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Extinction and periodic oscillations in an age-structured population model in a patchy environment

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Abstract

We consider an age-structured single-species population model in a patch environment consisting of infinitely many patches. Previous work shows that if the nonlinear birth rate is sufficiently large and the maturation time is small, then the model exhibits the usual transition from the trivial equilibrium to the positive (spatially homogeneous) equilibrium represented by a traveling wavefront. Here we show that (i) if the birth rate is so small that a patch alone cannot sustain a positive equilibrium then the whole population in the patchy environment will become extinct, and (ii) if the birth rate is large enough that each patch can sustain a positive equilibrium and if the maturation time is moderate then the model exhibits nonlinear oscillations characterized by the occurrence of multiple periodic traveling waves.

Keywords: Extinction; Oscillation; Nonlinear stability; Age structure; Energy norms

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1. Introduction

Recently, Weng et al. [3] derived the following system of delay differential equations for a single species population with two age classes distributed over a patchy environment consisting of the integer nodes $j \in \mathbf{Z} := \{0, \pm 1, \pm 2, \ldots\}$ of a one-dimensional lattice:

$$\frac{dw_j(t)}{dt} = \frac{\mu}{2\pi} \sum_{k=-\infty}^{\infty} \beta_\alpha(j-k) b\big(w_k(t-r)\big) + D_m\big[w_{j+1}(t) + w_{j-1}(t) - 2w_j(t)\big] - d_m w_j(t), \quad t > 0,\ j \in \mathbf{Z}. \tag{1.1}$$

In this equation, $w_j(t)$ denotes the total number of adults (i.e., the total number of age at least r) in the jth patch, and $r > 0$ is the length of the juvenile phase (maturation time). The function b denotes the birth function and satisfies $b(0) = 0$. The constants D_m and d_m are, respectively, the diffusion coefficient and death rate for the mature population, and the r-dependent parameters μ and α are given by

$$\mu = \exp\left(-\int_0^r d(a)\,da\right), \qquad \alpha = \int_0^r D(a)\,da, \tag{1.2}$$

where $D(a)$ and $d(a)$ in (1.2) above, and in (1.3) below, are the diffusion coefficient and death rate for the population at age a (thus μ and α above are defined in terms of the diffusion and death rates for the *immature* population while, for $a \geqslant r$, $D(a) = D_m$ and $d(a) = d_m$). The derivation of (1.1) (given in [3]) allows the diffusion coefficient and death rate for the immatures to be age-dependent as the notation in (1.2) suggests, but, for the mature population, these parameters must be age-independent. This is because the derivation of (1.1) utilizes the technique of integration along characteristics for the following well-known simple model for an age-structured population:

$$\frac{\partial u_j}{\partial t} + \frac{\partial u_j}{\partial a} = D(a)\big[u_{j+1}(t,a) + u_{j-1}(t,a) - 2u_j(t,a)\big] - d(a)u_j(t,a) \tag{1.3}$$

in which $u_j(t,a)$ is the density of age a at time t in the jth patch. Of course,

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

The coefficients $\beta_\alpha(l)$ in (1.1) are given by

$$\beta_\alpha(l) = 2e^{-2\alpha} \int_0^\pi \cos(l\omega) e^{2\alpha\cos\omega}\,d\omega, \tag{1.4}$$

and it was shown in [3] that these coefficients enjoy the following properties which will be important for the present paper:

(i) $\beta_\alpha(l) = \beta_\alpha(|l|)$ for all $l \in \mathbf{Z}$, i.e., $\beta_\alpha(l)$ is isotropic;
(ii) $\sum_{l=-\infty}^{\infty} \beta_\alpha(l) = 2\pi$;
(iii) $\beta_\alpha(l) = 0$ if $\alpha = 0$ and $l \in \mathbf{Z} \setminus \{0\}$, and $\beta_\alpha(l) > 0$ if $\alpha > 0$ and $l \in \mathbf{Z}$.

Spatially uniform equilibria (i.e., equilibria independent of j) of (1.1) satisfy $\mu b(w) = d_m w$. Of course, zero is an equilibrium. Weng et al. [3] were concerned with the situation when there is one other equilibrium $w^+ > 0$, and with the possibility of traveling wave-front solutions connecting 0 to the other equilibrium w^+. In this discrete-space setting such a solution is a solution of the single variable $j + ct$, where $c > 0$ is the wave speed. They showed that such a wave-front exists for all c exceeding some minimum value c_*, and they also proved that c_* is the asymptotic speed of wave propagation if r is not too large and the initial data satisfies certain biologically realistic conditions.

The present paper continues the study in [3] by investigating two further aspects of (1.1). The first of these is the situation when there is no nonzero spatially uniform equilibrium. In this case, by estimating a certain energy norm, we prove that the population will become extinct for any initial data that tends to zero as $|j| \to \infty$ sufficiently fast that $w(t) := \{w_j(t)\}_{j=-\infty}^{\infty}$ lies in the sequence space ℓ^2 for each $t \in [-r, 0]$. The second aspect we shall investigate is the occurrence of a Hopf bifurcation, when r is moderate, to periodic traveling waves from the positive equilibrium, when it exists. In fact, we shall establish the existence of multiple periodic waves by using the result of Rustichini [2].

In Section 2 we shall first prove that solutions of (1.1) enjoy a positivity preserving property, and then we shall consider the issue of extinction. In Section 3 periodic traveling waves will be investigated.

