

## Asymptotic speed of propagation of wave fronts in a lattice delay differential equation with global interaction

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In this paper, we derive a lattice model for a single species in a one-dimensional patchy environment with infinite number of patches connected locally by diffusion. Under the assumption that the death and diffusion rates of the mature population are age independent, we show that the dynamics of the mature population is governed by a lattice delay differential equation with global interactions. We study the well-posedness of the initial-value problem and obtain the existence of monotone travelling waves for wave speeds  $c > c_*$ . We show that the minimal wave speed  $c_*$  is also the asymptotic speed of propagation, which depends on the maturation period and the diffusion rate of mature population monotonically.

*Keywords:* lattice equation; age structure; delay; travelling wave; monotone iteration; asymptotic speed of propagation; global interaction.

### 1. Introduction

One of the recently developed continuous models for the dynamics of a single-species population involving age structures and spatial diffusion is given by

$$\frac{\partial}{\partial t}u(t, a, x) + \frac{\partial}{\partial a}u(t, a, x) = \bar{D}(a)\frac{\partial^2}{\partial x^2}u(t, a, x) - \bar{d}(a)u(t, a, x), \quad x \in \mathbf{R}, t > 0, \quad (1.1)$$

where  $u(t, a, x)$  is the population density (at time  $t$ , age  $a$  and spatial location  $x$ ) per unit age and per unit spatial length,  $\bar{D}(a)$  is the diffusion coefficient accounting for spatial dispersion and  $\bar{d}(a)$  is the death rate at age  $a \geq 0$ . See Metz & Diekmann (1986) and So *et al.* (2001).

The total mature population per unit spatial length at time  $t$  and location  $x$  is given by

$$w(t, x) = \int_r^\infty u(t, a, x) da,$$

where  $r$  is the length of maturation period. The equation for  $w$  can be derived using (1.1) as

$$\frac{\partial}{\partial t}w(t, x) = u(t, r, x) + \bar{D}_m\frac{\partial^2}{\partial x^2}w(t, x) - \bar{d}_m w(t, x), \quad x \in \mathbf{R}, t > 0, \quad (1.2)$$

assuming that  $\bar{D}(a) = \bar{D}_m$  and  $\bar{d}(a) = \bar{d}_m$  are constants when  $a \geq r$  and assuming  $u(t, \infty, x) = 0$ . The function  $u(t, r, x)$  can be obtained by Fourier transform (see So *et al.*, 2001 for the derivation) and is given by

$$u(t, r, x) = \frac{1}{\sqrt{4\pi\bar{\alpha}}} e^{-\int_0^r \bar{d}(z) dz} \int_{-\infty}^{\infty} b(w(t-r, y)) e^{-\frac{(x-y)^2}{4\bar{\alpha}}} dy, \quad (1.3)$$

where  $\bar{\alpha} = \int_0^r \bar{D}(z) dz$ , and  $b : \mathbf{R}_+ := [0, \infty) \rightarrow \mathbf{R}_+$  is the birth rate.

Equation (1.2) with (1.3) and

$$b(w) = pwe^{-aw} \quad w \geq 0, \quad (1.4)$$

was studied by So *et al.* (2001), where it was shown that if  $1 < \mu p/d_m \leq e$ , then there exist monotone travelling waves connecting two spatially homogeneous equilibria

$$w^0 = 0 \quad \text{and} \quad w^+ = \frac{1}{a} \ln \frac{\mu p}{d_m}, \quad (1.5)$$

where  $\mu = \exp\{-\int_0^r \bar{d}(z) dz\}$ .

The expression of  $u(t, r, x)$  in (1.3) involves an infinite integral which can be interpreted as a weighted spatial averaging of  $w$  over the entire spatial domain to account for the non-local interaction, and such a weight satisfies, for every fixed  $x \in \mathbf{R}$ ,

$$\frac{1}{\sqrt{4\pi\bar{\alpha}}} \int_{-\infty}^{\infty} e^{-\frac{(x-y)^2}{4\bar{\alpha}}} dy = 1. \quad (1.6)$$

It should be mentioned that the idea of weighted spatial averaging in a model with spatial diffusion and time delay was first introduced by Britton (1990) and further developed in Gourley & Britton (1996) and Gourley (2000).

In this paper, we develop a discrete analogue of model (1.1). Namely, we consider a single-species population with two age classes distributed over a patchy environment consisting of all integer nodes of a one-dimensional lattice. We consider only local interaction through spatial dispersal among adjacent patches. Nevertheless, due to this dispersal of the immature population during the maturation period we show that the dynamics of the mature population is governed by a lattice delay differential system with global interactions. It seems that this is the first time such a lattice system is rigorously derived and the global interaction term with delay adds new difficulties to the qualitative study of the model.

We perhaps should emphasize that by a ‘patch’, we do not necessarily mean a ‘water-surrounded’ island. In fact, the environment favoured by blowfly and their larvae (sheep farms, etc.) might be considered patchy. We refer to Wilcox (1980) and DeAngelis *et al.* (1986) for a long list of ecological scenarios with patch environment.

In Section 2, we derive the lattice system rigorously and prove some of the properties of the system of delay lattice differential equations. In Section 3, we prove the existence of monotone travelling waves which connect the trivial equilibrium 0 and a positive spatially homogeneous equilibrium  $w^+$  under the assumption that the birth function  $b$  is monotone in  $[0, w^+]$ . The classical monotone iteration technique is used in the analysis, with the construction of a pair of upper and lower solutions of the associated characteristic equation

at the trivial equilibrium. Analysis of the characteristic equation also provides the value of the minimal wave speed  $c_*$  whose biological significance will be illustrated in Section 5, where we show that the minimal wave speed  $c_*$  is in fact the asymptotic speed of propagation. Our analysis is a discrete analog of those employed in Diekmann (1978, 1979) and Thieme (1979), which is extended here to handle the global interaction with delay. In Section 4, we discuss the isotropic property of the solutions to the associated Cauchy initial-value problem.

Finally, we mention that more details on other models of population dynamics with interaction between patches and the existence of travelling waves can be found in Smith & Thieme (1991), So *et al.* (2000, 2001), Wu (1996), Wu & Zou (2001) and references therein, while discussions on asymptotic speed can be found in Aronson (1977), Aronson & Weinberger (1975, 1978), Diekmann (1978, 1979), Thieme (1979) and Weinberger (1978).

## 2. Model derivation

Let  $u_j(t, a)$  denote the density of the population of the species of the  $j$ th patch at time  $t \geq 0$  and age  $a \geq 0$ . Using  $D(a)$  and  $d(a)$  to denote the diffusion rate and death rate of the population at age  $a$ , and assuming the patches are located at the integer nodes of a one-dimensional lattice and assuming spatial diffusion occurs only at the nearest neighbourhood and is proportional to the difference of the densities of the population at adjacent patches, we obtain the following model:

$$\frac{\partial}{\partial t} u_j(t, a) + \frac{\partial}{\partial a} u_j(t, a) = D(a)[u_{j+1}(t, a) + u_{j-1}(t, a) - 2u_j(t, a)] - d(a)u_j(t, a),$$

$$t > 0, \quad j \in \mathbf{Z} := \{0, \pm 1, \pm 2, \dots\}. \quad (2.1)$$

It is natural to assume that

$$u_j(t, \infty) = 0 \quad \text{for } t \geq 0, \quad j \in \mathbf{Z}.$$

Clearly,

$$w_j(t) = \int_r^\infty u_j(t, a) \, da$$

is the total mature population at the  $j$ th patch. From (2.1), we obtain

$$\begin{aligned} \frac{dw_j(t)}{dt} &= \int_r^\infty \frac{\partial}{\partial t} u_j(t, a) \, da \\ &= \int_r^\infty \left\{ -\frac{\partial}{\partial a} u_j(t, a) + D(a)[u_{j+1}(t, a) + u_{j-1}(t, a) - 2u_j(t, a)] \right. \\ &\quad \left. - d(a)u_j(t, a) \right\} da. \end{aligned} \quad (2.2)$$

Assuming that the diffusion coefficient and the death rate of mature population are age independent, i.e.

$$D_m = D(a), \quad d_m = d(a) \quad \text{for } a \in [r, \infty)$$

are constants, we obtain from (2.2) and (2.1) that

$$\frac{dw_j(t)}{dt} = u_j(t, r) + D_m[w_{j+1}(t) + w_{j-1}(t) - 2w_j(t)] - d_m w_j(t) \quad \text{for } t > 0. \quad (2.3)$$

In order to obtain a closed system for  $w_j$ , we need to evaluate  $u_j(t, r)$ . For fixed  $s \geq 0$ , let

$$V_j^s(t) = u_j(t, t-s) \quad \text{for } s \leq t \leq s+r. \quad (2.4)$$

Since only the mature population can reproduce, we have

$$V_j^s(s) = u_j(s, 0) = b(w_j(s)),$$

where  $b: \mathbf{R}_+ \rightarrow \mathbf{R}_+$  is the birth function. From (2.1),

$$\begin{aligned} \frac{d}{dt} V_j^s(t) &= \frac{\partial}{\partial t} u_j(t, a)|_{a=t-s} + \frac{\partial}{\partial a} u_j(t, a)|_{a=t-s} \\ &= D(t-s)[V_{j+1}^s(t) + V_{j-1}^s(t) - 2V_j^s(t)] - d(t-s)V_j^s(t). \end{aligned} \quad (2.5)$$

Note that the grid function  $V_j^s(t)$  can be viewed as the discrete spectral of a periodic function  $v^s(t, \omega)$  by discrete Fourier transform (see Goldberg (1965) and Titchmarsh (1962)):

$$v^s(t, \omega) = \frac{1}{\sqrt{2\pi}} \sum_{j=-\infty}^{\infty} e^{-i(j\omega)} V_j^s(t), \quad (2.6)$$

$$V_j^s(t) = \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{\pi} e^{i(j\omega)} v^s(t, \omega) d\omega, \quad (2.7)$$

where  $i$  is the imaginary unit. Applying the discrete Fourier transform (2.6) to (2.5) yields

$$\begin{aligned} \frac{\partial}{\partial t} v^s(t, \omega) &= [D(t-s)(e^{i\omega} + e^{-i\omega} - 2) - d(t-s)]v^s(t, \omega) \\ &= [-4D(t-s)\sin^2(\frac{\omega}{2}) - d(t-s)]v^s(t, \omega). \end{aligned} \quad (2.8)$$

This equation can be solved easily as

$$v^s(t, \omega) = e^{-4\sin^2(\frac{\omega}{2}) \int_s^t D(z-s) dz - \int_s^t d(z-s) dz} v_s(s, \omega).$$

Using the inverse discrete Fourier transform (2.7) we obtain

$$V_j^s(t) = \frac{1}{\sqrt{2\pi}} e^{-\int_s^t d(z-s) dz} \int_{-\pi}^{\pi} e^{i(j\omega) - 4\alpha_s \sin^2(\frac{\omega}{2})} v_s^s(\omega) d\omega,$$

where  $\alpha_s = \int_s^t D(z-s) dz$ . Noting that  $V_j^s(s) = u_j(s, 0) = b(w_j(s))$ , by (2.6), we obtain

$$v_s(s, \omega) = \frac{1}{\sqrt{2\pi}} \sum_{k=-\infty}^{\infty} e^{-i(k\omega)} b(w_k(s)).$$

Hence,

$$V_j^s(t) = \frac{1}{2\pi} e^{-\int_s^t d(z-s) dz} \sum_{k=-\infty}^{\infty} b(w_k(s)) \int_{-\pi}^{\pi} e^{i[(j-k)\omega] - 4\alpha_s \sin^2(\frac{\omega}{2})} d\omega. \tag{2.9}$$

Let

$$s = t - r, \quad \mu = e^{-\int_0^r d(z) dz}, \quad \alpha = \int_0^r D(z) dz.$$

Then (2.9) yields

$$u_j(t, r) = \frac{\mu}{2\pi} \sum_{k=-\infty}^{\infty} \beta_\alpha(j - k) b(w_k(t - r)), \tag{2.10}$$

where

$$\beta_\alpha(l) = \int_{-\pi}^{\pi} e^{i(l\omega) - 4\alpha \sin^2(\frac{\omega}{2})} d\omega = 2e^{-\nu} \int_0^{\pi} \cos(l\omega) e^{\nu \cos \omega} d\omega \quad (\nu := 2\alpha), \tag{2.11}$$

for any  $l \in \mathbf{Z}$ . The following lemma describes the properties of  $\beta_\alpha(l)$ .

LEMMA 2.1 Let  $\beta_\alpha(l)$  be given in (2.11). Then

- (i)  $\beta_\alpha(l) = \beta_\alpha(|l|)$  for  $l \in \mathbf{Z}$ , that is,  $\beta_\alpha(l)$  is an isotropic function for any  $\alpha \geq 0$ ;
- (ii)  $\frac{1}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) = 1$ ;
- (iii)  $\beta_\alpha(l) \geq 0$  if  $\alpha = 0$  and  $l \in \mathbf{Z}$ ;  $\beta_\alpha(l) > 0$  if  $\alpha > 0$  and  $l \in \mathbf{Z}$ .

