2} a^2 \xi \alpha)$ , where

$$(3.12) \quad \mathcal{G} = e^{a^2 \xi^2/4} [\xi \sinh(\frac{1}{2} a^2 \xi \alpha) - 2\alpha \cosh(\frac{1}{2} a^2 \xi \alpha)] + \alpha \cosh^2(\frac{1}{2} a^2 \xi \alpha) + \alpha.$$

I will prove that  $\mathcal{G} > 0$  when  $\xi > 0$  and  $\alpha \in (0, \sqrt{2}/a)$ ; this implies that condition (ii) holds, completing the proof of the theorem.

I have been unable to find a single argument showing  $\mathcal{G}$  to be positive for all  $\xi > 0$ . Instead I will develop two arguments, holding for small and large values of  $\xi$ ; the ranges of validity of these two arguments overlap, so that the required result follows.

*Stage 3:  $\mathcal{G} > 0$  for large  $\xi$ .* I focus initially on the part of the formula (3.12) that is in square brackets:

$$(3.13) \quad \xi \sinh(\tfrac{1}{2}a^2\xi\alpha) - 2\alpha \cosh(\tfrac{1}{2}a^2\xi\alpha) = \alpha \cosh(\tfrac{1}{2}a^2\xi\alpha) [\tanh(\tfrac{1}{2}a^2\xi\alpha) \cdot \xi/\alpha - 2].$$

Now

$$\frac{d}{d\alpha} [\tanh(\tfrac{1}{2}a^2\xi\alpha) \cdot (1/\alpha)] = (1/\alpha^2) \cdot [(\tfrac{1}{2}a^2\xi\alpha)\operatorname{sech}^2(\tfrac{1}{2}a^2\xi\alpha) - \tanh(\tfrac{1}{2}a^2\xi\alpha)] < 0$$

using the inequality  $\tanh \vartheta > \vartheta \operatorname{sech}^2 \vartheta$ . (This is valid for all  $\vartheta > 0$  and is better known in the form  $\sinh 2\vartheta > 2\vartheta$ .) Therefore for  $0 < \alpha < \sqrt{2}/a$

$$[\tanh(\tfrac{1}{2}a^2\xi\alpha) \cdot (1/\alpha)] > [\tanh(\tfrac{1}{2}a^2\xi\alpha) \cdot (1/\alpha)]|_{\alpha=\sqrt{2}/a} = (a/\sqrt{2}) \tanh(a\xi/\sqrt{2}).$$

Substituting this into (3.13) gives

$$(3.14) \quad \xi \sinh(\tfrac{1}{2}a^2\xi\alpha) - 2\alpha \cosh(\tfrac{1}{2}a^2\xi\alpha) > \alpha \cosh(\tfrac{1}{2}a^2\xi\alpha) \left[ \tanh(a\xi/\sqrt{2}) \cdot a\xi/\sqrt{2} - 2 \right].$$

Substituting this into (3.12) implies

$$(3.15) \quad \begin{aligned} \mathcal{G} &> \alpha \cosh(\tfrac{1}{2}a^2\xi\alpha) \cdot [\mathcal{D}(\phi) + 2] + \alpha [\cosh(\tfrac{1}{2}a^2\xi\alpha) - 1]^2 \\ &\geq \alpha \cosh(\tfrac{1}{2}a^2\xi\alpha) [\mathcal{D}(\phi) + 2], \\ &\text{where } \phi = a\xi/\sqrt{2} \quad \text{and } \mathcal{D}(\phi) = \exp(\phi^2/2) \cdot (\phi \tanh \phi - 2). \end{aligned}$$

I now consider the form of  $\mathcal{D}(\cdot)$ , which is illustrated in Figure 3, and for which

$$\mathcal{D}'(\phi) = \tfrac{1}{2} \exp(\phi^2/2) (2 - \operatorname{sech}^2 \phi) (1 + \phi^2) [\tanh(2\phi) - 2\phi/(\phi^2 + 1)].$$

For  $\phi > 1$ ,  $2\phi/(\phi^2 + 1)$  is a decreasing function of  $\phi$  while  $\tanh(2\phi)$  is increasing; moreover  $\tanh(2\phi) < 2\phi/(\phi^2 + 1)$  at  $\phi = 1$  and  $\tanh(2\phi) > 2\phi/(\phi^2 + 1)$  for sufficiently large  $\phi$ . Therefore there is exactly one value of  $\phi > 1$ , which I denote by  $\phi_0$ , with  $\mathcal{D}'(\phi_0) = 0$ . Numerical calculation shows that  $\phi_0 \approx 1.1997$ . For  $\phi > \phi_0$ ,  $\mathcal{D}(\phi)$  is an increasing function of  $\phi$ . Moreover  $\mathcal{D}(\phi_0) < -2$ , while  $\mathcal{D}(\phi) > 0$  for sufficiently large  $\phi$ . Therefore there is exactly one value of  $\phi > \phi_0$ , which I denote by  $\phi^*$ , with  $\mathcal{D}(\phi^*) = -2$ . Hence  $\mathcal{G} > 0$  for  $\xi > \phi^* \sqrt{2}/a$ . Direct substitution into (3.15) shows that  $\mathcal{D}(\sqrt{2 \log 3}) > -2$ , implying that  $\phi^{*2}/2 < \log 3$ , a fact that I will use later in the proof. Numerical calculation shows that  $\phi^* \approx 1.463$ .

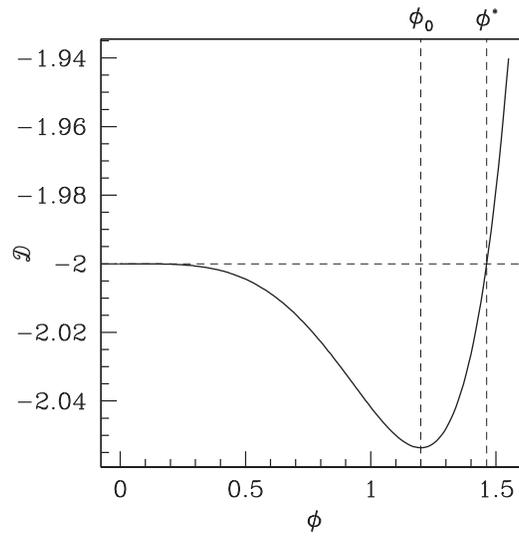


Figure 3. A numerical plot of the function  $\mathcal{D}(\cdot)$ , defined in (3.15).

