Dynamics of single species population over a patchy environment

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Appeared in *[Advanced Topics in Biomathematics, L. Chen et al eds., pp. 63-77, World Scientific, Singapore, 1998.]*

Abstract. The dynamics of a time delay single-species population over a patch environment with Allee effect is considered in this paper. By constructing a suitable Liapunov functional, we first establish the global asymptotical stability for the positive homogenous equilibrium of the system of functional differential equations. Then, using the symmetric Hopf bifurcation theory, we are able to show that time delay can induce Hopf bifurcation of periodic solutions including phase-lock oscillations and synchronous oscillations.

1 Introduction

Single species population models have been extensively studied. When the environment where the species inhabits is *homogeneous*, the growth of the population is usually described by an ordinary differential equation

$$\frac{du}{dt} = u\, f(u), \tag{1.1}$$

where f is called the growth rate. A typical and frequently used rate function is the so called logistic growth function

$$f(u) = r\left(1 - \frac{u}{K}\right), \tag{1.2}$$

where the constant $r > 0$ is the intrinsic growth rate and $K > 0$ is the carrying capacity. Equation (1.1) with a logistic growth function accounts for, to some extent, the competitive aspect of the population.

On the other hand, it has been widely observed in ecology and biology (e.g. Allee [1], Cushing [4], Sarukhan [12], Silvertown [13] and Watt [14]) that for many species, increased population levels are advantageous at low densities but disadvantageous at high densities. Such kind of effect is referred as *Allee effect* in the literature, and is easily observable in those species of small individual sizes. For example, it has been observed that in several species of beetles (Allee [1]) and insects (Watt [14]) increased low level densities result in increased fertility as well as enhanced survival. Concerning the beneficial effects of crowding on survival rates, one immediately thinks of the possible increased chance of survival of young as a result of increased care and nurturing within groups of animals. Indeed, herding, flocking, schooling, etc. can provide general protection to individual members from predators and adverse environment events. Also, survival can be enhanced by more efficient harvesting or hunting of prey resources by herds or packs. Studies showing enhanced survival for plant species in the presence of increased low densities are described by Sarukhan [12] for Ranunculus Bulbosa and by Silvertown [13] for Pinus Ponderosa.

A simple way to take into account Allee effect in the model (1.1) is to modify f in (1.2) as

$$g(u) = r\,\left[1 + \alpha\, u - \beta\, u^2\right], \tag{1.3}$$

where $\alpha > 0$ and $\beta > 0$, for it is easily seen that when $u > 0$ is small the growth function g is dominated by the term $1 + \alpha u(t)$, and when $u > 0$ is large it is dominated by the second order term βu^2. An ODE model with such a growth function was discussed in Zou [17].

When the population of a species distributes over a continuous heterogeneous environment, spatial variables must be corporated into the model. In such a situation, the growth of the population is often modeled by a reaction-diffusion equation

$$\frac{\partial u(t,x)}{\partial t} = h(u(t,x)) + \triangle u(t,x) \tag{1.4}$$

where $\triangle$ is the Laplacian with respect to the spatial variables. While the nonlinear term $h(u(t,x)) = u(t,x)f(u(t,x))$ in (1.4) just decribes the reaction term (local), $\triangle u$ accounts for the natural diffusion of the population, based on random walk.

Recently, Britton [3] proposed and analyzed a model of the form

$$\frac{\partial u}{\partial t} = u\,[\,1 + \alpha\, u - (1+\alpha)\, g * u\,] + \triangle u \tag{1.5}$$

to account for *local aggregation* and *global intraspecies competition*, where g is a given function and $g * u$ represents a convolution in the spatial-temporal variables. The term αu with $\alpha > 0$ represents an advantage (cooperative aspect) in local aggregation and the term $-(1+\alpha)g*u$ with $\alpha > -1$ explain the disadvantage (competitive aspect) of high global population levels. It was shown that various types of bifurcating spatial-temporal solutions including steady spatial periodic structures, periodic standing wave solutions and periodic traveling wave solutions can occur by varying certain parameters.

In the conclusion section of Britton [3], it was also suggested that Allee effect should be included in the local interaction term. Later, Gourley and Britton [7] studied the following modified model of (1.5)

$$\frac{\partial u}{\partial t} = u\,[\,1 + a\, u - b\, u^2 - (1 + a - b)\, g * u\,] + \triangle u \tag{1.6}$$

where $a > 0$, $b > 0$ and $1 + a - b > 0$. The asymptotic stability of the equilibrium $u \equiv 1$ was studied there.