*Proof.* The conclusion of (i) is obvious. Now we show conclusion (ii). Define

$$g_\alpha(\omega) = e^{-4\alpha \sin^2(\frac{\omega}{2})}, \quad a_l^\alpha = \frac{1}{\pi} \int_{-\pi}^{\pi} \cos(l\omega) g_\alpha(\omega) d\omega.$$

Noting that  $g_\alpha(\omega)$  is an even function of  $\omega$ , we know that  $a_l^\alpha, l = 0, 1, 2, \dots$ , are the coefficients of the Fourier series of  $g_\alpha(\omega)$  and  $a_l^\alpha = a_{-l}^\alpha$ , thus we obtain

$$\begin{aligned} \frac{1}{2\pi} \sum_{k=-\infty}^{\infty} \beta_\alpha(l) &= \frac{a_0^\alpha}{2} + \sum_{l=1}^{\infty} a_l^\alpha \\ &= \frac{a_0^\alpha}{2} + \sum_{l=1}^{\infty} a_l^\alpha \cos(l \cdot 0) \\ &= g_\alpha(0) = 1 \end{aligned}$$

by using the Fourier convergence theorem. This proves (ii).

When  $\alpha = 0$ , then  $\beta_\alpha(0) = 1$  and  $\beta_\alpha(l) = 0$  for  $l = \pm 1, \pm 2, \dots$ . The conclusion of (iii) clearly holds. When  $\alpha > 0$ , the conclusion (iii) is equivalent to

$$f_l(\nu) := \int_0^{\pi} \cos(l\omega) e^{\nu \cos \omega} d\omega > 0 \quad \text{for } \nu > 0, l \in \mathbf{N}^0 := \{0, 1, 2, \dots\} \tag{2.12}$$

by using the isotropic property of  $f_l$ .

A simple differentiation procedure and applications of triangle identities yield, for any integer  $m \geq 1$ , the following:

$$\begin{aligned}
 \frac{df_l(v)}{dv} &= \int_0^\pi \cos(l\omega) \cos \omega e^{v \cos \omega} d\omega = \frac{1}{2}[f_{l+1}(v) + f_{l-1}(v)], \\
 \frac{d^2 f_l(v)}{dv^2} &= \frac{1}{4}[f_{l+2}(v) + 2f_l(v) + f_{l-2}(v)], \\
 \frac{d^3 f_l(v)}{dv^3} &= \frac{1}{8}[f_{l+3}(v) + 3f_{l+1}(v) + 3f_{l-1}(v) + f_{l-3}(v)], \\
 &\vdots \\
 \frac{d^m f_l(v)}{dv^m} &= \frac{1}{m} \left[ f_{l+m}(v) + m f_{l+m-2}(v) + \frac{m(m-1)}{2} f_{l+m-4}(v) + \cdots \right. \\
 &\quad \left. + \frac{m(m-1) \cdots (m-k+1)}{k} f_{l+m-2k}(v) + \cdots + m f_{l-m+2}(v) + f_{l-m}(v) \right].
 \end{aligned} \tag{2.13}$$

Therefore,

$$\begin{aligned}
 f_0(0) &= \pi, \quad f_l(0) = 0, \quad l \neq 0 \text{ and } l \in \mathbf{N}^0, \\
 f_1'(0) &= \frac{\pi}{2}, \quad f_l'(0) = 0, \quad l \neq 1 \text{ and } l \in \mathbf{N}^0, \\
 f_2''(0) &= \frac{\pi}{4}, \quad f_0''(0) = \frac{\pi}{4}, \quad f_l''(0) = 0, \quad l \neq 0, 2 \text{ and } l \in \mathbf{N}^0, \\
 f_3^{(3)}(0) &= \frac{\pi}{8}, \quad f_1^{(3)}(0) = \frac{\pi}{8}, \quad f_l^{(3)}(0) = 0, \quad l \neq 1, 3 \text{ and } l \in \mathbf{N}^0,
 \end{aligned}$$

and in general, for  $m, n \in \mathbf{N}^0$ ,

$$\begin{aligned}
 f_m^{(m)}(0) &= \frac{\pi}{2^m}, \quad f_{m-2}^{(m)}(0) = \frac{m\pi}{2^m}, \dots, \quad f_0^{(m)}(0) = \frac{m(m-1) \cdots (m-n+1)\pi}{2^{mn}}, \\
 f_l^{(m)}(0) &= 0, \quad l \neq 0, 2, \dots, m \text{ and } l \in \mathbf{N}^0, \quad \text{if } m = 2n; \\
 f_m^{(m)}(0) &= \frac{\pi}{2^m}, \quad f_{m-2}^{(m)}(0) = \frac{m\pi}{2^m}, \dots, \quad f_1^{(m)}(0) = \frac{m(m-1) \cdots (m-n+1)\pi}{2^{mn}}, \\
 f_l^{(m)}(0) &= 0, \quad l \neq 1, 3, \dots, m \text{ and } l \in \mathbf{N}^0, \quad \text{if } m = 2n + 1.
 \end{aligned} \tag{2.14}$$

Let

$$v_l = \sup\{\bar{v} \mid v \in (0, \bar{v}), f_l(v) > 0\}.$$

We want to show that  $v_l = \infty$  for  $l \in \mathbf{N}^0$ .

Since

$$\begin{aligned}
 f_0(v) &= \int_0^\pi e^{v \cos \omega} d\omega > 0 \quad \text{for } v > 0, \\
 f_1(v) &= \int_0^\pi \cos \omega e^{v \cos \omega} d\omega = \int_0^{\frac{\pi}{2}} \cos \omega e^{v \cos \omega} d\omega + \int_{\frac{\pi}{2}}^\pi \cos \omega e^{v \cos \omega} d\omega \\
 &= \int_0^{\frac{\pi}{2}} \cos \omega e^{v \cos \omega} d\omega - \int_0^{\frac{\pi}{2}} \cos \omega e^{-v \cos \omega} d\omega > 0 \quad \text{for } v > 0,
 \end{aligned}
 \tag{2.15}$$

we know that  $v_0 = \infty$  and  $v_1 = \infty$ . By (2.14), we obtain

$$f_2(0) = 0, f_2^{(2n-1)}(0) = 0, f_2^{(2n)}(0) > 0 \quad \text{for } n \in \mathbf{N} := \{1, 2, \dots\},$$

which implies  $f_2^{(m)}(v) > 0$  and is strictly increasing in a right neighbourhood of  $v = 0$  for any  $m \in \mathbf{N}^0$ . Thus  $v_2 > 0$ . We claim that  $v_2 = \infty$ . Otherwise,  $v_2 < \infty$  and

$$f_2(v) > 0 \text{ for } v \in (0, v_2), f_2(v_2) = 0, f_2'(v_2) \leq 0.$$

According to the property of  $f_2'$  near zero, there exists  $a_1 \in (0, v_2)$  such that  $f_2'(a_1) = 0$ . But

$$f_2'(a_1) = \int_0^\pi \cos(2\omega) \cos \omega e^{a_1 \cos \omega} d\omega.$$

Note that  $\cos(2\omega)$  is symmetric about  $\omega = \frac{\pi}{2}$ , and  $\cos \omega$  is symmetric about the point  $(\frac{\pi}{2}, 0)$ . Thus,  $\cos(2\omega) \cos \omega$  is symmetric about the point  $(\frac{\pi}{2}, 0)$ . On the other hand,  $e^{a_1 \cos \omega}$  is strictly decreasing on  $[0, \pi]$ . Consequently, it is impossible to have  $f_2'(a_1) = 0$ . Therefore,  $v_2 = \infty$  must hold.

We now consider  $f_3(v)$ . We have from (2.14) that

$$f_3(0) = f_3'(0) = f_3''(0) = 0, f_3^{(2n-1)}(0) > 0, f_3^{(2n)}(0) = 0 \quad \text{for } n \geq 2.$$

Similarly, we derive that

$$f_3^{(m)}(v) > 0 \quad \text{for small } v > 0 \text{ and } m \geq 2,$$

and consequently,

$$f_3'(v) > 0, f_3(v) > 0 \quad \text{for small } v > 0.$$

If  $v_3 \neq \infty$ , then there is  $a_2 \in (0, v_3)$  such that

$$f_3'(a_2) = \int_0^\pi \cos(3\omega) \cos \omega e^{a_2 \cos \omega} d\omega = 0.$$

But again  $\cos(3\omega)$  is symmetric about the point  $(\frac{\pi}{2}, 0)$ , and thus a similar argument as above shows that  $f_3'(a_2) = 0$  is impossible. Therefore,  $v_3 = \infty$ .

Continuing the above procedure, we can obtain  $v_m = \infty$  for  $m \in \mathbf{N}^0$ . This completes the proof. □

### 3. Existence of travelling waves

In this section, we assume that the birth function  $b : \mathbf{R}_+ \rightarrow \mathbf{R}_+$  satisfies the following properties:

$(H_b)$ :  $b$  is continuous and

- (i)  $b(0) = 0$ ,  $b'(0) > \frac{d_m}{\mu}$ ,  $b(w) \leq b'(0)w$  for  $w \in \mathbf{R}_+$ ;
- (ii)  $b$  is non-decreasing on  $[0, K]$ , and  $\mu b(w) = d_m w$  has a unique solution  $w^+ \in (0, K]$ .

Note that  $\mu = \exp(-\int_0^r \bar{d}(z) dz)$  and hence  $b'(0) > d_m/\mu$  holds only when  $\int_0^r \bar{d}(z) dz$  is sufficiently small. In the case this term is large (this is particularly true if the maturation time is too long), then system (2.3) will not have a non-zero equilibrium and we suspect that every solution of (2.3) converges to zero, though this has not been verified yet.

A travelling wave of (2.3) is a solution of (2.3) of the form

$$w_j(t) = \phi(s), \quad (3.1)$$

where  $s = j + ct$  and  $c > 0$  is the wave speed. Substituting (3.1) into (2.3) yields

$$\begin{aligned} c \frac{d\phi(s)}{ds} &= D_m[\phi(s+1) + \phi(s-1) - 2\phi(s)] - d_m\phi(s) \\ &\quad + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) b(\phi(s+l-cr)). \end{aligned} \quad (3.2)$$

Denoting the characteristic equation of (3.2) at  $w^0 := 0$  by  $\Delta(\lambda, c, w^0) = 0$ , we have

$$\Delta(\lambda, c, w^0) \equiv -c\lambda + D_m(e^\lambda + e^{-\lambda} - 2) - d_m + \frac{b'(0)\mu}{2\pi} \left( \sum_{l=-\infty}^{\infty} \beta_\alpha(l) e^{\lambda l} \right) e^{-\lambda cr}, \quad (3.3)$$

which can be simplified as follows. Let

$$S(\alpha) = \frac{1}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) e^{\lambda l} = \frac{1}{\pi} \int_0^\pi \left( \sum_{l=-\infty}^{\infty} e^{\lambda l} \cos(l\omega) \right) e^{-4\alpha \sin^2(\frac{\omega}{2})} d\omega, \quad (3.4)$$

then

$$\begin{aligned} \frac{dS(\alpha)}{d\alpha} &= \frac{1}{\pi} \sum_{l=-\infty}^{\infty} e^{\lambda l} \int_0^\pi \cos(l\omega) \left[ -4 \sin^2\left(\frac{\omega}{2}\right) \right] e^{-4\alpha \sin^2(\frac{\omega}{2})} d\omega \\ &= \frac{2}{\pi} \sum_{l=-\infty}^{\infty} e^{\lambda l} \int_0^\pi \cos(l\omega) (\cos \omega - 1) e^{-4\alpha \sin^2(\frac{\omega}{2})} d\omega \\ &= \frac{1}{\pi} \sum_{l=-\infty}^{\infty} e^{\lambda l} \int_0^\pi \{\cos[(l+1)\omega] + \cos[(l-1)\omega] - 2\cos(l\omega)\} e^{-4\alpha \sin^2(\frac{\omega}{2})} d\omega \\ &= S(\alpha) (e^{-\lambda} + e^\lambda - 2). \end{aligned}$$

Since  $S(0) = 1$ ,

$$S(\alpha) = \exp\{[e^{-\lambda} + e^\lambda - 2]\alpha\} = e^{2(\cosh \lambda - 1)\alpha}. \quad (3.5)$$

Thus, we obtain

$$\frac{1}{2\pi} \sum_{l=-\infty}^{\infty} \beta_{\alpha}(l)e^{\lambda l} = e^{2(\cosh \lambda - 1)\alpha}. \tag{3.6}$$