Stage 4: *Small  $\xi$* :  $\mathcal{G} > 0$  for  $\alpha < \sqrt{2}/a$  if  $\mathcal{H} > 0$  for  $1 < C < 1 + y^2/3$ . Taylor series expansion shows that  $\mathcal{G} = O(\xi^4)$  as  $\xi \rightarrow 0$ , and this very slow approach to zero means that rather delicate inequalities are needed to prove that  $\mathcal{G} > 0$  for small  $\xi$ . I use Lazarević’s inequality  $(\sinh \vartheta)/\vartheta > (\cosh \vartheta)^{1/3}$ , which is valid for all  $\vartheta \neq 0$  [48, 49]. This implies

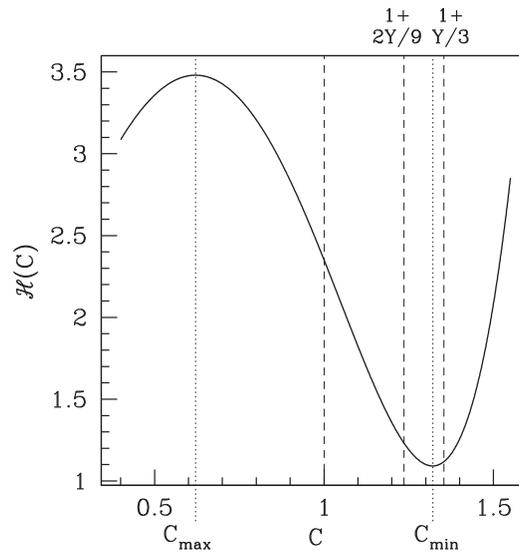
$$(3.16) \quad \mathcal{G}/\alpha > \mathcal{H} \equiv 2 \exp(y^2) [y^2 C - C^3] + C^6 + 1,$$

where  $y = a\xi/2$  and  $C = [\cosh(\frac{1}{2}a^2\xi\alpha)]^{1/3}$ . I will treat  $\mathcal{H}$  as a function of  $C$ , with  $y$  entering as a parameter. Working with  $\mathcal{H}$  rather than  $\mathcal{G}$  has two major advantages: there is no explicit dependence on  $\alpha$ , and hyperbolic functions are not explicitly involved. However, the second of these advantages is negated by the range of  $C$  over which  $\mathcal{H}$  must be considered: since  $0 < \alpha < \sqrt{2}/a$ , I must consider  $1 < C < [\cosh(\sqrt{2}y)]^{1/3}$ . To overcome this, I will consider instead a range of  $C$  whose upper limit depends algebraically on  $y$ , but which is larger than  $[\cosh(\sqrt{2}y)]^{1/3}$ . To do this I will make use of Lemma 3.4. I am restricting attention to  $\xi < \phi^* \sqrt{2}/a \Rightarrow y < \phi^*/\sqrt{2}$ . Therefore  $\cosh(\sqrt{2}y) < \cosh(\phi^*) < 125/8$ , and hence Lemma 3.4 implies  $\cosh(\sqrt{2}y) < (1 + y^2/3)^3$ . Therefore to complete the proof, it is sufficient to show that  $\mathcal{H}(C) > 0$  for all  $C \in (1, 1 + y^2/3)$  for  $y \in (0, \phi^*/\sqrt{2})$ .

Stage 5: *The form of  $\mathcal{H}(C)$* . I now consider the form of  $\mathcal{H}(C)$ , which is a hexic polynomial whose coefficients depend on  $y$ . Figure 4 shows the typical form of  $\mathcal{H}(\cdot)$ . For notational simplicity I write  $Y = y^2$ . Then

$$\mathcal{H}(C) = C^6 - 2e^Y C^3 + 2Ye^Y C + 1 \quad \Rightarrow \quad \mathcal{H}'(C) = 6C^5 - 6e^Y C^2 + 2Ye^Y.$$

Evaluating  $\mathcal{H}''(C)$  and  $\mathcal{H}'''(C)$  shows that  $\mathcal{H}'(C)$  has two turning points: a local maximum at  $C = 0$  and a local minimum at  $C = (\frac{2}{5}e^Y)^{1/3}$ . Moreover  $\mathcal{H}'(0) > 0$  and  $\mathcal{H}'((\frac{2}{5}e^Y)^{1/3}) < 0$  for all  $Y > 0$ . Therefore  $\mathcal{H}'(C)$  has exactly two zeros on  $C > 0$ ,  $C_{min}$  and  $C_{max}$  say, which correspond, respectively, to a local minimum and a local maximum of  $\mathcal{H}$ . The form of  $\mathcal{H}''$  implies that  $C_{max} < C_{min}$ .



**Figure 4.** A numerical plot of the function  $\mathcal{H}(\cdot)$ , defined in (3.16). The case shown is for  $y = 1.03$ ; this is just below  $\phi^*/\sqrt{2}$ , which is the largest value of  $y$  being considered in Stages 4–7 of the proof of Theorem 3.3. This relatively large value gives greater visual clarity.

**Stage 6:**  $\mathcal{H}(C) > 0$  for  $1 < C \leq 1 + \frac{2}{9}y^2$ . Taylor series expansion implies that  $C_{min} = 1 + \frac{2}{9}Y + O(Y^2)$  as  $Y \rightarrow 0$ . Motivated by this, I consider  $\mathcal{H}'(1 + \frac{2}{9}Y) = \mathcal{P}_5(Y) - \mathcal{P}_2(Y)e^Y$ . Here  $\mathcal{P}_5(\cdot)$  and  $\mathcal{P}_2(\cdot)$  are polynomials of degree 5 and 2 in which all of the coefficients are positive (details omitted for brevity). Therefore in a Taylor series expansion of  $\mathcal{H}'(1 + \frac{2}{9}Y)$  about  $Y = 0$ , the coefficients of  $Y^6$  and all higher powers must be negative. In addition, explicit calculation shows that the coefficients of  $Y^0, Y^1, \dots, Y^5$  are all negative, and thus  $\mathcal{H}'(1 + \frac{2}{9}Y) < 0$  for all  $Y > 0$ . Therefore  $C_{min} > 1 + \frac{2}{9}Y$  for all  $Y > 0$ . Moreover  $\mathcal{H}'(1) = 6 + (2Y - 6)e^Y < 0$  for  $Y \in (0, \frac{1}{2}\phi^{*2}) \Rightarrow C_{max} < 1$ . Therefore  $\mathcal{H}'(C) < 0$  for all  $C \in [1, 1 + \frac{2}{9}Y] \Rightarrow \mathcal{H}(C) > \mathcal{H}(1 + \frac{2}{9}Y)$ . I now use the fact that  $1 + (1 + \frac{2}{9}Y)^6 > 2(1 + \frac{2}{9}Y)(1 + \frac{4}{9}Y)$  for all  $Y > 0$ , which implies

$$\mathcal{H}(1 + \frac{2}{9}Y) = 1 + (1 + \frac{2}{9}Y)^6 + 2e^Y [Y - (1 + \frac{2}{9}Y)^2] (1 + \frac{2}{9}Y) > 2(1 + \frac{2}{9}Y)F_0(Y),$$

where  $F_0(Y) = 1 + \frac{4}{9}Y + e^Y(-1 + \frac{5}{9}Y - \frac{4}{81}Y^2)$ .

Now  $F_0''(Y) > 0$  for all  $Y \in (0, \frac{1}{2}\phi^{*2})$ ; also  $F_0'(0) = F_0(0) = 0$ . Therefore  $F_0(Y) > 0 \Rightarrow \mathcal{H}(1 + \frac{2}{9}Y) > 0$  for all  $Y \in (0, \frac{1}{2}\phi^{*2})$ .