2. Positivity and extinction criterion

Throughout the paper, denote

$$w(t) = \{w_j(t)\}_{j=-\infty}^{\infty}. \tag{2.1}$$

We shall need a classical result from [1] which states that:

Lemma 2.1. *Let X be a Banach space over* **R** *or* **C**. *Assume that $f : [0,\infty) \times X \to X$ is continuous and that there exists a constant $L \geqslant 0$ such that*

$$\left| f(t,x) - f(t,y) \right| \leqslant L|x-y|.$$

Then for any given $x^0 \in X$ there exists a unique continuously differentiable function $x : [0,\infty) \to X$ such that $\dot{x}(t) = f(t, x(t))$ for $t \in [0,\infty)$ and $x(0) = x^0$.

Applying this result to

$$\begin{aligned} &\dot{v}_j(t) = D\big[v_{j+1}(t) + v_{j-1}(t) - 2v_j(t)\big] - dv_j(t) + h_j(t), \quad j \in \mathbf{Z}, \\ &v_j(0) = c_j \in \mathbf{R}, \quad j \in \mathbf{Z}, \end{aligned} \tag{2.2}$$

with $c = (c_j)_{j\in\mathbf{Z}} \in \ell^\infty$, where D and d are positive constants, and ℓ^∞ is the Banach space

$$\ell^\infty = \Big\{ c = (c_j)_{j\in\mathbf{Z}};\ \|c\|_{\ell^\infty} := \sup_{j\in\mathbf{Z}} |c_j| < \infty \Big\},$$

$(h_j)_{j\in\mathbf{Z}} : [0,\infty) \to \ell^\infty$ is continuous, we conclude that (2.2) has a unique solution $v : [0,\infty) \to \ell^\infty$.

Using the definition of $\beta_\alpha(l)$, it is easy to verify that

$$v_j(t) = \frac{1}{2\pi} e^{-dt} \sum_{k=-\infty}^{\infty} \beta_{Dt}(k-j) c_k + \frac{1}{2\pi} \sum_{k=-\infty}^{\infty} \int_0^t e^{-d(t-s)} \beta_{D(t-s)}(k-j) h_k(s)\, ds \tag{2.3}$$

gives the explicit solution to the initial value problem (2.2). In particular, property (iii) of $\beta_\alpha(l)$ ensures that $v_j(t) \geqslant 0$ for all $j \in \mathbf{Z}$ and $t \geqslant 0$ as long as $c_j \geqslant 0$, $h_j(t) \geqslant 0$ for all $t \geqslant 0$ and $j \in \mathbf{Z}$. We can now prove that solutions of (1.1) enjoy a positivity preserving property.

Theorem 2.2. *Let $b : \mathbf{R} \to \mathbf{R}$ be a C^1-smooth bounded function. Then*:

(i) *For any continuous $\phi : [-r, 0] \to \ell^\infty$, Eq.* (1.1) *has a unique solution $w^\phi : [-r, \infty) \to \ell^\infty$ with $w^\phi(s) = \phi(s)$ on $[-r, 0]$*;
(ii) *If $\phi_j(s) \geqslant 0$ for all $j \in \mathbf{Z}$ and $s \in [-r, 0]$, then $w_j^\phi(t) \geqslant 0$ for all $j \in \mathbf{Z}$ and $t \geqslant 0$; if in addition $\phi \neq 0 \in \ell^\infty$, then $w_j^\phi(t) > 0$ for all $j \in \mathbf{Z}$ and $t > r$.*

Proof. (i) follows from Lemma 2.1 by solving Eq. (1.1) on consecutive intervals $[nr, (n+1)r]$, $n = 0, 1, 2, \ldots$. By a standard comparison technique, we know $w_j(t) \geqslant \tilde{w}_j(t)$ for all $j \in \mathbf{Z}$ and $t \geqslant 0$, where $\tilde{w}_j$ is the solution of the initial value problem

$$\frac{d\tilde{w}_j(t)}{dt} = D_m\big[\tilde{w}_{j+1}(t) + \tilde{w}_{j-1}(t) - 2\tilde{w}_j(t)\big] - d_m \tilde{w}_j(t), \quad t > 0,\ j \in \mathbf{Z},$$
$$\tilde{w}_j(0) = w_j(0), \quad j \in \mathbf{Z}. \tag{2.4}$$

Using the explicit expression (2.3), we then conclude that

$$w_j(t) \geqslant \tilde{w}_j(t) \geqslant 0 \quad \text{for } j \in \mathbf{Z} \text{ and } t \geqslant 0.$$

Using the analytic formula (2.3) for (1.1) with

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

we get, for $t \in [0, r]$, that

$$\begin{aligned} w_j(t) = {} & \frac{1}{2\pi} e^{-d_m t} \sum_{k=-\infty}^{\infty} \beta_{D_m t}(j-k) w_k(0) \\ & + \frac{1}{2\pi} \sum_{k=-\infty}^{\infty} \int_0^t e^{-d_m(t-s)} \beta_{D_m(t-s)}(k-j) \\ & \times \frac{\mu}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(k-l)\, b\big(w_l(s-r)\big)\, ds \end{aligned}$$

from which it follows that if $w \neq 0$ then

$$w_j(r) > 0 \quad \text{for all } j \in \mathbf{Z}.$$

Therefore, for $t \geqslant r$, we get

$$w_j(t) \geqslant \frac{1}{2\pi} e^{-d_m(t-r)} \sum_{k=-\infty}^{\infty} \beta_{D_m(t-r)}(j-k) w_k(r) > 0$$

for all $j \in \mathbf{Z}$.

