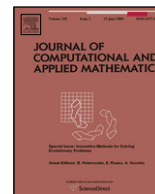




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Traveling wavefronts of a prey–predator diffusion system with stage-structure and harvesting[☆]

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ABSTRACT

From a biological point of view, we consider a prey–predator-type free diffusion fishery model with stage-structure and harvesting. First, we study the stability of the nonnegative constant equilibria. In particular, the effect of harvesting on the stability of equilibria is discussed and supported with numerical simulation. Then, employing the upper and lower solution method, we show that when the wave speed is large enough there exists a traveling wavefront connecting the zero solution to the positive equilibrium of the system. Numerical simulation is also carried out to illustrate the main result.

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1. Introduction

As we know, the exploitation of biological resources and harvesting of population species are commonly practiced in fishery, forestry and wildlife management. Harvesting has a strong impact on the dynamic evolution of a population [1–18]. In particular, stage-structure models have received much attention in recent years [5,6,10,11,13–16]. Based on predator–prey or host–parasite relationships, some researchers have used models of differential equations and difference equations to study a stage-structured population model with or without time delays (see, for example, [5,16]). They have focused on the effect of stage-structure on the dynamical behavior of the systems. In the absence of harvesting, a population can be free of extinction risk. However, harvesting can lead to the incorporation of a positive extinction probability and, therefore, to potential extinction in finite time. If a population is subject to a positive extinction rate then harvesting can drive the population density to a dangerously low level at which extinction becomes sure no matter how the harvester affects the population afterwards. Fishery, an ancient human tradition, has satisfied the food needs of mankind for thousands of years and has become economically, socially and culturally fundamental. Today, however, these fish are in trouble as their populations are being depleted to dangerously low levels and that necessitates further discussion in order to understand short- and long-term exploitation patterns [13]. Predator–prey systems incorporated with harvesting have been discussed by many authors with most of the research concentrating on optimal exploitation guided entirely by profits from harvesting [6,11,14]. But, in [2,3], Brauer and Soudack studied a class of predator–prey models under a constant rate of harvesting and under a constant quota of harvesting of both species simultaneously.

On the other hand, species have the natural tendency to move from areas of bigger population concentration to those of smaller population concentration. This kind of diffusion process is called free diffusion and it is not considered in the above

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mentioned references. In the literature, many researchers have directly introduced the free diffusion to ODEs and DDEs and have also explained why to do so. To name a few, see [19–32]. Moreover, such models or similar models with delays and free diffusion have also arisen from a variety of situations like infectious disease dynamics, porous medium, chemical reaction, and engineering control theory.

Based on the above discussion, it is necessary to consider stage-structured population models with diffusion and harvesting. This is the purpose of this paper. In particular, we study the following delayed reaction–diffusion system with harvesting,

$$\begin{aligned} u_t - d_1 u_{xx} &= ru \left(1 - \frac{u}{k}\right) - \frac{\alpha uv}{1 + au + bv} - q_1 E_1 u, \\ v_t - d_2 v_{xx} &= b_0 e^{-\gamma\tau} v(x, t - \tau) - \left(d_0 - \frac{\beta u}{1 + au + bv}\right) v - q_2 E_2 v, \end{aligned} \tag{1.1}$$

where $u = u(x, t)$ and $v = v(x, t)$ represent the density of prey and adult predator at position x at time t , respectively. The biological meanings of the constants and terms are as follows.

- r : intrinsic growth rate of prey
- k : carrying capacity of prey
- b_0 : birth rate of predator
- d_0 : maximum death rate of predator in the absence of food
- d_1, d_2 : diffusion coefficients
- $\frac{\alpha uv}{1 + au + bv}$: functional response known as the Beddington–DeAngelis response
- $\frac{\beta uv}{1 + au + bv}$: growth rate due to predation
- $b_0 e^{-\gamma\tau} v(x, t - \tau)$: transformation of juveniles to adults, which represent the juveniles who were born at time $t - \tau$ and survive at time t (with the immature death rate γ)
- $q_1 E_1 u, q_2 E_2 v$: catch rate functions based on the catch-per-unit-effort hypothesis, where q_1 and q_2 respectively represent the catch-ability coefficients of the prey and predator while E_1 and E_2 respectively denote the harvesting efforts for the prey and predator.

A similar model to system (1.1) without diffusion and stage-structure was studied in [4]. Note that the harvesting rates there are constant and hence are independent of the densities of the prey and predator.

There have been intensive developments in the theory of traveling wave solutions of partial differential equations since the 1970s. It was found that traveling waves can well model the oscillatory phenomenon and the propagation with finite speed of nature. For example, traveling wave solutions described that material transferred from one equilibrium to another equilibrium state in Physics, the concentration of the substance changed in a Chemical reaction, the species invaded and the spread of infectious diseases in Biology. Of particular importance is that traveling wave solutions for the information carried was never changed in the spread process. As we know that an increasing attention has been paid to traveling waves for reaction–diffusion model modeling a variety of biological phenomena in the recent years. Therefore, in this paper, we will study the existence of a traveling wavefront of (1.1). In order to study traveling wavefronts, we need to analyze the stability of the nonnegative constant equilibria first.