**Stage 7:**  $\mathcal{H} > 0$  for  $1 + \frac{2}{9}y^2 < C < 1 + \frac{1}{3}y^2$ . It remains to show that  $\mathcal{H}(C) > 0$  for  $C \in (1 + \frac{2}{9}Y, 1 + \frac{1}{3}Y)$ . For  $C$  in this interval,

$$\mathcal{H}(C) > \widehat{\mathcal{H}}(C) \equiv C^6 - 2e^Y C^3 + 2Ye^Y(1 + \frac{2}{9}Y) + 1.$$

$\widehat{\mathcal{H}}(C)$  is a quadratic in  $C^3$  whose minimum is at  $C = e^{Y/3} > 1 + \frac{1}{3}Y$ . Therefore for  $C \in (1 + \frac{2}{9}Y, 1 + \frac{1}{3}Y)$

$$\mathcal{H}(C) > \widehat{\mathcal{H}}(1 + \frac{1}{3}Y) = \frac{1}{729}Y^4(Y^2 + 18Y + 135) + \frac{2}{27}Y^2(Y + 3)(3 - e^Y) + 2F_1(Y),$$

(3.17) where  $F_1(Y) = \frac{7}{27}Y^3 + \frac{1}{2}Y^2 + Y + 1 - e^Y$ .

Figure 5 shows a numerical plot of  $F_1$ . Now  $\frac{1}{2}\phi^{*2} < \log 3$ . Therefore for  $C \in (1 + \frac{2}{9}Y, 1 + \frac{1}{3}Y)$  and  $Y \in (0, \frac{1}{2}\phi^{*2})$ ,  $\mathcal{H}(C) > 2F_1(Y)$ . Now  $F_1''(Y) = \frac{14}{9}Y + 1 - e^Y$ , which is  $> 0$  for  $Y \in (0, Y^*)$  and  $< 0$  for  $Y > Y^*$ , where  $Y^* \approx 0.827$ . Moreover Taylor series expansion shows that  $F_1'(Y) > 0$  for sufficiently small positive  $Y$ , while  $F_1'(Y) < 0$  for sufficiently large  $Y$ . Therefore there exists  $Y^{**} > Y^*$  such that  $F_1'(Y) > 0$  for  $Y \in (0, Y^{**})$  and  $< 0$  for  $Y > Y^{**}$ . Since  $F_1'(\log 3) > 0$  it follows that  $Y^{**} > \log 3$ . (Numerical calculation gives  $Y^{**} \approx 1.20$  while  $\log 3 \approx 1.10$ .) Now  $\frac{1}{2}\phi^{*2} < \log 3$ , and hence  $F_1(Y)$  is strictly increasing for  $0 < Y < \frac{1}{2}\phi^{*2}$ . Moreover Taylor series expansion shows that  $F_1(Y) > 0$  for sufficiently small  $Y$ . Therefore  $F_1(Y) > 0$  for  $Y \in (0, \frac{1}{2}\phi^{*2})$ . This implies the positivity of  $\mathcal{H}(C)$  for  $C \in (1 + \frac{2}{9}Y, 1 + \frac{1}{3}Y)$  and  $Y \in (0, \frac{1}{2}\phi^{*2})$ , which completes the proof. ■

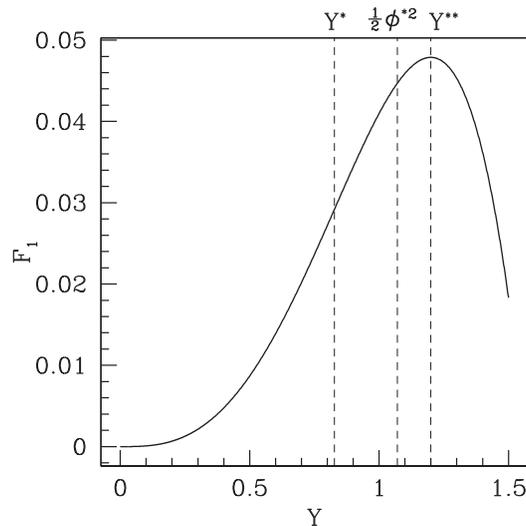
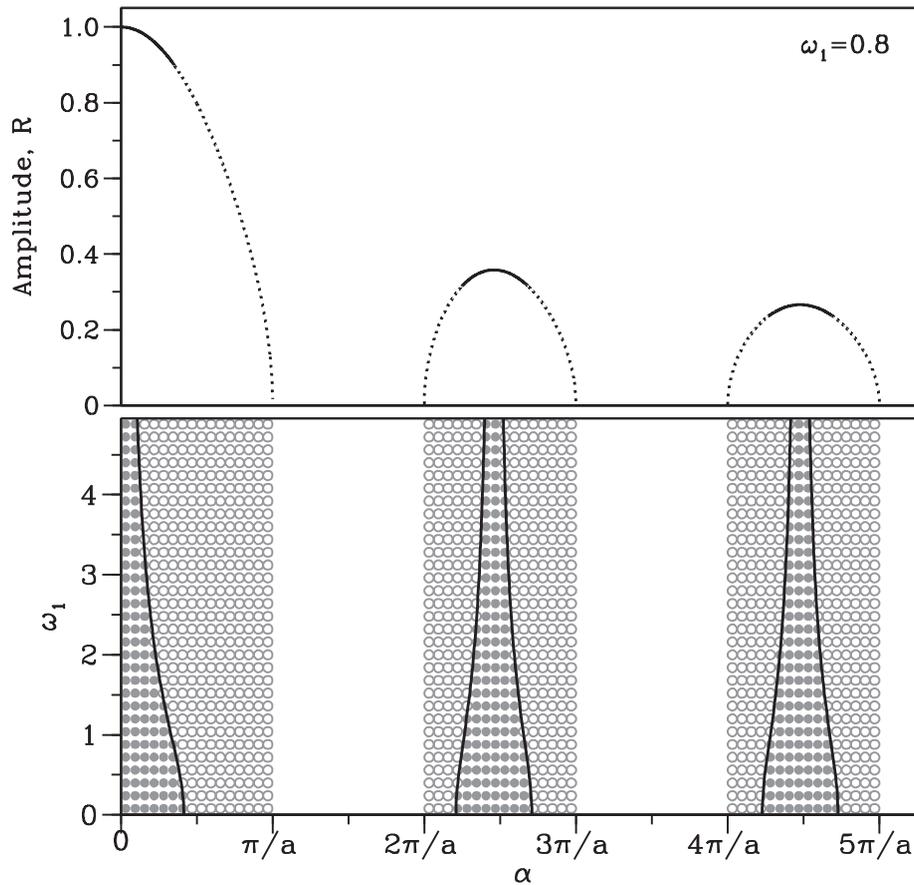


Figure 5. A numerical plot of the function  $F_1(\cdot)$ , defined in (3.17).