Next, we shall consider the issue of extinction. Recall that the condition $\mu b(w) < d_m w$ for all $w > 0$ ensures that there is no spatially homogeneous equilibrium other than 0 and is the weakest possible condition that ensures extinction for biologically sensible birth functions $b(w)$. The theorem below confirms that this is also a sufficient condition for extinction. More precisely the theorem essentially states that extinction will occur if there is no positive equilibrium and if the initial data decays to zero sufficiently fast as $|j| \to \infty$.

We shall let ℓ^2 denote the Hilbert space of sequences $\{\xi_j\}_{j=-\infty}^{\infty}$ such that $\sum_{j=-\infty}^{\infty} \xi_j^2 < \infty$, with the norm

$$\|\xi\|_{\ell^2} = \left(\sum_{j=-\infty}^{\infty} \xi_j^2 \right)^{1/2}. \qquad \square$$

Theorem 2.3. *Let the initial data* $\phi : [-r, 0] \to \ell^2$ *be continuous and* $\phi_j(s) \geqslant 0$ *for each* $s \in [-r, 0]$. *Assume also that* $\mu b(w) < d_m w$ *for all* $w > 0$ *and that* $\sup_{w \geqslant 0} |b'(w)| < \infty$. *Then*

$$\sup_{j \in \mathbf{Z}} w_j^{\phi}(t) \to 0 \quad \text{as } t \to \infty. \tag{2.5}$$

Proof. Applying Lemma 2.1 to Eq. (1.1) on consecutive intervals $[nr, (n+1)r]$, $n = 0, 1, 2, \ldots$, we conclude that $w(t) = w^{\phi}(t) \in \ell^2$ for all $t \geqslant 0$. Multiplying Eq. (1.1) by $w_j(t)$, summing over $j \in \mathbf{Z}$ and some rearranging gives

$$\begin{aligned}
\frac{1}{2} \frac{d}{dt} \sum_{j=-\infty}^{\infty} w_j^2(t)
&= \frac{\mu}{2\pi} \sum_{j=-\infty}^{\infty} \sum_{k=-\infty}^{\infty} \beta_\alpha(j-k) w_j(t) b\big(w_k(t-r)\big) - D_m \sum_{j=-\infty}^{\infty} \big(w_j(t) - w_{j-1}(t)\big)^2 \\
&\quad + D_m \sum_{j=-\infty}^{\infty} \big[w_j(t)\big(w_{j+1}(t) - w_j(t)\big) - w_{j-1}(t)\big(w_j(t) - w_{j-1}(t)\big)\big] \\
&\quad - d_m \sum_{j=-\infty}^{\infty} w_j^2(t).
\end{aligned}$$

The penultimate term on the right-hand side is a telescoping series which sums to zero, since $w_j(t) \to 0$ as $|j| \to \infty$. Thus

$$\begin{aligned}
&\frac{1}{2}\frac{d}{dt}\sum_{j=-\infty}^{\infty} w_j^2(t) + D_m \sum_{j=-\infty}^{\infty}\big(w_j(t)-w_{j-1}(t)\big)^2 + d_m \sum_{j=-\infty}^{\infty} w_j^2(t) \\
&\quad = \frac{\mu}{2\pi}\sum_{j=-\infty}^{\infty}\sum_{k=-\infty}^{\infty}\beta_\alpha(j-k)w_j(t)b\big(w_k(t-r)\big) \\
&\quad \leqslant \frac{d_m}{2\pi}\sum_{j=-\infty}^{\infty}\sum_{k=-\infty}^{\infty}\beta_\alpha(j-k)w_j(t)w_k(t-r) \\
&\quad \leqslant \frac{d_m}{4\pi}\left(\sum_{j=-\infty}^{\infty} w_j^2(t)\sum_{k=-\infty}^{\infty}\beta_\alpha(j-k) + \sum_{j=-\infty}^{\infty}\sum_{k=-\infty}^{\infty}\beta_\alpha(j-k)w_k^2(t-r)\right).
\end{aligned}$$

On interchanging the order of summation in the second double sum, and then using properties (i) and (ii) of $\beta_\alpha(l)$, we find

$$\begin{aligned}
&\frac{1}{2}\frac{d}{dt}\sum_{j=-\infty}^{\infty} w_j^2(t) + D_m \sum_{j=-\infty}^{\infty}\big(w_j(t)-w_{j-1}(t)\big)^2 + \frac{d_m}{2} \sum_{j=-\infty}^{\infty} w_j^2(t) \\
&\quad \leqslant \frac{d_m}{2}\sum_{j=-\infty}^{\infty} w_j^2(t-r).
\end{aligned}$$

Integrating with respect to time from 0 to t gives

$$\begin{aligned}
&\|w(t)\|_{\ell^2}^2 - \|w(0)\|_{\ell^2}^2 + 2D_m\int_0^t \sum_{j=-\infty}^{\infty}\big(w_j(s)-w_{j-1}(s)\big)^2\,ds + d_m\int_0^t \|w(s)\|_{\ell^2}^2\,ds \\
&\quad \leqslant d_m\int_0^t \|w(s-r)\|_{\ell^2}^2\,ds = d_m\int_{-r}^{t-r}\|w(s)\|_{\ell^2}^2\,ds \\
&\quad \leqslant d_m\int_{-r}^{0}\|w(s)\|_{\ell^2}^2\,ds + d_m\int_0^t\|w(s)\|_{\ell^2}^2\,ds.
\end{aligned}$$

Hence

$$\|w(t)\|_{\ell^2}^2 + 2D_m\int_0^t\sum_{j=-\infty}^{\infty}\bar{w}_j^2(s)\,ds \leqslant \|w(0)\|_{\ell^2}^2 + d_m\int_{-r}^{0}\|w(s)\|_{\ell^2}^2\,ds, \tag{2.6}$$

where $\bar{w}_j$ is defined in (2.8) below.

