TRAVELING WAVEFRONTS IN A DELAYED FOOD-LIMITED POPULATION MODEL[*]

CHUNHUA OU[†] AND JIANHONG WU[‡]

Abstract. In this paper we develop a new method to establish the existence of traveling wavefronts for a food-limited population model with nonmonotone delayed nonlocal effects. Our approach is based on a combination of perturbation methods, the Fredholm theory, and the Banach fixed point theorem. We also develop and theoretically justify Canosa's asymptotic method for the wavefronts with large wave speeds. Numerical simulations are provided to show that there exists a prominent hump when the delay is large.

Key words. traveling wave fronts, nonmonotone, nonlocal, food-limited

AMS subject classifications. 35K55, 35K57, 35R10, 92D25

DOI. 10.1137/050638011

1. Introduction. There has been some success in establishing the existence of traveling wavefronts for the reaction-diffusion equation with nonlocal delayed nonlinearity. When the nonlinearity is monotone, the existence of traveling wavefronts can be obtained by extension of the methods of the super/subsolution pair [1], [7], [29], homotopy [3], and Leray-Schauder degree [28]. Unfortunately, when the delayed nonlinearity is no longer monotone, very little has been achieved (except for the work in [9]). While one suspects that the method developed by Wu and Zou [29] and based on a nonstandard ordering could be applicable, the construction of a supersolution and subsolution pair is nontrivial, and it is almost as difficult as solving the original given equations. In this paper we develop a new approach to establish the existence of traveling wavefronts in the case when the delayed nonlinearity is nonmonotone. We shall demonstrate this approach by considering the following food-limited reaction-diffusion equation

$$(1.1) \qquad \frac{\partial u}{\partial t}(t,x) = \frac{\partial^2 u}{\partial x^2}(t,x) + u(t,x)\frac{1 - (f*u)(t,x)}{1 + \gamma(f*u)(t,x)},$$

where the parameter $\gamma > 0$, and the spatiotemporal convolution $f*u$ is defined by

$$(1.2) \qquad f*u = \int_{-\infty}^{t}\int_{-\infty}^{\infty} f(t,s,x,y)u(s,y)dyds,$$

with the kernel $f(t,s,x,y)$ satisfying the normalization condition

$$\int_{-\infty}^{t}\int_{-\infty}^{\infty} f(t,s,x,y)dyds = 1.$$

[†]Laboratory for Industrial and Applied Mathematics, Department of Mathematics and Statistics, York University, Toronto, Ontario, M3J 1P3, Canada. Current address: Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's, Canada (ou@math.mun.ca).

[‡]Laboratory for Industrial and Applied Mathematics, Department of Mathematics and Statistics, York University, Toronto, Ontario, M3J 1P3, Canada (wujh@mathstat.yorku.ca).

The simplest version of (1.1) without diffusion is the following ODE:

$$(1.3) \qquad \frac{du}{dt} = ru(t)\frac{K - u(t)}{K + \gamma u(t)},$$

where r, K, and γ are positive constants. This equation was first proposed by Smith [25] as a mathematical model for population of *Daphnia* (water flea), and a derivation of this equation is given in [23]. The equation can also be used to study the effects of environmental toxicants on aquatic populations [16].

The delayed food-limited model

$$(1.4) \qquad \frac{du}{dt} = ru(t)\frac{K - u(t - \tau)}{K + \gamma u(t - \tau)}, \quad \tau > 0,$$

has been studied recently by several authors; see [13], [17], [27], [18], and [8]. It seems that the best result for the local stability of the positive equilibrium $u = K$ is given in [27]. For the first time, the global stability of the positive equilibrium was established in [18]; see also [8] for further generalizations.

Equation (1.3) incorporating spatial dispersal was investigated by Feng and Lu [11]. They considered both the reaction-diffusion equation without time delay

$$(1.5) \qquad \frac{\partial u}{\partial t} - Au(t, x) = r(x)u(t, x)\frac{K(x) - u(t, x)}{K(x) + \gamma(x)u(t, x)}$$

and the corresponding time-delay model

$$(1.6) \qquad \frac{\partial u}{\partial t} - Au(t, x) = r(x)u(t, x)\frac{K(x) - au(t, x) - bu(t - \tau, x)}{K(x) + a\gamma(x)u(t, x) + b\gamma(x)u(t - \tau, x)},$$

where $x = (x_1, x_2, \ldots, x_n) \in \Omega \subseteq R^n$, with Ω bounded and the operator A, given by

$$A = \sum_{i,j=1}^{n} a_{ij}(x)\frac{\partial^2}{\partial x_i \partial x_j} + \sum_{j=1}^{n} \beta_j(x)\frac{\partial}{\partial x_j},$$

is uniformly strongly elliptic and has coefficient functions that are uniformly Hölder continuous in $\bar{\Omega}$. Feng and Lu studied the above problems subject to general boundary conditions that include both the zero-Dirichlet and zero-Neumann cases, and they established a global convergence result for the nonzero steady state.

We are here concerned about the general case (1.1), and we first note that this includes various types of special cases by choosing the kernel function f.

(i) If the kernel f is taken to be

$$f(t, s, x, y) = \delta(t - s)\delta(x - y),$$

(1.1) becomes the reaction-diffusion equation without delay

$$(1.7) \qquad \frac{\partial u}{\partial t}(t, x) = \frac{\partial^2 u}{\partial x^2}(t, x) + u(t, x)\frac{1 - u(t, x)}{1 + \gamma u(t, x)},$$

which is a special case of (1.5).

(ii) If the kernel function f has a discrete time lag τ and spatial averaging, that is,

$$f(t, s, x, y) = \frac{1}{\sqrt{4\pi(t - s)}}e^{-(x-y)^2/4(t-s)}\delta(t - s - \tau),$$

then (1.1) becomes

$$(1.8) \qquad \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u \frac{1 - \int_{-\infty}^{\infty} \frac{e^{-(x-y)^2/4\tau}}{\sqrt{4\pi\tau}} u(t-\tau, y) dy}{1 + \gamma \int_{-\infty}^{\infty} \frac{e^{-(x-y)^2/4\tau}}{\sqrt{4\pi\tau}} u(t-\tau, y) dy} \ .$$

A derivation of this type of model, using probabilistic arguments, was given in [4]. In this model, the movement of individuals to their present positions from where they have been at previous times is accounted for by a spatial convolution with a kernel that spreads normally with a dependence on the delay.

(iii) If $f(t, s, x, y) = \delta(x - y)G(t - s)$, where

$$(1.9) \qquad G(t) = \frac{1}{\tau} e^{-t/\tau} \quad \text{or} \quad G(t) = \frac{t}{\tau^2} e^{-t/\tau},$$

(1.1) becomes a model of reaction diffusion equation with distributed delay:

$$(1.10) \qquad \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u \frac{1 - \int_{-\infty}^{t} G(t-\eta)u(\eta, x)d\eta}{1 + \gamma \int_{-\infty}^{t} G(t-\eta)u(\eta, x)d\eta}.$$

The parameter τ measures time delay and is comparable to the discrete delay τ in (1.8). The two kernel functions G in (1.9) are used frequently in the literature on delay differential equations. The first of the two functions G is sometimes called the "weak" generic kernel because it implies that the importance of events in the past decreases exponentially. The second kernel (the "strong" generic case) is different because it implies that a particular time in the past, namely, τ time units ago, is more important than any other since this kernel achieves its unique maximum when $t = \tau$. This kernel can be viewed as a smoothed out version of the case $G(t) = \delta(t-\tau)$, which gives rise to the discrete delay model.

(iv) If the kernel f is taken to be

$$f(t, s, x, y) = \frac{1}{\sqrt{4\pi(t-s)}} e^{-(x-y)^2/4(t-s)} G(t-s),$$

then (1.1) is a reaction diffusion equation with both distributed delay and spatial averaging. In the distributed delay case with $G(t) = \frac{1}{\tau} e^{-t/\tau}$, a formal asymptotic expansion of traveling wavefront to (1.1) when τ is small was found recently by Gourley and Chaplain by using the so-called linear chain techniques; see [14], [15]. But the convergence of this series or the proof of validity of this expansion has been absent. The central idea of this trick is to recast the traveling wave equation into a higher dimensional system of ODEs without delay. When τ is small, Fenichel's geometrical singular perturbation theory (see [12] or part two of [2]) is applicable. As mentioned in [14], if $G(t) = \frac{t}{\tau^2} e^{-t/\tau}$, linear chain techniques are still applicable, but the system of traveling wave profile equation is six-dimensional. While the trick remains to be effective theoretically, it will be much more difficult in practice. Apparently, it is well known that the drawback of this method is that it is applicable only for models with the special distributed delays. One cannot extend this technique to the discrete case. Another disadvantage of this approach is that if the unperturbed system ($\tau = 0$) is a higher dimensional system, the construction of a traveling wavefront is extraordinarily difficult.

As mentioned in section 3 of [14], traveling wave solutions to (1.1) in the discrete case are much more difficult to study than in the distributed case with specific kernels, because we are no longer able to recast the wave profile equation of (1.8) into

a nondelay equation, and thus Fenichel's geometrical singular perturbation theory cannot be directly used to find a heteroclinic connection in a finite dimensional manifold. Generally, it is well known that in this case the search for traveling wavefronts becomes a much more difficult task.

The purpose of this paper is to develop a completely new approach suitable for all of the aforementioned cases for the existence of traveling wavefronts. The principal result can be stated as follows.