**3.4. Periodic traveling waves for the top hat kernel with (1.2) and  $\lambda_0 = 1$ .** For (1.4), (1.2) with both the Laplace and Gaussian kernels, the properties of PTW solutions are strongly analogous to those for the reaction-diffusion system (1.1), (1.2). Wave amplitude is a decreasing function of wavenumber, and there is a critical wavenumber that divides the wave family into stable and unstable solutions. Moreover, PTWs are stable if and only if they are Eckhaus stable. The only real qualitative difference between PTW solutions of the integrodifferential equation (1.4), (1.2) with these kernels, and those of the reaction-diffusion system (1.1), (1.2), is that in the former case with  $\lambda_0 > 1$  the wave family terminates when the spatial period  $\rightarrow 0$  at finite wave amplitude; this behavior cannot occur in reaction-diffusion equations.

However, this type of close qualitative similarity between PTW solutions of (1.4) and (1.1) does not apply for all dispersal kernels. To illustrate this I consider the example of the top hat kernel (3.3), again with  $\lambda(\cdot)$  and  $\omega(\cdot)$  given by (1.2). To simplify the algebra I will restrict attention to  $\lambda_0 = \lambda_1 = 1$ . I will show that in this case wave amplitude does not depend monotonically on wavenumber, and Eckhaus stability does not imply stability.

In this case, (2.2) gives  $R^2 = \sin(\alpha a)/(\alpha a)$ . Therefore PTWs exist for  $\alpha \in [0, \pi/a] \cup$



**Figure 6.** An illustration of the existence and Eckhaus stability of PTW solutions of (1.4) for the top hat kernel (3.3). The top panel shows wave amplitude as a function of  $\alpha$  for  $\omega_1 = 0.8$ , with solid and dotted lines indicating waves that are Eckhaus stable and Eckhaus unstable, respectively. The lower panel shows Eckhaus stability as a function of  $\alpha$  and  $\omega_1$ , with solid and open circles indicating waves that are Eckhaus stable and Eckhaus unstable, respectively. Theorem 3.5 shows that all waves with  $\alpha \geq 2\pi/a$  are unstable, irrespective of their Eckhaus stability. Numerical calculations of the spectrum suggest that for  $\alpha \leq \pi/a$ , waves are stable if and only if they are Eckhaus stable; however, I have not proved this.

$[2\pi/a, 3\pi/a] \cup [4\pi/a, 5\pi/a] \cup \dots$ , with wave amplitude being zero at  $\alpha = n\pi/a$  for all  $n \in \mathbb{Z}^+$  (illustrated in Figure 6). This nonmonotonic dependence of amplitude on wavenumber and the fact that the set of wavenumbers giving PTWs is disconnected are immediate points of difference between this PTW family and that for (1.1), (1.2).

Considering stability, the condition (2.6) for Eckhaus stability is

$$(3.18) \quad \omega_1^2 < \mathcal{T}(\tilde{\alpha}) \equiv \frac{\tilde{\alpha}^2 \tan^2 \tilde{\alpha} - \tilde{\alpha}^2 + 4\tilde{\alpha} \tan \tilde{\alpha} - 3 \tan^2 \tilde{\alpha}}{(\tan \tilde{\alpha} - \tilde{\alpha})^2},$$

where  $\tilde{\alpha} = \alpha a$ . For  $\tilde{\alpha} = (n + \frac{1}{2})\pi$  ( $n \in \mathbb{Z}$ ), the expression in (3.18) is not formally defined, but I define  $\mathcal{T}$  by continuity, as  $\tilde{\alpha}^2 - 3$ . The main result in this section is the following.

**Theorem 3.5.** *When  $K(\cdot)$  is given by (3.3) and  $\lambda(\cdot)$  and  $\omega(\cdot)$  are given by (1.2) with  $\lambda_0 = \lambda_1 = 1$ , there exist  $\tilde{\alpha}_0 \in (0, \pi)$ ,  $\tilde{\alpha}_{L,1} < \tilde{\alpha}_{U,1} \in (2\pi, 3\pi)$ ,  $\tilde{\alpha}_{L,2} < \tilde{\alpha}_{U,2} \in (4\pi, 5\pi)$ , etc., such that PTWs are stable to perturbations with sufficiently small wavenumber if and only if  $\alpha a \in [0, \tilde{\alpha}_0) \cup (\tilde{\alpha}_{L,1}, \tilde{\alpha}_{U,1}) \cup (\tilde{\alpha}_{L,2}, \tilde{\alpha}_{U,2}) \cup \dots$ . However, all PTWs with  $\alpha a \geq 2\pi$  are unstable.*

Note that this theorem holds for all values of  $\omega_1$ ; in fact my proof implies the additional result that  $\tilde{\alpha}_0$  and the  $\tilde{\alpha}_{U,n}$ 's are decreasing functions of  $|\omega_1|$ , while the  $\tilde{\alpha}_{L,n}$ 's are increasing functions of  $|\omega_1|$ . The key implication of this theorem is that Eckhaus stability does not imply stability, since PTWs with  $\alpha \in (\tilde{\alpha}_{L,n}, \tilde{\alpha}_{U,n})$  ( $n \geq 1$ ) are unstable, but are Eckhaus stable. This is another major point of difference between PTW properties for (1.4) and (1.1). Figure 7 shows numerically calculated spectra for values of  $\tilde{\alpha}$  on either side of  $\tilde{\alpha}_0$  and  $\tilde{\alpha}_{L,1}$ . In both cases there is a change in the curvature of the spectrum at the origin, i.e., a change in Eckhaus stability. This corresponds to a change in stability in the former case but not in the latter, since there is a part of the spectrum away from the origin that is in the right half of the eigenvalue complex plane for  $\tilde{\alpha}$  on either side of  $\tilde{\alpha}_{L,1}$ . Note that Theorem 3.5 makes no claim about stability for  $\alpha a \in [0, \tilde{\alpha}_0)$ . Numerical investigation suggests that all such PTWs are stable, but I have not proved this.

*Proof.* The essence of the proof is a determination of the qualitative form of  $\mathcal{T}(\cdot)$ , defined in (3.18), and I will establish this in stages. As a reference point, I show in Figure 8 a numerical plot of  $\mathcal{T}(\cdot)$ .