In many circumstances, a species may live in a *patchy environment* which is also heterogeneous. In such a case, the spatial variables belong to a discrete set, and thus the growth of the population is described by a system of ordinary/functional differential equations. In Madras, Wu and Zou [11], a single species population over a ring of n identical patches connected by dispersion between adjacent patches was considered. They derived a model of the following form

$$\begin{aligned}\frac{d\,u_i(t)}{dt} &= r\,u_i(t)\left[1+\alpha u_i(t)-(1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}u_j(t-\tau)\right] \\ &\quad + d\,\left[u_{i+1}(t)+u_{i-1}(t)-2u_i(t)\right], \quad i=1,\dots,n\ (mod\ n), \end{aligned} \tag{1.7}$$

where $u_i(t)$ is the population of the species in patch i at time t, $r>0$ is the intrinsic growth rate of the population in each patch, $d\geq 0$ is the parameter measuring the strength of dispersion of the populations between patches, and $\tau\geq 0$ is the time delay. Note that the discrete Laplacian $\triangle_d$ defined by

$$(\triangle_d u(t))_i = u_{i+1}(t)+u_{i-1}(t)-2u_i(t)$$

is the discretization of the $\triangle u(t,x)$ along the one-dimensional spatial variable x. So, (1.7) is actually a discrete version of (1.5). The basic assumptions for (1.7) in [11] is

$$\alpha>-1, \quad \beta_j\geq 0, \quad \beta_{n-j}=\beta_j,\ j=1,\dots,n\ (mod\ n) \quad and \quad \sum_{j=1}^{n}\beta_j=1, \tag{1.8}$$

reflecting the ring structure of the inhibiting patches. While the term αu_i and $-(1+\alpha)\beta_0 u_i(t-\tau)$ exhibit the local effect in patch i, the terms $-(1+\alpha)\beta_{|j-i|}u_j(t-\tau),\ j\neq i$, stands for the nonlocal competitive effect from patch j to patch i, and hence, $-(1+\alpha)\sum_{j=0}^{n-1}\beta_{|j-i|}u_j(t-\tau)$ reflects the global intraspecies competition. It was shown [11] that spatially heterogeneous steady state solutions can bifurcate from a spatially homogeneous steady state solution if the dispersion rate is large, and that Hopf bifurcations of periodic solutions including phase-locked oscillations and synchronous oscillations can occur when the delay in the global intraspecies competition reaches a critical value.

In this paper, we modify (1.7), as a discrete analog of (1.6), to include Allee effect in the model system. In other words, we consider the following system

$$\begin{aligned}\frac{d\,u_i(t)}{dt} &= r_i\,u_i(t)\left[1+a_i u_i(t)-b_i u_i^2(t)-(1+a_i-b_i)\sum_{j=1}^{n}\beta_{|j-i|}u_j(t-\tau_{ij})\right] \\ &\quad + d_i\,\left[u_{i+1}(t)+u_{i-1}(t)-2u_i(t)\right], \quad i=1,\dots,n\ (mod\ n), \end{aligned} \tag{1.9}$$

where $r_i > 0$, $d_i > 0$, $b_i \geq 0$ and $\tau_{ij} \geq 0$ for $i, j = 1, 2, \ldots, n$. Note that we allow in (1.9) different dispersion strengthes, different intrinsic growth rates and different delays in different patches. Moreover, we assume

(H1) $\beta_{n-j} = \beta_j,\ j = 1, \ldots, n\ (mod\ n)$ *and* $\sum_{j=1}^{n} \beta_j = 1.$

Here,(H1) again describes the ring structure of the patchy environment and is in the normalized form. Also note that we do not require a_i, $1+a_i-b_i$ and β_i, $i = 1, \ldots, n$, to be positive, which means nonlocal interaction could be either advantageous (cooperative) or disadvantageous (competitive). When $a_i > 0$ and $b_i > 0$, Allee effect is reflected in the model too.

The justification for system (1.9) can be similarly done as for (1.7) in [11], by considering a species of land (or amphibious) animals that live on the shores of a lake. The patches correspond to segments of the shoreline, and thus form a ring. In such an environment, the nonlocal interaction is complicated and could be due to, among other things, the migration of the population, the resulting competition for resources and the accumulation of populations waste production in the environment. For detailed argument on this context, we refer to [11] and [3]. We mention that a simpler version of (1.9) with $r_i = r$, $a_i = a, b_i = b$ and $d_i = d$ for $i = 1, \ldots, n$ was considered in Wu and Zou [16] where some *local stability* and Hopf bifurcation results were obtained. But so far no global stability result has ever been addressed for such models.

The purpose of this paper is to present some global stability and Hopf bifurcation results for (1.9). Section 2 deals with homogeneous equilibria of (1.9) and their stability. In particular, we establish a global asymptotic stability result for the positive homogeneous equilibrium, by Liapunov methods. Section 3 is devoted to the existence of periodic solutions. By using some symmetric Hopf bifurcation theorem developed by Geba, Krawcewicz and Wu [6], Krawcewicz, Vivid and Wu [9], and Krawcewicz and Wu [10] based on equivariant degree theory, we are able to obtain the existence of phase-locked oscillations (or discrete waves) or synchronous oscillations, which are special periodic solutions with certain symmetries.