The rest of the paper is organized as follows. We first use linearized method to study the stability of the nonnegative constant equilibria of (1.1) in Section 2. The effect of harvesting is discussed and demonstrated with numerical simulations. Then, applying the method of upper and lower solutions, we establish the existence of the traveling wavefronts of (1.1) in Section 3, which is demonstrated with a numerical example.

2. Asymptotical stability of the nonnegative constant equilibria

It is easy to verify that (1.1) has at most three nonnegative constant equilibria. $C_0(0, 0)$ is always one of them; if (H1)

$$r > q_1 E_1$$

then one has another boundary equilibria $C_1\left(k\left(1 - \frac{q_1 E_1}{r}\right), 0\right)$; moreover, the positive equilibrium $C_2(c_1^*, c_2^*)$ exists if (H1)–(H3) are satisfied. Here

(H2)

$$d_0 + q_2 E_2 > b_0 e^{-\gamma\tau},$$

(H3)

$$0 < \frac{2br\Delta}{k\alpha\beta - ak\alpha\Delta} < \frac{a}{\beta}\Delta + \frac{b}{\alpha}(r - q_1 E_1) - 1,$$

and

$$c_1^* = \frac{\frac{a}{\beta} \Delta + \frac{b}{\alpha} (r - q_1 E_1) - 1 + \sqrt{\left[\frac{a}{\beta} \Delta + \frac{b}{\alpha} (r - q_1 E_1) - 1\right]^2 + \frac{4br}{k\alpha\beta} \Delta}}{\frac{2br}{k\alpha}},$$

$$c_2^* = \frac{[\beta - a\Delta]c_1^* - \Delta}{\Delta},$$

where $\Delta = d_0 + q_2 E_2 - b_0 e^{-\gamma\tau}$.

The linearized system of (1.1) about a nonnegative constant equilibrium (u^*, v^*) is

$$u_t = d_1 u_{xx} + \left(r - \frac{2ru^*}{k} - q_1 E_1 - \frac{\alpha v^* (1 + bv^*)}{(1 + au^* + bv^*)^2} \right) u - \frac{\alpha u^* (1 + au^*)}{(1 + au^* + bv^*)^2} v,$$

$$v_t = d_2 v_{xx} + b_0 e^{-\gamma\tau} v(x, t - \tau) - \left(d_0 + q_2 E_2 - \frac{\beta u^* (1 + au^*)}{(1 + au^* + bv^*)^2} \right) v + \frac{\beta v^* (1 + bv^*)}{(1 + au^* + bv^*)^2} u. \tag{2.1}$$

System (2.1) admits nontrivial solutions of the form $\begin{pmatrix} c_1 \\ c_2 \end{pmatrix} e^{\lambda t + i\sigma x}$ if and only if

$$\frac{\alpha\beta u^* v^* (1 + au^*) (1 + bv^*)}{(1 + au^* + bv^*)^4} + \left(\lambda + d_1 \sigma^2 - r + \frac{2ru^*}{k} + q_1 E_1 + \frac{\alpha v^* (1 + bv^*)}{(1 + au^* + bv^*)^2} \right) \\ \times \left(\lambda + d_2 \sigma^2 - b_0 e^{-\gamma\tau - \lambda\tau} + d_0 + q_2 E_2 - \frac{\beta u^* (1 + au^*)}{(1 + au^* + bv^*)^2} \right) = 0. \tag{2.2}$$

where λ is a complex number and σ is a real number (see, for example, [20] and the references therein). In the following, we discuss the stability of the possible equilibria one by one.

2.1. Asymptotical stability of $C_0(0, 0)$

In this case, Eq. (2.2) reduces to

$$(\lambda + d_1 \sigma^2 - r + q_1 E_1)(\lambda + d_2 \sigma^2 - b_0 e^{-\gamma\tau - \lambda\tau} + d_0 + q_2 E_2) = 0.$$

Thus either

$$\lambda + d_1 \sigma^2 - r + q_1 E_1 = 0 \tag{2.3}$$

or

$$\lambda + d_2 \sigma^2 - b_0 e^{-\gamma\tau - \lambda\tau} + d_0 + q_2 E_2 = 0. \tag{2.4}$$

It follows from (2.3) that

$$\lambda + d_1 \sigma^2 = r - q_1 E_1.$$

Then $\text{Re} \lambda < 0$ if $r < q_1 E_1$ while there exists at least one (λ_0, σ_0) satisfying (2.3) such that $\text{Re} \lambda_0 > 0$ if $r > q_1 E_1$, i.e., (H1) holds.