*Stage 1:  $\mathcal{T}$  is decreasing on  $(0, \sqrt{2})$ , with a zero.*

$$(3.19) \quad \mathcal{T}'(\tilde{\alpha}) = -2(\sin \tilde{\alpha} - \tilde{\alpha} \cos \tilde{\alpha})^{-3} [(\tilde{\alpha}^3 - 2\tilde{\alpha}) \sin \tilde{\alpha} + (\tilde{\alpha}^2 + \sin^2 \tilde{\alpha}) \cos \tilde{\alpha}].$$

Now  $\cos \vartheta \geq 1 - \frac{1}{2}\vartheta^2$  for all  $\vartheta$ , so that

$$\begin{aligned} [(\tilde{\alpha}^3 - 2\tilde{\alpha}) \sin \tilde{\alpha} + (\tilde{\alpha}^2 + \sin^2 \tilde{\alpha}) \cos \tilde{\alpha}] &\geq [(\tilde{\alpha}^3 - 2\tilde{\alpha}) \sin \tilde{\alpha} + \frac{1}{2}(\tilde{\alpha}^2 + \sin^2 \tilde{\alpha})(2 - \tilde{\alpha}^2)] \\ &= (1 - \frac{1}{2}\tilde{\alpha}^2)(\tilde{\alpha} - \sin \tilde{\alpha})^2 > 0 \text{ for } \tilde{\alpha} \in (0, \sqrt{2}). \end{aligned}$$

Also  $\sin \vartheta > \vartheta \cos \vartheta$  for  $\vartheta \in (0, \frac{1}{2}\pi) \supset (0, \sqrt{2})$ . Therefore  $\mathcal{T}'(\tilde{\alpha}) < 0$  for  $\tilde{\alpha} \in (0, \sqrt{2})$ . Moreover  $\mathcal{T}(\tilde{\alpha}) \rightarrow \infty$  as  $\tilde{\alpha} \rightarrow 0^+$ , and  $\mathcal{T}(\sqrt{2}) < 0$ , implying that  $\mathcal{T}$  has a zero on  $(0, \sqrt{2})$ . (Numerical evaluation gives  $\mathcal{T}(\sqrt{2}) \approx -0.260$ .)

*Stage 2:  $\mathcal{T}$  is negative on  $[\sqrt{2}, \pi/2)$ .* By removing the  $-\tilde{\alpha}^2$  term in the numerator of formula (3.18) for  $\mathcal{T}$ , one obtains

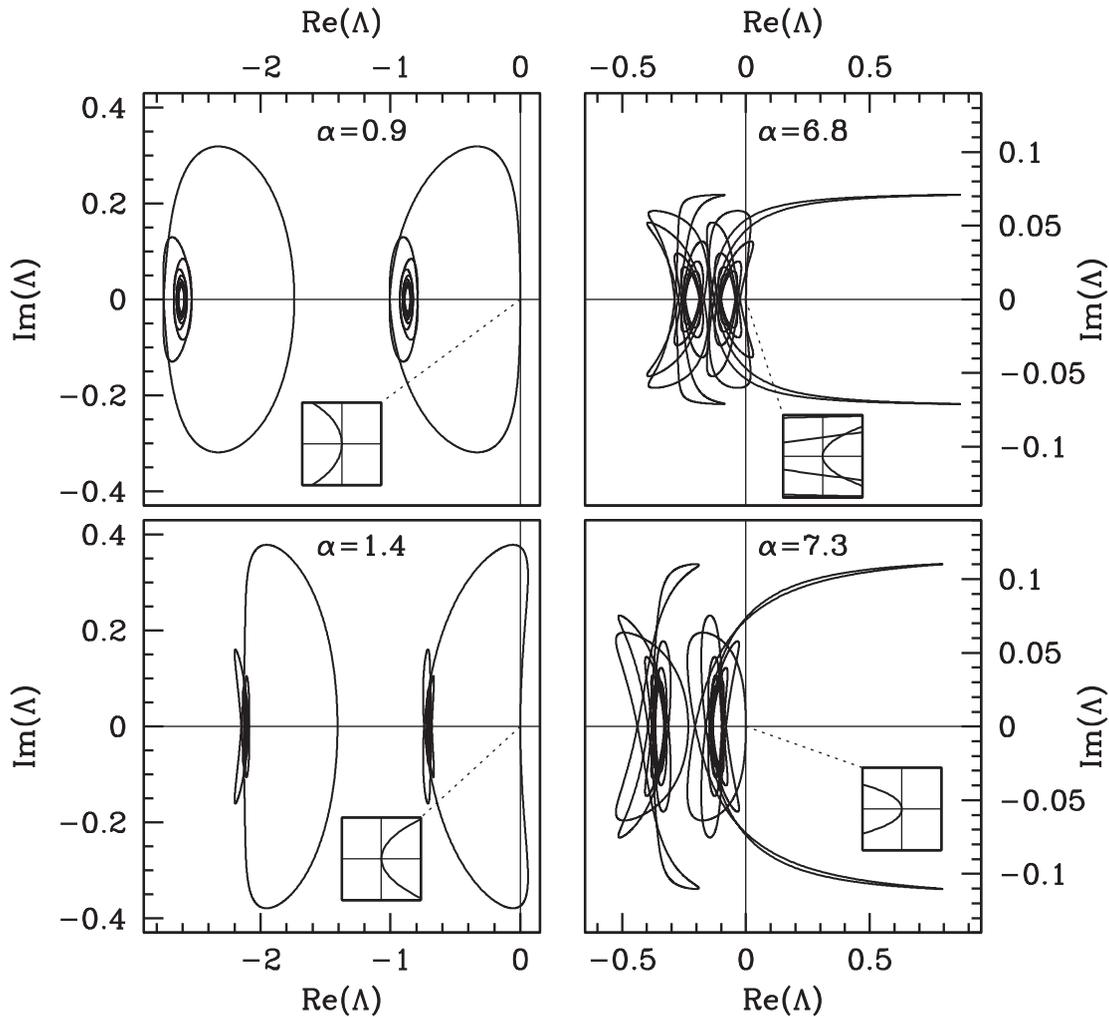
$$(3.20) \quad \mathcal{T}(\tilde{\alpha}) < \frac{\tan \tilde{\alpha}}{(\tan \tilde{\alpha} - \tilde{\alpha})^2} [4\tilde{\alpha} - (3 - \tilde{\alpha}^2) \tan \tilde{\alpha}]$$

for all  $\tilde{\alpha} > 0$ . Now

$$\frac{d}{d\vartheta} [(\frac{1}{2}\pi - \vartheta) \tan \vartheta] = \frac{1}{2} \sec^2 \vartheta [(\pi - 2\vartheta) - \sin(\pi - 2\vartheta)]$$

$> 0$  for  $\vartheta \in (0, \frac{1}{2}\pi)$ . Therefore  $\tan \vartheta > (\frac{1}{2}\pi - \sqrt{2}) \tan(\sqrt{2}) / (\frac{1}{2}\pi - \vartheta)$  for  $\vartheta \in (\sqrt{2}, \frac{1}{2}\pi)$ . Substituting this into (3.20) gives

$$\mathcal{T}(\tilde{\alpha}) < \frac{(\frac{1}{2}\pi - \sqrt{2}) \tan(\sqrt{2}) \tilde{\alpha} \tan \tilde{\alpha}}{(\tan \tilde{\alpha} - \tilde{\alpha})^2} \left[ \frac{4}{(\frac{1}{2}\pi - \sqrt{2}) \tan(\sqrt{2})} - \frac{3 - \tilde{\alpha}^2}{\tilde{\alpha}(\frac{1}{2}\pi - \tilde{\alpha})} \right].$$