THEOREM 1.1. *For any fixed constant $c \geq 2$, there exists a real number $\delta = \delta(c) > 0$ so that for $\tau \in [0, \delta]$, (1.1) possesses a traveling wavefront $u(t, x) = U(x - ct)$ satisfying $U(-\infty) = 1$ and $U(\infty) = 0$.*

We should remark that our approach here can be developed to study more general equations including

$$\frac{\partial u}{\partial t}(t, x) = \frac{\partial^2 u}{\partial t^2}(t, x) + u(t, x)H((f * u)(t, x)),$$

with $H(\cdot)$ a decreasing function; we refer to [20] for this development.

Although the main result should be of interest, we wish to emphasize the novelty of the approach that we develop. This approach is based on a combination of the perturbation analysis, the Fredholm operator theory, and the fixed point theorems and is expected to find applications in other models as well. A detailed proof is given for case (ii) and is sketched to emphasize the key differences for cases (iii) and (iv). This approach does not work when the delay is not small. In the case where the delay is arbitrary, we develop in section 5 Faria, Huang, and Wu's perturbation method [9] for traveling wavefronts with large wave speeds. We shall provide both theoretical justifications and numerical simulations for this method.

2. The discrete-delay and spatial-averaging case. In the discrete-delay and spatial-averaging case, i.e., the case when the delayed term involves an evaluation of the dependence exactly time τ ago and a convolution in space to account for the movement of individuals to their present positions from their past positions at previous times, (1.1) becomes

$$(2.1) \qquad \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(t, x) \left(\frac{1 - \int_{-\infty}^{\infty} 1/\sqrt{4\pi\tau} e^{-(x-y)^2/(4\tau)} u(t - \tau, y) dy}{1 + \gamma \int_{-\infty}^{\infty} 1/\sqrt{4\pi\tau} e^{-(x-y)^2/(4\tau)} u(t - \tau, y) dy} \right).$$

Our intention here is to establish the existence of traveling waves to (2.1) connecting the two uniform steady states $u = 0$ and $u = 1$. For this purpose, we first show the existence of such wavefronts when the delay τ is zero.

Letting $\tau \to 0^+$, we arrive at the following nondelay version of the food-limited model:

$$(2.2) \qquad \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u \frac{1 - u}{1 + \gamma u},$$

which is actually a modified version of the well-known Fisher's equation. Obviously, (2.2) has two uniform steady-state solutions $u = 0$ and $u = 1$. Considering the traveling wavefront form by setting $u(t, x) = U_0(z) = U_0(x - ct)$ in (2.2), we obtain the following second-order ODE for $U_0(z)$:

$$(2.3) \qquad U_0'' + cU_0' + U_0 \frac{1 - U_0}{1 + \gamma U_0} = 0$$

or equivalently the following first-order coupled system

$$(2.4) \qquad \begin{cases} U_0' = V_0, \\ V_0' = -cV_0 - U_0 \frac{1-U_0}{1+\gamma U_0}. \end{cases}$$

The existence of traveling wavefronts to (2.4) can be established by using the standard phase-plane techniques. Here we present only the result below.

THEOREM 2.1. *If $c \geq 2$, then in the (U_0, V_0) phase plane, a heteroclinic connection exists between the critical points $(U_0, V_0) = (1, 0)$ and $(0, 0)$. Furthermore, the traveling front $U_0(z)$ is strictly monotonically decreasing.*

It is easy to see that the equilibrium $(1, 0)$ is a saddle and the origin $(0, 0)$ is a stable node.

To obtain an extension when $\tau > 0$, we need the following estimate on the derivative of the wave profile U_0.

THEOREM 2.2. *Let U_0 be a traveling wavefront solution to (2.3). Then*

$$(2.5) \qquad -\frac{1}{2\sqrt{\gamma}} < U_0'(z) \leq 0 \ \text{ for all } z \in (-\infty, \infty).$$

Proof. Since U_0 is strictly monotonically decreasing, it is obvious that $U_0'(z) \leq 0$. It remains to prove that $U_0'(z) > -1/(2\sqrt{\gamma})$. Note that (2.3) can be rewritten as

$$(2.6) \qquad U_0'' + cU_0' - \frac{1}{\gamma}U_0 + \left(1 + \frac{1}{\gamma}\right) \frac{U_0}{1 + \gamma U_0} = 0.$$

Let

$$\lambda_1 = \frac{-c - \sqrt{c^2 + 4/\gamma}}{2} < 0, \quad \lambda_2 = \frac{-c + \sqrt{c^2 + 4/\gamma}}{2} > 0.$$

Then it follows from (2.6) that

$$U_0(z) = \frac{(1 + \frac{1}{\gamma})}{\lambda_2 - \lambda_1} \left[\int_{-\infty}^{z} e^{\lambda_1(z-s)} \frac{U_0}{1 + \gamma U_0} ds + \int_{z}^{\infty} e^{\lambda_2(z-s)} \frac{U_0}{1 + \gamma U_0} ds \right],$$

and hence using the fact that $0 < U_0 < 1$, we have

$$\begin{aligned} U_0'(z) &= \frac{(1 + \frac{1}{\gamma})}{\lambda_2 - \lambda_1} \left[\lambda_1 \int_{-\infty}^{z} e^{\lambda_1(z-s)} \frac{U_0}{1 + \gamma U_0} ds + \lambda_2 \int_{z}^{\infty} e^{\lambda_2(z-s)} \frac{U_0}{1 + \gamma U_0} ds \right] \\ &> \frac{(1 + \frac{1}{\gamma})\lambda_1}{\lambda_2 - \lambda_1} \int_{-\infty}^{z} e^{\lambda_1(z-s)} \frac{U_0}{1 + \gamma U_0} ds \\ &\geq \frac{(1 + \frac{1}{\gamma})\lambda_1}{\lambda_2 - \lambda_1} \max \left(\frac{U_0}{1 + \gamma U_0} \right) \int_{-\infty}^{z} e^{\lambda_1(z-s)} ds \\ &= -\frac{(1 + \frac{1}{\gamma})}{(1 + \gamma)\sqrt{c^2 + 4/\gamma}} \geq -\frac{1}{2\sqrt{\gamma}}. \end{aligned}$$

The proof is complete.   ☐

Now we are in a position to establish the existence of traveling wavefronts to (2.1). We will show that the traveling fronts to (2.1) can be approximated by the corresponding wavefronts $U_0(z)$ of (2.3) when τ is small. First, we introduce some

notations. Let $C(R, R)$ be the Banach space of continuous and bounded functions from R to R equipped with the standard norm $||\phi||_C = \sup\{|\phi(t)|, t \in R\}$. Let $C^1 = C^1(R, R) = \{\phi \in C : \phi' \in C\}$, $C^2 = \{\phi \in C : \phi'' \in C\}$, $C_0 = \{\phi \in C : \lim_{t \to \pm\infty} \phi = 0\}$, and $C_0^1 = \{\phi \in C_0 : \phi' \in C_0\}$, where the corresponding norms are defined by

$$||\phi||_{C_0} = ||\phi||_C, \ ||\phi||_{C^1} = ||\phi||_{C_0^1} = ||\phi||_C + ||\phi'||_C,$$

and

$$||\phi||_{C^2} = ||\phi||_C + ||\phi'||_C + ||\phi''||_C.$$

Set $u(t, x) = U(z) = U(x - ct)$ in (2.1). Then $U(z)$ satisfies the profile equation

$$-cU' = U'' + U\frac{1 - H(U)(z)}{1 + \gamma H(U)(z)}, \tag{2.7}$$

where

$$H(U)(z) = \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}} e^{-y^2/(4\tau)} U(z - y + c\tau) dy.$$

We suppose that U can be approximated by U_0 and hence assume that $U = U_0 + W$. Then an equation for W is given by

$$-cW' = W'' + (U_0 + W)\frac{1 - H(U_0 + W)(z)}{1 + \gamma H(U_0 + W)(z)} - U_0\frac{1 - U_0(z)}{1 + \gamma U_0(z)}. \tag{2.8}$$

Applying Taylor's expansions to

$$(U_0 + W)\frac{1 - H(U_0 + W)(z)}{1 + \gamma H(U_0 + W)(z)}$$

yields

$$
\begin{aligned}
(U_0 + W)\frac{1 - H(U_0 + W)(z)}{1 + \gamma H(U_0 + W)(z)} = \ & U_0\frac{1 - H(U_0)}{1 + \gamma H(U_0)} \\
& + W\frac{1 - H(U_0)}{1 + \gamma H(U_0)} - \frac{(1 + \gamma)U_0}{(1 + \gamma H(U_0))^2} H(W) \\
& + R_1(z, \tau, W),
\end{aligned} \tag{2.9}
$$

where $R_1(z, \tau, W)$ is the remainder (higher order terms) of this expansion, and for the time being we write it as

$$
\begin{aligned}
R_1(z, \tau, W) = \ & (U_0 + W)\frac{1 - H(U_0 + W)(z)}{1 + \gamma H(U_0 + W)(z)} \\
& - U_0\frac{1 - H(U_0)}{1 + \gamma H(U_0)} \\
& - W\frac{1 - H(U_0)}{1 + \gamma H(U_0)} + \frac{(1 + \gamma)U_0}{(1 + \gamma H(U_0))^2} H(W).
\end{aligned} \tag{2.10}
$$

Let $g(x) = x\frac{1-x}{1+\gamma x}$. Then we have

$$g'(x) = \frac{1 - x}{1 + \gamma x} - \frac{(1 + \gamma)x}{(1 + \gamma x)^2}.$$

Therefore, by (2.9), (2.8) becomes

$$-cW' = W'' + g'(U_0(z))W(z)$$
$$+ R_1(z, \tau, W) + R_2(z, \tau) + R_3(z, \tau, W),$$