2 Global Asymptotic Stability

For biological reasons, we are only interested in solutions in the non-negative cone $\mathbb{R}^n_+$ where

$$\mathbb{R}^n_+ = \{u = (u_1, u_2, \ldots, n)^n \in \mathbb{R}^n; u_i \geq 0, i = 1, 2, \ldots, n\}.$$

Let $\tau = \max\{\tau_{ij}; i,j = 1,2,\ldots,n\}$. Then, fundamental theory of existence and uniqueness in Hale [8] shows that for any initial function $\phi \in C([-\tau,0],\mathbb{R}^n_+)$, there exists a unique solution $u(t) = (u_1(t),u_2(t),\ldots,u_n(t))^T$ of (1.9) such that $u(s) = \phi(s)$ for $s \in [-\tau,0]$.

Theorem 2.1. *For any $\phi \in C([-\tau,0],\mathbb{R}^n_+)$, the corresponding solution $u(t)$ remains in $\mathbb{R}^n_+$ in the interval of existence and is bounded, and therefore, the existence is global.*

The positivity is trivial, as the ith component of the right-hand side of (1.9) is non-negative at $t \geq 0$ such that $u_i(t) = 0$ and $u_j(t) \geq 0$ for $j \neq i$. The proof of the boundedness is also obvious because of the negativity of the higher order terms $-b_i u_i^2(t)$, $i = 1,2,\ldots,n$, in the equations.

Note that there are two explicit spatially homogeneous equilibria, i.e.,$(0,0,\ldots,0)^T$, $(1,1,\ldots,1)^T$ in $\mathbb{R}^n_+$. The trivial equilibrium $(0,0,\ldots,0)^T$ is always unstable, for the linearized system at this equilibrium

$$\frac{d}{dt}u_i(t) \;=\; r_i\, u_i(t) + \; d_i\; [u_{i+1}(t) + u_{i-1}(t) - 2u_i(t)]\,, \quad i = 1,\ldots,n\ (mod\ n) \tag{2.1}$$

is unstable. The instability of (2.1) can be easily established by considering the positive invariance of (2.1) and a Liapunov function $V(u) = \sum_{i=1}^n \frac{1}{d_i}u_i$. For the positive equilibrium $(1,1,\ldots,1)^T$, we have

Theorem 2.2. *Assume that*

$$a_i + \sum_{j=1}^n \frac{1}{2}\left[|1+a_i-b_i| + \frac{d_i}{d_j}\frac{r_j}{r_i}|1+a_j-b_j|\right]|\beta_{|i-j|}| < b_i, \quad i = 1,2,\cdots,n. \tag{2.2}$$

Then the positive equilibrium $(1,1,\ldots,1)^T$ is globally attractive in the sense that all positive solutions of (1.9) converge to $(1,1,\ldots,1)^T$.

Proof. Assume $u(t) = (u_1(t),u_2(t),\cdots,u_n(t))^T$ is a positive solution of (1.9). Let

$$x_i = log u_i, \qquad y_i = e^{x_i} - 1, \qquad i = 1,\cdots,n.$$

Then

$$u_i(t) = e^{x_i(t)}, \qquad y_i(t) = u_i(t) - 1.$$

Since $(1, 1, \cdots, 1)$ is a positive equilibrium of (1.9), using the above relations, we can write (1.9) as follows:

$$\begin{aligned}\dot{x}_i(t) &= r_i\left(a_i y_i(t) - b_i[y_i(t)+2]y_i(t) - (1+a_i-b_i)\sum_{j=1}^{n}\beta_{|j-i|}y_j(t-\tau_{ij})\right) \\ &\quad + d_i[e^{x_{i+1}(t)-x_i(t)} + e^{x_{i-1}(t)-x_i(t)} - 2]. \qquad (2.3)\end{aligned}$$

Define

$$V_i(x_i) = \int_0^{x_i}[e^s - 1]ds$$

and

$$V(x) = \sum_{i=1}^{n}\frac{1}{d_i}V_i(x_i).$$

¿From (2.3) we have

$$\begin{aligned}\frac{d}{dt}V(x(t)) &= \sum_{i=1}^{n}\frac{1}{d_i}y_i(t)\dot{x}_i(t) \\ &= \sum_{i=1}^{n}\frac{r_i}{d_i}\bigg(a_i y_i^2(t) - b_i[y_i(t)+2]y_i^2(t) \\ &\quad -(1+a_i-b_i)\sum_{j=1}^{n}\beta_{|j-i|}y_i(t)y_j(t-\tau_{ij})\bigg) \\ &\quad +\sum_{i=1}^{n}[e^{x_i(t)}-1][e^{x_{i+1}(t)-x_i(t)} + e^{x_{i-1}(t)-x_i(t)} - 2]. \qquad (2.4)\end{aligned}$$