**Figure 7.** Numerical plots of spectra of PTW solutions of (1.4) when  $K(\cdot)$  is the top hat kernel (3.3) with  $a = 1$  and  $\lambda(\cdot)$  and  $\omega(\cdot)$  are given by (1.2) with  $\lambda_0 = \lambda_1 = \omega_1 = 1$ . For these parameters,  $\tilde{\alpha}_0 \approx 1.04$  and  $\tilde{\alpha}_{L,1} \approx 7.11$ . The left- and right-hand columns of panels show spectra for  $\tilde{\alpha}$  on either side of  $\tilde{\alpha}_0$  and  $\tilde{\alpha}_{L,1}$ , respectively. In both cases there is a change in the curvature of the spectrum at the origin as  $\alpha$  is increased from the value in the upper panel to that in the lower panel. This corresponds to a change in stability in the left-hand panels but not in the right-hand panels, since there is a part of the spectrum away from the origin that is in the right half of the eigenvalue complex plane for  $\tilde{\alpha}$  on either side of  $\tilde{\alpha}_{L,1}$ . The curves in each panel of the figure are given by plotting  $(\text{Re}\Lambda_+, \text{Im}\Lambda_+)$  and  $(\text{Re}\Lambda_-, \text{Im}\Lambda_-)$  as  $\xi$  is varied; here  $\Lambda_{\pm}$  are defined in (2.5). The insets show detail of the behavior near the origin. The axes' ranges in the insets are  $|\text{Re}\Lambda| < 0.008$  and  $|\text{Im}\Lambda| < 0.1$  in the two left-hand panels and  $|\text{Re}\Lambda| < 0.008$  and  $|\text{Im}\Lambda| < 0.04$  in the two right-hand panels.

Differentiation shows that  $(3 - \tilde{\alpha}^2)/[\tilde{\alpha}(\frac{1}{2}\pi - \tilde{\alpha})]$  is an increasing function of  $\tilde{\alpha} \in (\sqrt{2}, \frac{1}{2}\pi)$ . Therefore

$$\mathcal{T}(\tilde{\alpha}) < \frac{(\frac{1}{2}\pi - \sqrt{2}) \tan(\sqrt{2}) \tilde{\alpha} \tan \tilde{\alpha}}{(\tan \tilde{\alpha} - \tilde{\alpha})^2} \left[ \frac{4}{(\frac{1}{2}\pi - \sqrt{2}) \tan(\sqrt{2})} - \frac{1}{\sqrt{2}(\frac{1}{2}\pi - \sqrt{2})} \right],$$

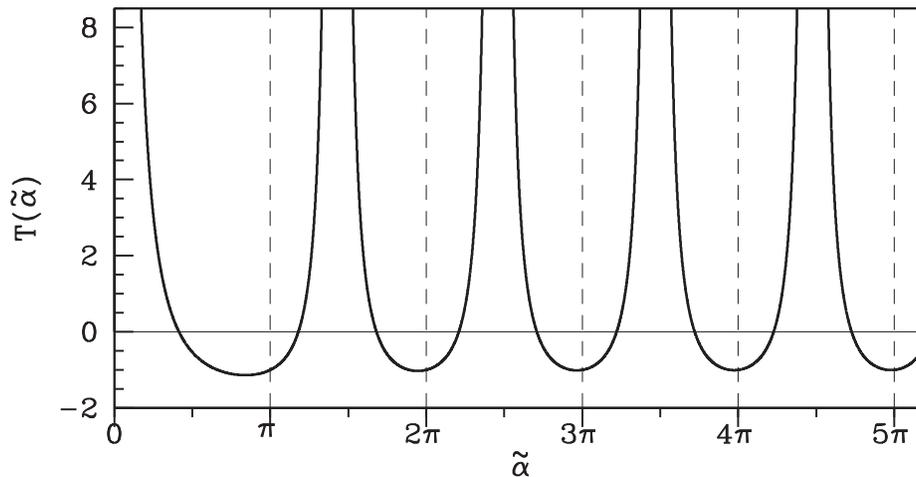


Figure 8. A numerical plot of the function  $\mathcal{T}(\cdot)$ , defined in (3.18).

which is  $< 0$  for  $\tilde{\alpha} \in [\sqrt{2}, \frac{1}{2}\pi)$ . (The part of the right-hand side of the above inequality in square brackets  $\approx -0.483$ .)

*Stage 3:  $\mathcal{T}$  is negative on  $[\pi/2, \sqrt{3}]$ .*  $\mathcal{T}(\frac{1}{2}\pi) = \frac{1}{4}\pi^2 - 3 < 0$ . For  $\tilde{\alpha} \in (\pi/2, \sqrt{3}]$ ,  $\tan \tilde{\alpha} < 0$  and  $3 - \tilde{\alpha}^2 \geq 0$ . Therefore (3.20) implies immediately that  $\mathcal{T}(\tilde{\alpha}) < 0$  on this interval.

*Stage 4:  $\mathcal{T}$  is negative on  $(\sqrt{3}, \pi)$ .* Since  $\vartheta^{-1} \tan \vartheta$  is increasing for  $\vartheta \in (0, \frac{1}{2}\pi)$ , it follows that  $\tan \vartheta < \vartheta \cdot (\nu^{-1} \tan \nu)$  whenever  $0 < \vartheta < \nu < \frac{1}{2}\pi$ . Substituting  $\vartheta = \pi - \tilde{\alpha}$  and  $\nu = \pi - \sqrt{3}$  gives  $\tan \tilde{\alpha} > \kappa \cdot (\tilde{\alpha} - \pi)$  for  $\tilde{\alpha} \in (\sqrt{3}, \pi)$ . Here  $\kappa = (\pi - \sqrt{3})^{-1} \tan(\pi - \sqrt{3}) \approx 4.36$ . Combining this inequality with (3.20) implies

$$(3.21) \quad \mathcal{T}(\tilde{\alpha}) < \frac{-\tan \tilde{\alpha}}{(\tan \tilde{\alpha} - \tilde{\alpha})^2} [\kappa \cdot (3 - \tilde{\alpha}^2)(\tilde{\alpha} - \pi) - 4\tilde{\alpha}] .$$

It is straightforward to show that the right-hand side of (3.21) is negative for all  $\tilde{\alpha} > 0$ . (For example, the part in square brackets is a cubic polynomial in  $\tilde{\alpha}$  with a negative real root and two turning points, at both of which the polynomial is negative.) Therefore  $\mathcal{T}(\tilde{\alpha}) < 0$  for  $\tilde{\alpha} \in (\sqrt{3}, \pi)$ .

Thus far, I have shown that  $\mathcal{T}$  attains any given positive value exactly once on  $(0, \pi)$ . Noting the condition (3.18) for stability, this implies the existence of  $\tilde{\alpha}_0$  as claimed in the theorem. I now consider the form of  $\mathcal{T}(\tilde{\alpha})$  for  $\tilde{\alpha} \in (2n\pi, 2n\pi + \pi)$  ( $n \in \mathbb{Z}^+$ ); recall that it is unnecessary to consider  $\tilde{\alpha} \in (2n\pi - \pi, 2n\pi)$  because there are then no PTW solutions.