Therefore, we have

$$\Delta(\lambda, c, w^0) = b'(0)\mu e^{2\alpha(\cosh \lambda - 1) - \lambda cr} - c\lambda + D_m(e^{\lambda} + e^{-\lambda} - 2) - d_m.$$

Differentiating with respect to  $\lambda$ , we obtain

$$\frac{\partial}{\partial \lambda} \Delta(\lambda, c, w^0) = b'(0)\mu(2\alpha \sinh \lambda - cr)e^{2\alpha(\cosh \lambda - 1) - \lambda cr} - c + D_m(e^{\lambda} - e^{-\lambda}),$$

and

$$\begin{aligned} \frac{\partial^2}{\partial \lambda^2} \Delta(\lambda, c, w^0) &= b'(0)\mu(2\alpha \sinh \lambda - cr)^2 e^{2\alpha(\cosh \lambda - 1) - \lambda cr} \\ &\quad + b'(0)\mu(2\alpha \cosh \lambda)e^{2\alpha(\cosh \lambda - 1) - \lambda cr} + D_m(e^{\lambda} + e^{-\lambda}). \end{aligned}$$

Since  $\frac{\partial^2}{\partial \lambda^2} \Delta(\lambda, c, w^0) > 0$  for  $\lambda \in \mathbf{R}$ , the graph of  $\Delta(\lambda, c, w^0)$  as a function of  $\lambda \in \mathbf{R}$  is convex. Furthermore, it can be easily verified that

$$\begin{aligned} \lim_{\lambda \rightarrow \infty} \Delta(\lambda, c, w^0) &= +\infty, \quad \Delta(0, c, w^0) = b'(0)\mu - d_m > 0, \\ \frac{\partial}{\partial \lambda} \Delta(\lambda, c, w^0)|_{\lambda=0} &= -(b'(0)\mu r + 1)c < 0 \end{aligned} \tag{3.7}$$

when  $c > 0$  and  $(H_b)$  holds. In addition, we can show that  $\Delta(\lambda, 0, w^0) > 0$  and  $\Delta(\lambda, \infty, w^0) < 0$  for any given  $\lambda$ , therefore we can make the following observations.

LEMMA 3.1 There exists a pair of  $c_*$  and  $\lambda_*$  such that

- (i)  $\Delta(\lambda_*, c_*, w^0) = 0, \quad \frac{\partial}{\partial \lambda} \Delta(\lambda_*, c_*, w^0) = 0;$
- (ii) for  $0 < c < c_*$  and any  $\lambda > 0, \Delta(\lambda, c, w^0) > 0;$
- (iii) for any  $c > c_*$ , the equation  $\Delta(\lambda, c, w^0) = 0$  has two positive real roots  $0 < \lambda_1 < \lambda_2$ , and there exists  $\epsilon_0 > 0$  such that for any  $\epsilon \in (0, \epsilon_0)$  with

$$0 < \lambda_1 < \lambda_1 + \epsilon < \lambda_2,$$

we have

$$\Delta(\lambda_1 + \epsilon, c, w^0) < 0. \tag{3.8}$$

We now define  $C = C(\mathbf{R}, [0, K])$ , and

$$S = \left\{ \phi \in C : \begin{array}{l} \text{(i) } \phi(s) \text{ is non-decreasing for } s \in \mathbf{R}, \\ \text{(ii) } \lim_{s \rightarrow -\infty} \phi(s) = w^0, \quad \lim_{s \rightarrow \infty} \phi(s) = w^+, \end{array} \right\}$$

and an operator on  $C$  as

$$H(\phi)(s) = \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_{\alpha}(l)b(\phi(s+l-cr)), \quad \phi \in C, s \in \mathbf{R}.$$

The following lemma summarizes some useful properties of  $H$ .

LEMMA 3.2 Assume that  $b : \mathbf{R}_+ \rightarrow \mathbf{R}_+$  satisfies  $(H_b)$ . Then we have

- (i) if  $\phi \in S$ , and  $\phi(s) \geq 0$  for  $s \in \mathbf{R}$ , then  $H(\phi)(s) \geq 0$  for  $s \in \mathbf{R}$ ;
- (ii) if  $\phi \in S$ , then  $H(\phi)(s)$  is non-decreasing for  $s \in \mathbf{R}$ ;
- (iii)  $H(\psi)(s) \leq H(\phi)(s)$  for  $s \in \mathbf{R}$  provided that  $\psi, \phi \in C$  and  $\psi(s) \leq \phi(s) \leq K$  for  $s \in \mathbf{R}$ .

*Proof.* If  $\phi, \psi \in C$  and  $\psi(s) \leq \phi(s) \leq K$  for  $s \in \mathbf{R}$ , then

$$\psi(s + l - cr) \leq \phi(s + l - cr) \leq K \quad \text{for } s \in \mathbf{R}, l \in \mathbf{Z}.$$

Therefore, by the positivity of  $\beta_\alpha(l)$  and monotonicity of  $b$  on  $[0, K]$ , we have

$$H(\phi)(s) \geq H(\psi)(s) \quad \text{for } s \in \mathbf{R}.$$

This proves (iii). The proofs of (i) and (ii) are straightforward. □

DEFINITION 3.1 A function  $U \in C$  is called an upper solution of (3.2) if it is differentiable almost everywhere (a.e.) and satisfies the inequality

$$cU'(s) \geq D_m[U(s + 1) + U(s - 1) - 2U(s)] - d_m U(s) + H(U)(s) \quad \text{a.e. in } \mathbf{R}.$$

Similarly, a function  $L \in C$  is called a lower solution of (3.2) if it is differentiable almost everywhere and satisfies

$$cL'(s) \leq D_m[L(s + 1) + L(s - 1) - 2L(s)] - d_m L(s) + H(L)(s) \quad \text{a.e. in } \mathbf{R}.$$

Suppose that

$$U(s) = \begin{cases} w^+, & s \geq 0, \\ e^{\lambda_1 s} w^+, & s \leq 0, \end{cases} \tag{3.9}$$

and

$$L(s) = \begin{cases} 0, & s \geq 0, \\ \zeta(1 - e^{\epsilon s})e^{\lambda_1 s}, & s \leq 0, \end{cases} \tag{3.10}$$

where  $\lambda_1, \epsilon$  are given as in Lemma 3.1, and  $\zeta > 0$  is chosen so that  $L(s) \leq U(s)$  for  $s \in \mathbf{R}$ . Clearly, we have  $0 \leq L(s) \leq U(s) \leq w^+ \leq K$  and  $L(s) \neq 0$  for  $s \in \mathbf{R}$ .

LEMMA 3.3  $U$  given by (3.9) and  $L$  given by (3.10) are a pair of upper and lower solutions of (3.2).

*Proof.* If  $s \geq 0$ , then we have from (iii) of Lemma 3.2 and the fact that  $\frac{1}{2\pi} \sum_{-\infty}^{\infty} \beta_\alpha(l) = 1$  and  $b(w) \leq b(w^+)$  for  $w \leq w^+$  the following:

$$\begin{aligned} & -c \frac{dU(s)}{ds} + D_m[U(s + 1) + U(s - 1) - 2U(s)] - d_m U(s) + H(U)(s) \\ & \leq 0 + D_m(w^+ + w^+ - 2w^+) - d_m w^+ + \frac{b(w^+)\mu}{2\pi} \sum_{-\infty}^{\infty} \beta_\alpha(l) = 0. \end{aligned}$$

Note that  $U(s) \leq e^{\lambda_1 s} w^+$  for  $s \in \mathbf{R}$  and  $b(\phi) \leq b'(0)\phi$  for  $\phi \geq 0$ . Therefore, if  $s \leq 0$ , then

$$\begin{aligned} & -c \frac{dU(s)}{ds} + D_m[U(s+1) + U(s-1) - 2U(s)] - d_m U(s) + H(U)(s) \\ \leq & -c\lambda_1 e^{\lambda_1 s} w^+ + D_m w^+ [e^{\lambda_1(s+1)} + e^{\lambda_1(s-1)} - 2e^{\lambda_1 s}] \\ & - d_m w^+ e^{\lambda_1 s} + \frac{b'(0)\mu}{2\pi} \sum_{-\infty}^{\infty} \beta_\alpha(l) U(s+l-cr) \\ \leq & e^{\lambda_1 s} w^+ \left\{ -c\lambda_1 + D_m [e^{\lambda_1} + e^{\lambda_1} - 2] - d_m + \frac{b'(0)\mu}{2\pi} \sum_{-\infty}^{\infty} \beta_\alpha(l) e^{\lambda_1(l-cr)} \right\} \\ = & 0. \end{aligned}$$

Hence,  $U$  is an upper solution of (3.2).

Note that  $L(s) \geq 0$  and thus  $H(L)(s) \geq 0$  for  $s \in \mathbf{R}$ . Therefore, for  $s \geq 0$ , we have

$$-c \frac{dL(s)}{ds} + D_m[L(s+1) + L(s-1) - 2L(s)] - d_m L(s) + H(L)(s) \geq 0.$$

Note also that  $\zeta(1 - e^{\epsilon s})e^{\lambda_1 s} \leq 0$  for  $s \geq 0$  and

$$L(s) \geq \zeta(1 - e^{\epsilon s})e^{\lambda_1 s} =: h(s) \quad \text{for } s \in \mathbf{R}.$$

Therefore,

$$H(L)(s) \geq H(h)(s) \quad \text{for } s \in \mathbf{R}.$$

Consequently, if  $s \leq 0$ , then

$$\begin{aligned} & -c \frac{dL(s)}{ds} + D_m[L(s+1) + L(s-1) - 2L(s)] - d_m L(s) + H(L)(s) \\ \geq & -c\lambda_1 \zeta e^{\lambda_1 s} + c(\lambda_1 + \epsilon) \zeta e^{(\lambda_1 + \epsilon)s} + D_m[\zeta(1 - e^{\epsilon(s+1)})e^{\lambda_1(s+1)} \\ & + \zeta(1 - e^{\epsilon(s-1)})e^{\lambda_1(s-1)} - 2\zeta(1 - e^{\epsilon s})e^{\lambda_1 s}] - d_m \zeta(1 - e^{\epsilon s})e^{\lambda_1 s} + H(h)(s) \\ = & e^{\lambda_1 s} \Delta(\lambda_1, c, w^0) - \zeta \Delta(\lambda_1 + \epsilon, c, w^0) e^{(\lambda_1 + \epsilon)s} > 0. \end{aligned}$$

Hence,  $L$  is a lower solution of (3.2). This completes the proof. □

We now consider the following equivalent form of (3.2):

$$\frac{d\phi(s)}{ds} + \delta\phi(s) = F(\phi)(s), \tag{3.11}$$

where

$$F(\phi)(s) = \left( \delta - \frac{d_m}{c} - \frac{2D_m}{c} \right) \phi(s) + \frac{D_m}{c} [\phi(s+1) + \phi(s-1)] + \frac{1}{c} H(\phi)(s),$$

and  $\delta > 0$  is chosen so that

$$\delta - \frac{d_m}{c} - \frac{2D_m}{c} > 0.$$

Then,  $F(\phi)(s) \geq F(\psi)(s)$  for  $s \in \mathbf{R}$  provided that  $\phi(s) \geq \psi(s)$  for  $s \in \mathbf{R}$ . Moreover,

$$F(w^0) = \delta w^0, \quad F(w^+) = \delta w^+.$$

For bounded solutions  $\phi : \mathbf{R} \rightarrow \mathbf{R}$ , (3.11) is equivalent to

$$\phi(s) = e^{-\delta s} \int_{-\infty}^s e^{\delta t} F(\phi)(t) dt. \quad (3.12)$$

It is thus natural to define an operator  $T : S \rightarrow C$  by

$$(T\phi)(s) = e^{-\delta s} \int_{-\infty}^s e^{\delta t} F(\phi)(t) dt, \quad \phi \in S, t \in \mathbf{R}. \quad (3.13)$$

And it is straightforward to verify the following lemma.

LEMMA 3.4 The operator  $T$  defined in (3.13) has the following properties:

- (i) if  $\phi \in S$ , then  $T\phi \in S$ ;
- (ii) if  $\phi$  is an upper (a lower) solution of (3.2), then  $\phi(s) \geq (T\phi)(s)$  ( $\phi(s) \leq (T\phi)(s)$ ) for  $s \in \mathbf{R}$ ;
- (iii) if  $\phi(s) \geq \psi(s)$  for  $s \in \mathbf{R}$ , then  $(T\phi)(s) \geq (T\psi)(s)$  for  $s \in \mathbf{R}$ ;
- (iv) if  $\phi$  is an upper (a lower) solution of (3.2), then  $T\phi$  is also an upper (a lower) solution of (3.2).