Let us now rewrite the original equation (1.1) as

$$\begin{aligned}
\frac{dw_j}{dt} = {}& \frac{\mu}{2\pi}\sum_{k=-\infty}^{\infty}\beta_\alpha(k)b\big(w_{j-k}(t-r)\big) + D_m\big[w_{j+1}(t)+w_{j-1}(t)-2w_j(t)\big] \\
& - d_m w_j(t).
\end{aligned} \tag{2.7}$$

Define

$$\bar{w}_j(t) = w_j(t) - w_{j-1}(t), \qquad \bar{w}(t) = \{\bar{w}_j(t)\}_{j=-\infty}^{\infty}. \tag{2.8}$$

Then from (2.7) we obtain

$$\begin{aligned}
\frac{d\bar{w}_j}{dt} &= \frac{\mu}{2\pi} \sum_{k=-\infty}^{\infty} \beta_\alpha(k)\big\{b\big(w_{j-k}(t-r)\big) - b\big(w_{j-1-k}(t-r)\big)\big\} \\
&\quad + D_m\big[\bar{w}_{j+1}(t) + \bar{w}_{j-1}(t) - 2\bar{w}_j(t)\big] - d_m\bar{w}_j(t) \\
&= \frac{\mu}{2\pi} \sum_{k=-\infty}^{\infty} \beta_\alpha(k)\bar{w}_{j-k}(t-r)b'\big(\hat{w}_{j-k}(t-r)\big) \\
&\quad + D_m\big[\bar{w}_{j+1}(t) + \bar{w}_{j-1}(t) - 2\bar{w}_j(t)\big] - d_m\bar{w}_j(t)
\end{aligned}$$

by the mean value theorem, where $\hat{w}_j(t)$ is between $w_j(t)$ and $w_{j-1}(t)$. Multiplying by $d\bar{w}_j/dt$ and summing over j gives, after some rearranging on the D_m terms, we get

$$\begin{aligned}
\left\|\frac{d\bar{w}}{dt}\right\|_{\ell^2}^2 &= \frac{\mu}{2\pi} \sum_{j=-\infty}^{\infty} \sum_{k=-\infty}^{\infty} \beta_\alpha(k)\frac{d\bar{w}_j(t)}{dt}\bar{w}_{j-k}(t-r)b'\big(\hat{w}_{j-k}(t-r)\big) \\
&\quad - \frac{1}{2}D_m\frac{d}{dt}\sum_{j=-\infty}^{\infty}\big(\bar{w}_j(t) - \bar{w}_{j-1}(t)\big)^2 \\
&\quad + D_m\sum_{j=-\infty}^{\infty}\bigg\{\frac{d\bar{w}_j(t)}{dt}\big(\bar{w}_{j+1}(t) - \bar{w}_j(t)\big) \\
&\quad - \frac{d\bar{w}_{j-1}(t)}{dt}\big(\bar{w}_j(t) - \bar{w}_{j-1}(t)\big)\bigg\} \\
&\quad - \frac{1}{2}d_m\frac{d}{dt}\sum_{j=-\infty}^{\infty}\bar{w}_j^2(t)
\end{aligned}$$

which again contains a telescoping series that sums to zero. Integrating from 0 to t gives

$$\begin{aligned}
&\int_0^t \left\|\frac{d\bar{w}(s)}{dt}\right\|_{\ell^2}^2 ds + \frac{1}{2}D_m\left[\sum_{j=-\infty}^{\infty}\big(\bar{w}_j(s) - \bar{w}_{j-1}(s)\big)^2\right]_{s=0}^{s=t} \\
&\quad + \frac{1}{2}d_m\left[\sum_{j=-\infty}^{\infty}\bar{w}_j^2(s)\right]_{s=0}^{s=t} \\
&= \frac{\mu}{2\pi}\sum_{j=-\infty}^{\infty}\sum_{k=-\infty}^{\infty}\beta_\alpha(k)\int_0^t \frac{d\bar{w}_j(s)}{dt}\bar{w}_{j-k}(s-r)b'\big(\hat{w}_{j-k}(s-r)\big)\,ds \\
&\leqslant \frac{\mu B}{2\pi}\sum_{j=-\infty}^{\infty}\sum_{k=-\infty}^{\infty}\beta_\alpha(k)\int_0^t \left|\frac{d\bar{w}_j(s)}{dt}\bar{w}_{j-k}(s-r)\right| ds
\end{aligned}$$

$$\leqslant \frac{\mu B}{4\pi} \sum_{j=-\infty}^{\infty} \sum_{k=-\infty}^{\infty} \beta_\alpha(k) \left\{ \int_0^t \varepsilon \left(\frac{d\bar{w}_j(s)}{dt} \right)^2 ds + \int_0^t \frac{1}{\varepsilon} \bar{w}_{j-k}^2(s-r)\, ds \right\}$$

$$\leqslant \frac{\varepsilon \mu B}{2} \int_0^t \left\| \frac{d\bar{w}(s)}{dt} \right\|_{\ell^2}^2 ds + \frac{\mu B}{4\pi \varepsilon} \sum_{j=-\infty}^{\infty} \sum_{k=-\infty}^{\infty} \beta_\alpha(k) \int_0^t \bar{w}_{j-k}^2(s-r)\, ds,$$

where we have used $xy \leqslant (1/2)(\varepsilon x^2 + (1/\varepsilon) y^2)$ with $\varepsilon > 0$ to be chosen, and where $B = \sup_{w \geqslant 0} |b'(w)|$. In fact, we shall choose $\varepsilon = (\mu B)^{-1}$, giving