*Stage 5:  $\mathcal{T}$  has one turning point on  $(2n\pi, 2n\pi + \pi)$ .* Equation (3.19) implies that

$$(3.22) \quad \mathcal{T}'(\tilde{\alpha}) = 0 \Leftrightarrow \tan \tilde{\alpha} = f(\tilde{\alpha}) \equiv \frac{\tilde{\alpha}^2 + \sin^2 \tilde{\alpha}}{2\tilde{\alpha} - \tilde{\alpha}^3} .$$

Since I am considering only values of  $\tilde{\alpha} > \sqrt{2}$ ,  $f(\tilde{\alpha}) < 0$  and thus (3.22) cannot hold for  $\tilde{\alpha} \in (2n\pi, 2n\pi + \frac{1}{2}\pi]$ . Now  $f(2n\pi + \frac{1}{2}\pi)$  is finite, while  $\tan \tilde{\alpha} \rightarrow -\infty$  as  $\tilde{\alpha} \rightarrow (2n\pi + \frac{1}{2}\pi)^+$ , and  $f(2n\pi + \pi) < \tan(2n\pi + \pi) = 0$ . Therefore  $f$  must have one or more zeros on this interval.

To prove that there is only one zero, I consider

$$\begin{aligned}
 f'(\tilde{\alpha}) &= (2\tilde{\alpha} - \tilde{\alpha}^3)^{-2} [\tilde{\alpha}^4 - \tilde{\alpha}^3 \sin(2\tilde{\alpha}) + \tilde{\alpha}^2(2 + 3 \sin^2 \tilde{\alpha}) + 2\tilde{\alpha} \sin(2\tilde{\alpha}) - 2 \sin^2 \tilde{\alpha}] \\
 &< (2\tilde{\alpha} - \tilde{\alpha}^3)^{-2} [\tilde{\alpha}^4 + 2\tilde{\alpha}^3 + 5\tilde{\alpha}^2 + 4\tilde{\alpha}] \\
 &< (2\tilde{\alpha} - \tilde{\alpha}^3)^{-2} [\tilde{\alpha}^4 + 2\tilde{\alpha}^4 + 5\tilde{\alpha}^4 + 4\tilde{\alpha}^4] \quad \text{since } \tilde{\alpha} > 1 \\
 &< (\frac{1}{2}\tilde{\alpha}^3)^{-2} \cdot (11\tilde{\alpha}^4) \quad \text{since } \tilde{\alpha} > 2 \Rightarrow |2 - \tilde{\alpha}^2| = \tilde{\alpha}^2 - 2 > \frac{1}{2}\tilde{\alpha}^2 \\
 &= 44\tilde{\alpha}^{-2} < 44(\frac{5}{2}\pi)^{-2} < 1.
 \end{aligned}$$

In comparison  $(d/d\tilde{\alpha})(\tan \tilde{\alpha}) \geq 1$ , so that there can be at most one solution of (3.22) on  $(2n\pi + \frac{1}{2}\pi, 2n\pi + \pi)$ . My arguments show further that the unique turning point is a local minimum.

*Stage 6: Deduction of the form of  $\mathcal{T}$  on  $(2n\pi, 2n\pi + \pi)$ .* The form of  $\mathcal{T}$  on  $(2n\pi, 2n\pi + \pi)$  is clarified by two further simple observations. First,  $\mathcal{T}(2n\pi) = \mathcal{T}(2n\pi + \pi) = -1$ , and second,  $\mathcal{T}(\tilde{\alpha}) \rightarrow +\infty$  as  $\tilde{\alpha} \rightarrow$  any root of  $\tan \tilde{\alpha} = \tilde{\alpha}$ , which occurs once in  $(2n\pi, 2n\pi + \pi)$ , at  $\tilde{\alpha} = \tilde{\alpha}_{\infty, n}$ , say. Therefore  $\mathcal{T}(\tilde{\alpha})$  increases from  $-1$  to  $+\infty$  as  $\tilde{\alpha}$  increases from  $2n\pi$  to  $\tilde{\alpha}_{\infty, n}$ . It then decreases from  $+\infty$  to a value less than  $-1$  at its local minimum, after which it increases to  $-1$  at  $2n\pi + \pi$ . It follows that  $\mathcal{T}$  attains any given positive value exactly twice on  $(2n\pi, 2n\pi + \pi)$ , once on each side of  $\tilde{\alpha}_{\infty, n}$ . This implies the existence of  $\tilde{\alpha}_{L, n}$  and  $\tilde{\alpha}_{U, n}$ , as claimed in the theorem.

*Stage 7: All PTWs with  $\tilde{\alpha} \geq 2\pi$  are unstable.* When  $\lambda(\cdot)$  and  $\omega(\cdot)$  are given by (1.2) with  $\lambda_0 = \lambda_1 = 1$ , the formula (2.5) implies

$$\text{Re}\Lambda_{\pm} = \mathcal{I} - 2R^2 \pm \left\{ \frac{1}{2} \left( R^4 + \mathcal{J}^2 + \left[ (R^4 + \mathcal{J}^2)^2 + 4\omega_1^2 R^4 \mathcal{J}^2 \right]^{1/2} \right) \right\}^{1/2},$$

where  $\mathcal{I}$  and  $\mathcal{J}$  are defined in (2.4). Therefore to prove that a PTW is unstable, it is sufficient to prove that  $\mathcal{I} - 2R^2 > 0$  for some  $\xi$ . Substituting  $\xi = \alpha$  into (2.4) with  $K(\cdot)$  given by (3.3) gives  $\mathcal{I} = (2\tilde{\alpha} + \sin 2\tilde{\alpha})/(4\tilde{\alpha})$ . Recall also that  $R^2 = \sin \tilde{\alpha}/\tilde{\alpha}$ . Therefore

$$\mathcal{I} - 2R^2 = \frac{2\tilde{\alpha} + \sin 2\tilde{\alpha} - 8 \sin \tilde{\alpha}}{4\tilde{\alpha}} \geq \frac{2\tilde{\alpha} - 9}{4\tilde{\alpha}}.$$

Therefore  $\mathcal{I} - 2R^2 > 0$  for  $\xi = \alpha$  whenever  $\tilde{\alpha} \geq 2\pi > \frac{9}{2}$ . ■

**4. Periodic traveling waves for the Cauchy kernel.** In sections 2 and 3 I have assumed that the dispersal kernel  $K(\cdot)$  is thin-tailed (i.e., exponentially bounded). However, in some ecological applications, fat-tailed kernels are more relevant [21, 40]. I will not attempt a comprehensive study of PTWs for fat-tailed kernels; this important topic is a natural area for future work. Rather, I will consider just one example, the Cauchy kernel:

$$(4.1) \quad K(s) = [\pi a (1 + s^2/a^2)]^{-1}$$

( $a > 0$ ), which is one of the most commonly used fat-tailed kernels [37, 50, 51]. Many of the arguments used in sections 2 and 3 are not valid for this kernel. In particular, the derivation of (2.6) involves taking derivatives of  $\mathcal{I}$  and  $\mathcal{J}$  with respect to  $\xi$  inside the integral signs, which is not permissible for (4.1); indeed the integral  $\mathcal{C}_2$ , which appears in (2.6), does not converge

when  $K(\cdot)$  is given by (4.1). However, formulae (2.2) and (2.5) are valid for any kernel, and I use these as the starting points for my investigation of PTW existence and stability for (4.1).