By the definition of y_i, we know that

$$y_i(t) + 2 \geq 1.$$

Note that

$$\begin{aligned}&\sum_{i=1}^{n}[e^{x_i(t)}-1][e^{x_{i+1}(t)-x_i(t)} + e^{x_{i-1}(t)-x_i(t)} - 2] \\ &= \sum_{i=1}^{n}\left[(e^{x_{i+1}(t)}-1) + (e^{x_{i-1}(t)}-1) - 2(e^{x_i(t)}-1)\right] \\ &\quad -\sum_{i=1}^{n}\left[e^{x_{i+1}(t)-x_i(t)} + e^{x_{i-1}(t)-x_i(t)} - 2\right]. \qquad (2.5)\end{aligned}$$

But

$$\sum_{i=1}^{n}\left[(e^{x_{i+1}(t)}-1)+(e^{x_{i-1}(t)}-1)-2(e^{x_i(t)}-1)\right]=0, \tag{2.6}$$

and

$$\sum_{i=1}^{n}\left[e^{x_{i+1}(t)-x_i(t)}+e^{x_{i-1}(t)-x_i(t)}-2\right]=\sum_{i=1}^{n}\left[e^{\frac{1}{2}(x_{i+1}(t)-x_i(t)}-e^{\frac{1}{2}(x_i(t)-x_{i+1}(t)}\right]^2. \tag{2.7}$$

Using (2.4)-(2.7), we obtain

$$\begin{aligned}\tfrac{d}{dt}V(x(t)) \leq \ & \sum_{i=1}^{n}\frac{r_i}{d_i}\bigg[(a_i-b_i)y_i^2(t)\\ & +\frac{1}{2}|1+a_i-b_i|\sum_{j=1}^{n}|\beta_{|j-i|}|(y_i^2(t)+y_j^2(t-\tau_{ij}))\bigg].\end{aligned} \tag{2.8}$$

Let

$$W(x_t)=\sum_{i,j=1}^{n}\frac{r_i}{d_i}\frac{1}{2}|1+a_i-b_i||\beta_{|j-i|}|\int_{t-\tau_{ij}}^{t}y_j^2(s)ds.$$

Then, using $|\beta_{|i-j|}|=|\beta_{|j-i|}|$, we have

$$\begin{aligned}&\frac{d}{dt}[V(x(t))+W(x_t)]\\ &\leq\sum_{i=1}^{n}\frac{r_i}{d_i}\bigg[(a_i-b_i)y_i^2(t)\\ &\quad+\frac{1}{2}|1+a_i-b_i|\sum_{j=1}^{n}|\beta_{|j-i|}|(y_i^2(t)+y_j^2(t))\bigg]\\ &=\sum_{i=1}^{n}\left[\frac{r_i}{d_i}(a_i-b_i)+\frac{1}{2}\sum_{j=1}^{n}\left(\frac{r_i}{d_i}|1+a_i-b_i|+\frac{r_j}{d_j}|1+a_j-b_j|\right)|\beta_{|i-j|}|\right]y_i^2(t)\\ &=-\sum_{i=1}^{n}\theta_i y_i^2(t),\end{aligned} \tag{2.9}$$

where

$$\theta_i=\frac{r_i}{d_i}(b_i-a_i)-\frac{1}{2}\sum_{j=1}^{n}\left(\frac{r_i}{d_i}|1+a_i-b_i|+\frac{r_j}{d_j}|1+a_j-b_j|\right)|\beta_{|i-j|}|,\quad i=1,2,\cdots,n.$$

¿From (2.2), we know $\theta_i > 0, \ \ i = 1, 2, \cdots, n$. Therefore

$$0 \le V(x(t)) + W(x_t) + \int_0^t \sum_{i=1}^n \theta_i y_i^2(s)\, ds \le V(x(0)) + W(x_0), \quad \text{for} \quad t > 0. \tag{2.10}$$

Thus, nonnegativity of V and W and (2.10) imply

$$\int_0^\infty \sum_{i=1}^n y_i^2(t)\, dt < \infty. \tag{2.11}$$

But, by the boundedness of $u_i, \ \ i = 1, 2, \cdots, n$ and (1.9), we know $\dot{y}_i(t) = \dot{u}_i(t)$ is also bounded, and hence, $\sum_{i=1}^n y_i^2(t)$ is uniformly continuous. ¿From a useful lemma in Barbálat [2] (also see Gopalsamy [5]), we obtain

$$\lim_{t\to\infty} \sum_{i=1}^n y_i^2(t) = 0,$$

that is,

$$\lim_{t\to\infty} y_i(t) = 0, \qquad i = 1, 2, \cdots, n. \tag{2.12}$$

By the definition of $y_i(t)$, we conclude that

$$\lim_{t\to\infty} u_i(t) = 1, \qquad i = 1, 2, \cdots, n.$$

This complete the proof.