(2.11)

where

$$R_2(z, \tau) = U_0 \frac{1 - H(U_0)}{1 + \gamma H(U_0)} - g(U_0),$$

and

$$R_3(z, \tau, W) = W \frac{1 - H(U_0)}{1 + \gamma H(U_0)} - \frac{(1 + \gamma)U_0}{(1 + \gamma H(U_0))^2} H(W) - g'(U_0(z))W(z).$$

Next we transform (2.11) into an integral equation as follows. Recall that the equation

$$W'' + cW' - W = 0$$

has the characteristic equation

$$\lambda^2 + c\lambda - 1 = 0$$

that has two real roots

$$\lambda_1 = \frac{-c - \sqrt{c^2 + 4}}{2} < 0, \quad \lambda_2 = \frac{-c + \sqrt{c^2 + 4}}{2} > 0.$$

Thus (2.11) is equivalent to the following integral equation:

$$(2.12) \quad W = \frac{1}{\lambda_2 - \lambda_1} \left(\begin{array}{c} \int_{-\infty}^{z} e^{\lambda_1(z-s)} \left[(1 + g'(U_0(s)))W(s) + R_1 + R_2 + R_3 \right] ds \\ + \int_{z}^{\infty} e^{\lambda_2(z-s)} \left[(1 + g'(U_0(s)))W(s) + R_1 + R_2 + R_3 \right] ds \end{array} \right).$$

We will study the existence of a solution $W \in C_0$ to (2.12). For this purpose, we define a linear operator $L : C_0 \to C_0$ by

$$L(W)(z) = W - \frac{\int_{-\infty}^{z} e^{\lambda_1(z-s)}(1 + g'(U_0(s)))W(s)ds}{\lambda_2 - \lambda_1}$$
$$- \frac{\int_{z}^{\infty} e^{\lambda_2(z-s)}(1 + g'(U_0(s)))W(s)ds}{\lambda_2 - \lambda_1}.$$

It is obvious that $L(W) \in C_0$ if $W \in C_0$. In order to verify the existence of a solution $W \in C_0$ to (2.12), we need to establish some estimates for the terms in the right-hand side of (2.12) when $W \in C_0$. We have the following.

LEMMA 2.3. *For each $\delta > 0$, there is a $\sigma > 0$ such that*

$$(2.13) \quad ||R_1(z, \tau, \phi) - R_1(z, \tau, \varphi)||_{C_0} \leq \delta ||\phi - \varphi||_{C_0}$$

and

$$\int_{-\infty}^{z} e^{\lambda_1(z-s)} |R_1(s, \tau, \phi) - R_1(s, \tau, \varphi)| ds + \int_{z}^{\infty} e^{\lambda_2(z-s)} |R_1(s, \tau, \phi) - R_1(s, \tau, \varphi)| ds$$
$$\leq \delta ||\phi - \varphi||_{C_0}$$

(2.14)

for all finite τ and all $\phi, \varphi \in B(\sigma)$, where $B(\sigma)$ is the ball in C_0 with radius σ and the center at the origin.

Proof. Since R_1 is the remainder of Taylor's expansion and $||H\phi|| \leq ||\phi||$ for any $\phi \in C$, we have

$$(2.15) \qquad ||R_1(\cdot, \tau, \phi)|| = O(||\phi||_{C_0}^2) \text{ as } ||\phi||_{C_0} \to 0,$$

uniformly for all finite τ. Obviously $R_1(\cdot, \tau, \phi)$, $(R_1)_\phi(\cdot, \tau, \phi)$ (the derivative of R_1 with respect to ϕ), and $(R_1)_{\phi\phi}(\cdot, \tau, \phi)$ (the second derivative of R_1 with respect to ϕ) are continuous for ϕ in a neighborhood of the origin in C_0, and $\tau \in [0, \tau_0]$, where τ_0 is a positive number. Therefore, (2.13) and (2.14) follow from (2.15). □

LEMMA 2.4. *As $\tau \to 0$, we have*

$$\left| \int_{-\infty}^{z} e^{\lambda_1(z-s)} R_2(s, \tau) ds + \int_{z}^{\infty} e^{\lambda_2(z-s)} R_2(s, \tau) ds \right| = O(\sqrt{\tau})$$

uniformly for all $z \in (-\infty, \infty)$.

Proof. Since

$$\begin{aligned}
R_2(z, \tau) &= U_0 \frac{1 - H(U_0)}{1 + \gamma H(U_0)} - g(U_0) \\
&= U_0 \frac{1 - H(U_0)}{1 + \gamma H(U_0)} - U_0 \frac{1 - U_0}{1 + \gamma U_0},
\end{aligned}$$

we need to show only that when τ is small, the following:

$$(2.16) \qquad \int_{-\infty}^{z} e^{\lambda_1(z-s)} |H(U_0)(s) - U_0(s)| \, ds = O(\sqrt{\tau})$$

and

$$(2.17) \qquad \int_{z}^{\infty} e^{\lambda_1(z-s)} |H(U_0)(s) - U_0(s)| \, ds = O(\sqrt{\tau})$$

hold. In fact, we have

$$\begin{aligned}
& \int_{-\infty}^{z} e^{\lambda_1(z-s)} |H(U_0)(s) - U_0(s)| \, ds \\
&= \int_{-\infty}^{z} e^{\lambda_1(z-s)} \left| \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}} e^{-y^2/4\tau} U_0(s - y + c\tau) dy - U_0(s) \right| ds \\
&= \int_{-\infty}^{z} e^{\lambda_1(z-s)} \left| \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}} e^{-y^2/4\tau} [U_0(s - y + c\tau) - U_0(s)] \, dy \right| ds \\
&\leq \int_{-\infty}^{z} e^{\lambda_1(z-s)} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}} e^{-y^2/4\tau} (|y| + c\tau) dy ds ||U_0'|| \\
&= O(\sqrt{\tau}).
\end{aligned}$$

Similarly we can show (2.17). □

LEMMA 2.5. *There exists an $M_0 > 0$ such that for all $W \in C_0$, the following inequality:*

$$(2.18) \quad \left| \int_{-\infty}^{z} e^{\lambda_1(z-s)} R_3(s, \tau, W) ds + \int_{z}^{\infty} e^{\lambda_2(z-s)} R_3(s, \tau, W) ds \right| \leq \sqrt{\tau} M_0 ||W||_{C_0}$$

holds. Furthermore for any two elements ϕ and φ in C_0, we have

$$\left|\int_{-\infty}^{z} e^{\lambda_1(z-s)}(R_3(s,\tau,\phi)-R_3(s,\tau,\varphi))ds + \int_{z}^{\infty} e^{\lambda_2(z-s)}(R_3(s,\tau,\phi)-R_3(s,\tau,\varphi))ds\right|$$
$$= O(\sqrt{\tau})\|\phi-\varphi\|_{C_0}.$$

(2.19)

Proof. We rewrite R_3 as

$$R_3(z,\tau,W) = W\left(\frac{1-H(U_0)}{1+\gamma H(U_0)}-\frac{1-U_0}{1+\gamma U_0}\right)$$
$$-H(W)\left(\frac{(1+\gamma)U_0}{(1+\gamma H(U_0))^2}-\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}\right)$$
(2.20)
$$-\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}(H(W)-W).$$

Therefore, for the integrations of the first and the second lines on the right-hand side of (2.20), we have from (2.16) the following estimates:

$$(2.21)\qquad \left|\int_{-\infty}^{z} e^{\lambda_1(z-s)}W\left(\frac{1-H(U_0)}{1+\gamma H(U_0)}-\frac{1-U_0}{1+\gamma U_0}\right)ds\right| = O(\sqrt{\tau}\|W\|),$$

and

$$(2.22)\quad \left|\int_{-\infty}^{z} e^{\lambda_1(z-s)}H(W)\left(\frac{(1+\gamma)U_0}{(1+\gamma H(U_0))^2}-\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}\right)ds\right| = O(\sqrt{\tau}\|W\|),$$

due to the fact $\|H(W)\| \le \|W\|$. For the integration of the function in the last line of (2.20), if $W \in C_0^1$, by exchanging the order of integration and integration by parts, we have

$$\int_{-\infty}^{z} e^{\lambda_1(z-s)}\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}(H(W)-W)\,ds$$
$$=\int_{-\infty}^{z} e^{\lambda_1(z-s)}\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}\int_{-\infty}^{\infty}\frac{1}{\sqrt{4\pi\tau}}e^{-y^2/(4\tau)}(W(s-y+c\tau)-W(s))\,dyds$$
$$=\int_{-\infty}^{z} e^{\lambda_1(z-s)}\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}\int_{-\infty}^{\infty}\frac{1}{\sqrt{4\pi\tau}}e^{-y^2/(4\tau)}\int_{0}^{-y+c\tau} W'(s+\eta)d\eta dyds$$
$$=\int_{-\infty}^{\infty}\frac{1}{\sqrt{4\pi\tau}}e^{-y^2/(4\tau)}\int_{0}^{-y+c\tau}\int_{-\infty}^{z} e^{\lambda_1(z-s)}\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}W'(s+\eta)dsd\eta dy$$
$$=\frac{(1+\gamma)U_0(z)}{(1+\gamma U_0(z))^2}\int_{-\infty}^{\infty}\frac{1}{\sqrt{4\pi\tau}}e^{-y^2/(4\tau)}\int_{0}^{-y+c\tau} W(z+\eta)d\eta dy$$
$$-\int_{-\infty}^{\infty}\frac{1}{\sqrt{4\pi\tau}}e^{-y^2/(4\tau)}\int_{0}^{-y+c\tau}\int_{-\infty}^{z} W(s+\eta)\left[e^{\lambda_1(z-s)}\frac{(1+\gamma)U_0}{(1+\gamma U_0)^2}\right]'dsd\eta dy$$
$$= O(\sqrt{\tau}\|W\|).$$