$$\frac{1}{2} \int_0^t \left\| \frac{d\bar{w}(s)}{dt} \right\|_{\ell^2}^2 ds + \frac{1}{2} D_m \left[\sum_{j=-\infty}^{\infty} \big(\bar{w}_j(s) - \bar{w}_{j-1}(s) \big)^2 \right]_{s=0}^{s=t}$$

$$+ \frac{1}{2} d_m \left[\sum_{j=-\infty}^{\infty} \bar{w}_j^2(s) \right]_{s=0}^{s=t}$$

$$\leqslant \frac{\mu^2 B^2}{4\pi} \sum_{j=-\infty}^{\infty} \sum_{k=-\infty}^{\infty} \beta_\alpha(k) \int_0^t \bar{w}_{j-k}^2(s-r)\, ds$$

$$= \frac{\mu^2 B^2}{4\pi} \int_0^t \sum_{k=-\infty}^{\infty} \beta_\alpha(k) \sum_{j=-\infty}^{\infty} \bar{w}_{j-k}^2(s-r)\, ds = \frac{\mu^2 B^2}{2} \int_0^t \left\| \bar{w}(s-r) \right\|_{\ell^2}^2 ds$$

$$\leqslant \frac{\mu^2 B^2}{2} \int_{-r}^0 \left\| \bar{w}(s) \right\|_{\ell^2}^2 ds + \frac{\mu^2 B^2}{2} \int_0^t \left\| \bar{w}(s) \right\|_{\ell^2}^2 ds$$

$$\leqslant \frac{\mu^2 B^2}{2} \int_{-r}^0 \left\| \bar{w}(s) \right\|_{\ell^2}^2 ds + \frac{\mu^2 B^2}{4 D_m} \left(\left\| w(0) \right\|_{\ell^2}^2 + d_m \int_{-r}^0 \left\| w(s) \right\|_{\ell^2}^2 ds \right)$$

using (2.6). Hence

$$\int_0^t \left\| \frac{d\bar{w}(s)}{dt} \right\|_{\ell^2}^2 ds + D_m \sum_{j=-\infty}^{\infty} \big(\bar{w}_j(t) - \bar{w}_{j-1}(t) \big)^2 + d_m \left\| \bar{w}(t) \right\|_{\ell^2}^2$$

$$\leqslant D_m \sum_{j=-\infty}^{\infty} \big(\bar{w}_j(0) - \bar{w}_{j-1}(0) \big)^2 + d_m \left\| \bar{w}(0) \right\|_{\ell^2}^2$$

$$+ \mu^2 B^2 \int_{-r}^0 \left\| \bar{w}(s) \right\|_{\ell^2}^2 ds + \frac{\mu^2 B^2}{2 D_m} \left(\left\| w(0) \right\|_{\ell^2}^2 + d_m \int_{-r}^0 \left\| w(s) \right\|_{\ell^2}^2 ds \right). \tag{2.9}$$

Now let

$$f(t) := \left\| \bar{w}(t) \right\|_{\ell^2}^2 = \sum_{j=-\infty}^{\infty} \bar{w}_j^2(t).$$

Then

$$\int_0^\infty \left|f(t)\right| dt = \int_0^\infty \sum_{j=-\infty}^{\infty} \bar{w}_j^2(t)\, dt < \infty$$

by (2.6), with $t \to \infty$. Also,

$$\left|f'(t)\right| = 2\left|\sum_{j=-\infty}^{\infty} \bar{w}_j(t)\frac{d\bar{w}_j(t)}{dt}\right| \leqslant \sum_{j=-\infty}^{\infty} \bar{w}_j^2(t) + \sum_{j=-\infty}^{\infty}\left(\frac{d\bar{w}_j(t)}{dt}\right)^2$$

and therefore

$$\begin{aligned}\int_0^\infty \left|f'(t)\right| dt &\leqslant \int_0^\infty \sum_{j=-\infty}^{\infty} \bar{w}_j^2(t)\, dt + \int_0^\infty \sum_{j=-\infty}^{\infty}\left(\frac{d\bar{w}_j(t)}{dt}\right)^2 dt \\ &= \int_0^\infty \sum_{j=-\infty}^{\infty} \bar{w}_j^2(t)\, dt + \int_0^\infty \left\|\frac{d\bar{w}(t)}{dt}\right\|_{\ell^2}^2 dt < \infty\end{aligned}$$

by (2.6) and (2.9) with $t \to \infty$.

It is known that if a differentiable function $f(t)$ satisfies $\int_0^\infty |f(t)|\, dt < \infty$ and $\int_0^\infty |f'(t)|\, dt < \infty$ then $\lim_{t\to\infty} f(t) = 0$. Therefore,

$$\lim_{t\to\infty} \left\|\bar{w}(t)\right\|_{\ell^2} = 0.$$

It can be shown (see Appendix A) that, for sequences $\{\xi_j\}_{j=-\infty}^{\infty} \in \ell^2$,

$$\sup_{j\in\mathbf{Z}} |\xi_j| \leqslant \sqrt{2}\left(\sum_{j=-\infty}^{\infty} \xi_j^2\right)^{1/4}\left(\sum_{j=-\infty}^{\infty} (\xi_j - \xi_{j-1})^2\right)^{1/4}. \tag{2.10}$$

With $\xi_j = w_j(t)$, and knowing that $w_j(t)$ is positive, tells us that

$$\sup_{j\in\mathbf{Z}} w_j(t) \leqslant \sqrt{2}\, \left\|w(t)\right\|_{\ell^2}^{1/2} \left\|\bar{w}(t)\right\|_{\ell^2}^{1/2},$$

which tends to zero as $t \to \infty$ (note that (2.6) assures us that $\|w(t)\|_{\ell^2}$ is bounded independently of t). The proof of the theorem is complete. □

3. Periodic traveling waves

In this section we consider the case when (1.1) has a positive uniform equilibrium state. Our aim is to prove the existence of a family of periodic traveling waves, arising via a Hopf bifurcation from this uniform equilibrium state. Our approach will be via the following Hopf bifurcation theory for functional differential equations of mixed type, due to Rustichini [2].