Remark 2.3. *When*

$$r_i = r, \ \ a_i = a, \ \ b_i = b, \ \ d_i = d, \ \ \tau_{ij} = \tau, \ \ i, j = 1, 2, \cdots, n, \tag{2.13}$$

(1.9) reduces to the system studied in [16]. It was shown in [16] that if $\beta_i \ge 0, \ \ i = 1, 2, \cdots, n$ *and*

$$\frac{1}{2} < b - a < 1 \quad (\textit{or equivalently } 0 < 1 + a - b < \frac{1}{2}), \tag{2.14}$$

then the positive equilibrium $(1, 1, \cdots, 1)^T$ *is locally asymptotically stable. Note that under the assumptions (2.13) and* $\beta_i \ge 0, \ \ i = 1, 2, \cdots, n$*, condition (2.2) in Theorem 2.2 becomes*

$$|1 + a - b| < b - a \tag{2.15}$$

which is weaker than (2.14), but the conclusion in Theorem 2.2 is stronger. So, Theorem 2.2 not only generalizes but also improves the corresponding result in [16].

3 Synchronous oscillations and phase-locked oscillations

This section deals with the Hopf bifurcation of system (1.9). As mentioned in the previous section, $(0,0,\cdots,0)^T$ and $(1,1,\cdots,n)^T$ are two spatially homogeneous equilibria. Since the trivial equilibrium is always unstable for any $\tau_{ij}\geq 0$ and $r_i>0,\;\; i,j=1,2,\cdots,n$, we will concentrate on the positive equilibrium $(1,1,\cdots,1)^T$ and look for Hopf bifurcation from this equilibrium. For simplicity, we will assume, in the remainder of this section, $r_i=r,\;\; a_i=a,\;\; b_i=b,\;\; d_i=d,\;\; \tau_{ij}=\tau,\;\; i,\, j=1,2,\cdots,n$, and consider

$$\begin{aligned}\tfrac{d\,u_i(t)}{dt} \;&=\; r\,u_i(t)\left[1+au_i(t)-bu_i^2(t)-(1+a-b)\sum_{j=1}^{n}\beta_{|j-i|}u_j(t-\tau_{ij})\right]\\ &\quad + d\,\left[u_{i+1}(t)+u_{i-1}(t)-2u_i(t)\right],\quad i=1,\ldots,n\ (mod\ n). \qquad (3.1)\end{aligned}$$

Set $x_i(t)=u_i(t)-1,\;\; i=1,1,\cdots,n$. Then (3.1) becomes

$$\begin{aligned}\tfrac{dx_i(t)}{dt} =\;& r\,[x_i(t)+1]\Bigg[ax_i(t)-bx_i(t)\,(\,x_i(t)+2\,)\\ & -(\,1+a-b\,)\sum_{j=1}^{n}\beta_{|j-i|}x_j(t-\tau)\Bigg]\\ & +d\,[\,x_{i+1}(t)+x_{i-1}(t)-2x_i(t)\,],\;\; i=1,\ldots,n\ (mod\ n). \quad (3.2)\end{aligned}$$

We consider the equivalent system (3.2) and the corresponding equilibrium $(0,\ldots,0)^T$. The linearization of (3.2) at this point is

$$\begin{aligned}\tfrac{dx_i(t)}{dt} =\;& r\left[(a-2b)\,x_i(t)\;-\;(1+a-b)\sum_{j=1}^{n}\beta_{|j-i|}x_j(t-\tau)\right]\\ & +d\,[\,x_{i+1}(t)+x_{i-1}(t)-2x_i(t)\,],\quad i=1,\ldots,n\ \ (mod\ n).\ (3.3)\end{aligned}$$

When $\tau=0$, (3.3) only has real eigenvalues, for the coefficient matrix is symmetric, and hence no Hopf bifurcation occurs if $\tau=0$. In the rest of this section, we will use $\tau>0$ as the bifurcation parameter and detect the occurrence of Hopf bifurcations.

Normalizing the delay by $y_i(t)=x_i(\tau\,t)$, (3.3) becomes

$$\frac{d}{dt}y(t)\;=\;[\,\tau r(a-2b)\,Id\;+\;\tau dN]\;y(t)\;-\;\tau r\,(1+a-b)\,M\,y(t-1),\quad (3.4)$$

where Id is the $n \times n$ identity matrix and

$$M = \begin{pmatrix} \beta_0 & \beta_1 & \beta_2 & \dots & \beta_{n-2} & \beta_{n-1} \\ \beta_1 & \beta_2 & \beta_3 & \dots & \beta_{n-3} & \beta_{n-2} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \beta_{n-1} & \beta_{n-2} & \beta_{n-3} & \dots & \beta_1 & \beta_0 \end{pmatrix},$$

$$N = \begin{pmatrix} -2 & 1 & 0 & \dots & 0 & 1 \\ 1 & -2 & 1 & \dots & 0 & 0 \\ 0 & 1 & -2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 1 & 0 & 0 & \dots & 1 & -2 \end{pmatrix}.$$

In what follows, we assume, in addition to (H1), the following

(H2) $1 + a - b \neq 0$.