We now construct a series of functions by the following iterative scheme:  $U_n = TU_{n-1}$ ,  $n \geq 1$ , with  $U_0 = U$ . By Lemma 3.4, we have

$$w^0 \leq L(s) \leq \dots \leq U_n(s) \leq U_{n-1}(s) \leq \dots \leq U(s) \leq w^+.$$

Using Lebesgue's dominated convergence theorem, we know that the limit function  $U_*(s) = \lim_{n \rightarrow \infty} U_n(s)$  exists and is a fixed point of  $T$ . This gives a solution of (3.2). Furthermore,  $U_*$  lies in  $S$  and is non-decreasing, and satisfies

$$\lim_{s \rightarrow -\infty} U_*(s) = w^0, \quad \lim_{s \rightarrow \infty} U_*(s) = w^+. \quad (3.14)$$

Summarizing the above discussions, we obtain the following existence theorem of travelling waves.

THEOREM 3.1 Assume that  $b : \mathbf{R}_+ \rightarrow \mathbf{R}_+$  satisfies  $(H_b)$ . Then there exists  $c_* > 0$ , such that for every  $c > c_*$ , (2.3) has a monotone travelling wave solution  $\phi : \mathbf{R} \rightarrow \mathbf{R}$  satisfying the boundary condition

$$\lim_{s \rightarrow -\infty} \phi(s) = w^0, \quad \lim_{s \rightarrow \infty} \phi(s) = w^+.$$

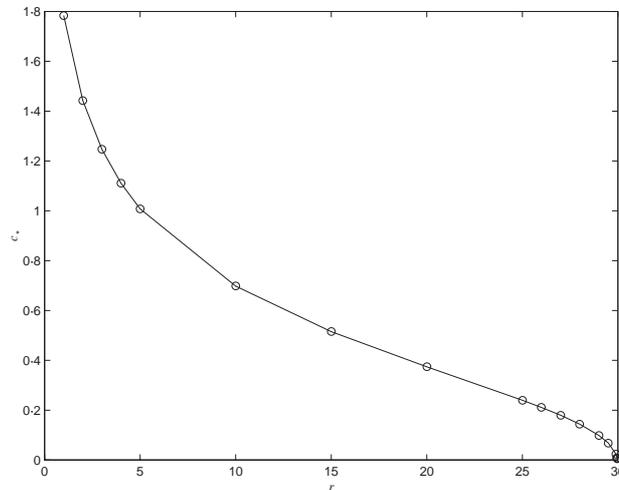


FIG. 1. The graph of  $c_* = c_*(r)$  as a function of  $r$  is a decreasing curve and  $x_*(r) \rightarrow 0$  when  $r \rightarrow 30$ , where  $b'(0) = 2$ ,  $d_i = 0.1$ ,  $d_m = 0.1$ ,  $D_i = 1$ ,  $D_m = 1$ ,  $\alpha = r$ ,  $\mu = \exp(-r)$ .

REMARK 3.1 The value of  $c_*$  is given by Lemma 3.1. For reasons to be explained in Section 5, it is important to know how its value depends on the parameters involved. This can be easily achieved numerically using Maple. For example, let

$$b'(0) = 2, \quad d_i = 0.1, \quad D_i = 1, \quad \alpha = \int_0^r D_i \, da = r, \quad \mu = e^{-\int_0^r d_i \, da} = e^{-r},$$

$d_m = 0.1$ , and fix  $D_m = 1$ . Then we can solve the system

$$\Delta(\lambda, c, w^0) = 0, \quad \frac{\partial}{\partial \lambda} \Delta(\lambda, c, w^0) = 0 \quad (3.15)$$

to obtain a function  $c_*(r)$ , and we find that  $c_* = c_*(r)$  is a decreasing function of  $r \geq 0$ , as shown in Fig. 1. Similarly, if we fix  $r = 2$ , and solve the system (3.15) for  $c_* = c_*(D_m)$ , we find that  $c_* = c_*(D_m)$  is an increasing function of  $D_m$ , see Fig. 2.

#### 4. Existence and isotropic properties of IVBs

In this section, we shall investigate the existence and isotropic properties of solutions for the initial-value problem of model (2.3) with  $u_j(t, r)$  defined in (2.10). For the convenience

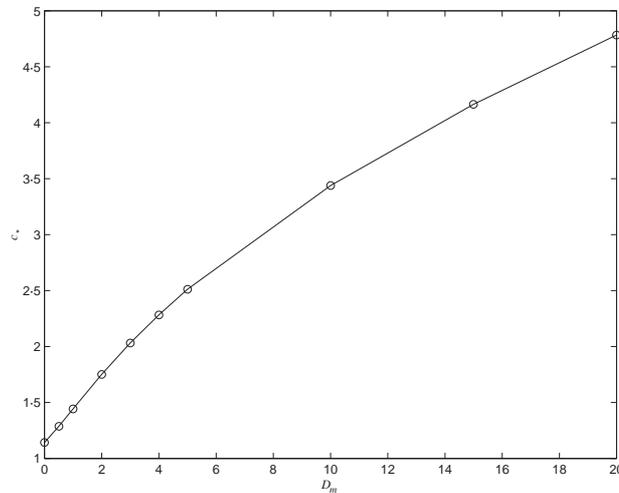


FIG. 2. The graph of  $c_* = c_*(D_m)$  as a function of  $D_m$  is an increasing curve, where  $b'(0) = 2$ ,  $r = 2$ ,  $d_i = 0.1$ ,  $d_m = 0.1$ ,  $D_i = 1$ ,  $\alpha = 2$ ,  $\mu = \exp(-2)$ .

of discussion, we first list some notation to be used:

$$B_N = \{j \in \mathbf{N} \mid |j| \leq N, N \in \mathbf{N}\},$$

$$C_K^+[-r, 0] = C([-r, 0], [0, K]), \quad C_K^+[-r, T] = C([-r, T], [0, K]),$$

$$w_j(t) = w(t, j), \quad j \in \mathbf{Z},$$

$$W(t) = W(t, \cdot) = \{w_j(t)\}_{j \in \mathbf{Z}},$$

$\text{supp } W(t, \cdot) = \{j \mid w(t, j) \neq 0\}$  is the support of  $W(t, \cdot)$ ,

$$W(t) \geq V(t) \text{ if } w_j(t) \geq v_j(t) \text{ for } j \in \mathbf{Z},$$

$$W(t) > V(t) \text{ if } W(t) \geq V(t) \text{ and } w_j(t) > v_j(t) \text{ for } j \in \text{supp } V(t, \cdot).$$

Also we say  $W$  is isotropic on an interval  $I$  if  $w_j(t) = w_{-j}(t)$  for  $j \in \mathbf{Z}$  and  $t \in I$ .

In the remaining part of this paper, we assume that the birth function  $b$  has the following properties:

$(H'_b)$ :  $b : \mathbf{R}_+ \rightarrow \mathbf{R}_+$  is continuous and

- (i)  $b(0) = 0$ ,  $b'(0) > \frac{d_m}{\mu}$ ,  $|b(w) - b(v)| \leq b'(0)|w - v|$  for  $w, v \in \mathbf{R}_+$ ;
- (ii)  $b$  is non-decreasing on  $[0, K]$ , and  $\mu b(w) = d_m w$  has a unique solution  $w^+ \in (0, K]$ ;
- (iii)  $\mu b(w) > d_m w$  for  $w \in (0, w^+)$ , and  $\mu b(w) < d_m w$  for  $w \in (w^+, \infty)$ .

Clearly, the birth function  $b(w) = pwe^{-aw}$  in Nicholson's blowfly model satisfies the above assumptions, when the parameters are in appropriate ranges.

The initial-value problem of (2.3) can be written as

$$\begin{cases} w_j(t) = e^{-\delta t} w_j(0) + \int_0^t e^{-\delta(t-s)} \{D_m[w_{j+1}(s) + w_{j-1}(s)] \\ \quad + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l)b(w_{l+j}(s-r))\} ds, & j \in \mathbf{Z}, t \geq 0, \\ w_j(t) = w_j^o(t), & j \in \mathbf{Z}, t \in [-r, 0], \end{cases} \quad (4.1)$$

where  $\delta = 2D_m + d_m$ , and  $w_j^o(t), t \in [-r, 0], j \in \mathbf{Z}$  are given initial data. A simple change of variable yields an equivalent form of (2.3) as

$$\begin{aligned} w_j(t) = e^{-\delta t} w_j(0) + \int_0^t e^{-\delta s} \{D_m[w_{j+1}(t-s) + w_{j-1}(t-s)] \\ + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l)b(w_{l+j}(t-s-r))\} ds, & j \in \mathbf{Z}, t \geq 0. \end{aligned} \quad (4.2)$$

The existence and isotropic properties of the solution to the initial-value problem is given by the following theorem.

**THEOREM 4.1** For any given function

$$W^o = \{w_j^o\}_{j \in \mathbf{Z}}, \quad w_j^o \in C_K^+[-r, 0], \quad j \in \mathbf{Z},$$

(4.1) has a unique solution  $W(t) = \{w_j(t)\}_{j \in \mathbf{Z}}$  with  $w_j \in C_K^+[-r, \infty)$ . If  $W^o$  is isotropic on  $\mathbf{Z}$  on  $[-r, 0]$ , then  $W$  is isotropic on  $\mathbf{R}_+$ .

*Proof.* For  $W^o = \{w_j^o\}_{j \in \mathbf{Z}}$  with  $w_j^o \in C_K^+[-r, 0]$  and for every  $T \in (0, \infty]$ , define a set

$$S_T = \{W = \{w_j\}_{j \in \mathbf{Z}} \mid w_j \in C_K^+[-r, T), w_j(t) = w_j^o(t), t \in [-r, 0]\}$$

and an operator  $F^T = \{F_j^T\}_{j \in \mathbf{Z}}$  on  $S_T$ , where for every  $W \in S_T, j \in \mathbf{Z}$ ,

$$F_j^T[W](t) = \begin{cases} e^{-\delta t} w_j(0) + \int_0^t e^{-\delta(t-s)} \{D_m[w_{j+1}(s) + w_{j-1}(s)] \\ \quad + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l)b(w_{l+j}(s-r))\} ds, & j \in \mathbf{Z}, t \geq 0, \\ w_j^o(t), & i \in \mathbf{Z}, t \in [-r, 0]. \end{cases}$$

Clearly, for fixed  $T > 0, F^T[W](t)$  is continuous in  $t \in [-r, T)$ . Note that if  $W \in S^T$ , then we have

$$\begin{aligned} 0 \leq F_j^T[W](t) &\leq e^{-\delta t} K + [2D_m K + \mu b(K)] \int_0^t e^{-\delta(t-s)} ds \\ &\leq e^{-\delta t} K + \frac{1}{\delta} [2D_m K + d_m K] (1 - e^{-\delta t}) = K, \end{aligned}$$

for  $t \in [0, T)$  and  $j \in \mathbf{Z}$ . Therefore,  $F^T(S_T) \subseteq S_T$ .

For any  $W \in S_T$  and  $\lambda > 0$ , define a norm as follows:

$$\|W\|_\lambda := \sup_{t \in [0, T], j \in \mathbf{Z}} |w_j(t)| e^{-\lambda t}.$$

For any  $W, \bar{W} \in S_T$ , let  $\phi_j(t) = w_j(t) - \bar{w}_j(t)$  and  $\Phi(t) = \{\phi_j(t)\}_{j \in \mathbf{Z}}$ , then for  $t \geq 0$  we have

$$\begin{aligned} & F_j^T[W](t) - F_j^T[\bar{W}](t) \\ &= \int_0^t e^{-\delta(t-s)} \{D_m[\phi_{j+1}(s) + \phi_{j-1}(s)] \\ & \quad + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) [b(w_{l+j}(s-r)) - b(\bar{w}_{l+j}(s-r))]\} ds, \\ &= \int_0^t e^{-\delta(t-s)} D_m[\phi_{j+1}(s) + \phi_{j-1}(s)] ds \\ & \quad + \begin{cases} \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) \int_0^{t-r} e^{-\delta(t-s-r)} [b(w_{l+j}(s)) - b(\bar{w}_{l+j}(s))] ds, & t-r > 0, \\ 0, & t-r \leq 0. \end{cases} \end{aligned}$$

When  $t - r > 0$ , using property (i) in  $(H'_b)$ , we have

$$\begin{aligned} |F_j^T[W](t) - F_j^T[\bar{W}](t)| &\leq \int_0^t e^{-\delta(t-s)} D_m[|\phi_{j+1}(s)| + |\phi_{j-1}(s)|] ds \\ & \quad + \frac{\mu b'(0)}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) \int_0^{t-r} e^{-\delta(t-s-r)} |\phi_{l+j}(s)| ds \end{aligned}$$

which leads to

$$\begin{aligned} |F_j^T[W](t) - F_j^T[\bar{W}](t)| e^{-\lambda t} &\leq D_m \int_0^t e^{-\lambda s} e^{-\lambda(t-s)} [|\phi_{j+1}(s)| + |\phi_{j-1}(s)|] ds \\ & \quad + \frac{\mu b'(0)}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) \int_0^{t-r} e^{-\lambda s} e^{-\lambda(t-s)} |\phi_{l+j}(s)| ds. \end{aligned}$$

Thus

$$\begin{aligned} & \|F^T[W](t) - F^T[\bar{W}](t)\|_\lambda \\ &\leq 2D_m \|\Phi\|_\lambda \int_0^t e^{-\lambda(t-s)} ds + \mu b'(0) \|\Phi\|_\lambda \int_0^{t-r} e^{-\lambda(t-s)} ds \tag{4.3} \\ &= \frac{2D_m}{\lambda} \|\Phi\|_\lambda (1 - e^{-\lambda t}) + \frac{\mu b'(0)}{\lambda} \|\Phi\|_\lambda (e^{-\lambda r} - e^{-\lambda t}). \end{aligned}$$

Since

$$\lim_{\lambda \rightarrow \infty} \frac{2D_m}{\lambda} (1 - e^{-\lambda t}) + \frac{\mu b'(0)}{\lambda} (e^{-\lambda r} - e^{-\lambda t}) = 0 \tag{4.4}$$

and  $S_T$  is a Banach space with norm  $\|\cdot\|_\lambda$ , we have from (4.3) and (4.4) that  $F^T$  is a contracting map and hence has a unique fixed point  $W$  in  $S_T$  if  $\lambda > 0$  is sufficiently large. This shows that a unique solution of (4.1) exists on  $[0, T]$  for any  $T > 0$ , which leads to the uniqueness and existence of solution  $W$  to (4.1) on  $[0, \infty)$ .