Let τ be a given positive real number, and denote by $C = C([-\tau, \tau], R^n)$ the Banach space of continuous functions from the interval $[-\tau, \tau]$ to R^n, endowed with the supremum norm. Consider the following functional differential equation of mixed type:

$$\dot{x} = F(x_t, \alpha),$$

where $\alpha \in (-\alpha_0, \alpha_0)$ is a real parameter and α_0 is a given constant, $F : C \times (-\alpha_0, \alpha_0) \to R^n$ is of class C^2 and $F(\hat{K}, \alpha) = 0$ for all $\alpha \in (-\alpha_0, \alpha_0)$, where K is a given constant, and $\hat{K}$ is the mapping from $[-\tau, \tau]$ into R^n identically taking the value K on $[-\tau, \tau]$. For a continuous mapping $x : R \to R$, $x_t \in C$ is defined by $x_t(s) = x(t + s)$ for $s \in [-\tau, \tau]$.

Denote by $F'(\phi, \alpha)$ the Frechét derivative of the functional $F(\cdot, \alpha)$, evaluated at ϕ, and write its representation as

$$F'(\phi, \alpha)(\psi) = \int_{-\tau}^{\tau} d\eta(\phi, \alpha)(s)\psi(s)$$

for $\psi \in C$, where $\eta(\cdot, \alpha)$ is a function of bounded variation.

We denote the characteristic matrix at $\alpha = 0$ of the equilibrium K as

$$\Delta(s, \alpha) = sI - \int_{-\tau}^{\tau} d\eta(\theta, \alpha)e^{s\theta}.$$

We then have

Theorem 3.1. *Assume that there exists $z > 0$ such that*

(i) $\det \Delta(iz, 0) = 0$ *and iz is a simple zero of* $\det \Delta(\lambda, 0) = 0$;
(ii) *There exists no $\omega \neq \pm z$ with* $\det \Delta(i\omega, 0) = 0$;
(iii) $\operatorname{Re} \lambda'(0) \neq 0$, *where $\lambda(\alpha)$ is the C^1-curve such that* $\det \Delta(\lambda(\alpha), \alpha) = 0$ *for small* $\alpha > 0$.

Then there exists a one-parameter family of periodic solutions of periods close to $2\pi/z$ bifurcating from the steady-state solution K.

Keeping in mind the various properties of $\beta_\alpha(l)$ described in Section 1, Eq. (1.1) can be recast in the following form which is slightly more convenient for the present section:

$$\begin{cases} \dot{w}_j(t) = u_j(t, r) + D_m[w_{j+1}(t) + w_{j-1}(t) - 2w_j(t)] - d_m w_j(t), \\ u_j(t, r) = \frac{\mu}{2\pi} \sum_{k=-\infty}^{\infty} \beta(j, k) b(w_k(t - r)), \\ \beta(j, k) = \beta_\alpha(k - j), \\ \beta_\alpha(l) = \int_{-\pi}^{\pi} \exp[-il\omega - 4\alpha \sin^2(\omega/2)]\, d\omega. \end{cases} \tag{3.1}$$

To apply Theorem 3.1, we also assume $b \in C^2$. We are interested in seeking traveling waves of the type

$$w_j(t) = \phi(t + cj), \quad \phi : R \to R.$$

Letting $s = t + cj$, we get

$$\dot{\phi}(s) = D_m\big[\phi(s+c) + \phi(s-c) - 2\phi(s)\big] - d_m\phi(s) + \frac{\mu}{2\pi}\sum_{k=-\infty}^{\infty}\beta_\alpha(k-j)b\big(\phi(s-r+(k-j)c)\big).$$

Therefore, we obtain the profile equation

$$\dot{\phi}(s) = D_m\big[\phi(s+c) + \phi(s-c) - 2\phi(s)\big] - d_m\phi(s) + \frac{\mu}{2\pi}\sum_{l=-\infty}^{\infty}\beta_\alpha(l)b\big((\phi(s-r+lc)\big). \tag{3.2}$$

We are interested in a periodic wave of period $2\pi/\omega$ (with $\omega > 0$) and so

$$\phi(s+2\pi/\omega) = \phi(s), \quad s \in \mathbf{R}.$$

Our approach is to seek a Hopf bifurcation of (3.2) from the steady state K, where $K > 0$ satisfies

$$d_m K = \mu b(K), \quad K > 0. \tag{3.3}$$

Of course, we assume here that the parameters d_m, μ and the birth function $b(w)$ are such that a positive root K exists to (3.3) (ecologically realistic choices for $b(w)$ include the case that $b(w)$ increases linearly with w when w is small, reaches a maximum and tends to zero as $w \to \infty$; in this case it is clear that a root $K > 0$ can be found for (3.3) for suitable values of the parameters d_m, μ and those associated with $b(w)$). If no root $K > 0$ can be found for (3.3) this will be (for ecologically realistic $b(w)$) because $\mu b(w) < d_m w$ on $w \in (0, \infty)$, and in this case extinction of the population is predicted in the last section.