(2.23)

To obtain the above result, we have used the fact that

$$\int_{-\infty}^{z}\left|\frac{d}{ds}\left[e^{\lambda_1(z-s)}\frac{(1+\gamma)U_0(s)}{(1+\gamma U_0(s))^2}\right]\right|ds$$

is uniformly bounded for all $z \in (-\infty, \infty)$. Therefore, from (2.21), (2.22), and (2.23) it follows that there exists a constant M_1 such that

$$(2.24) \qquad \left| \int_{-\infty}^{z} e^{\lambda_1 (z-s)} R_3(s, \tau, W) ds \right| \leq \sqrt{\tau} M_1 ||W||_{C_0}.$$

Similarly, we can prove that there exists a constant M_2 so that

$$(2.25) \qquad \left| \int_{z}^{\infty} e^{\lambda_2 (z-s)} R_3(s, \tau, W) ds \right| \leq \sqrt{\tau} M_2 ||W||_{C_0}.$$

Therefore, it follows from (2.24) and (2.25) that for any $W \in C_0^1$, we have

$$\left| \int_{-\infty}^{z} e^{\lambda_1 (z-s)} R_3(s, \tau, W) ds + \int_{z}^{\infty} e^{\lambda_2 (z-s)} R_3(s, \tau, W) ds \right| \leq \sqrt{\tau} M_0 ||W||_{C_0},$$

with

$$M_0 = \sum_{j=1}^{2} M_j.$$

Since C_0^1 is dense in C_0, the inequality (2.18) holds for all $W \in C_0$. Thus (2.19) is satisfied due to the fact that $R_3(s, \tau, W)$ is a linear functional of W.

We should mention that for each $\tau > 0$ and $W \in C_0$, we have $R_1, R_2,$ and $R_3 \in C_0$ and hence

$$\int_{-\infty}^{z} e^{\lambda_1 (z-s)} (R_1 + R_2 + R_3) ds + \int_{z}^{\infty} e^{\lambda_2 (z-s)} [R_1 + R_2 + R_3] ds \in C_0.$$

Now we are ready to prove our main result. $\quad \square$

THEOREM 2.6. *For any $c \geq 2$, there exists a constant $\delta = \delta(c) > 0$ so that for any $\tau \in [0, \delta]$, (2.1) possesses a traveling wavefront $u(t, x) = U(x - ct)$ satisfying $U(-\infty) = 1$ and $U(\infty) = 0$.*

Proof. Define an operator $T : \Psi \in C^2 \to C$ from the homogeneous part of (2.11) as follows:

$$(2.26) \qquad T\Psi(z) = c\Psi'(z) + \Psi''(z) + g'(U_0(z))\Psi(z).$$

The formal adjoint equation of $T\Psi = 0$ is given by

$$(2.27) \qquad -c\Phi'(z) + \Phi''(z) + g'(U_0(z))\Phi(z) = 0, \quad z \in R.$$

We now divide our proof into five steps.

Step 1. We claim that if $\Phi \in C$ is a solution of (2.27) and Φ is C^2-smooth, then $\Phi = 0$. Moreover, we have $\Re(T) = C$, where $\Re(T)$ is the range space of T.

Indeed, when $z \to \infty$, $U_0(z) \to 0$ and $g'(U_0(z)) \to 1$. Then (2.27) tends asymptotically to an equation with constant coefficients

$$(2.28) \qquad -c\Phi'(z) + \Phi''(z) + \Phi(z) = 0.$$

The corresponding characteristic equation of (2.28) is

$$(2.29) \qquad \lambda^2 - c\lambda + 1 = 0.$$

Both roots of (2.29) have a positive real part as $c \geq 2$, and thus we can conclude that any bounded solution to (2.28) must be the zero solution. So as $z \to \infty$, any solution to (2.27) other than the zero solution must grow exponentially for large z. Then the only solution satisfying $\Phi(\pm\infty) = 0$ is the zero solution. By the Fredholm theory (see Lemma 4.2 in [22]) we have that $\Re(T) = C$.

Step 2. Let $\Theta \in C_0$ be given. We conclude that if Ψ is a bounded solution of $T\Psi = \Theta$, then we have $\lim_{z \to \pm\infty} \Psi(z) = 0$.

In fact when $z \to \infty$, the equation

$$(2.30) \qquad c\Psi'(z) + \Psi''(z) + g'(U_0(z))\Psi(z) = \Theta$$

tends asymptotically to

$$(2.31) \qquad c\Psi'(z) + \Psi''(z) + \Psi(z) = 0.$$

Note for (2.31), the ω-limit set of every bounded solution is just the critical point $\Psi = 0$. Using Theorem 1.8 from [19], we find that every bounded solution of (2.30) also satisfies

$$\lim_{z \to \infty} \Psi(z) = 0.$$

When $z \to -\infty$, (2.30) tends asymptotically to

$$(2.32) \qquad c\Psi'(z) + \Psi''(z) + g'(1)\Psi(z) = 0.$$

Since $g'(1) = -1$, the characteristic equation of (2.32) has two eigenvalues: $\bar{\lambda}_1 < 0$ and $\bar{\lambda}_2 > 0$. Thus every bounded solution of (2.32) must satisfy

$$\lim_{z \to -\infty} \Psi(z) = 0.$$

Inverting the time from z to $-z$ and using the result in [19] again, we know that any bounded solution to (2.30) satisfies $\lim_{z \to -\infty} \Psi(z) = 0$. Hence the claim of Step 2 holds.

Step 3. For a linear operator $L : C_0 \to C_0$ defined by

$$L(W)(z) = W - \frac{1}{\lambda_2 - \lambda_1} \left(\begin{array}{c} \int_{-\infty}^{z} e^{\lambda_1(z-s)}(1 + g'(U_0(s)))W(s)ds \\ + \int_{z}^{\infty} e^{\lambda_2(z-s)}(1 + g'(U_0(s)))W(s)ds \end{array} \right),$$

we want to prove that $\Re(L) = C_0$; that is, for each $Z \in C_0$, we have a $W \in C_0$ so that

$$W - \frac{1}{\lambda_2 - \lambda_1} \left(\begin{array}{c} \int_{-\infty}^{z} e^{\lambda_1(z-s)}(1 + g'(U_0(s)))W(s)ds \\ + \int_{z}^{\infty} e^{\lambda_2(z-s)}(1 + g'(U_0(s))W(s))ds \end{array} \right) = Z(z).$$

To see this, we assume that $\xi(z) = W(z) - Z(z)$ and obtain an equation for ξ as follows:

$$\xi(z) = \frac{1}{\lambda_2 - \lambda_1} \left(\begin{array}{c} \int_{-\infty}^{z} e^{\lambda_1(z-s)}(1 + g'(U_0(s)))\xi(s)ds \\ + \int_{z}^{\infty} e^{\lambda_2(z-s)}(1 + g'(U_0(s)))\xi(s)ds \end{array} \right)$$
$$+ \frac{1}{\lambda_2 - \lambda_1} \left(\begin{array}{c} \int_{-\infty}^{z} e^{\lambda_1(z-s)}(1 + g'(U_0(s)))Z(s)ds \\ + \int_{z}^{\infty} e^{\lambda_2(z-s)}(1 + g'(U_0(s)))Z(s)ds \end{array} \right).$$

Differentiating both sides twice yields

$$(2.33) \qquad -c\xi' - \xi''(z) - g'(U_0(z))\xi(z) = (1 + g'(U_0(z)))Z(z).$$

Using the results that $\Re(T) = C$ in Step 1 and $Z \in C_0$, we obtain by Step 2 that there exists a solution $\xi(z)$ satisfying (2.33) and $\xi(\pm\infty) = 0$. Returning to the variable W, we have $W = \xi + Z \in C_0$.

Step 4. Let $N(L)$ be the null space of operator L. By Lemma 5.1 in [9], there is a subspace $N^\perp(L)$ in C_0 so that

$$C_0 = N^\perp(L) \oplus N(L);$$

see also [10]. It is clear that $N^\perp(L)$ is a Banach space. If we let $S = L|_{N^\perp(L)}$ be the restriction of L to $N^\perp(L)$, then $S : N^\perp(L) \to C_0$ is one-to-one and onto. By the well-known Banach inverse operator theorem, we have that $S^{-1} : C_0 \to N^\perp(L)$ is a linear bounded operator.