For (2.4), first we assume that $d_0 + q_2 E_2 < b_0 e^{-\gamma\tau}$. Let

$$f_\sigma(\lambda) = \lambda + d_2 \sigma^2 - b_0 e^{-\gamma\tau - \lambda\tau} + d_0 + q_2 E_2.$$

Then $f_\sigma(0) = d_2 \sigma^2 - b_0 e^{-\gamma\tau} + d_0 + q_2 E_2$ and hence there exists a $\sigma_1 > 0$ such that $f_{\sigma_1}(0) < 0$. Noting that $f_{\sigma_1}(\lambda) \rightarrow \infty$ as $\lambda \rightarrow \infty$, we know that there exists a $\lambda_1 > 0$ such that (λ_1, σ_1) satisfying (2.4). Now, we assume that $d_0 + q_2 E_2 > b_0 e^{-\gamma\tau}$, i.e., (H2) holds. We claim that $\lambda < 0$ for all (λ, σ) satisfying (2.4). Otherwise, suppose that there exists a (λ_2, σ_2) satisfying (2.4) such that $\text{Re} \lambda_2 \geq 0$. Then

$$\text{Re} \lambda_2 + d_2 \sigma_2^2 + d_0 + q_2 E_2 \leq |\lambda_2 + d_2 \sigma_2^2 + d_2 + q_2 E_2| = |b_0 e^{-\gamma\tau - \lambda_2 \tau}| \leq b_0 e^{-\gamma\tau},$$

which is impossible as $d_0 + q_2 E_2 > b_0 e^{-\gamma\tau}$. This proves the claim.

In summary, we have proved the following result.

Theorem 2.1. *The equilibrium $C_0(0, 0)$ is (locally) asymptotically stable if and only if $r < q_1 E_1$ and (H2) holds.*

2.2. Asymptotical stability of $C_1(k(1 - \frac{q_1 E_1}{r}), 0)$

Recall that C_1 exists only when (H1) holds. At $C_1(k(1 - \frac{q_1 E_1}{r}), 0)$, Eq. (2.2) holds if and only if either

$$\lambda + d_1\sigma^2 + r - q_1E_1 = 0 \tag{2.5}$$

or

$$\lambda + d_2\sigma^2 - b_0e^{-\gamma\tau - \lambda\tau} + d_0 + q_2E_2 - \frac{\beta k(r - q_1E_1)}{r + ak(r - q_1E_1)} = 0. \tag{2.6}$$

Obviously, $\text{Re}\lambda < 0$ if (λ, σ) satisfies (2.5) as $r > q_1E_1$. Applying similar arguments as those for (2.4), we can show that $\text{Re}\lambda < 0$ for all (λ, σ) satisfying (2.6) if $d_0 + q_2E_2 - \frac{\beta k(r - q_1E_1)}{r + ak(r - q_1E_1)} > b_0e^{-\gamma\tau}$ and there exists at least one (λ_3, σ_3) satisfying (2.6) such that $\text{Re}\lambda_3 > 0$ if $d_0 + q_2E_2 - \frac{\beta k(r - q_1E_1)}{r + ak(r - q_1E_1)} < b_0e^{-\gamma\tau}$.

To summarize, we have shown

Theorem 2.2. Assume that (H1) holds. Then (1.1) has an equilibrium $C_1\left(k\left(1 - \frac{q_1E_1}{r}\right), 0\right)$. Moreover, C_1 is (locally) asymptotically stable if and only if $d_0 + q_2E_2 - \frac{\beta k(r - q_1E_1)}{r + ak(r - q_1E_1)} > b_0e^{-\gamma\tau}$.

2.3. Asymptotical stability of $C_2(c_1^*, c_2^*)$

When C_2 exists, one can show that $c_1^* > \frac{ak}{\beta r}(r - q_1E_1)$. At $C_2(c_1^*, c_2^*)$, we have from (2.2) that

$$\begin{aligned} & \frac{\alpha\beta c_1^*c_2^*(1 + ac_1^*)(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^4} + \left(\lambda + d_1\sigma^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2} \right) \\ & \times \left(\lambda + d_2\sigma^2 - b_0e^{-\gamma\tau - \lambda\tau} + d_0 + q_2E_2 - \frac{\beta c_1^*(1 + ac_1^*)}{(1 + ac_1^* + bc_2^*)^2} \right) = 0. \end{aligned} \tag{2.7}$$

Obviously, if (λ, σ) satisfies (2.7) then $\lambda + d_1\sigma^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2} \neq 0$. Thus we rewrite (2.7) as

$$\lambda = -\frac{\frac{\alpha\beta c_1^*c_2^*(1 + ac_1^*)(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^4}}{\lambda + d_1\sigma^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}} - d_2\sigma^2 + b_0e^{-\gamma\tau - \lambda\tau} - d_0 - q_2E_2 + \frac{\beta c_1^*(1 + ac_1^*)}{(1 + ac_1^* + bc_2^*)^2}. \tag{2.8}$$