The integral  $\mathcal{C}_0$  can be evaluated explicitly, giving  $\lambda(R) = 1 - e^{-a\alpha}$ . Since  $\lambda(0) > 0$  and  $\lambda(\cdot)$  is a strictly decreasing function with a simple zero, it follows that  $R$  is a strictly decreasing function of  $\alpha$ . The case  $\alpha = 0$  corresponds to the zero of  $\lambda$ , with spatially homogeneous oscillations for  $u$  and  $v$ . If  $\lambda(0) < 1$ , then the wave family terminates at a finite value of  $\alpha$ , when  $R = 0$ . However, if  $\lambda(0) \geq 1$ , then there are PTWs for all values of  $\alpha$ , with the speed and spatial period  $\rightarrow 0$  as  $\alpha \rightarrow \infty$ . These results on wave existence correspond directly with those for thin-tailed kernels; however, this correspondence does not apply for wave stability.

Evaluating the necessary integrals gives

$$\mathcal{I} = \frac{1}{2} \left[ e^{-a|\xi-\alpha|} + e^{-a|\xi+\alpha|} \right], \quad \mathcal{J} = \frac{1}{2} \left[ e^{-a|\xi-\alpha|} - e^{-a|\xi+\alpha|} \right].$$

Substituting these into (2.5) and expanding as a Taylor series in  $\xi$  gives

$$(4.2) \quad \text{Re}\Lambda_+ = \frac{1}{2}a^2\xi^2e^{-a\alpha} \left[ 1 - \frac{2e^{-a\alpha}}{R\lambda'(R)} \left( 1 + \frac{\omega'(R)^2}{\lambda'(R)^2} \right) \right] + O(\xi^4)$$

as  $\xi \rightarrow 0$ , provided  $\alpha > 0$ . For  $\alpha = 0$ , a different expansion applies, but in fact the eigenvalues can be calculated explicitly:  $\Lambda_- < \Lambda_+ = e^{-a|\xi|} - 1$ . Therefore the limiting (spatially homogeneous) PTW with  $\alpha = 0$  is stable. However, (4.2) implies that all other PTWs are Eckhaus unstable (and hence unstable). This is quite different from the situation for thin-tailed kernels, for which Theorem 2.1(iii) implies stability for a range of small values of  $\alpha$ .

**5. Discussion.** PTWs have been detected in many ecological data sets [11]. Mathematical modeling has identified a number of potential causes for these spatiotemporal patterns, including invasions [26, 27, 52, 53, 54, 55, 56], heterogeneous habitats [9, 57, 58, 59], migration between subpopulations [60], migration driven by pursuit and evasion [61], and hostile habitat boundaries [13, 14, 62]. Each of these mechanisms selects one member of the family of PTW solutions of the model equations. Therefore a thorough investigation of the wave family is an important precursor to a detailed study of PTW occurrence in ecological models. In this paper I have undertaken the first such investigation for models in which dispersal is represented by convolution with a dispersal kernel. My results are restricted to the normal form equations close to a standard supercritical Hopf bifurcation, and to dispersal coefficients being the same for each of the interacting populations. This is clearly a very special case, and it is important to consider the prospects for extending my results in future work. The assumption of equal dispersal coefficients is mathematically convenient because it implies simple dispersal terms in the normal form equations. More generally, one would obtain ‘‘cross-dispersal’’ terms, i.e., nonlocal terms involving  $v$  in the  $u$  equation, and vice versa. The resulting analysis would be more complicated, but all of the various aspects of my approach could potentially be generalized to this case. This is directly analogous to using  $\lambda$ - $\omega$ -type reaction-diffusion systems as a stepping stone to studying the complex Ginzburg–Landau equation, which has proved highly effective (see, e.g., [63]). The assumption of a standard supercritical Hopf bifurcation is also potentially generalizable. For  $\lambda$ - $\omega$ -type reaction-diffusion equations, Ermentrout, Chen, and Chen [64] investigated wave fronts connecting PTWs and a uniform equilibrium for the

$\lambda$ - $\omega$  system corresponding to a standard subcritical Hopf bifurcation, building on earlier results for the supercritical case [42]. A similar extension of the results in this paper may be possible. However, a fundamental feature of my approach that is not amenable to extension is that of being close to a Hopf bifurcation. All of my methods rely on being able to reformulate the model equations in terms of amplitude and phase, which is only possible close to Hopf bifurcation. Even for reaction-diffusion equations, which have been actively studied for more than 40 years, the same limitation applies. For the normal form of reaction-diffusion equations close to a Hopf bifurcation, there is now a very detailed understanding of PTW solutions [12, 31, 33, 64, 65]. However, away from Hopf bifurcation there are to my knowledge almost no analytical results; the one exception concerns stability of PTWs that have very small wavenumber and are thus close to a homogeneous oscillation [66, 67]. Analytical results for the more difficult case of nonlocal dispersal are likely to be even more elusive. Instead, one must rely on numerical calculations of wave existence and stability. For reaction-diffusion equations, the analytical understanding of PTWs close to Hopf bifurcation has proved to be an invaluable reference point for such numerical work, and the same promises to be true for models with nonlocal dispersal.

A large part of this paper has concerned the subdivision of the PTW family into stable and unstable solutions. This is important because initial and/or boundary conditions may select a PTW that is either stable or unstable; in the latter case, the long-term behavior is typically spatiotemporal chaos [35, 44]. In fact, distinguishing between stable and unstable waves is only able to give a partial explanation of the spatiotemporal dynamics that result from PTW generation [65]. Unstable PTWs can themselves be subdivided according to whether the instability is absolute or convective [68, 69]. In the latter case, PTWs can be a long-term feature of model solutions, as persistent spatiotemporal transients. For example, the invasion of a prey population by predators can generate a fixed-width band of convectively unstable PTWs behind the invasion front, with spatiotemporal chaos behind the band [44, 70]. To my knowledge, the distinction between absolute and convective instability has never been investigated for integrodifferential equations, and its study for PTW solutions of models with nonlocal dispersal terms is an important area for future research.

In summary, this paper has two main messages. The first is my specific results on PTW existence for general kernels, and on PTW stability for the Laplace and Gaussian kernels. The qualitative form of the stability results for these two kernels is very similar to that for reaction-diffusion equations of  $\lambda$ - $\omega$  type. However, my second main message is that this qualitative similarity does not apply in general. In particular, Eckhaus stability does not necessarily imply stability for nonlocal dispersal, as shown by the example of the top hat kernel. And for fat-tailed kernels, waves of arbitrarily small (but nonzero) wavenumber can be unstable, as shown by the example of the Cauchy kernel. My work leaves many unanswered questions about PTWs in models with nonlocal dispersal, but it provides a starting point for the investigation of these questions.

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