Linearizing (3.2) at the constant solution K and letting

$$b'(K) = B, \tag{3.4}$$

we obtain

$$\dot{\phi}(s) = D_m\big[\phi(s+c) + \phi(s-c) - 2\phi(s)\big] - d_m\phi(s) + \frac{\mu}{2\pi}B\sum_{l=-\infty}^{\infty}\beta_\alpha(l)\phi(s-r+lc). \tag{3.5}$$

Let $\phi(s) = e^{\lambda s}$. This gives the characteristic equation

$$\lambda = D_m[e^{\lambda c} + e^{-\lambda c} - 2] - d_m + \frac{\mu}{2\pi}B\sum_{l=-\infty}^{\infty}\beta_\alpha(l)e^{-\lambda r + l\lambda c}. \tag{3.6}$$

Letting $\lambda = iz$ in (3.6), with $z \geqslant 0$, gives

$$iz = 2D_m\big[\cos(cz) - 1\big] - d_m + \frac{\mu}{2\pi}Be^{-izr}\sum_{l=-\infty}^{\infty}\beta_\alpha(l)\big[\cos(lzc) + i\sin(lzc)\big]. \tag{3.7}$$

Noting that $\beta_\alpha(l) = \beta_\alpha(-l)$, we obtain

$$iz = 2D_m\big[\cos(cz) - 1\big] - d_m + \frac{\mu}{2\pi}Be^{-izr}\left[\beta_\alpha(0) + 2\sum_{l=1}^{\infty}\beta_\alpha(l)\cos(lzc)\right]. \tag{3.8}$$

We now need to develop an explicit formula for $\beta_\alpha(0) + 2\sum_{l=1}^{\infty} \beta_\alpha(l)\cos(lzc)$.

Lemma 3.2. *For any $x \geqslant 0$, we have*

$$\beta_\alpha(0) + 2\sum_{l=1}^{\infty} \beta_\alpha(l)\cos(lx) = 2\pi e^{-4\alpha\sin^2(x/2)}. \tag{3.9}$$

Proof. Let $c_j = e^{ijx}$ and $h_j(t) = 0$ in (2.2). It is easily verified that in this case the solution of (2.2) is

$$v_j(t) = e^{\lambda t} e^{ijx},$$

where $\lambda = -4D\sin^2(x/2) - d$. But also, the solution $v_j(t)$ can be found from expression (2.3). Comparing the two expressions, we get

$$\frac{1}{2\pi} e^{-dt} \sum_{k=-\infty}^{\infty} \beta_{Dt}(k-j) e^{ikx} = e^{-(4D\sin^2(x/2)+d)t} e^{ijx}.$$

Accordingly,

$$\frac{1}{2\pi} \sum_{k=-\infty}^{\infty} \beta_{Dt}(k-j) e^{ikx} = e^{-4D\sin^2(x/2)t} e^{ijx}$$

which, with $\alpha = Dt$, yields

$$\frac{1}{2\pi} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) e^{ilx} = e^{-4\alpha\sin^2(x/2)}.$$

Since $\beta_\alpha(l) = \beta_\alpha(-l)$, we conclude that

$$\beta_\alpha(0) + 2\sum_{l=1}^{\infty} \beta_\alpha(l)\cos(lx) = 2\pi e^{-4\alpha\sin^2(x/2)}.$$

This completes the proof. □

With the results of Lemma 3.2 in mind, (3.8) becomes

$$iz = -4D_m\sin^2(cz/2) - d_m + \mu B e^{-izr} e^{-4\alpha\sin^2(cz/2)}.$$

Separating the real and imaginary parts gives

$$\begin{cases} 0 = -4D_m\sin^2(cz/2) - d_m + e^{-4\alpha\sin^2(cz/2)}\mu B\cos(zr), \\ -z = e^{-4\alpha\sin^2(cz/2)}\mu B\sin(zr). \end{cases} \tag{3.10}$$

Thus, we have

$$4D_m\sin^2(cz/2) + d_m = e^{-4\alpha\sin^2(cz/2)}\mu B\cos(zr) \tag{3.11}$$

and

$$-z = e^{-4\alpha\sin^2(cz/2)}\mu B\sin(zr). \tag{3.12}$$

Lemma 3.3. *Assume that* $\mu|B| > d_m$. *Let*

$$x^* = \min\{x \in [0,1];\ \mu|B|e^{-4\alpha x} > 4D_m x + d_m\},$$
$$z_0 = \sqrt{(\mu B)^2 - d_m^2},$$
$$z_1 = \sqrt{(\mu B e^{-4\alpha x^*})^2 - (4D_m x^* + d_m)^2},$$
$$r_0 = \frac{1}{z_0}\left[\pi - \arctan\frac{z_0}{d_m}\right],$$
$$r_1 = \frac{1}{z_1}\left[\pi - \arctan\frac{z_1}{4D_m x^* + d_m}\right].$$

Then for every fixed $r \in (r_0, r_1)$ *there exists a unique pair* (c, z) *with* $c = c(r)$ *and* $\omega = \omega(r) > 0$ *such that* (3.11) *and* (3.12) *are satisfied and* $zr \in (\pi/2, \pi)$, $\omega(r) = 2\pi/z(r)$.