We claim that $\mu < 0$ if $(\lambda, \sigma) = (\mu + i\nu, \sigma)$ satisfies (2.8). Otherwise, suppose that there exists a $(\mu_4 + i\nu_4, \sigma_4)$ satisfying (2.8) such that $\mu_4 \geq 0$. Then direct computation gives us

$$\begin{aligned} 0 \leq \mu_4 &= -\frac{\alpha\beta c_1^*c_2^*(1 + ac_1^*)(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^4} \times \frac{\mu_4 + d_1\sigma_4^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}}{\left(\mu_4 + d_1\sigma_4^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}\right)^2 + \nu_4^2} \\ & - d_2\sigma_4^2 + b_0e^{-\gamma\tau - \mu_4\tau} \cos(\nu_4\tau) - d_0 - q_2E_2 + \frac{\beta c_1^*(1 + ac_1^*)}{(1 + ac_1^* + bc_2^*)^2} \\ & \leq -\frac{\alpha\beta c_1^*c_2^*}{(1 + ac_1^* + bc_2^*)^4} \times \frac{\frac{2rc_1^*}{k} + q_1E_1 - r + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}}{\left(\mu_4 + d_1\sigma_4^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}\right)^2 + \nu_4^2} \\ & + b_0e^{-\gamma\tau} - d_0 - q_2E_2 + \frac{\beta c_1^*}{1 + ac_1^* + bc_2^*} \\ & \leq -\frac{\alpha\beta c_1^*c_2^*}{(1 + ac_1^* + bc_2^*)^4} \times \frac{\frac{rc_1^*}{k} - \frac{\alpha c_2^*}{1 + ac_1^* + bc_2^*} + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}}{\left(\mu_4 + d_1\sigma_4^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}\right)^2 + \nu_4^2} \\ & = -\frac{\alpha\beta c_1^*c_2^*}{(1 + ac_1^* + bc_2^*)^4} \times \frac{\frac{rc_1^*}{k} - \frac{\alpha ac_1^*c_2^*}{(1 + ac_1^* + bc_2^*)^2}}{\left(\mu_4 + d_1\sigma_4^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}\right)^2 + \nu_4^2} \\ & < -\frac{\alpha\beta c_1^*c_2^*}{(1 + ac_1^* + bc_2^*)^4} \times \frac{\frac{rc_1^*}{k} - \frac{a}{\beta}(r - q_1E_1)}{\left(\mu_4 + d_1\sigma_4^2 - r + \frac{2rc_1^*}{k} + q_1E_1 + \frac{\alpha c_2^*(1 + bc_2^*)}{(1 + ac_1^* + bc_2^*)^2}\right)^2 + \nu_4^2} \\ & < 0 \end{aligned}$$

as $c_1^* > \frac{ak}{\beta r}(r - q_1E_1) > 0$, a contradiction. This proves the claim. As a result, we have proved.

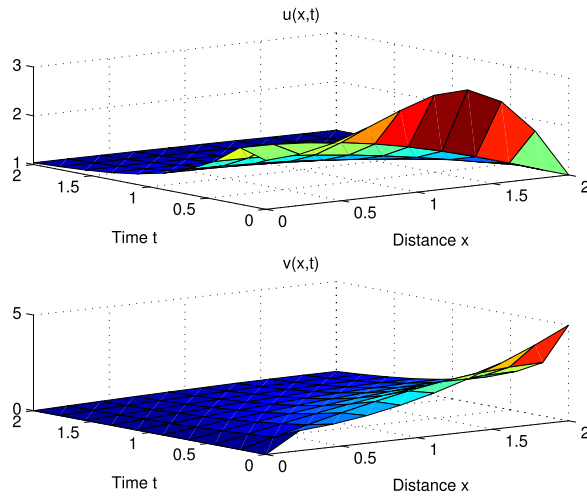


Fig. 1. $E_1 = E_2 = 1.25$.

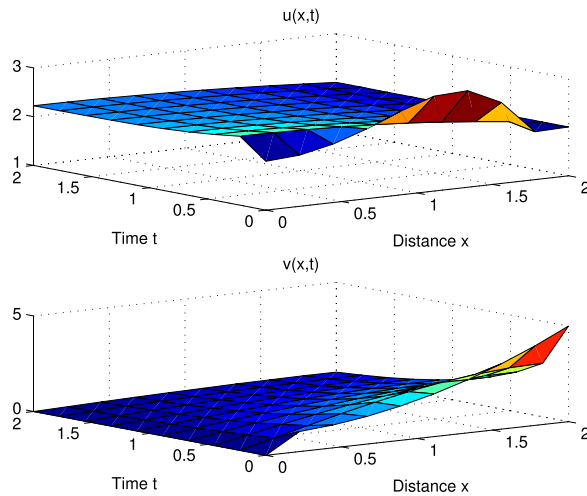


Fig. 2. $E_1 = E_2 = 1.235$.