For fixed $r > 0$, $d \geq 0$ and $b > 0$, let

$$\Lambda_\tau(\lambda) := [\lambda - \tau r(a - 2b)]\, Id + e^{-\lambda}\tau r(1 + a - b)\, M - \tau d\, N.$$

Then, considering the restriction of $\Lambda_\tau(\lambda)$ on the one-dimensional complex subspace spanned by $(1, e^{i\frac{2\pi}{n}j}, \cdots, e^{i\frac{2\pi}{n}(n-1)j})^T$, we can get the following (see, for example [11])

Lemma 3.1. *Suppose (H1) holds. Then*

$$det\, \Lambda_\tau(\lambda) \;=\; \prod_{k=0}^{n-1} q_k(\tau,\, \lambda)$$

where

$$q_k(\tau,\, \lambda) = \lambda - \tau r(a - 2b) + e^{-\lambda}\tau r(1 + a - b)\, B_k + 4\tau d \sin^2 \frac{k\pi}{n},$$

$$B_k = \sum_{j=0}^{n-1} \beta_j\, \xi^{jk}, \quad k = 0, 1, \dots, n-1,\ \xi = e^{i\frac{2\pi}{n}}.$$

By a standard application of the well-known result about the zeros of $\lambda + A + Be^{-\lambda} = 0$(see, for example Hale [8]), we obtain

Lemma 3.2. *The following statements hold:*

(i) The equation

$$q_k(\tau,\, \lambda) = 0 \tag{3.5}$$

has purely imaginary roots λ if and only if

$$(A_k) \qquad |B_k| > \frac{|r(a-2b) - 4d\, \sin^2 \frac{k\pi}{n}|}{r\,|1+a-b|}$$

holds;

(ii) For each $k \in \{0, 1, \ldots, n-1\}$ satisfying (A_k), the least positive τ for $(3.5)_k$ to have purely imaginary roots and the corresponding pair $\pm\omega_k$ of the purely imaginary roots are given by

$$\begin{cases} \tau_k = \frac{\omega_k}{B_k r(1+a-b)\, \sin\, \omega_k}, \\ \omega_k = \begin{cases} \arccos \frac{r(a-2b)-4d\, \sin^2\, \frac{k\pi}{n}}{rB_k(1+a-b)} & if\ \ B_k(1+a-b) > 0; \\ 2\pi - \arccos \frac{r(a-2b)-4d\, \sin^2\, \frac{k\pi}{n}}{rB_k(1+a-b)} & if\ \ B_k(1+a-b) < 0. \end{cases} \end{cases}$$

(iii) For each $k \in \{0, 1, \ldots, n-1\}$ satisfying (A_k), there exist $\delta_k > 0$ and a continuously differentiable $\lambda:\ (\tau_k - \delta_k,\, \tau_k + \delta_k) \to \mathbb{C}$ such that $q_k(\tau,\, \lambda(\tau)) = 0$ for $(\tau_k - \delta_k,\, \tau_k + \delta_k)$, $\lambda(\tau_k) = i\omega_k$ and

$$\frac{d}{dt} Re(\,\lambda(\tau)\,)\bigg|_{\tau=\tau_k} = \frac{\omega_k^2}{\tau_k \left[\left(1 - \tau_k r(a-2b) + 4d\tau_k\, \sin^2\, \frac{k\pi}{n}\,\right)^2 + \omega_k^2\right]} > 0.$$

Suppose that there exists $k \in \{0, 1, \ldots, n-1\}$ satisfying (A_k). Then the characteristic equation

$$det\, \Lambda_\tau(\lambda) = 0 \tag{3.6}$$

has purely imaginary roots at $\tau = \tau_k$. Sine $\sin^2\, \frac{(n-k)\pi}{n} = \sin^2\, \frac{k\pi}{n}$ and $B_{n-k} = B_k$, we observe that these purely imaginary roots of (3.6) at $\tau = \tau_k$ will not be simple unless $k = 0$, or $k = \frac{n}{2}$ when n is even. This observation implies that the standard Hopf bifurcation theorem is not applicable in the case $k \neq 0$ and $k \neq \frac{n}{2}$ when n is even. Fortunately, the symmetry of (3.2) arising from the ring structure of the patchy environment makes the newly developed *symmetric bifurcation theory* for functional differential equations in [6,9,10] applicable.