Step 5. When L is restricted to $N^\perp(L)$, (2.12) can be written as

$$S(W)(z) = \frac{1}{\lambda_2 - \lambda_1} \left(\begin{array}{c} \int_{-\infty}^z e^{\lambda_1(z-s)} \left[R_1 + R_2 + R_3\right] ds \\ + \int_z^\infty e^{\lambda_2(z-s)} \left[R_1 + R_2 + R_3\right] ds \end{array} \right).$$

Since the norm $||S^{-1}||$ is independent of τ, it follows from Lemmas 2.3, 2.4, and 2.5 that there exist $\sigma > 0, \delta > 0$, and $0 < \rho < 1$ such that for all $\tau \in (0, \delta]$ and $W, \varphi, \psi \in B(\sigma) \cap N^\perp(L)$,

$$||F(z, W)|| \le \frac{1}{3} (||W|| + \sigma)$$

and

$$||F(z, \varphi) - F(z, \psi)|| \le \rho ||\varphi - \psi||,$$

where

$$F(z, W) = \frac{1}{\lambda_2 - \lambda_1} S^{-1} \left(\begin{array}{c} \int_{-\infty}^z e^{\lambda_1(z-s)} \left[R_1 + R_2 + R_3(\tau, s, W)\right] ds \\ + \int_z^\infty e^{\lambda_2(z-s)} \left[R_1 + R_2 + R_3(\tau, s, W)\right] ds \end{array} \right).$$

It is easy to know that for any $W \in B(\sigma) \cap N^\perp(L)$, we have

$$||F(z, W)|| \le \frac{1}{3} (||W|| + \sigma) \le \sigma.$$

Hence $F(z, \varphi)$ is a uniform contractive mapping for $W \in N^\perp(L) \cap B(\sigma)$. By using the Banach contraction principle, it follows that for $\tau \in [0, \delta]$, equation (2.12) has a unique solution $W \in N^\perp(L)$. Returning to the original variable, $W + U_0$ is a heteroclinic connection between the two equilibria 1 and 0. This completes the proof. $\square$

3. The distributed delay case. In this section we consider (1.1) with the kernel function

$$f(t, s, x, y) = G(t - s)\delta(x - y),$$

where

$$(3.1) \qquad G(t) = \frac{1}{\tau}e^{-t/\tau} \quad \text{or} \quad G(t) = \frac{t}{\tau^2}e^{-t/\tau}.$$

We shall focus on the following equation

$$(3.2) \qquad \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u\frac{1 - \int_{-\infty}^{t} \frac{t-\eta}{\tau^2}e^{-(t-\eta)/\tau}u(\eta,x)d\eta}{1 + \gamma \ \int_{-\infty}^{t} \frac{t-\eta}{\tau^2}e^{-(t-\eta)/\tau}u(\eta,x)d\eta}$$

since the corresponding analysis for the weak kernel $G(t) = \frac{1}{\tau}e^{-t/\tau}$ is much easier. Instead of using the linear chain trick which is valid only for the kernels in (3.1), we shall use the approach in section 2 to prove rigorously that traveling fronts exist when τ is small.

As in section 2, assume that $u(t,x) = U(z)$, $z = x - ct$, where $c \geq 2$. Substituting $u = U(z)$ into (3.2), we have a wave equation for U

$$-cU' = U'' + U\frac{1 - \int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}U(z + c\eta)d\eta}{1 + \gamma \ \int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}U(z + c\eta)d\eta}.$$

Let $U = U_0 + W$, where U_0 is the traveling fronts for (2.4). Then we have an equation for W of the form

$$(3.3) \qquad -cW' = W'' - W + (U_0 + W)h[U_0 + W] - U_0\frac{1 - U_0}{1 + \gamma U_0},$$

where the functional h is defined by

$$h[U](z) = \frac{1 - \int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}U(z + c\eta)d\eta}{1 + \gamma \int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}U(z + c\eta)d\eta}.$$

Applying Taylor's expansion to $h[U_0 + W]$, we have

$$h[U_0 + W](z) = \frac{1 - \int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}[U_0(z + c\eta) + W(z + c\eta)]dyd\eta}{1 + \gamma \int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}[U_0(z + c\eta) + W(z + c\eta)]dyd\eta}$$

$$= \ h[U_0](z) - \frac{(1 + \gamma)}{\left(1 + \gamma\int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}U_0(z + c\eta)d\eta\right)^2}\int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}W(z + c\eta)d\eta + \cdots.$$

Thus (3.3) becomes

$$-cW' = W'' + g'(U_0(z))W(z)$$
$$(3.4) \qquad\qquad + R_1(z, \tau, W) + R_2(z, \tau) + R_3(z, \tau, W),$$

where

$$R_1(z, \tau, W) = (U_0 + W)h[U_0 + W](z) - U_0h[U_0](z)$$
$$(3.5) \qquad\qquad + U_0\frac{(1 + \gamma)}{\left(1 + \gamma\int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}U_0(z + c\eta)d\eta\right)^2}\int_0^{\infty} \frac{\eta}{\tau^2}e^{-\eta/\tau}W(z + c\eta)d\eta$$
$$\qquad\qquad - h[U_0]W,$$

$$(3.6) \qquad\qquad R_2(z, \tau) = U_0h[U_0](z) - U_0\frac{1 - U_0}{1 + \gamma U_0},$$

and

$$R_3(z, \tau, W) = \frac{(1+\gamma)\, U_0 \int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} W(z + c\eta) d\eta}{\left(1 + \gamma \int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} U_0(z + c\eta) d\eta\right)^2}$$

(3.7)
$$+ h[U_0] W(z) - g'(U_0(z)) W(z).$$

To obtain the existence of the traveling fronts when τ is small, we need to prove that Lemmas 2.3, 2.4, and 2.5 hold. The proofs are quite similar to those in the discrete case, so we shall prove only Lemma 2.5 as an illustration and leave the proofs of Lemmas 2.3 and 2.4 to interested readers.

Proof of Lemma 2.5 *in the case of distributed delay.* Note that

$$g'(U_0(z)) = \frac{1 - U_0}{1 + \gamma U_0} - \frac{(1+\gamma)U_0}{(1 + \gamma U_0)^2}.$$

So

$$R_3(z, \tau, W) = \bar{F}(U_0)(z) \left(\int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} W(z + c\eta) d\eta - W(z) \right)$$
$$- \left(\frac{(1+\gamma)\, U_0}{\left(1 + \gamma \int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} U_0(z + c\eta) d\eta\right)^2} - \frac{(1+\gamma)U_0}{(1 + \gamma U_0)^2} \right) W$$
$$+ \left(h[U_0] - \frac{1 - U_0}{1 + \gamma U_0} \right) W,$$

where

$$\bar{F}(U_0)(z) = -\frac{(1+\gamma)U_0}{\left(1 + \gamma \int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} U_0(z + c\eta) d\eta\right)^2}.$$

We note that when τ is small,

$$\int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} U_0(z + c\eta) d\eta - U_0(z) = O(\tau)$$

holds uniformly for any $z \in (-\infty, \infty)$. Therefore, we have

$$\int_{-\infty}^z e^{\lambda_1(z-s)} \left(\frac{(1+\gamma)\, U_0}{\left(1 + \gamma \int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} U_0(s + c\eta) d\eta\right)^2} - \frac{(1+\gamma)U_0}{(1 + \gamma U_0)^2} \right) W(s) ds$$
$$= O(\tau\|W\|)$$

and

$$\int_{-\infty}^z e^{\lambda_1(z-s)} \left(h[U_0] - \frac{1 - U_0}{1 + \gamma U_0} \right) W(s) ds = O(\tau\|W\|).$$

We now prove that

$$\int_{-\infty}^z e^{\lambda_1(z-s)} \bar{F}(U_0)(s) \left(\int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} \left(W(s + c\eta) - W(s) \right) d\eta \right) ds = O(\tau\|W\|).$$

Using the fact that

$$\bar{F}(U_0)(s) = O(1)$$

for any $s \in (-\infty, \infty)$, we need only prove that

$$\int_{-\infty}^{z} e^{\lambda_1(z-s)} \left(\int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} \left(W(s+c\eta) - W(s) \right) d\eta \right) ds = O(\tau\|W\|).$$

Indeed, when $W \in C_0^1$, we have

$$W(s+c\eta) - W(s) = \int_0^{c\eta} W'(s+v)dv.$$

Exchanging the order of integration and using the integration by parts, we obtain

$$\int_{-\infty}^{z} e^{\lambda_1(z-s)} \left(\int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} \left(W(s+c\eta) - W(s) \right) d\eta \right) ds$$
$$= \int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} \left(\int_0^{c\eta} \int_{-\infty}^{z} e^{\lambda_1(z-s)} W'(s+v) ds dv \right) d\eta$$
$$= O(\tau\|W\|_{C_0}).$$

Continuing the process as in section 2, we can show that Lemma 2.5 remains true, and so does the result in Theorem 2.6 for (3.2).

Similarly, we can prove that Theorem 2.6 is true if the kernel function is replaced by

$$f(t, s, x, y) = \frac{1}{\tau} e^{-(t-s)} \delta(x-y). \qquad \square$$

4. The distributed delay and spatial-averaging case. In this section, we consider (1.1) with the distributed delay and spatial averaging. Namely, we study the following equation:

(4.1)
$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(t,x) \left(\frac{1 - \int_{-\infty}^{0} \frac{t-\eta}{\tau^2} e^{-(t-\eta)/\tau} \int_{-\infty}^{\infty} \frac{\exp(-(x-y)^2/(4(t-\eta)))}{\sqrt{4\pi(t-\eta)}} u(\eta,y) dy d\eta}{1 + \int_{-\infty}^{0} \frac{t-\eta}{\tau^2} e^{-(t-\eta)/\tau} \int_{-\infty}^{\infty} \frac{\exp(-(x-y)^2/(4(t-\eta)))}{\sqrt{4\pi(t-\eta)}} u(\eta,y) dy d\eta} \right).$$

As before, by a traveling wavefront, we mean a solution $u(t,x) = U(z) = U(-ct+x)$, where $c > 0$ is the wave speed. Thus this specific kind of solution satisfies the following second-order ODE:

(4.2)
$$-cU' = U'' + U \frac{1 - H_1(U)(z)}{1 + \gamma H_1(U)(z)},$$

where

$$H_1(U)(z) = \int_0^\infty \frac{\eta}{\tau^2} e^{-\eta/\tau} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\eta}} e^{-y^2/4\eta} U(z-y+c\eta) dy d\eta.$$

We suppose that U can be approximated by U_0 and hence assume that $U = U_0 + W$. Then we obtain the equation for W as follows:

(4.3)
$$-cW' = W'' + (U_0+W) \frac{1 - H_1(U_0+W)(z)}{1 + \gamma H_1(U_0+W)(z)} - U_0 \frac{1 - U_0(z)}{1 + \gamma U_0(z)}.$$

Applying Taylor's expansions to

$$(U_0 + W)\frac{1 - H_1(U_0 + W)(z)}{1 + \gamma H_1(U_0 + W)(z)},$$

we have

$$
\begin{aligned}
(U_0 + W)\frac{1 - H_1(U_0 + W)(z)}{1 + \gamma H_1(U_0 + W)(z)} = \;& U_0\frac{1 - H_1(U_0)}{1 + \gamma H_1(U_0)} \\
& + W\frac{1 - H_1(U_0)}{1 + \gamma H_1(U_0)} - \frac{(1 + \gamma)\,U_0}{(1 + \gamma H_1(U_0))^2}H_1(W) \\
& + R_1(z, \tau, W),
\end{aligned}
$$

(4.4)

where $R_1(z, \tau, W)$ is the remainder (higher order terms) of this expansion, and this can be rewritten as

$$
\begin{aligned}
R_1(z, \tau, W) = \;& (U_0 + W)\frac{1 - H_1(U_0 + W)(z)}{1 + \gamma H_1(U_0 + W)(z)} \\
& - U_0\frac{1 - H_1(U_0)}{1 + \gamma H_1(U_0)} \\
& - W\frac{1 - H_1(U_0)}{1 + \gamma H_1(U_0)} + \frac{(1 + \gamma)U_0}{(1 + \gamma H_1(U_0))^2}H_1(W).
\end{aligned}
$$

(4.5)

Recall that

$$g(x) = x\frac{1 - x}{1 + \gamma x} \text{ and } g'(x) = \frac{1 - x}{1 + \gamma x} - \frac{(1 + \gamma)x}{(1 + \gamma x)^2}.$$

Therefore, in view of (4.4), (4.3) becomes

$$
\begin{aligned}
-cW' = \;& W'' + g'(U_0(z))W(z) \\
& + R_1(z, \tau, W) + R_2(z, \tau) + R_3(z, \tau, W),
\end{aligned}
$$

(4.6)

where

$$R_2(z, \tau) = U_0\frac{1 - H_1(U_0)}{1 + \gamma H_1(U_0)} - g(U_0)$$

and

$$R_3(z, \tau, W) = W\frac{1 - H_1(U_0)}{1 + \gamma H_1(U_0)} - \frac{(1 + \gamma)U_0}{(1 + \gamma H_1(U_0))^2}H_1(W) - g'(U_0(z))W(z).$$

As before, we transform (4.6) into the following integral equation

$$
(4.7) \quad W = \frac{1}{\lambda_2 - \lambda_1}\left(
\begin{array}{l}
\int_{-\infty}^{z} e^{\lambda_1(z-s)}\left[(1 + g'(U_0(s)))W(s) + R_1 + R_2 + R_3\right]ds \\[2mm]
+ \int_{z}^{\infty} e^{\lambda_2(z-s)}\left[(1 + g'(U_0(s)))W(s) + R_1 + R_2 + R_3\right]ds
\end{array}
\right).
$$

Now the above argument can be repeated to show that Theorem 2.6 holds for (4.1).

Similarly, we can prove Theorem 2.6 for (1.1) with the kernel function

$$(4.8) \qquad f(t, s, x, y) = \frac{1}{\tau}e^{-(t-s)}\frac{1}{\sqrt{4\pi(t-s)}}e^{-(x-y)^2/(4(t-s))}.$$

5. Traveling wavefronts with large wave speed. In section 2, we obtained a traveling wavefront for our model by assuming that the maturation time τ is small. In this section we utilize the idea of Canosa [6] to investigate the existence of traveling wavefront for (2.1) without the smallness requirement of τ. Although the method is originally a formal asymptotic analysis as the front speed approaches infinity, it is known that for Fisher's equation the method generates a solution that is accurate within a few percent of the true solution, even at the minimum speed. The method has also been applied to other reaction-diffusion equations, including coupled systems, with a very good accuracy; see [21] and [24]. The main purpose here is to give a theoretical justification of the method for our food-limited model by showing the fact that when the wave speed tends to infinity, our traveling wavefront approaches a heteroclinic solution (the leading term of Canosa's expansions) of the original model without diffusion. The main idea of this section is from [9], except that we use some known results of global stability of the positive equilibrium instead of applying Smith and Thieme's order preserving semiflows theory [26].

Linearizing (2.7) for U far ahead of the front, where $U \to 0$, gives

$$-cU'(z) = U''(z) - U(z).$$

To ensure that we are studying ecologically realistic fronts that are positive for all values of z, we assume, as in Fisher's equation, that the wave speed $c \geq 2$. Following Canosa's approach, we introduce the small parameter

$$\varepsilon = 1/c^2 \leq \frac{1}{4}$$

and seek a solution of the form

$$U(z) = G(\zeta), \quad \zeta = \sqrt{\varepsilon}z.$$

Equation (2.7) becomes

$$(5.1) \qquad \varepsilon G'' + G' + G \frac{1 - \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}} e^{-y^2/4\tau} G(\zeta - \sqrt{\varepsilon}y + \tau)dy}{1 + \gamma \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}} e^{-y^2/4\tau} G(\zeta - \sqrt{\varepsilon}y + \tau)dy} = 0.$$

When $\varepsilon = 0$, (5.1) reduces to

$$(5.2) \qquad G' + G \frac{1 - G(\zeta + \tau)}{1 + \gamma G(\zeta + \tau)} = 0.$$

For (5.2), we have the following result concerning the heteroclinic orbit connecting the two equilibria $G = 0$ and $G = 1$.

THEOREM 5.1. *Assume $\tau/(1 + \gamma) < \frac{3}{2}$. Then* (5.2) *has a heteroclinic orbit $g_0(\zeta)$ connecting the two equilibria $G = 1$ and $G = 0$.*

Proof. When $\varepsilon = 0$, we set $g_0(\zeta) = G(-\zeta)$ to invert (5.2) into a delay differential equation

$$(5.3) \qquad g_0' = g_0 \frac{1 - g_0(\zeta - \tau)}{1 + \gamma g_0(\zeta - \tau)}.$$

By the result in [18] or [8], we know that the equilibrium $g_0 = 1$ is a global attractor as long as the initial value $g_0(s) = \phi(s)$, $s \in [-\tau, 0]$, satisfies

$$\phi(0) > 0 \text{ and } \phi(s) \geq 0 \text{ for s} \in [-\tau, 0].$$

Linearizing (5.3) around $g_0 = 0$, we have

$$(5.4) \qquad\qquad g_0' = g_0.$$

Therefore, the unstable space E_u of the trivial solution in the usual phase space $C_\tau = C([-\tau, 0]; R)$ of continuous functions equipped with the sup-norm $||\cdot||$ is spanned by $\chi(s) = e^s, s \in [-\tau, 0]$. Let E_s be the subspace in C_τ so that $C_\tau = E_s \oplus E_u$; then there exists $\epsilon_0 > 0$ and a C^1-map $w : E_u \to E_s$, with $w(0) = 0$ and $Dw(0) = 0$ so that a local unstable manifold of $g_0 = 0$ is given by $\epsilon\chi + w(\epsilon\chi)$ for $\epsilon \in (-\epsilon_0, \epsilon_0)$. Choose $\epsilon_0 > 0$ sufficiently small so that the operator norm $||Dw(\epsilon\chi)|| < e^{-\tau}$ for $\epsilon \in (0, \epsilon_0)$. Then pick up $\epsilon \in (0, \epsilon_0)$ and consider $\phi = \epsilon\chi + w(\epsilon\chi)$. We have

$$\phi(s) = \epsilon e^s + w(\epsilon\chi)(s) > \epsilon e^s - e^{-\tau}\epsilon||\chi|| \geq \epsilon(e^{-\tau} - e^{-\tau}) \geq 0.$$

So the solution from the point ϕ on the local unstable manifold of $g_0 = 0$ is positive and tends to 1 due to the global attractivity of the positive equilibrium $g_0 = 1$. Returning to the original variable, we have an orbit G connecting the two equilibria $G = 1$ and $G = 0$. This completes the proof. □

For (5.3), the positive equilibrium 1 is a node, and all of the conditions in Theorem 1.1 in [9] are satisfied. Thus direct application of this result gives the following.

THEOREM 5.2. *Assume $\tau/(1 + \gamma) < \frac{3}{2}$. There is a constant $c^* > 0$ such that for any $c > c^*$, (5.1) has a traveling wave solution $G(x - ct)$ connecting the two equilibria 0 and 1. When the wave speed $c \to \infty$, the wave profile $G(\xi)$ converges to a solution to (5.2).*

Although the result is a consequence of Theorem 1.1 in [9], for the completeness of this paper and the convenience of readers, we outline the proof of this theorem as follows.