Theorem 2.3. Assume that (H1)–(H3) hold. Then (1.1) has a positive equilibrium C_2 , which is locally asymptotically stable.

Theorems 2.1–2.3 tell us that the harvesting efforts affect not only the existence of equilibria but also the stability of them. Therefore, it is possible to use E_1 and E_2 as controls to make the system approach a required state. Let us support this with some numerical simulations.

Fix $r = 2, k = 100, \alpha = 0.4, a = 5, b = 20, \beta = 0.24, q_1 = 1.584, q_2 = 1.854, d_0 = 0.1, d_1 = 3, d_2 = 2$ and $b_0 e^{-0.001\gamma} = 2.36$. All these parameters are biologically realistic (see [14]). If we take $E_1 = E_2 = 1.25$, then the assumptions of Theorem 2.2 hold and hence the equilibrium $C_1(1, 0)$ is asymptotically stable. Fig. 1 illustrates this with the initial conditions $u(x, 0) = 2 + \sin(x^2), v(x, 0) = x^2 + 1$. On the other hand, if we take $E_1 = E_2 = 1.235$ then (H1) holds but $d_0 + q_2 E_2 - \frac{\beta k(r - q_1 E_1)}{r + ak(r - q_1 E_1)} < b_0 e^{-\gamma\tau}$. Thus it follows from Theorem 2.2 that the equilibrium $C_1(2.2, 0)$ is unstable. This is supported with the same initial conditions (see Fig. 2).

3. Traveling wavefronts solution with large wave speed

A traveling wave solution of (1.1) is a special translation invariant solution of the form $(u(x, t), v(x, t)) = (\phi_1(x + ct), \psi_2(x + ct))$ with wave speed c . Various methods including the monotone iteration technique [23,28,31] and the degree theory [21,26] have been adopted to study the existence of traveling wave solutions to reaction–diffusion systems with delays.

In this section, we use the approach introduced in [33] to establish the existence of traveling wave solutions connecting the zero solution to the positive equilibrium $C_2(c_1^*, c_2^*)$ with large wave speeds. To seek such a pair of traveling wavefronts

of (1.1), we substitute $u(x, t) = \phi_1(s)$ and $v(x, t) = \phi_2(s)$, where $s = x + ct$, into (1.1) to obtain

$$\begin{aligned} d_1\phi_1''(s) - c\phi_1'(s) + r\phi_1(s) \left(1 - \frac{1}{k}\phi_1(s)\right) - \frac{\alpha\phi_1(s)\phi_2(s)}{1 + a\phi_1(s) + b\phi_2(s)} - q_1E_1\phi_1(s) &= 0, \\ d_2\phi_2''(s) - c\phi_2'(s) + b_0e^{-\gamma\tau}\phi_2(s - c\tau) - d_0\phi_2(s) + \frac{\beta\phi_1(s)\phi_2(s)}{1 + a\phi_1(s) + b\phi_2(s)} - q_2E_2\phi_2(s) &= 0, \\ \phi_i(-\infty) = 0, \quad \phi_i(\infty) = c_i^*, \quad i = 1, 2. \end{aligned} \tag{3.1}$$

Now, we follow the approach of Canosa [33] to construct a uniformly valid asymptotic approximation to the wavefronts for large values of the wave speed c . Suppose that c is large enough. Then $\epsilon = 1/c^2$ is a small parameter. We aim to seek a pair of solutions to (3.1) of the form

$$\begin{pmatrix} \phi_1(s) \\ \phi_2(s) \end{pmatrix} = \begin{pmatrix} \psi_1(\eta) \\ \psi_2(\eta) \end{pmatrix} \quad \text{with } \eta = \sqrt{\epsilon}s = s/c.$$

Then (3.1) becomes

$$\begin{aligned} \epsilon d_1\psi_1''(\eta) - \psi_1'(\eta) + r\psi_1(\eta) - \frac{r}{k}\psi_1^2(\eta) - q_1E_1\psi_1(\eta) - \frac{\alpha\psi_1(\eta)\psi_2(\eta)}{1 + a\phi_1(\eta) + b\phi_2(\eta)} &= 0, \\ \epsilon d_2\psi_2''(\eta) - \psi_2'(\eta) + b_0e^{-\gamma\tau}\psi_2(\eta - \tau) - d_0\psi_2(\eta) + \frac{\beta\psi_1(\eta)\psi_2(\eta)}{1 + a\psi_1(\eta) + b\psi_2(\eta)} - q_2E_2\psi_2(\eta) &= 0, \\ \psi_i(-\infty) = 0, \quad \psi_i(+\infty) = c_i^*, \quad i = 1, 2. \end{aligned} \tag{3.2}$$