To apply these results, we now explore the symmetry of system (3.2). Define

$$\mathbb{Z}_n = \left\{ e^{i\frac{2\pi}{n}j};\ 0 \le j \le n-1 \right\}.$$

Then, $\mathbb{Z}_n$ is a group with the usual operation:

$$e^{i\frac{2\pi}{n}j_1} \cdot e^{i\frac{2\pi}{n}j_2} = e^{i\frac{2\pi}{n}(j_1+j_2)},\ \ j_1,\ j_2\ \ (mod\ n).$$

Define the orthogonal representation $\rho:\ \mathbb{Z}_n \to GL(\mathbb{R}^n)$ of the $\mathbb{Z}_n$ cyclic permutation on $\mathbb{R}^n$ by

$$\left(\rho\left(e^{i\frac{2\pi}{n}k}\right)x\right)_j = x_{j-k}, \quad x \in \mathbb{R}^n \quad and \quad j,\ k\ \ (mod\ n).$$

Then, under (H1) we can verify that system (3.2) is equivariant with respect to the above $\mathbb{Z}_n$ action.

Now we can apply the *symmetric bifurcation theory* in [6,9,10] (see [11] or [15] for a simpler version applicable to (3.2)) to obtain

Theorem 3.3. *Assume (H1), (H2) and*

(H3) $\ rB_k\,(1+a-b) - r(a-2b) + 4d\sin^2\frac{k\pi}{n} \neq 0,\ \ k \in \{0,1,\ldots,n-1\}$ *are satisfied. Suppose* (A_{k_0}) *hold for some* $k_0 \in \{0,1,\ldots,n-1\}$*. Then, there exists a sequence of triples* $\left\{u^{(l)}(t),\, \tau^{(l)},\, \omega^{(l)}\right\}$ *such that*

(i) $\tau^{(l)} \to \tau_{k_0},\quad \omega^{(l)} \to \omega_{k_0}$ *as* $l \to \infty$ *and* $u^{(l)}(t) = \left(u_1^{(l)}(t),\ldots,u_n^{(l)}(t)\right)^T \to (1,\ldots,1)^T$ *uniformly for* $t \in \mathbb{R}$ *as* $l \to \infty$.

(ii) $u^{(l)}(t) = \left(u_1^{(l)}(t),\ldots,u_n^{(l)}(t)\right)^T$ *is a* $\frac{2\pi}{\omega^{(l)}}-$*periodic solution of (3.1) with* $\tau = \tau^{(l)}$ *for* $l = 1,2,\ldots$.

(iii) $u_{j-1}^{(l)}(t) = u_j^{(l)}\left(t - \frac{2\pi}{\omega^{(l)}}\frac{k_0}{n}\right)$ *for* $t \in \mathbb{R},\ \ l = 1,2,\ldots$ *and* $j = 1,2,\ldots,n$ *(mod n).*

Remark 3.4. *If* $k_0 = 0$*, the bifurcated periodic solutions are spatially homogeneous and are called synchronous oscillations, and if* $k_0 \neq 0$*, they are spatially heterogeneous and are called discrete waves or phase-locked oscillations.*

We now discuss some special cases. If $1+a-b<0$, then we have

$$\frac{|a-2b|}{|1+a-b|} = \frac{(b-a)+b}{(b-a)-1} \ge 1 \quad for\ \ b \ge -1. \tag{3.7}$$

So, as $b \ge 0$, (A_0) cannot hold. Hence it is necessary that $1+a-b>0$ in order for synchronous oscillations to occur.

Corollary 3.5. *If*

$$a > -\frac{1}{2} \quad \textit{and} \quad 0 \ \leq b < \frac{2a+1}{3}, \tag{3.8}$$

then there exist synchronous oscillations for (3.1).

Proof. (3.8) implies that $1 + a - b > (1+a) - \frac{2}{3}(1+a) = \frac{1}{3}(1+a) > 0$, $a-2b > b-a-1 = -(1+a-b)$ and $a-2b \leq (a-b)+1$. Thus, $|a-2b| < 1+a-b$, and hence (A_0) holds. Therefore, by Theorem 3.3, synchronous oscillations occur near $\tau = \tau_0$.

We have seen that the conditions of Corollary 3.5 imply $\frac{|a-2b|}{1+a-b} < 1$ and hence

$$\frac{|r(a-2b)| - 4d\, \sin^2 \frac{k\pi}{n}|}{r(1+a-b)} < 1 \tag{3.9}$$

for $k = 0, 1, \ldots, [\frac{n}{2}]$ for sufficiently small $d > 0$. Note also that $B_k = 1,\ k = 0, 1, \ldots, n-1$, if $\beta_j = 0$ for $j \neq 0$ and $\beta_0 = 1$, and hence (3.9_k) is equivalent to (A_k) in this case. This means that if we ignore the non-local interactions, then under the condition (3.8), there will also occur phase-locked oscillations, in addition to synchronous oscillations.