Proof. Note that if $\mu|B| > d_m$ and x^* is defined as above, then

$$\Omega(x) := \sqrt{\mu^2 B^2 e^{-8\alpha x} - (4D_m x + d_m)^2}$$

is a monotonically decreasing function of $x \in [0, x^*]$ with $\Omega(0) = z_0$ and $\Omega(x^*) = z_1$. Therefore,

$$R(x) := \frac{1}{\Omega(x)}\left[\pi - \arctan\left(\frac{\Omega(x)}{4D_m x + d_m}\right)\right]$$

is an increasing function of $x \in [0, x^*]$ with $R(0) = r_0$ and $R(x^*) = r_1$. Therefore, if $r \in (r_0, r_1]$ then there exists a unique $x = x(r) \in (0, x^*] \subset (0, 1]$ so that $R(x(r)) = r$. Let $\omega := \omega(r) = \Omega(x(r))$. Then

$$z^2 + (4D_m x + d_m)^2 = \mu^2 B^2 e^{-8\alpha x}$$

and

$$\tan(zr) = -\frac{\omega}{4D_m x + d_m}.$$

By letting $x = \sin^2(c\omega)$, we complete the proof. □

Let $\lambda = \lambda(c)$ be the C^1-smooth curve of solutions of (3.6) such that $\lambda(c) = iz$. Differentiating (3.6) with respect to c, we obtain

$$\lambda' = D_m(e^{\lambda c} - e^{-\lambda c})(\lambda' c + \lambda) + \frac{\mu B}{2\pi} e^{-\lambda r}(-\lambda' r) \sum_{l=-\infty}^{\infty} \beta_\alpha(l) e^{l\lambda c}$$
$$+ \frac{\mu B}{2\pi} e^{-\lambda r} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) l[\lambda' c + \lambda].$$

Using the fact that $\beta_\alpha(l) = \beta_\alpha(-l)$, we obtain

$$\sum_{l=-\infty}^{\infty} \beta_\alpha(l) l = 0.$$

Therefore,

$$\lambda' = \frac{D_m(e^{\lambda c} - e^{-\lambda c})\lambda}{1 - D_m(e^{\lambda c} - e^{-\lambda c})c + \frac{\mu B}{2\pi} r e^{-\lambda r} \sum_{l=-\infty}^{\infty} \beta_\alpha(l) e^{\lambda l c}}.$$

Therefore, when $\lambda(c) = iz$, we get

$$\begin{aligned}\lambda' &= \frac{D_m(e^{izc} - e^{-izc})(iz)}{1 - D_m(e^{izc} - e^{-izc})c + r[\lambda + d_m - D_m(e^{izc} + e^{-izc} - 2)]} \\ &= \frac{-2D_m z \sin(zc)}{1 - 2i D_m \sin(zc) + r[iz + d_m + 4D_m \sin^2(zc/2)]}.\end{aligned}$$

Consequently, we have

$$\operatorname{Re} \lambda' = -2D_m z \sin(zc) \frac{1 + r d_m + 4D_m r \sin^2(zc/2)}{[1 + d_m r + 4D_m r \sin^2(zc/2)]^2 + [rz - 2D_m \sin(zc)]^2} < 0.$$

Therefore, applying Theorem 3.1, we obtain

Theorem 3.4. *Let r_0 and r_1 be defined as in Lemma* 3.3. *Then, for every $r \in (r_0, r_1)$,* (1.1) *has a family of periodic traveling waves $w_j(t) = \phi(t + cj)$, $j \in \mathbf{Z}$, of period $2\pi/\omega(r)$, for c near $c(r)$, where ω is close to $\omega(r)$ and $c(r)$ and $\omega(r)$ are the unique solutions of* (3.11) *and* (3.12) *with $2\pi r/\omega(r) \in (\pi/2, \pi)$.*

Appendix A

In this appendix we derive inequality (2.10). First, we shall show that, for $f \in W_0^{1,2}(\mathbf{R})$,

$$\|f\|_{L^\infty} \leqslant \sqrt{2}\, \|f\|_{L^2}^{1/2} \|f_x\|_{L^2}^{1/2}. \tag{A.1}$$

To see this, note that

$$\begin{aligned}\big(f(x)\big)^2 = \big(f(x)\big)^2 - \big(f(-\infty)\big)^2 &= \int_{-\infty}^{x} \frac{d}{ds}\big(f(s)\big)^2\, ds \\ &= 2\int_{-\infty}^{x} f(s) f'(s)\, ds \leqslant 2\|f\|_{L^2}\|f_x\|_{L^2}\end{aligned}$$

which establishes (A.1). Now let $f \in W_0^{1,2}(\mathbf{R})$ be the piecewise linear function such that $f(j) = \xi_j$, $j \in \mathbf{Z}$. Then

$$\|f\|_{L^2}^2 = \frac{1}{3} \sum_{j=-\infty}^{\infty} \big(\xi_j \xi_{j+1} + \xi_{j+1}^2 + \xi_j^2\big) \leqslant \sum_{j=-\infty}^{\infty} \xi_j^2$$

while

$$\|f_x\|_{L^2}^2 = \sum_{j=-\infty}^{\infty} (\xi_{i+1} - \xi_i)^2.$$

Thus (A.1) becomes

$$\sup_{j\in\mathbf{Z}}|\xi_j| \leqslant \sqrt{2}\left(\sum_{j=-\infty}^{\infty}\xi_j^2\right)^{1/4}\left(\sum_{j=-\infty}^{\infty}(\xi_{i+1}-\xi_i)^2\right)^{1/4}$$

so that (2.10) holds.

References

[1] K. Deimling, Ordinary Differential Equations in Banach Spaces, in: Lecture Notes in Biomathematics, Vol. 596, Springer-Verlag, New York, 1977.

[2] A. Rustichini, Hopf bifurcation for functional differential equations of mixed type, J. Dynam. Differential Equations 1 (1989) 145–177.

[3] P. Weng, H. Huang, J. Wu, Asymptotic speed of propagation of wave fronts in a lattice delay differential equation with global interaction, IMA J. Appl. Math. 68 (2003) 409–439.