Denote

$$\psi_i(\eta, \epsilon) = \psi_{i0}(\eta) + \epsilon\psi_{i1}(\eta) + \epsilon^2\psi_{i2}(\eta) + \dots, \quad i = 1, 2,$$

and substitute them into (3.2). It turns out that $\psi_{10}(\eta)$ and $\psi_{20}(\eta)$ satisfy

$$\begin{aligned} \psi_{10}'(\eta) &= r\psi_{10}(\eta) - \frac{r}{k}\psi_{10}^2(\eta) - q_1E_1\psi_{10}(\eta) - \frac{\alpha\psi_{10}(\eta)\psi_{20}(\eta)}{1 + a\phi_{10}(\eta) + b\phi_{20}(\eta)}, \\ \psi_{20}'(\eta) &= b_0e^{-\gamma\tau}\psi_{20}(\eta - \tau) - d_0\psi_{20}(\eta) - q_2E_2\psi_{20}(\eta) + \frac{\beta\psi_{10}(\eta)\psi_{20}(\eta)}{1 + a\psi_{10}(\eta) + b\psi_{20}(\eta)}, \\ \psi_{i0}(-\infty) = 0, \quad \psi_{i0}(+\infty) = c_i^*, \quad i = 1, 2. \end{aligned} \tag{3.3}$$

For simplicity of notation, we still denote $\psi_{10}(\eta)$, $\psi_{20}(\eta)$ by $\phi_1(s)$, $\phi_2(s)$, respectively. Then (3.3) becomes

$$\begin{aligned} \phi_1'(s) &= r\phi_1(s) - \frac{r}{k}\phi_1^2(s) - q_1E_1\phi_1(s) - \frac{\alpha\phi_1(s)\phi_2(s)}{1 + a\phi_1(s) + b\phi_2(s)}, \\ \phi_2'(s) &= b_0e^{-\gamma\tau}\phi_2(s - \tau) - d_0\phi_2(s) - q_2E_2\phi_2(s) + \frac{\beta\phi_1(s)\phi_2(s)}{1 + a\phi_1(s) + b\phi_2(s)}, \\ \phi_i(-\infty) = 0, \quad \phi_i(+\infty) = c_i^*, \quad i = 1, 2. \end{aligned} \tag{3.4}$$

Now, we are ready to state and prove the following result by the upper and lower solution technique developed in [31].

Theorem 3.1. Assume that (H1)–(H3) hold. Then (1.1) has a traveling wavefront connecting $(0, 0)$ to (c_1^*, c_2^*) .

Proof. The proof is divided into the following two steps.

Step I: Verify a quasi-monotonicity condition. For this purpose, we define the functional $f_c(\phi) = (f_{c1}(\phi), f_{c2}(\phi))^T$ by

$$\begin{aligned} f_{c1}(\phi) &= r\phi_1(0) - \frac{r}{k}\phi_1^2(0) - q_1E_1\phi_1(0) - \frac{\alpha\phi_1(0)\phi_2(0)}{1 + a\phi_1(0) + b\phi_2(0)}, \\ f_{c2}(\phi) &= b_0e^{-\gamma\tau}\phi_2(-\tau) - d_0\phi_2(0) - q_2E_2\phi_2(0) + \frac{\beta\phi_1(0)\phi_2(0)}{1 + a\phi_1(0) + b\phi_2(0)}. \end{aligned} \tag{3.5}$$

For arbitrary $(\phi_1, \phi_2)^T$ and $(\psi_1, \psi_2)^T \in C([-\tau, 0], \mathbb{R}^2)$ such that

$$0 \leq \psi(s) \leq \phi(s) \leq c^* := (c_1^*, c_2^*) \quad \text{for } s \in [-\tau, 0]$$

and

$$\phi_2(0) - \psi_2(0) < \theta(\phi_1(0) - \psi_1(0)) \quad \text{for some } \theta > 0$$

we have

$$\begin{aligned} f_{c_1}(\phi) - f_{c_1}(\psi) &= (r - q_1E_1)(\phi_1(0) - \psi_1(0)) - \frac{r}{k}(\phi_1(0) + \psi_1(0))(\phi_1(0) - \psi_1(0)) \\ &\quad - \left(\frac{\alpha\phi_1(0)\phi_2(0)}{1 + a\phi_1(0) + b\phi_2(0)} - \frac{\alpha\psi_1(0)\psi_2(0)}{1 + a\psi_1(0) + b\psi_2(0)} \right) \\ &\geq \left(r - q_1E_1 - \frac{2rc_1^*}{k} \right) (\phi_1(0) - \psi_1(0)) - \alpha(\phi_2(0)(\phi_1(0) - \psi_1(0)) + \psi_1(0)(\phi_2(0) - \psi_2(0))) \\ &\geq \left(r - q_1E_1 - \frac{2rc_1^*}{k} - \alpha c_1^*\theta - \alpha c_2^* \right) (\phi_1(0) - \psi_1(0)), \end{aligned}$$