The isotropic property of the solution on  $[-r, \infty)$  starting from an isotropic initial data  $W^o$  on  $[-r, 0]$  can be verified by noting that the subspace of  $S_T^I$  of  $S_T$ , consisting of all elements which are isotropic on  $[-r, \infty)$ , is closed and  $F^T(S_T^I) \subset S_T^I$ .  $\square$

### 5. Asymptotic speed of wave propagation

To start this section, we first rewrite  $\Delta(\lambda, c, 0) = 0$  as

$$1 = \frac{1}{\delta + \lambda c} \left[ D_m(e^\lambda + e^{-\lambda}) + \mu b'(0)e^{2\alpha(\cosh \lambda - 1) - \lambda c} \right]. \quad (5.1)$$

Let

$$L_c(\lambda) = \frac{1}{\delta + \lambda c} \left[ D_m(e^\lambda + e^{-\lambda}) + \mu b'(0)e^{2\alpha(\cosh \lambda - 1) - \lambda c} \right],$$

then the minimum speed defined in Lemma 3.1 can also be written as

$$c_* := \inf\{c > 0 \mid L_c(\lambda) = 1 \text{ for some } \lambda \in \mathbf{R}_+\}.$$

Define

$$\bar{L}_c(\lambda) = \frac{1}{\delta + \lambda c} \left[ D_m(e^\lambda + e^{-\lambda}) + \mu b'(0)e^{2\alpha(\cosh \lambda - 1)} \right],$$

$$\bar{c}_* = \inf\{c > 0 \mid \bar{L}_c(\lambda) = 1 \text{ for some } \lambda \in \mathbf{R}_+\},$$

$$\bar{\Delta}(\lambda, c, 0) = D_m(e^\lambda + e^{-\lambda}) + \mu b'(0)e^{2\alpha(\cosh \lambda - 1)} - \delta - \lambda c.$$

A similar analysis to that for Lemma 3.1 shows that there exists  $\bar{\lambda}_* \in \mathbf{R}_+$  such that  $\bar{\Delta}(\bar{\lambda}_*, \bar{c}_*, 0) = 0$  and  $(\bar{\lambda}_*, \bar{c}_*)$  is the solution of

$$\bar{\Delta}(\bar{\lambda}_*, \bar{c}_*, 0) = 0, \quad \frac{\partial}{\partial \lambda} \bar{\Delta}(\bar{\lambda}_*, \bar{c}_*, 0) = 0. \quad (5.2)$$

In the following, we will show that  $c_*$  is the asymptotic speed of wave propagation in the sense that the solution of (4.1) satisfies

$$\lim_{t \rightarrow \infty} \sup\{w_j(t) \mid |j| \geq ct\} = 0 \quad \text{for } c \in (c_*, \infty), \quad (5.3)$$

$$\liminf_{t \rightarrow \infty} \min\{w_j(t) \mid |j| \leq ct\} \geq w^+ \quad \text{for } c \in (0, c_*), \quad (5.4)$$

if the initial function  $W^o$  satisfies some biologically realistic conditions to be specified in the following theorems.

**THEOREM 5.1** Assume that

(i)  $W^o = \{w_j^o\}_{j \in \mathbf{Z}}$ , with  $w_j^o \in C_K^+[-r, 0]$  for  $j \in \mathbf{Z}$ , is isotropic on  $[-r, 0]$ , and there exists an integer  $\bar{N} \in \mathbf{N}$  such that  $\text{supp } W^o(t, \cdot) \subseteq B_{\bar{N}}$  for  $t \in [-r, 0]$ ;

(ii)  $r > 0$  is sufficiently small so that

$$e^{(\delta + \lambda_* \bar{c}_*)r} - 1 - e^{\delta r} \leq 0,$$

or

$$\mu b'(0)e^{2\alpha(\cosh \lambda_* - 1)} [e^{(\delta + \lambda_* \bar{c}_*)r} - 1 - e^{\delta r}] \leq D_m.$$

Then for any  $c > c_*$ , we have

$$\lim_{t \rightarrow \infty} \sup\{w_j(t) \mid |j| \geq ct\} = 0.$$

*Proof.* Define a sequence of maps by

$$W^{(n)} = F^\infty[W^{(n-1)}](t) \quad \text{for } n \in \mathbf{N}, \quad t \geq -r, \quad W^{(0)}(t) = \{w_j^{(0)}(t)\}_{j \in \mathbf{Z}},$$

$$w_j^{(0)}(t) = \begin{cases} w_j^o(t), & t \in [-r, 0], \\ w_j^o(0), & t \in (0, \infty). \end{cases}$$

Then  $W^{(0)}$  is isotropic and  $\text{supp } W^{(0)}(t, \cdot) \subset B_{\bar{N}}$  for  $t \geq -r$ . By an argument similar to that for Theorem 4.1, we obtain the convergence of  $\{W^{(n)}\}$  on  $[0, \infty)$ . Let

$$W(t) = \lim_{n \rightarrow \infty} W^{(n)}(t), \quad t \in [0, \infty).$$

Then  $W$  is a solution of (4.1) with the isotropic property due to Lebesgue’s theorem of dominated convergence.

Using the assumption on  $W^{(0)}$ , we can find  $M > 0$  and  $N \in \mathbf{N}$  such that

$$w_j^{(0)}(t)e^{\lambda j} \leq Me^{\lambda N} \quad \text{for } t \geq -r, \quad j \in \mathbf{Z}. \tag{5.5}$$

Note that  $L_c(\lambda) < \bar{L}_c(\lambda)$  for any  $c > 0$ . In addition,  $\bar{L}_c(\lambda)$  and  $L_c(\lambda)$  are decreasing functions of  $c$  for any  $\lambda > 0$ . As a result, we have  $c_* < \bar{c}_*$ . For any  $c_1 > c_*$ , there are two possibilities:  $c_1 > \bar{c}_*$  or  $c_1 \in (c_*, \bar{c}_*]$ .

*Case 1.*  $c_1 > \bar{c}_*$ . Let  $c_2 \in (\bar{c}_*, c_1)$ , for  $t \geq 0$ , we have from (5.5) that

$$\begin{aligned} & w_j^{(1)}(t)e^{\lambda(j-c_2t)} \\ &= e^{-(\delta+\lambda c_2)t} \left\{ w_j^{(0)}(0)e^{\lambda j} + \int_0^t D_m[w_{j+1}^{(0)}(s)e^{\lambda(j+1)}e^{-\lambda} + w_{j-1}^{(0)}(s)e^{\lambda(j-1)}e^\lambda] ds \right. \\ & \quad \left. + \frac{\mu}{2\pi} \sum_{l=-\infty}^\infty \beta_\alpha(l) \int_0^t e^{\delta s} b(w_{l+j}^{(0)}(s-r))e^{\lambda(j+l)}e^{-\lambda l} ds \right\} \\ &\leq e^{-(\delta+\lambda c_2)t} \left\{ Me^{\lambda N} + D_m \int_0^t Me^{\lambda N} e^{(\delta+\lambda c_2)s} (e^{-\lambda} + e^\lambda) ds \right. \\ & \quad \left. + \frac{\mu b'(0)}{2\pi} e^{2\alpha(\cosh \lambda - 1)} Me^{\lambda N} \int_0^t e^{(\delta+\lambda c_2)s} ds \right\} \\ &= e^{-(\delta+\lambda c_2)t} Me^{\lambda N} \left\{ 1 + [D_m(e^{-\lambda} + e^\lambda) + \mu b'(0)e^{2\alpha(\cosh \lambda - 1)}] \int_0^t e^{(\delta+\lambda c_2)s} ds \right\} \\ &\leq Me^{\lambda N} [1 + \bar{L}_{c_2}(\lambda)]. \end{aligned} \tag{5.6}$$

By induction we obtain

$$w_j^{(n)}(t)e^{\lambda(j-c_2t)} \leq Me^{\lambda N} [1 + \bar{L}_{c_2}(\lambda) + \dots + (\bar{L}_{c_2}(\lambda))^n]. \tag{5.7}$$

Since  $c_2 > \bar{c}_*$ , we can choose  $\lambda > 0$  such that  $\bar{L}_{c_2}(\lambda) < 1$ . For this choice of  $\lambda$ , the right-hand side of (5.7) is bounded from above uniformly for  $n$ . From (5.6) and the isotropic

property of  $W$ , we obtain that for  $j \in \mathbf{Z}$ ,

$$w_j(t) \leq \frac{M e^{\lambda N}}{1 - \bar{L}_{c_2}(\lambda)} e^{\lambda(c_2 t - j)},$$

for  $t \geq 0$ . Thus

$$w_j(t) \leq \frac{M e^{\lambda N}}{1 - \bar{L}_{c_2}(\lambda)} e^{\lambda(c_2 t - |j|)}.$$

Therefore, we have

$$\sup\{w_j(t) \mid |j| \geq c_1 t\} \leq \frac{M e^{\lambda N}}{1 - \bar{L}_{c_2}(\lambda)} e^{\lambda(c_2 - c_1)t} \rightarrow 0 \text{ as } t \rightarrow \infty$$

which leads to

$$\lim_{t \rightarrow \infty} \sup\{w_j(t) \mid |j| \geq c_1 t\} = 0, \quad c_1 > \bar{c}_*.$$

Case 2.  $c_1 \in (c_*, \bar{c}_*]$ . By choosing  $c_2 \in (c_*, c_1)$  and an estimate similar to (5.6), we obtain, for  $t \geq r$ , that

$$\begin{aligned} w_j^{(1)}(t) e^{\lambda(j - c_2 t)} &= e^{-(\delta + \lambda c_2)t} \left\{ w_j^{(o)}(0) e^{\lambda j} \right. \\ &\quad + \int_0^t D_m e^{\delta s} [w_{j+1}^{(o)}(s) e^{\lambda(j+1)} e^{-\lambda} + w_{j-1}^{(o)}(s) e^{\lambda(j-1)} e^{\lambda}] ds \\ &\quad + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) \int_0^r e^{\delta s} b(w_{l+j}^{(o)}(s-r)) e^{\lambda(j+l)} e^{-\lambda l} ds \\ &\quad \left. + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \int_r^t e^{\delta s} b(w_{l+j}^{(o)}(s-r)) e^{\lambda(j+l)} e^{-\lambda l} ds \right\} \\ &\leq e^{-(\delta + \lambda c_2)t} \left\{ M e^{\lambda N} \left[ 1 + D_m \int_0^t e^{(\delta + \lambda c_2)s} (e^{-\lambda} + e^{\lambda}) ds \right] \right. \\ &\quad + \mu b'(0) e^{2\alpha(\cosh \lambda - 1)} M e^{\lambda N} \int_0^r e^{(\delta + \lambda c_2)s} ds \\ &\quad \left. + \mu b'(0) e^{2\alpha(\cosh \lambda - 1) - \lambda c_2 r} \int_r^t M e^{\lambda N} e^{(\delta + \lambda c_2)s} ds \right\} \\ &\leq M e^{\lambda N} [1 + L_{c_2}(\lambda)] \\ &\quad + \frac{M e^{\lambda N} e^{-(\delta + \lambda c_2)t}}{\delta + \lambda c_2} \left\{ \mu b'(0) e^{2\alpha(\cosh \lambda - 1)} [e^{(\delta + \lambda c_2)r} - 1 - e^{\delta r}] \right. \\ &\quad \left. - D_m (e^{-\lambda} + e^{\lambda}) \right\}. \end{aligned} \tag{5.8}$$