We next consider the order of the occurrences of these oscillations. First, we note that $B_k(1+a-b) = 1+a-b > 0$ and

$$\frac{r(a-2b) - 4d\, \sin^2 \frac{(k+1)\pi}{n}}{r(1+a-b)} < \frac{r(a-2b) - 4d\, \sin^2 \frac{k\pi}{n}}{r(1+a-b)}, \quad k = 0, 1, \ldots, [\frac{n}{2}] - 1. \tag{3.10}$$

Thus, we have

$$\begin{aligned} \omega_{k+1} &= arccos \frac{r(a-2b) - 4d\, \sin^2 \frac{(k+1)\pi}{n}}{r(1+a-b)} \\ &> \frac{r(a-2b) - 4d\, \sin^2 \frac{k\pi}{n}}{r(1+a-b)} = \omega_k, \quad k = 0, 1, \ldots, [\frac{n}{2}] - 1 \end{aligned} \tag{3.11}$$

which leads to

$$\begin{aligned} \tau_{k+1} &= \frac{1}{r(1+a-b)} \frac{\omega_{k+1}}{\sin\, \omega_{k+1}} \\ &> \frac{1}{r(1+a-b)} \frac{\omega_k}{\sin\, \omega_k} = \tau_k, \quad k = 0, 1, \ldots, [\frac{n}{2} - 1]. \end{aligned} \tag{3.12}$$

Thus, $\tau_0 < \tau_1 < \cdots < \tau_{[\frac{n}{2}]}$, and hence we have

Corollary 3.6. *Assume (3.8) is satisfied. If* $\beta_j = 0$ *for* $j \neq 0$, *and* $d > 0$ *is sufficiently small, then there occur synchronous oscillations first, and then phase-locked oscillations, as* $\tau > 0$ *increases to* $\tau_0 < \tau_1 < \cdots < \tau_{[\frac{n}{2}]}$ *respectively.*

Remark 3.7. *When* $b = 0$, *Corollary 3.5 implies that for any* $a \in (-\frac{1}{2}, \infty)$, (A_0) *always holds. Hence, Hopf bifurcations for (3.1) always exist. Now, for any fixed* $a \in (-\frac{1}{2}, \infty)$, *we can choose* $b > 0$ *such that* $\frac{1}{2} < b - a < 1$ *(say* $b = a + \frac{2}{3}$*) which implies, by Theorem 2.2, that* $(1, \ldots, 1)^T$ *is asymptotically stable for any* $\tau > 0$. *Therefore, no Hopf bifurcation will occur as* $\tau > 0$ *increases. This shows that appropriate* $b > 0$ *prevents Hopf bifurcations.*

Corollary 3.6 claims the existence of phase-locked oscillations under the conditions that $\beta_j = 0$ for $j \neq 0$ and that $d > 0$ is sufficiently small. Such phase-locked oscillations are unstable under small perturbations because when τ is near $\tau_k > \tau_0$ for $k \neq 0$, the characteristic equation (3.6) always has zeros with positive real parts. The only phase-locked oscillations which are possibly stable will be those occurring at $\tau = \tau_{k_0} = min\,\{\tau_k : k \in \{0, 1, \ldots, n-1\}$ *and* (A_k) *holds*$\}$ for some $k_0 \neq 0$. The next result shows that such phase-locked oscillations exist, due to non-local interactions.

Corollary 3.8. *Assume* $\beta_j = 0$ *for* $j > 1$, *and let* $\beta_1 = -\theta$ *and* $\beta_0 = 1 + 2\theta$ *where* $\theta > 0$. *If* $1 + a - b < 0$, *then for sufficiently large* $\theta > 0$, *(3.1) has (and only has) phase-locked oscillations.*

Proof. By (H1), we can obtain $B_k = 1 + 4\theta \sin^2 \frac{k\pi}{n}$ and hence, (A_k) becomes

$$\frac{|r(a-2b) - 4d\,\sin^2 \frac{k\pi}{n}|}{r\,|1 + a - b\,|} < 1 + 4\theta\,\sin^2 \frac{k\pi}{n}$$

which would hold for each $k \in \{1, 2, \ldots, n-1\}$, provided that $\theta > 0$ is sufficiently large. Therefore, by Theorem 3.3 and Remark 3.4, we know that (3.1) has phase-locked oscillations near $\tau = \tau_k,\ k = 1, 2, \ldots, n-1$. On the other hand, discussion as argued before, $1 + a - b < 0$ implies that (A_0) does not hold, and hence no synchronous oscillations would occur. Therefore $min\,\{\tau_k : k \in \{0, 1, \ldots, n-1\}$ *and* (A_k) *holds*$\} = \tau_{k_0}$ for some $k_0 \neq 0$. This completes the proof.

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