which implies

$$\begin{aligned} f_{c_1}(\phi) - f_{c_1}(\psi) + \delta_1(\phi_1(0) - \psi_1(0)) &\geq (\delta_1 + r - q_1E_1 - \frac{2rc_1^*}{k} - \alpha c_1^*\theta - \alpha c_2^*)(\phi_1(0) - \psi_1(0)) \\ &\geq 0, \end{aligned}$$

provided that δ_1 is chosen such that $\delta_1 > -r + q_1E_1 + \frac{2rc_1^*}{k} + \alpha c_1^*\theta + \alpha c_2^*$. Similarly, we can get

$$f_{c_2}(\phi) - f_{c_2}(\psi) + \delta_2(\phi_2(0) - \psi_2(0)) \geq (\delta_2 - d_0 - q_2E_2)(\phi_2(0) - \psi_2(0)) \geq 0,$$

provided that δ_2 is chosen such that $\delta_2 > d_0 + q_2E_2$. This proves the quasi-monotonicity condition.

Step II: Establish the existence of a pair of upper and lower solutions. To achieve this, we look for wavefront solutions of (3.1) in the following profile set

$$\Gamma = \left\{ \phi = \begin{pmatrix} \phi_1(s) \\ \phi_2(s) \end{pmatrix} \in C(\mathbb{R}, \mathbb{R}^2) : \begin{array}{l} \text{(i) } \phi \text{ is component-wise nondecreasing in } \mathbb{R}, \\ \text{(ii) } \lim_{s \rightarrow -\infty} \phi(s) = 0, \lim_{s \rightarrow \infty} \phi(s) = c^* \end{array} \right\}.$$

Note that $r + \alpha c_2^* - q_1E_1 > 0$ and $b_0e^{-\gamma\tau} + \beta c_1^* - d_0 - q_2E_2 > 0$. Choose λ such that $\lambda > \max\{r + \alpha c_2^* - q_1E_1, b_0e^{-\gamma\tau} + \beta c_1^* - d_0 - q_2E_2\}$. Define

$$\phi_1(s) = \min\{c_1^*e^{\lambda s}, c_1^*\} \quad \text{and} \quad \phi_2(s) = \min\{c_2^*e^{\lambda s}, c_2^*\}.$$

Then $\phi = (\phi_1(s), \phi_2(s))^T \in \Gamma$. We distinguish two cases to show that $(\phi_1(s), \phi_2(s))^T$ is a pair of upper solutions to (3.4).

Case I: $s < 0$. It is easy to see that

$$\phi_1(s) = c_1^*e^{\lambda s}, \quad \phi_2(s) = c_2^*e^{\lambda s} \quad \text{and} \quad \phi_2(s - \tau) = c_2^*e^{\lambda(s-\tau)}.$$

Thus

$$\begin{aligned} \phi_1'(s) - r\phi_1(s) + \frac{r}{k}\phi_1^2(s) + q_1E_1\phi_1(s) - \frac{\alpha\phi_1(s)\phi_2(s)}{1 + a\phi_1(s) + b\phi_2(s)} &\geq \lambda c_1^*e^{\lambda s} - rc_1^*e^{\lambda s} + \frac{r}{k}c_1^*e^{2\lambda s} + q_1E_1c_1^*e^{\lambda s} - \alpha c_1^*c_2^*e^{2\lambda s} \\ &\geq c_1^*e^{\lambda s} \left(\lambda - r + \frac{r}{k}c_1^*e^{\lambda s} + q_1E_1 - \alpha c_2^*e^{\lambda s} \right) \\ &\geq c_1^*e^{\lambda s}(\lambda - r + q_1E_1 - \alpha c_2^*) > 0. \end{aligned}$$

Similarly,

$$\begin{aligned} \phi_2'(s) - b_0e^{-\gamma\tau}\phi_2(s - \tau) + d_0\phi_2(s) + q_2E_2\phi_2(s) - \frac{\beta\phi_1(s)\phi_2(s)}{1 + a\phi_1(s) + b\phi_2(s)} &\geq \lambda c_2^*e^{\lambda s} - b_0e^{-\gamma\tau}c_2^*e^{\lambda(s-\tau)} + d_0c_2^*e^{\lambda s} + q_2E_2c_2^*e^{\lambda s} - \beta c_1^*c_2^*e^{2\lambda s} \\ &\geq c_2^*e^{\lambda s}(\lambda - b_0e^{-\gamma\tau} + d_0 + q_2E_2 - \beta c_1^*) > 0. \end{aligned}$$

Case II: $s \geq 0$. We have

$$\phi_i(s) = c_i^* \quad (i = 1, 2), \quad \phi_2(s - \tau) = \begin{cases} c_2^*, & \text{if } s \geq \tau, \\ c_2^*e^{\lambda(s-\tau)}, & \text{if } s < \tau, \end{cases}$$

which implies that

$$\phi_2(s - \tau) \leq c_2^* \quad \text{for } s \geq 0.$$

Therefore,

$$\begin{aligned} \phi_1'(s) - r\phi_1(s) + \frac{r}{k}\phi_1^2(s) + q_1E_1\phi_1(s) + \frac{\alpha\phi_1(s)\phi_2(s)}{1 + a\phi_1(s) + b\phi_2(s)} &= -rc_1^* + \frac{r}{k}c_1^* + q_1E_1c_1^* + \frac{\alpha c_1^*c_2^*}{1 + a c_1^* + b c_2^*} \\ &= 0, \end{aligned}$$