Since the equation  $1 = L_{c_2}(\lambda)$  has two positive solutions  $\lambda_1 < \lambda_* < \lambda_2$ , we can choose  $\lambda \in (\lambda_1, \lambda_*)$  so that  $L_{c_2}(\lambda) < 1$ . By assumption (ii), we have

$$e^{(\delta + \lambda c_2)r} - 1 - e^{\delta r} \leq e^{(\delta + \lambda_* \bar{c}_*)r} - 1 - e^{\delta r} \leq 0$$

or

$$\begin{aligned} & \mu b'(0)e^{2\alpha(\cosh \lambda - 1)}[e^{(\delta + \lambda c_2)r} - 1 - e^{\delta r}] - D_m(e^{-\lambda} + e^\lambda) \\ & \leq \mu b'(0)e^{2\alpha(\cosh \lambda_* - 1)}[e^{(\delta + \lambda_* \bar{c}_*)r} - 1 - e^{\delta r}] - D_m \leq 0, \end{aligned}$$

and this, together with (5.8), leads to

$$w_j^{(1)}(t)e^{\lambda(j - c_2 t)} \leq M e^{\lambda N} [1 + L_{c_2}(\lambda)] \quad \text{for } t \geq r.$$

Again by a similar argument and by induction, we have

$$w_j^{(n)}(t)e^{\lambda(j - c_2 t)} \leq M e^{\lambda N} [1 + L_{c_2}(\lambda) + \dots + (L_{c_2}(\lambda))^n] \quad \text{for } t \geq r.$$

This shows

$$\lim_{t \rightarrow \infty} \sup\{w_j(t) \mid |j| \geq c_1 t\} = 0,$$

and completes the proof. □

In order to obtain (5.4), we follow the approaches used by Aronson (1977), Aronson & Weiberger (1975, 1978), Diekmann (1979), Thieme (1979) and Weinberger (1978), to develop a comparison principle and to construct a suitable sub-solution of (4.2).

For any  $T > 0$ , we define a map on  $M_\infty = \{\Phi = \{\phi_j\}_{j \in \mathbf{Z}} \mid \phi_j \in C_K^+[-r, \infty)\}$  by

$$E^T = \{E_j^T\}_{j \in \mathbf{Z}},$$

where for  $\Phi \in M_\infty, t \geq T, j \in \mathbf{Z}$ ,

$$\begin{aligned} E_j^T[\Phi](t) = & \int_0^T e^{-\delta s} \{D_m[\phi_{j+1}(t-s) + \phi_{j-1}(t-s)] \\ & + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l)b(\phi_{l+j}(t-s-\tau))\} ds. \end{aligned}$$

LEMMA 5.1 Consider

$$E^T[\Phi](t) > \Phi(t) \quad \text{for } t \geq T, \tag{5.9}$$

where  $\Phi \in M_\infty$  satisfies

- (i) for any  $t' > 0$ , there exists an  $N = N(t') \in \mathbf{N}$  such that for any  $t \in [0, t']$ ,  $\text{supp } \Phi(t, \cdot) \subset B_N$ ;
- (ii) if  $\{(t_n, j_n)\}_{n=1}^\infty \subset \mathbf{R}_+ \times \mathbf{Z}, j_n \in \text{supp } \Phi(t_n, \cdot)$ , and  $\lim_{n \rightarrow \infty} (t_n, j_n) = (t_0, j_0)$ , then  $j_0 \in \text{supp } \Phi(t_0, \cdot)$ .

If there exists a  $\bar{t} \geq 0$  such that the solution of (4.2) satisfies

$$W(\bar{t} + t) > \Phi(t) \quad \text{for } t \in [0, T],$$

then

$$W(\bar{t} + t) > \Phi(t) \quad \text{for } t \in [0, \infty).$$

*Proof.* Let

$$t_0 = \sup\{t \geq T \mid W(\bar{t} + t) > \Phi(t)\}.$$

If  $t_0 < \infty$ , since  $W(t)$  is non-negative, there exists  $\{(t_n, j_n)\}_{n=1}^\infty$  such that

- (a)  $t_n \downarrow t_0, n \rightarrow \infty,$
- (b)  $j_n \in \text{supp } \bar{\Phi}(t_n, \cdot),$
- (c)  $w_{j_n}(\bar{t} + t_n) \leq \phi_{j_n}(t_n).$

Under assumption (i),  $\{j_n\}$  must be bounded. Thus,  $\{j_n\}$  is composed of finite integers and hence contains a convergent sub-sequence, which is a constant sequence  $\{j_0\}$ . By (b) and (c), we know that  $j_0 \in \text{supp } \bar{\Phi}(t_0, \cdot)$  and  $w_{j_0}(\bar{t} + t_0) \leq \phi_{j_0}(t_0).$

Noting that  $t_0 \geq T$  and  $\bar{t} \geq 0,$  we obtain from the definition of  $t_0$  and (5.9) that

$$\begin{aligned} w_{j_0}(\bar{t} + t_0) &\geq \int_0^T e^{-\delta s} \left\{ D_m[w_{j_0+1}(\bar{t} + t_0 - s) + w_{j_0-1}(\bar{t} + t_0 - s)] \right. \\ &\quad \left. + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l)b(w_{j_0+l}(\bar{t} + t_0 - s - r)) \right\} ds \\ &\geq \int_0^T e^{-\delta s} \left\{ D_m[\phi_{j_0+1}(t_0 - s) + \phi_{j_0-1}(t_0 - s)] \right. \\ &\quad \left. + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l)b(\phi_{j_0+l}(t_0 - s - r)) \right\} ds \\ &= E_{j_0}^T[\bar{\Phi}](t_0) > \phi_{j_0}(t_0), \end{aligned}$$

which is a contradiction. Therefore,  $t_0 = \infty.$  This completes the proof. □

Defining  $K_c = K_c(h, T, N, \lambda)$  as

$$\begin{aligned} K_c(h, T, N, \lambda) &= \int_0^T e^{-(\delta+\lambda c)s} \left\{ D_m[e^{-\lambda} + e^\lambda] + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l)e^{\lambda l - \lambda cr} \right\} ds \\ &= \frac{1 - e^{-(\delta+\lambda c)T}}{\delta + \lambda c} \left\{ D_m[e^{-\lambda} + e^\lambda] + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l)e^{\lambda l - \lambda cr} \right\}, \end{aligned} \tag{5.10}$$

we have the following lemma.

LEMMA 5.2 For any  $c \in (0, c_*)$ , there exist  $h \in (0, b'(0)), T > 0$  and  $N \in \mathbf{N},$  such that

$$K_c(h, T, N, \lambda) > 1 \quad \text{for } \lambda \in \mathbf{R}. \tag{5.11}$$

*Proof.* By the definition of  $K_c(h, T, N, \lambda),$  we have

$$K_c(h, T, N, -\lambda) \geq K_c(h, T, N, \lambda) \quad \text{for } \lambda \geq 0.$$

Therefore, we only need to show that

$$K_c(h, T, N, \lambda) > 1 \quad \text{for } \lambda \geq 0.$$

We claim that there exist  $N_0 > 0, \lambda_0 > 0, h_0 \in (0, b'(0))$  and  $T_0 > 0$  such that

$$K_c(h, T, N, \lambda) > 1 \quad \text{for } \lambda \geq \lambda_0, N \geq N_0, h \geq h_0, \text{ and } T \geq T_0.$$

In fact, since

$$\frac{1}{2\pi} \sum_{l=-\infty}^{\infty} \beta_{\alpha}(l)e^{\lambda l} = e^{2\alpha(\cosh \lambda - 1)} \geq 1,$$

which holds uniformly for  $\lambda \in \mathbf{R}$ , we can choose  $N_0 > 0$  and  $h_0 \in (0, b'(0))$  ( $h_0$  can be chosen arbitrarily), such that for  $N \geq N_0$  and  $h \geq h_0$ , we have

$$\frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_{\alpha}(l)e^{\lambda l} > 0.$$

Since

$$\lim_{\lambda \rightarrow \infty} \frac{e^{\lambda}}{\lambda c_* + \delta} = \infty,$$

we can choose  $T_0 > 0$  and  $\lambda_0 > 0$  such that for  $T \geq T_0$  and  $\lambda \geq \lambda_0$ , we have

$$1 - e^{-(\lambda c + \delta)T} \geq 1 - e^{-\delta T} \geq 1 - e^{-\delta T_0} > 0,$$

and

$$\frac{D_m}{\lambda c + \delta} (1 - e^{-\delta T_0})e^{\lambda} \geq \frac{D_m}{\lambda_0 c_* + \delta} (1 - e^{-\delta T_0})e^{\lambda_0} \geq 1.$$

Then for  $N \geq N_0, T \geq T_0, h \geq h_0$  and  $\lambda \geq \lambda_0$ , we have

$$K_c(h, T, N, \lambda) > \frac{D_m}{\lambda_0 c_* + \delta} (1 - e^{-\delta T_0})e^{\lambda_0} \geq 1.$$

If (5.11) is not true, then there exist  $\{h_n\}, \{T_n\}, \{\lambda_n\}, \{N_n\}$  satisfying  $h_n \uparrow b'(0), T_n \uparrow \infty, N_n \uparrow \infty, \{\lambda_n\} \subset [0, \lambda_0]$  and

$$K_c(h_n, T_n, N_n, \lambda_n) \leq 1, \quad n = 1, 2, \dots$$

Since  $\{\lambda_n\}$  is bounded, we can choose a sub-sequence  $\{\lambda_{n_k}\}$  which has a finite limit, say  $\bar{\lambda}$ . By Fatou's Lemma, we have

$$1 < L_c(\bar{\lambda}) \leq \liminf_{k \rightarrow \infty} K_c(h_{n_k}, T_{n_k}, N_{n_k}, \lambda_{n_k}) \leq 1,$$

which is impossible. This completes the proof. □

We define a function with two parameters  $\omega, \beta$  as

$$q(y; \omega, \zeta) = \begin{cases} e^{-\omega y} \sin(\zeta y) & \text{for } y \in [0, \frac{\pi}{\zeta}], \\ 0 & \text{for } y \in \mathbf{R}/[0, \frac{\pi}{\zeta}]. \end{cases}$$

We have the following lemma.

LEMMA 5.3 Let  $c \in (0, c_*)$ . There exist  $\zeta_0 > 0$ , a continuous function  $\tilde{\omega} = \tilde{\omega}(\zeta)$  defined on  $[0, \zeta_0]$ , and a positive number  $\delta_1 \in (0, 1)$  such that

$$\int_0^T e^{-\delta s} \left\{ D_m[q(m + cs + 1) + q(m + cs - 1)] + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_{\alpha}(l)q(m + l + cs + cr) \right\} ds \geq q(m - \delta_1) \quad (5.12)$$

for  $m \in \mathbf{Z}$ , where  $q(y) = q(y; \tilde{\omega}(\zeta), \zeta)$ .