For (5.1), set $\bar{G}(\zeta) = G(-\zeta)$. Then $\bar{G}$ satisfies the equation

$$\varepsilon\bar{G}'' - \bar{G}' + \bar{G}\frac{1 - \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}}e^{-y^2/4\tau}\bar{G}(\zeta + \sqrt{\varepsilon}y - \tau)dy}{1 + \gamma\int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}}e^{-y^2/4\tau}\bar{G}(\zeta + \sqrt{\varepsilon}y - \tau)dy} = 0.$$

Now when ε is small, we use g_0 to approximate the wavefront $\bar{G}(\zeta)$ in (5.1). Let $\bar{G} = g_0 + W$. Then we have an equation for W

$$(5.5) \qquad W' = \varepsilon W'' + \varepsilon g_0'' + (g_0 + W)\frac{1 - h_1(g_0 + W)}{1 + \gamma h_1(g_0 + W)} - g_0\frac{1 - g_0(\zeta - \tau)}{1 + \gamma g_0(\zeta - \tau)},$$

where the functional h_1 is given by

$$(5.6) \qquad h_1[U](\zeta) = \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi\tau}}e^{-\eta^2/4\tau}U(\zeta + \sqrt{\varepsilon}\eta - \tau)d\eta.$$

By means of Taylor's expansion, we have

$$(5.7) \qquad \begin{aligned} (g_0 + W)\frac{1 - h_1(g_0 + W)(\zeta)}{1 + \gamma h_1(g_0 + W)(\zeta)} &= g_0\frac{1 - h_1(g_0)}{1 + \gamma h_1(g_0)} \\ &+ W\frac{1 - h_1(g_0)}{1 + \gamma h_1(g_0)} - \frac{(1 + \gamma)g_0}{(1 + \gamma h_1(g_0))^2}h_1(W) \\ &+ R_1(\zeta, \tau, W), \end{aligned}$$

where $R_1(\zeta, \tau, W)$ is the remainder (higher order terms) of this expansion. Therefore by (5.7), (5.5) becomes

$$(5.8) \qquad W' = \varepsilon W'' + P^0 W(z) + R_1(\zeta, \tau, W) + R_2(\zeta, \tau) + R_3(\zeta, \tau, W),$$

where the linear operator $P^0 : C \to C$ is defined by

$$P^0 W(\zeta) = \frac{1 - g_0(\zeta - \tau)}{1 + \gamma g_0(\zeta - \tau)} W(\zeta) - g_0 \frac{(1 + \gamma)}{(1 + \gamma g_0(\zeta - \tau))^2} W(\zeta - \tau),$$

$$R_2(\zeta, \tau) = g_0 \frac{1 - h_1(g_0)}{1 + \gamma h_1(g_0)} - g_0 \frac{1 - g_0(\zeta - \tau)}{1 + \gamma g_0(\zeta - \tau)} + \varepsilon g_0'',$$

and

$$R_3(\zeta, \tau, W) = W \frac{1 - h_1(g_0)}{1 + \gamma h_1(g_0)} - g_0 \frac{(1 + \gamma)}{(1 + \gamma h_1(g_0))^2} h_1(W)$$
$$- W \frac{1 - g_0(\zeta - \tau)}{1 + \gamma g_0(\zeta - \tau)} + g_0 \frac{(1 + \gamma)}{(1 + \gamma g_0(\zeta - \tau))^2} h_1(W).$$

Now we prove that there exists a $W \in C_0$ satisfying (5.8) when ε is small. Equation (5.8) can be transformed into an integral equation as follows. We first write (5.8) as

$$(5.9) \qquad \varepsilon W'' - W' - W = -W - P^0 W - R_1 - R_2 - R_3.$$

Since the equation

$$\varepsilon \lambda^2 - \lambda - 1 = 0$$

has two real zeros λ_1 and λ_2, with

$$(5.10) \qquad \lambda_1 = \frac{1 - \sqrt{1 + 4\varepsilon}}{2\varepsilon} < 0, \quad \lambda_2 = \frac{1 + \sqrt{1 + 4\varepsilon}}{2\varepsilon} > 0,$$

(5.9) is equivalent to the integral equation

$$W(\zeta) = \frac{1}{\sqrt{1 + 4\varepsilon}} \int_{-\infty}^{\zeta} e^{\lambda_1(\zeta - t)} [W(t) + P^0 W(t)] dt$$
$$+ \frac{1}{\sqrt{1 + 4\varepsilon}} \int_{\zeta}^{\infty} e^{\lambda_2(\zeta - t)} [W(t) + P^0 W(t)] dt$$
$$+ \frac{1}{\sqrt{1 + 4\varepsilon}} \int_{-\infty}^{\zeta} e^{\lambda_1(\zeta - t)} [R_1 + R_2 + R_3] dt$$
$$(5.11) \qquad + \frac{1}{\sqrt{1 + 4\varepsilon}} \int_{\zeta}^{\infty} e^{\lambda_2(\zeta - t)} [R_1 + R_2 + R_3] dt.$$

It is easy to show that

$$\lim_{\varepsilon \to 0^+} \lambda_1 = -1, \quad \lim_{\varepsilon \to 0^+} \lambda_2 = +\infty.$$

Thus we have, from (5.11), that

$$W(\zeta) - \int_{-\infty}^{\zeta} e^{-(\zeta-t)}[W(t) + P^0 W(t)]dt$$

$$= \int_{-\infty}^{\zeta} \left[\frac{e^{\lambda_1(\zeta-t)}}{\sqrt{1+4\varepsilon}} - e^{-(\zeta-t)} \right] [W(t) + P^0 W(t)]dt$$

$$+ \frac{1}{\sqrt{1+4\varepsilon}} \int_{\zeta}^{\infty} e^{\lambda_2(\zeta-t)}[W(t) + P^0 W(t)]dt$$

$$+ \frac{1}{\sqrt{1+4\varepsilon}} \int_{-\infty}^{\zeta} e^{\lambda_1(\zeta-t)}[R_1 + R_2 + R_3]dt$$

(5.12)
$$+ \frac{1}{\sqrt{1+4\varepsilon}} \int_{\zeta}^{\infty} e^{\lambda_2(\zeta-t)}[R_1 + R_2 + R_3]dt.$$

For the right-hand side of (5.12), in a similar manner as in section 2, we can prove that

$$\int_{-\infty}^{\zeta} \left[\frac{e^{\lambda_1(\zeta-t)}}{\sqrt{1+4\varepsilon}} - e^{-(\zeta-t)} \right] [W(t) + P^0 W(t)]dt = O(\sqrt{\varepsilon}\|W\|_{C_0}),$$

$$\frac{1}{\sqrt{1+4\varepsilon}} \int_{\zeta}^{\infty} e^{\lambda_2(\zeta-t)}[W(t) + P^0 W(t)]dt = O(\sqrt{\varepsilon}\|W\|_{C_0}),$$

$$\frac{1}{\sqrt{1+4\varepsilon}} \left(\int_{-\infty}^{\zeta} e^{\lambda_1(\zeta-t)} R_1 \, dt + \int_{\zeta}^{\infty} e^{\lambda_2(\zeta-t)} R_1 dt \right) = O(\|W\|^2),$$

$$\frac{1}{\sqrt{1+4\varepsilon}} \left(\int_{-\infty}^{\zeta} e^{\lambda_1(\zeta-t)} R_2 \, dt + \int_{\zeta}^{\infty} e^{\lambda_2(\zeta-t)} R_2 dt \right) = O(\sqrt{\varepsilon}),$$

and

$$\frac{1}{\sqrt{1+4\varepsilon}} \left(\int_{-\infty}^{\zeta} e^{\lambda_1(\zeta-t)} R_3 \, dt + \int_{\zeta}^{\infty} e^{\lambda_2(\zeta-t)} R_3 dt \right) = O(\sqrt{\varepsilon}\|W\|_{C_0}).$$

Let L be the linear operator defined by the left-hand side of (5.12), namely,

$$[LW](\zeta) = W(\zeta) - \int_{-\infty}^{\zeta} e^{-(\zeta-t)}[W(t) + P^0 W(t)]dt.$$

It is obvious that if $W \in C_0$, then $LW \in C_0$. In order to use the argument in section 2 to prove our result, we need to prove that $\Re(L) = C_0$, where $\Re(L)$ is the range space of L; that is, for each $u \in C_0$, we need to show that equation $LW = u$ or, equivalently,

$$W(\zeta) - \int_{-\infty}^{\zeta} e^{-(\zeta-t)}[W(t) + P^0 W(t)]dt = u(\zeta), \quad \zeta \in (-\infty, \infty)$$

has a solution in C_0. For this purpose, we set $w = W - u$. Upon substitution, we have an equation for w:

(5.13)
$$w' = P^0 w(\zeta) + u(\zeta) + P^0 u(\zeta).$$

Define an operator $T : C_0^1 \to C_0$ by

$$[Tw](\zeta) = w'(\zeta) - P^0 w(\zeta)$$

and the formal adjoint equation of $Tw = 0$ by

$$(5.14) \qquad \phi'(t) = -\frac{1 - g_0(t - \tau)}{1 + \gamma g_0(t - \tau)}\phi(t) + \frac{g_0(1 + \gamma)}{(1 + \gamma g_0(t - \tau))^2}\phi(t + \tau), \ t \in (-\infty, \infty).$$

When $t \to \infty$, (5.14) tends asymptotically to

$$\phi'(t) = \frac{1}{1 + \gamma}\phi(t + \tau).$$

When $\tau/(1 + \gamma) < \frac{\pi}{2}$, it is easy to see that if ϕ is a bounded solution to (5.14), then $\phi = 0$. From p. 7 of Chow, Lin, and Mallet-Paret [5], we see that T is Fredholm and $\Re(T) = C_0$. Therefore, (5.13) has a solution $w \in C_0$. From now on we can use the same argument as in sections 4 and 5 in [9] to verify that (5.12) has a solution $W \in C_0$.

6. Summary and simulations. In this paper we have studied the existence of traveling wavefronts for the food-limited population model that involves nonmonotone delayed nonlocal response. The classical phase-plane approach or super/subsolution technique does not work for this type of model due to the lack of monotonicity. Hence, we develop a perturbation argument based on some analytical tools such as the contraction mapping principle and the Fredholm theory to establish the existence of traveling wavefronts. We consider three cases with spatiotemporal averaging when the delay is small. In the general case where the smallness condition on the delay is no longer required, we also developed Canosa's method to establish traveling wavefronts with large wave speeds.