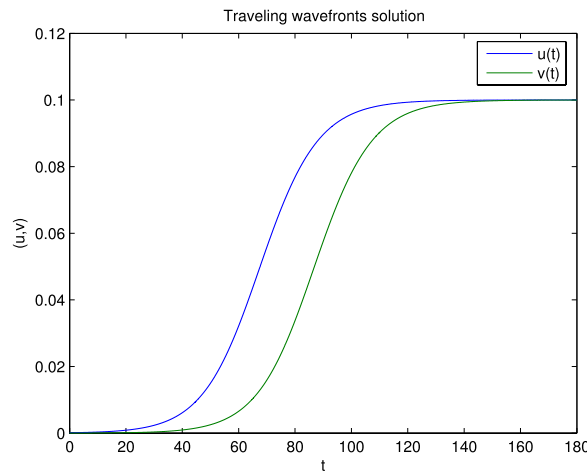


Fig. 3. Existence of traveling wavefront of system (1.1).

and

$$\begin{aligned} & \phi_2'(s) - b_0 e^{-\gamma\tau} \phi_2(s - \tau) + d_0 \phi_2(s) + q_2 E_2 \phi_2(s) - \frac{\beta \phi_1(s) \phi_2(s)}{1 + a \phi_1(s) + b \phi_2(s)} \\ & \geq -b_0 e^{-\gamma\tau} c_2^* + d_0 c_2^* + q_2 E_2 c_2^* - \frac{\beta c_1^* c_2^*}{1 + a c_1^* + b c_2^*} \\ & = 0. \end{aligned}$$

The above discussion tells us that $(\phi_1(s), \phi_2(s))^T$ is an upper solution to (3.4). Now, define

$$\psi_1(s) = \begin{cases} \varepsilon e^{\lambda_1 s}, & \text{if } s < 0 \\ \varepsilon, & \text{if } s \geq 0 \end{cases} \quad \text{and} \quad \psi_2(s) = 0, \tag{3.6}$$

where

$$0 < \varepsilon < \min \left\{ c_1^*, \frac{k}{r} (r - \lambda_1 - q_1 E_1) \right\}, \tag{3.7}$$

and the positive λ_1 satisfies

$$0 < \lambda_1 < r - q_1 E_1. \tag{3.8}$$

Using (3.6)–(3.7) we have

$$\psi_1'(s) - r \psi_1(s) + \frac{r}{k} \psi_1^2(s) + q_1 E_1 \psi_1(s) + \frac{\alpha \psi_1(s) \psi_2(s)}{1 + a \psi_1(s) + b \psi_2(s)} = \varepsilon \left(-r + \frac{r}{k} \varepsilon + q_1 E_1 \right) < 0$$

if $s \geq 0$ and

$$\begin{aligned} & \psi_1'(s) - r \psi_1(s) + \frac{r}{k} \psi_1^2(s) + q_1 E_1 \psi_1(s) + \frac{\alpha \psi_1(s) \psi_2(s)}{1 + a \psi_1(s) + b \psi_2(s)} \\ & = \varepsilon e^{\lambda_1 s} \left(\lambda - r + \frac{r}{k} \varepsilon e^{\lambda_1 s} + q_1 E_1 \right) \leq \varepsilon e^{\lambda_1 s} \left(\lambda - r + \frac{r}{k} \varepsilon + q_1 E_1 \right) < 0 \end{aligned}$$

if $s \leq 0$. This proves that $(\psi_1(s), \psi_2(s))^T$ is a pair of lower solutions to (3.4).

So far, we have verified all the assumptions in the theory developed in [31]. Therefore, there exists at least one solution in the set Γ , that is, system (1.1) has a traveling wavefront solution connecting $(0, 0)$ to (c_1^*, c_2^*) . This completes the proof. \square

To conclude this paper, we now give an example to illustrate Theorem 3.1. Take $r = 2, k = 100, \alpha = 0.4, a = 5, b = 15, \beta = 0.24, q_1 = 0.994, q_2 = 1.004, d_0 = 0.36, b_0 e^{-0.001\gamma} = 2.36$, and $E_1 = E_2 = 2$. Straightforward calculations show that system (1.1) has the trivial steady state $E_0(0, 0)$ and the positive steady state $E^*(0.1, 0.1)$. One can easily check that (H1)–(H3) are satisfied. Therefore, by Theorem 3.1, system (1.1) has a traveling wavefront solution connecting $(0, 0)$ to $(0.1, 0.1)$ (see Fig. 3).

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