*Proof.* Define

$$L(\lambda) = \int_0^T e^{-\delta s} \left\{ D_m [e^{-\lambda(cs+1)} + e^{\lambda(cs-1)}] + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) e^{-\lambda(l+cs+cr)} \right\} ds,$$

where  $T, h, N$  are defined in Lemma 5.2. We can choose  $N$  sufficiently large so that  $-N + c_*(T + r) < 0$ . Using Lemma 5.2 we have

$$L(\lambda) = K_c(h, T, N, \lambda) > 1 \quad \text{for all } \lambda \in \mathbf{R}. \tag{5.13}$$

Let  $\lambda = \omega + i\zeta$ , we have

$$L(\lambda)|_{\lambda=\omega+i\zeta} = \text{Re}[L(\lambda)] + i \text{Im}[L(\lambda)],$$

where

$$\begin{aligned} \text{Re}[L(\lambda)] &= D_m \int_0^T e^{-\delta s} \{ e^{-\omega(cs+1)} \cos \zeta(cs+1) + e^{-\omega(cs-1)} \cos \zeta(cs-1) \} ds \\ &\quad + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) \int_0^T e^{-\delta s} e^{-\omega(l+cs+cr)} \cos \zeta(l+cs+cr) ds, \\ \text{Im}[L(\lambda)] &= -D_m \int_0^T e^{-\delta s} \{ e^{-\omega(cs+1)} \sin \zeta(cs+1) + e^{-\omega(cs-1)} \sin \zeta(cs-1) \} ds \\ &\quad - \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) \int_0^T e^{-\delta s} e^{-\omega(l+cs+cr)} \sin \zeta(l+cs+cr) ds. \end{aligned}$$

Since  $L''(\lambda) > 0$  and  $\lim_{|\lambda| \rightarrow \infty} L(\lambda) = \infty$ , we conclude that  $L(\lambda)$  can achieve its minimum, say at  $\lambda = \theta$ . Then we obtain

$$\begin{aligned} L'(\theta) &= -D_m \int_0^T e^{-\delta s} [(cs+1)e^{-\theta(cs+1)} + (cs-1)e^{-\theta(cs-1)}] ds \\ &\quad - \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) \int_0^T e^{-\delta s} (cs+l+cr)e^{-\theta(cs+l+cr)} ds = 0. \end{aligned}$$

We now define a function  $H = H(\omega, \zeta)$  by

$$\begin{cases} H(\omega, \zeta) = \frac{1}{\zeta} \text{Im}[L(\lambda)] & \text{for } \zeta \neq 0, \\ H(\omega, 0) = \lim_{\zeta \rightarrow 0} H(\omega, \zeta) = L'(\omega). \end{cases}$$

Then  $H(\theta, 0) = 0$  and

$$\frac{\partial H}{\partial \omega}(\theta, 0) = L''(\theta) > 0.$$

The implicit function theorem implies that there exist  $\zeta_1 > 0$  and a continuous function  $\tilde{\omega} = \tilde{\omega}(\zeta)$  defined on  $[0, \zeta_1]$  with  $\tilde{\omega}(0) = \theta$  such that  $H(\tilde{\omega}(\zeta), \zeta) = 0$  for  $\zeta \in [0, \zeta_1]$ . Hence, we have

$$\text{Im}[L(\lambda)]|_{\lambda=\tilde{\omega}(\zeta)+i\zeta} = 0 \quad \text{for } \zeta \in [0, \zeta_1]. \tag{5.14}$$

By (5.13), we have

$$\operatorname{Re}[L(\omega + i\zeta)]|_{\omega=\theta, \zeta=0} = L(\theta) > 1.$$

Thus there exists  $\zeta_2 > 0$  such that

$$\operatorname{Re}[L(\tilde{\omega}(\zeta) + i\zeta)] > 1 \quad \text{for } \zeta \in [0, \zeta_2]. \quad (5.15)$$

Let  $0 < \zeta \leq \zeta_0 := \min\left\{\zeta_1, \zeta_2, \frac{\pi}{N+c_*(T+r)}\right\}$ . For  $m \in [0, \frac{\pi}{\zeta}]$ ,  $|l| \geq N$  and  $s \in [0, T]$ , we have

$$-\frac{\pi}{\zeta} < -N \leq l \leq m + l + cs + cr \leq m + l + c(T+r) \leq N + c_*(T+r) + \frac{\pi}{\zeta} \leq \frac{2\pi}{\zeta}.$$

Since

$$\sin \zeta(m + l + c(s+r)) < 0 \quad \text{for } m + l + c(s+r) \in \left(-\frac{\pi}{\zeta}, 0\right) \cup \left(\frac{\pi}{\zeta}, \frac{2\pi}{\zeta}\right), \quad (5.16)$$

for  $m \in [0, \frac{\pi}{\zeta}]$ , we have from (5.16) that

$$\begin{aligned} & \int_0^T e^{-\delta s} \{D_m[q(m+cs+1) + q(m+cs-1)] \\ & \quad + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) q(m+l+cs+cr)\} ds \\ \geq & D_m \int_0^T e^{-\delta s} \left\{ e^{-\tilde{\omega}(\zeta)(m+cs+1)} \sin(\zeta(m+cs+1)) \right. \\ & \quad \left. + e^{-\tilde{\omega}(\zeta)(m+cs-1)} \sin(\zeta(m+cs-1)) \right\} ds \\ & \quad + \frac{\mu h}{2\pi} \int_0^T e^{-\delta s} \sum_{|l| \leq N} \beta_\alpha(l) e^{-\tilde{\omega}(\zeta)(m+l+cs+cr)} \sin(\zeta(m+l+cs+cr)) ds. \end{aligned} \quad (5.17)$$

Using  $\sin \zeta(m+a) = \sin \zeta m \cos \zeta a + \sin \zeta a \cos \zeta m$  for any  $a$ , we obtain from (5.17), (5.14) and (5.15) that

$$\begin{aligned} & \int_0^T e^{-\delta s} \{D_m[q(m+cs+1) + q(m+cs-1)] \\ & \quad + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) q(m+l+cs+cr)\} ds \\ = & e^{-\tilde{\omega}(\zeta)m} \sin(\zeta m) \operatorname{Re}[L(\lambda)]|_{\lambda=\tilde{\omega}(\zeta)+i\zeta} + e^{-\tilde{\omega}(\zeta)m} \cos(\zeta m) \operatorname{Im}[L(\lambda)]|_{\lambda=\tilde{\omega}(\zeta)+i\zeta} \\ \geq & e^{-\tilde{\omega}(\zeta)m} \sin(\zeta m) = q(m). \end{aligned} \quad (5.18)$$

We should emphasize that (5.18) is a strict inequality for  $m \in (0, \frac{\pi}{\zeta})$ . On the other hand, if  $m = 0$  or  $m = \frac{\pi}{\zeta}$ , (5.18) is a strict inequality by using (5.16) and (5.17). In fact, if  $m = \frac{\pi}{\zeta}$  and  $l = N$ , we have

$$m + l + c(s+r) > \frac{\pi}{\zeta}.$$

Similarly, if  $m = 0$  and  $l = -N$ , we have

$$m + l + c(s + r) < -N + c_*(T + r) < 0.$$

However, for both cases, we have

$$q(m + l + cs + sr) = 0 \quad \text{and} \quad \sin(\zeta(m + l + cs + sr)) < 0,$$

and thus (5.17) is a strict inequality. Therefore, for  $m \in [0, \frac{\pi}{\zeta}]$ , we have

$$\int_0^T e^{-\delta s} \left\{ D_m[q(m + cs + 1) + q(m + cs - 1)] + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) q(m + l + cs + cr) \right\} ds > q(m). \tag{5.19}$$

Note that if  $m \notin [0, \frac{\pi}{\zeta}]$ , we still have (5.19) since  $q(m) = 0$  in this case. Thus we have (5.19) for  $m \in \mathbf{R}$ . Inequality (5.12) follows immediately from the continuity consideration. This completes the proof.  $\square$

Now we consider the following family of functions:

$$R(y; \omega, \zeta, \gamma) : = \max_{\eta \geq -\gamma} q(y + \eta; \omega, \zeta) = \begin{cases} M & \text{for } y \leq \gamma + \rho, \\ q(y - \gamma; \omega, \zeta) & \text{for } \gamma + \rho \leq y \leq \gamma + \frac{\pi}{\zeta}, \\ 0 & \text{for } y \geq \gamma + \frac{\pi}{\zeta}, \end{cases} \tag{5.20}$$

where

$$M = M(\omega, \zeta) := \max \left\{ q(y; \omega, \zeta) \mid 0 \leq y \leq \frac{\pi}{\zeta} \right\}, \tag{5.21}$$

and  $\rho = \rho(\omega, \zeta)$  is the point where the above maximum  $M$  is achieved. The following lemma gives a sub-solution of (4.2).

**LEMMA 5.4** Let  $c \in (0, c_*)$  be given, then there exist  $T > 0, \zeta > 0, \omega \in \mathbf{R}, D > 0$  and  $\sigma_0 > 0$  such that for any  $\sigma \in (0, \sigma_0)$  and for any  $t \geq T$

$$E^T[\sigma \Phi](t) > \sigma \Phi(t) \quad \text{for } t \geq T, \tag{5.22}$$

where  $\Phi(t) = \{\phi_j(t)\}_{j \in \mathbf{Z}}, \phi_j(t) = R(|j|; \omega, \zeta, D + ct)$ .

*Proof.* Let  $h \in (0, b'(0)), T > 0, N > 0$  be chosen such that  $K_c(h, T, N, \lambda) > 1$  for all  $\lambda \in \mathbf{R}$ . According to Lemma 5.3, we can choose  $\zeta > 0, \omega = \tilde{\omega}(\zeta)$  and  $\delta_1 \in (0, 1)$  such that (5.12) holds.

Let  $\sigma_h$  be the smallest positive root of the equation  $b(w) = hw$ . Then  $b(w) > hw$  for  $w \in (0, \sigma_h)$ . Choose  $\sigma_0 \in (0, \sigma_h M^{-1})$ , where  $M$  is defined in (5.21). Let  $\sigma \in (0, \sigma_0)$  and

$t \geq T$ , then

$$\begin{aligned}
 E_j^T[\sigma \Phi](t) &= \sigma \int_0^T e^{-\sigma s} \left\{ D_m[\phi_{j+1}(t-s) + \phi_{j-1}(t-s)] \right. \\
 &\quad \left. + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) b(\phi_{j+l}(t-s-r)) \right\} ds \\
 &\geq \sigma \int_0^T e^{-\sigma s} \left\{ D_m[\phi_{j+1}(t-s) + \phi_{j-1}(t-s)] \right. \\
 &\quad \left. + \frac{\mu}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) b(\phi_{j+l}(t-s-r)) \right\} ds. \tag{5.23}
 \end{aligned}$$

We now distinguish two cases.

Case (i)  $|j| \leq D + \rho + c(t - T) - N$ . If  $|l| \leq N$ ,  $s \in [0, T]$ , then

$$|l + j| \leq D + \rho + c(t - T) \leq D + \rho + c(t - s)$$

and consequently

$$\begin{aligned}
 E_j^T[\sigma \Phi](t) &= \sigma \left\{ 2D_m \sigma M + \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) b(\sigma M) \right\} \int_0^T e^{-\delta s} ds \\
 &> \sigma M K_c(h, T, N, 0) > \sigma M. \tag{5.24}
 \end{aligned}$$

Case (ii)  $D + \rho + c(t - T) - N \leq |j| \leq \frac{\pi}{\zeta} + D + ct$ . If  $|l| \leq N$  and  $t \geq T$ , then

$$\begin{aligned}
 |l + j| &= (l^2 + 2Lj + j^2)^{\frac{1}{2}} \leq |j| + \frac{lj}{|j|} + \frac{l^2}{2|j|} \\
 &\leq |j| + \frac{lj}{|j|} + \frac{N^2}{D + \rho - N} \leq |j| + \frac{lj}{|j|} + \delta_1,
 \end{aligned}$$

provided  $D \geq \frac{N^2}{2\delta_1} - \rho + N$ . Since  $\phi_j(t)$  is decreasing with respect to  $|j|$ , we have from

(5.23) that

$$\begin{aligned}
 E_j^T[\sigma \Phi](t) &\geq \sigma \int_0^T e^{-\delta s} \left\{ D_m \left[ \max_{\eta \geq -D-c(t-s)} q(|j| + 1 + \delta_1 + \eta) \right. \right. \\
 &\quad \left. \left. + \max_{\eta \geq -D-c(t-s)} q(|j| - 1 + \delta_1 + \eta) \right] \right. \\
 &\quad \left. + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) \max_{\eta \geq -D-c(t-s-r)} q(|j| + l + \delta_1 + \eta) \right\} ds \\
 &= \sigma \int_0^T e^{-\delta s} \left\{ D_m \left[ \max_{\eta \geq -D-ct} q(|j| + 1 + cs + \delta_1 + \eta) \right. \right. \\
 &\quad \left. \left. + \max_{\eta \geq -D-ct} q(|j| - 1 + cs + \delta_1 + \eta) \right] \right. \\
 &\quad \left. + \frac{\mu h}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) \max_{\eta \geq -D-ct} q(|j| + l + cs + cr + \delta_1 + \eta) \right\} ds \\
 &\geq \sigma \max_{\eta \geq -D-ct} q(|j| + \eta).
 \end{aligned}$$

Combining (i) and (ii), we obtain (5.22) and complete the proof. □

The following result is an easy observation from (4.1).