Our work shows how our perturbation analyses based on some analytical tools are particularly useful for models with small delay or for wavefronts with large wave speeds. We believe the smallness condition on τ and the largeness condition on the wave speed can be removed by a certain homotopy argument, and this remains to be a subject for future study.

We should emphasize the difficulty caused by the nonmonotonicity of the delayed nonlocal response. In particular, we note that the traveling wavefronts obtained have prominent humps as the following two numerical simulations show.

The first numerical simulation, reported in Figure 1, is for (2.1), carried out by using Matlab on a spatial domain $-L_0 \le x \le L_0$ (for some $L_0 > 0$) with homogeneous Neumann boundary conditions at both ends. For initial data, we set a nonzero steady state value 1 at the left side and zero elsewhere for all $t \in [-\tau, 0]$. The solution stabilizes to a wavefront when time t goes on. For τ sufficiently small, the resulting traveling fronts appear to be strictly monotone. Increasing the value τ, we find that the monotonicity is lost and a prominent hump is exhibited. When $\gamma = 1$ and $\tau = 2$, the solutions at two different times are shown in Figure 1.

The second numerical simulation is about (4.1) with the kernel given by (4.8). Set

$$v(t, x) = \int_{-\infty}^{t} \frac{1}{\tau}e^{-(t-s)} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi(t - s)}}e^{-(x-y)^2/(4(t-s))}u(s, y)dyds.$$

Then it is easy to recast (1.1) into the form

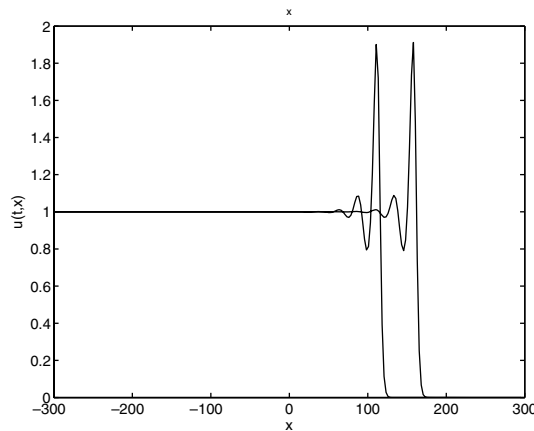$$\begin{cases} u_t = u_{xx} + u\frac{1-v}{1+\gamma v} \\ v_t = v_{xx} + \frac{1}{\tau}(u - v). \end{cases}$$

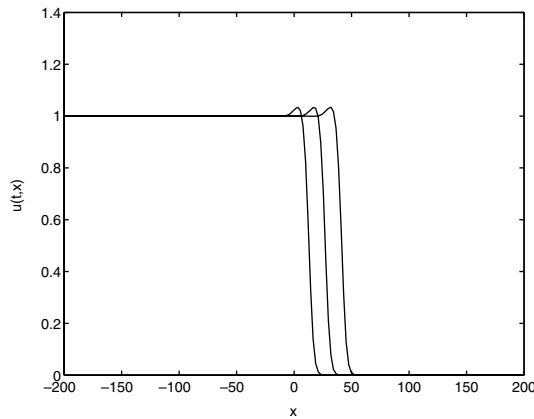FIG. 1. $\gamma = 1, \tau = 2$. *There exists a prominent hump in the front.*

FIG. 2. $\gamma = 1, \tau = 1$. *There exists a prominent hump in the front.*

Using the method of lines, we find again the solution to the above equations with step initial functions and the Neumann boundary conditions stabilizes to a wavefront with a hump. The solution pattern at three different times with $\gamma = 1, \tau = 1$ are shown in Figure 2.

Acknowledgment. We thank the reviewers whose constructive comments lead to a significant improvement of the manuscript.

REFERENCES

[1] J. F. M. AL-OMARI AND S. A. GOURLEY, *Stability and traveling fronts in Lotka-Volterra competition models with stage structure*, SIAM J. Appl. Math., 63 (2003), pp. 2063–2086.
[2] L. ARNOLD, C. JONES, K. MISCHAIKOW, AND G. RAUGEL, *Dynamical systems*, Lectures given at the Second C.I.M.E. Session held in Montecatini Terme, 1994, R. Johnson, ed., Lect. Notes Math. 1609, Springer-Verlag, Berlin, 1995.
[3] P. W. BATES, P. C. FIFE, X. REN, AND X. WANG, *Traveling waves in a convolution model for phase transitions*, Arch. Ration. Mech. Anal., 138 (1997), pp. 105–136.
[4] N. F. BRITTON, *Spatial structures and periodic travelling waves in an integro-differential reaction-diffusion population model*, SIAM J. Appl. Math., 50 (1990), pp. 1663–1688.

[5] S.-N. Chow, X.-B. Lin, and J. Mallet-Paret, *Transition layers for singularly perturbed delay differential equations with monotone nonlinearities*, J. Dynam. Differential Equations, 1 (1989), pp. 3–43.

[6] J. Canosa, *On a nonlinear diffusion equation describing population growth*, IBM J. Res. Develop., 17 (1973), pp. 307–313.

[7] X. Chen, *Existence, uniqueness, and asymptotic stability of traveling waves in nonlocal evolution equations*, Adv. Differential Equations, 2 (1997), pp. 125–160.

[8] T. Faria, E. Liz, J. Oliveira, and S. Trofimchuk, *On a generalized Yorke condition for scalar delayed population models*, Discrete Contin. Dyn. Syst., 12 (2005), pp. 481–500.

[9] T. Faria, W. Huang, and J. Wu, *Traveling waves for delayed reaction-diffusion equations with global response*, Proc. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci., 462 (2006), pp. 229–261.

[10] T. Faria and S.Trofimchuk, *Non-monotone traveling waves in a single species reaction-diffusion equation with delay*, J. Differential Equations, 228 (2006), pp. 357–376.

[11] W. Feng and X. Lu, *On diffusive population models with toxicants and time delays*, J. Math. Anal. Appl., 233 (1999), pp. 373–386.

[12] N. Fenichel, *Geometric singular perturbation theory for ordinary differential equations*, J. Differential Equations, 31 (1979), pp. 53–98.

[13] K. Gopalsamy, M. S. C. Kulenovic, and G. Ladas, *Time lags in a "food-limited" population model*, Appl. Anal., 31 (1988), pp. 225–237.

[14] S. A. Gourley and M. A. J. Chaplain, *Travelling fronts in a food-limited population model with time delay*, Proc. Roy. Soc. Edinburgh Sect. A, 132 (2002), pp. 75–89.

[15] S. A. Gourley and S. Ruan, *Convergence and travelling fronts in functional differential equations with nonlocal terms: a competition model*, SIAM J. Math. Anal., 35 (2003), pp. 806–822.

[16] T. G. Hallam, R. R. Lassiter, and S. A. L. M. Kooijman, *Effects of toxicants on aquatic populations*, in Applied Mathematical Ecology (Trieste, 1986), Biomathematics 18, Springer-Verlag, Berlin, 1989, pp. 352–382, 92A17.

[17] E. Liz, V. Tkachenko, and S. Trofimchuk, *York and Wright 3/2-stability theorems from a unified point of view*, Discrete Contin. Dyn. Syst., 2003, suppl., pp. 580–589.

[18] M. Pinto, G. Robledo, E. Liz, V. Tkachenko, and S. Trofimchuk, *Wright type delay differential equations with negative Schwarzian*, Discrete Contin. Dyn. Syst., 9 (2003), pp. 309–321.

[19] K. Mischaikow, H. Smith, and H. R. Thieme, *Asymptotically autonomous semiflows: chain recurrence and Lyapunov functions*, Trans. Amer. Math. Soc., 347 (1995), pp. 1669–1685.

[20] C. H. Ou and J. Wu, *Persistence of wavefronts in delayed non-local reaction diffusion equations*, J. Differential Equations, 235 (2007), pp. 219–261.

[21] J. D. Murray, *Mathematical Biology*, in Biomathematics 19, Springer-Verlag, Berlin, 1989.

[22] K. J. Palmer, *Exponential dichotomies and transversal homoclinic points*, J. Differential Equations, 55 (1984), pp. 225–256.

[23] E. C. Pielou, *Introduction to Mathematical Ecology*, Wiley, New York, 1969.

[24] J. A. Sherratt, *Wavefront propagation in a competition equation with a new motility term modelling contact inhibition between cell populations*, Proc. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci., 456 (2000), pp. 2365–2386.

[25] F. E. Smith, *Population dynamics in Daphnia magna*, Ecology, 44 (1963), pp. 651–663.

[26] H. L. Smith and H. R. Thieme, *Strongly order preserving semiflows generated by functional-differential equations*, J. Differential Equations, 93 (1991), pp. 332–363.

[27] J. W.-H.So and J. S. Yu, *On the uniform stability for a "food-limited" population model with time delay*, Proc. Roy. Soc. Edinburgh Sect. A, 125 (1995), pp. 991–1002.

[28] A. I. Volpert, V. A. Volpert, and V. A. Volpert, *Traveling Wave Solutions of Parabolic Systems*, Trans. Math. Monogr. 140, American Mathematical Society, Providence, RI, 1994. Translated from the Russian manuscript by James F. Heyda.

[29] J. Wu and X. Zou, *Traveling wave fronts of reaction-diffusion systems with delay*, J. Dynam. Differential Equations, 13 (2001), pp. 651–687.