LEMMA 5.5 Assume that  $W = \{w_j\}_{j \in \mathbf{Z}}$  is a solution of (4.1), and assume that

- (i)  $W^o = \{w_j^o\}_{j \in \mathbf{Z}}$ , with  $w_j^o \in C_K^+[-r, 0]$ , is isotropic on  $[-r, 0]$ ;
- (ii) there exists  $N_1 \in \mathbf{N}$  such that

$$\text{supp } W^o(t, \cdot) \subset B_{N_1} \text{ for } t \in [-r, 0], \quad \text{and } w_j^o(0) > 0 \text{ for } |j| \leq N_1.$$

Then there exists  $t_0 > r$  such that

$$w_j(t) > 0 \text{ for } t \in [t_0, \infty) \text{ and } j \in \mathbf{N}.$$

LEMMA 5.6 Let  $\{Q_n(t, N)\}$  be defined by  $Q_1(t, N) \equiv a \in [0, w^+)$ , and

$$Q_{n+1}(t, N) = \frac{1}{\delta} [2D_m Q_n(t, N) + \frac{\mu}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) b(Q_n(t, N))] (1 - e^{-\delta t}), \quad n = 1, 2, \dots \tag{5.25}$$

Then for any  $\epsilon > 0$ , there exist  $\bar{t}(\epsilon)$ ,  $\bar{N}(\epsilon)$  and  $\bar{n}(\epsilon)$  such that for any  $t \geq \bar{t}(\epsilon)$ ,  $N \geq \bar{N}(\epsilon)$  and  $n \geq \bar{n}(\epsilon)$ ,

$$Q_n(t, N) \geq w^+ - \epsilon.$$

*Proof.* First, we note that

$$\frac{2D_m w^+ + \mu b(w^+)}{\delta} = w^+,$$

and

$$0 < Q_1(t, N) < w^+, \quad 0 < \frac{1}{\delta}(1 - e^{-\delta t}) < 1 \quad \text{and} \quad 0 < \frac{1}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) < 1.$$

Therefore, we have by induction that  $0 < Q_n(t, N) \leq K$  for all  $n \in \mathbf{N}$ ,  $t \geq 0$  and  $N \in \mathbf{N}$ .

Let  $\epsilon > 0$ . Since

$$2D_m w + \mu b(w) > (2D_m + d_m)w \quad \text{for } 0 < w < w^+,$$

we have

$$\sup \left\{ \frac{2D_m w + \mu b(w)}{(2D_m + d_m)w} \mid 0 < w \leq w^+ - \epsilon \right\} > 1.$$

Choose  $\alpha(\epsilon) < 1$  so that

$$\alpha(\epsilon)[2D_m w + \mu b(w)] > (2D_m + d_m)w \quad \text{for } 0 < w \leq w^+ - \epsilon.$$

Define a sequence as follows:

$$M_1 \equiv a, \quad M_{n+1} = \frac{\alpha(\epsilon)}{\delta} [2D_m M_n + \mu b(M_n)], \quad n \geq 2.$$

Then we have the following observations:

(i) if  $0 < M_n \leq w^+ - \epsilon$ , then  $M_{n+1} \geq M_n$ ;

(ii) if  $M_n > w^+ - \epsilon$ , then

$$M_{n+1} \geq \frac{\alpha(\epsilon)}{\delta} [2D_m(w^+ - \epsilon) + \mu b(w^+ - \epsilon)] \geq w^+ - \epsilon.$$

We now claim that  $M_n > w^+ - \epsilon$  for large  $n$ . If not, then using (ii) we can assume that  $M_n \leq w^+ - \epsilon$  for all  $n$ . Then by (i)  $\lim_{n \rightarrow \infty} M_n = M < \infty$  exists and we have

$$M = \frac{\alpha(\epsilon)}{\delta} [2D_m M + \mu b(M)],$$

which is impossible. Therefore, there is  $\bar{n}(\epsilon) > 0$  such that  $M_n > w^+ - \epsilon$  for all  $n > \bar{n}(\epsilon)$ .

Choose  $\bar{t}(\epsilon)$  and  $\bar{N}(\epsilon)$  such that

$$\frac{1}{2\pi} (1 - e^{-\delta \bar{t}(\epsilon)}) \sum_{|l| \leq \bar{N}(\epsilon)} \beta_\alpha(l) \geq \alpha(\epsilon).$$

Then, for any  $t \geq \bar{t}(\epsilon)$  and  $N \geq \bar{N}(\epsilon)$ , we have  $Q_1(t, N) = a \geq M_1$  and

$$\begin{aligned} Q_{n+1}(t, N) &\geq \frac{1}{\delta} (1 - e^{-\delta \bar{t}(\epsilon)}) \left[ 2D_m Q_n(t, N) + \frac{\mu}{2\pi} \sum_{|l| \leq \bar{N}(\epsilon)} \beta_\alpha(l) b(Q_n(t, N)) \right] \\ &> \frac{1}{\delta} \alpha(\epsilon) [2D_m Q_n(t, N) + \mu b(Q_n(t, N))]. \end{aligned}$$

Using the monotonicity of  $b$  on  $[0, K]$  and by induction, we obtain  $Q_n(t, N) \geq M_n \geq w^+ - \epsilon$  for all  $n > \bar{n}(\epsilon)$ . This completes the proof.  $\square$

**THEOREM 5.2** Assume that  $W^o$  satisfies all conditions in Lemma 5.5. Then for any  $c \in (0, c_*)$ , we have

$$\liminf_{t \rightarrow \infty} \min\{w_j(t) \mid |j| \leq ct\} \geq w^+.$$

*Proof.* Fix  $c_1 \in (0, c_*)$  and choose  $c_2 \in (c_1, c_*)$ . According to Lemma 5.4, there exist  $T > 0, \zeta > 0, \omega \in \mathbf{R}, D > 0$  and  $\sigma_0 > 0$  such that for any  $\sigma \in (0, \sigma_0)$  and any  $t \geq T$ ,

$$E^T[\sigma \Phi](t) > \sigma \Phi(t),$$

where  $\Phi(t) = \{\phi_j(t)\}_{j \in \mathbf{Z}}, \phi_j(t) := R(|j|; \omega, \zeta, D + c_2 T)$ . By Lemma 5.5, we can find  $t_0 > r$  so that

$$w_j(t) > 0 \quad \text{for } t \in [t_0, t_0 + T], \quad |j| \leq D + c_2 T + \frac{\pi}{\zeta}.$$

Then we can choose  $\sigma_1 \in (0, \sigma_0)$  such that

$$\sigma_1 M < w^+, \quad w_j(t_0 + t) > \sigma_1 \phi_j(t) \quad \text{for } t \in [0, T]. \tag{5.26}$$

We infer from the comparison principle (Lemma 5.1) that (5.26) holds for  $t \geq 0$ . Hence by (5.20) and the definition of  $\phi_j(t)$ , we have

$$w_j(t_0 + t) \geq \sigma_1 M \quad \text{for } t \geq 0, \quad |j| \leq \rho + D + c_2 t. \tag{5.27}$$

By (4.2), we obtain

$$\begin{aligned} w_j(t_0 + t) &\geq \int_0^t e^{-\delta s} \{D_m[w_{j+1}(t_0 + t - s) + w_{j-1}(t_0 + t - s)] \\ &\quad + \frac{\mu}{2\pi} \sum_{|l| \leq N} \beta_\alpha(l) b(w_{l+j}(t_0 + t - s - r))\} ds. \end{aligned} \tag{5.28}$$

Let  $a = \sigma_1 M = Q_1(t, N)$  and let  $Q_n(t, N)$  be defined in Lemma 5.6. Then by induction and using (5.27)–(5.28), we have

$$w_j(t_0 + t) \geq Q_n(t, N) \quad \text{for } t \geq 0, \quad |j| \leq \rho + D + c_2 t - nN.$$

Therefore, for any  $\epsilon > 0$  we can find  $\bar{t}(\epsilon), \bar{N}(\epsilon)$  and  $\bar{n}(\epsilon)$  such that

$$w_j(t) \geq w^+ - \epsilon \quad \text{for } t \geq t_0 + \bar{t}(\epsilon), \quad |j| \leq \rho + D + c_2(t - t_0) - \bar{n}(\epsilon)\bar{N}(\epsilon). \tag{5.29}$$

Define

$$t_1 = \max \left\{ t_0 + \bar{t}(\epsilon), \frac{\bar{n}(\epsilon)\bar{N}(\epsilon) + c_2 t_0 - \rho - D}{c_2 - c_1} \right\}.$$

Since  $c_2 > c_1$ , we have from (5.29) that

$$w_j(t) \geq w^+ - \epsilon \quad \text{for } t \geq t_1, \quad |j| \leq c_1 t.$$

This completes the proof. □

## 6. Conclusions and remarks

We derived a lattice model for a single species in a one-dimensional patchy environment with infinite number of patches connected locally by diffusion, under the assumption that the death and diffusion rates of the mature population are age independent. It was shown that the dynamics of the mature population is governed by a lattice delay differential equation with global interactions.

It was shown that the initial-value problem is well posed and that the model system admits a family of monotone travelling waves with wave speeds  $c > c_*$  under the technical condition  $(H_b)$ . It was established that the minimal wave speed  $c_*$  coincides with the asymptotic speed of propagation.

We numerically investigated the dependence of the minimal wave speed on the maturation period and the diffusion rate of the mature population, and we illustrated that the minimal wave speed  $c_*$  as a function of the maturation period  $r$  is a decreasing function that approaches zero when  $r$  is sufficiently large, and  $c_*$  is a monotonically increasing function of the diffusion rate of the mature population.

Many of the aforementioned results were obtained under the assumption  $b'(0) > d_m/\mu$ . This assumption holds only when  $\int_0^r \bar{d}(z) dz$  is sufficiently small. In the case that this term is large (this is particularly true if the maturation time is too long), then the model system will not have a non-zero equilibrium and we suspect that every solution of the model converges to zero, though this has not been verified yet.

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## REFERENCES

- ARONSON, D. G. & WEINBERGER, H. F. (1975) Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. *Partial Differential Equations and Related Topics* (J. A. Goldstein, ed.). Lecture Notes in Mathematics, vol. 446. Berlin: Springer, pp. 5–49.
- ARONSON, D. G. (1977) The asymptotic speed of a propagation of a simple epidemic. *Nonlinear Diffusion* (W. E. Fitzgibbon & H. F. Walker, eds). Research Notes in Mathematics, vol. 14. London: Pitman, pp. 1–23.
- ARONSON, D. G. & WEINBERGER, H. F. (1978) Multidimensional nonlinear diffusion arising in population genetics. *Advances in Math.*, **30**, 33–76.
- BRITTON, N. F. (1990) Spatial structures and periodic travelling waves in an integro-differential reaction–diffusion population model. *SIAM J. Appl. Math.*, **50**, 1663–1688.
- DEANGELIS, D. L., POST, W. M. & TRAVIS, C. C. (1986) *Positive Feedback in Natural Systems* Biomathematics, vol. 15. New York: Springer.
- DIEKMANN, O. (1978) Thresholds and travelling waves for the geographical spread of infection. *J. Math. Biol.*, **69**, 109–130.
- DIEKMANN, O. (1979) Run for your life, a note on the asymptotic speed of propagation of an epidemic. *J. Diff. Eqns.*, **33**, 58–73.

- GOURLEY, S. A. & BRITTON, N. F. (1996) A predator–prey reaction–diffusion system with nonlocal effects. *J. Math. Biol.*, **34**, 297–333.
- GOURLEY, S. A. (2000) Travelling front solutions of a nonlocal Fisher equation. *J. Math. Biol.*, **41**, 272–284.
- GOLDBERG, R. R. (1965) *Fourier Transform*. New York: Cambridge University Press.
- METZ, J. A. J. & DIEKMANN, O. (1986) *The Dynamics of Physiologically Structured Populations*. New York: Springer.
- SMITH, H. & THIEME, H. (1991) Strongly order preserving semiflows generated by functional differential equations. *J. Diff. Eqns.*, **93**, 332–363.
- SO, J. W. H., WU, J. H. & ZOU, X. F. (2001) A reaction–diffusion model for a single species with age structure I: Travelling wavefronts on unbounded domain. *Proc. Roy. Soc. Lond. A*, **457**, 1841–1853.
- SO, J. W. H., WU, J. H. & ZOU, X. F. (2001) Structured population on two patches: modelling dispersal and delay. *J. Math. Biol.*, **43**, 37–51.
- SO, J. W. H., WU, J. H. & YANG, Y. (2000) Numerical Hopf bifurcation analysis on the diffusive Nicholson’s blowflies equation. *Appl. Math. Comput.*, **111**, 53–69.
- THIEME, H. (1979) Asymptotic estimates of the solutions of nonlinear integral equations and asymptotic speeds for the spread of populations. *J. Reine angew. Math.*, **306**, 94–121.
- TITCHMARSH, E. C. (1962) *Introduction to the Theory of Fourier Integrals*. Oxford: Clarendon Press.
- WEINBERGER, H. F. (1978) Asymptotic behaviours of a model in population genetics. *Nonlinear Partial Differential Equations and Applications* (J. M. Chadam, ed.). Lecture Notes in Mathematics, vol. 648. Berlin: Springer.
- WILCOX, B. A. (1980) Insular Ecology and Conservation. *Conservation Ecology*. (M. E. Soule & B. A. Wilcox, eds). Massachusetts: Sinauer Associates.
- WU, J. H. (1996) *Theory and Applications of Partial Functional Differential Equations* Applied Mathematical Sciences, vol. 119. New York: Springer.
- WU, J. H. & ZOU, X. F. (2001) Travelling wave fronts of reaction–diffusion systems with delay. *J. Dynam. Diff. Eqns*, **13**, 651–687.