CANADIAN APPLIED
MATHEMATICS QUARTERLY
Volume 4, Number 1, Winter 1996

LOCAL-NONLOCAL INTERACTION AND SPATIAL-TEMPORAL PATTERNS IN SINGLE SPECIES POPULATION OVER A PATCHY ENVIRONMENT

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ABSTRACT. A system of functional differential equations is proposed to describe the dynamics of a single-species population distributed over a patchy environment. Of major concern is the impact of the interaction between local aggregation and global delayed competition on the dynamics and the spatial-temporal patterns of the considered system. It is shown that spatially heterogeneous steady state solutions can bifurcate from a spatially homogeneous steady state solution if the dispersion rate is large. Moreover, Hopf bifurcation of periodic solutions including phase-locked oscillations and synchronous oscillations can occur when the time delay in the global intraspecies competition reaches a critical value. Examples are provided to exhibit the complexity of the dynamics and the co-existence of phase-locked oscillations and heterogeneous steady state solutions.

1. Introduction. Single species population models with or without delay have been extensively investigated and the interaction of spatial diffusion/dispersal with time delay has also been studied. For details, we refer to [**1, 2, 4–8, 13–16, 19, 22–27, 31–39**] and the references therein.

In [**7**], Britton proposed and analyzed a model of the form

$$\frac{\partial u}{\partial t} = u[1 + \alpha u - (1+\alpha) g * u] + \triangle u \tag{1.1}$$

to account for local aggregation and global intraspecies competition, where g is a given function and $g * u$ represents a convolution in

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Received by the editors in revised form on August 24, 1995.
Key words and phrases. Hopf bifurcation, bifurcation of equilibria, local and nonlocal interaction, phase-locked oscillation, synchronous oscillation, heterogeneity, patchy environment, delay, dispersion.
AMS (MOS) *Subject Classifications.* 34K15, 34C10.
Research partially supported by Natural Sciences and Engineering Research Council of Canada.

the spatial-temporal variables. The term αu with $\alpha > 0$ represents an advantage in local aggregation and the term $-(1+\alpha)g * u$ with $\alpha > -1$ represents a disadvantage 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 this paper, we propose a system of ordinary functional differential equations as a discrete analog of Britton's model to describe the dynamics of a single species population distributed over a patchy environment. We will justify the assumption that growth rate decreases as the total population increases due to the accumulation of population's waste products in the environment, and we will point out that the nonlocal competitive effect due to the migration of the population and the resulting competition for resources is more complicated than the case described in Britton's model at the probability level. We will show, by using several existing bifurcation theorems, that the proposed system exhibits spatially heterogeneous steady state solutions and discrete wave solutions bifurcating from a spatially homogeneous equilibrium. More precisely, we prove that a bifurcation of spatially heterogeneous steady state solutions takes place when we increase the strength of the dispersal to a critical value, and discrete waves (or phase-locked oscillations) bifurcate (from a spatially homogeneous equilibrium) when the delay passes through another critical value. This demonstrates the possible co-existence of several spatial heterogeneous positive equilibria and periodic solutions, in addition to some spatially homogeneous equilibria and periodic solutions.

The rest of this paper is organized as follows. The model is derived in Section 2. The steady state bifurcation and spatial-temporal structure are described in Section 3 and Section 4 respectively.

2. The model.

The focus of this paper is on a single species population over a ring of n identical patches connected by dispersion between adjacent patches. For concreteness, we consider 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. The lake serves as the animals' principal source of water, and it is also where their waste products accumulate. We assume that each particle of waste floats randomly around the lake, until it is removed, e.g., via a stream that flows out of the lake. We shall use the following probabilities to describe the free motion of a waste particle:

$$\begin{aligned} p_{j,i}(s) = \Pr\{&\text{a particle is in patch } i \text{ at time } t+s, \\ &\text{given that the particle is produced at patch } j \text{ at time } t\}. \end{aligned}$$

Here we assume time-homogeneity so that the probabilities are independent of the initial time t. We emphasize that $p_{j,i}(s)$ describes the motion of a hypothetical particle under the condition that it remains in the lake forever. The amount of time that a real particle spends in the lake is modeled by a random variable T. We describe the probability distribution of T by

$$\begin{aligned} w(s) &= \Pr\{T \geq s\} \\ &= \Pr\{\text{a particle is still in the lake at time } t+s, \\ &\qquad \text{given that the particle is produced at time } t\}. \end{aligned}$$

Therefore, for a waste particle that was produced at time t in patch j, the probability that it is still in the lake at time $t+s$ and is in patch i at that time is $p_{j,i}(s)w(s)$. Therefore the expected number of waste particles that are in patch i at time t is proportional to

$$\int_0^\infty \sum_{j=1}^n u_j(t-s)p_{j,i}(s)w(s)\,ds$$

where $u_j(t)$ is the population of the species in patch j at time t and the proportionality constant is scaled to one. This gives us a measure of the water quality in patch i at time t. If we assume that the birth rate is influenced (linearly) by the water quality, then we arrive at the model

$$\begin{aligned} \frac{d}{dt}u_i(t) = r\,u_i(t)\left[1+\gamma u_i(t) - A\sum_{j=1}^n \int_0^\infty u_j(t-s)p_{j,i}(s)w(s)\,ds\right] \\ + d[u_{i+1}(t) - 2u_i(t) + u_{i-1}(t)], \quad i \pmod n \end{aligned} \tag{2.1}$$

for some constant A, where $r > 0$ 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 $\gamma > 0$ (< 0) represents the advantage (disadvantage) of local aggregation.

In the present paper, we shall analyze a version of this model that has been simplified in two ways. Firstly, instead of integrating over all possible time delays, we shall work with a single time delay τ and assume that the waste quality at time t depends only on the population accounts at time $t-\tau$. Mathematically, this is done by replacing the delay weights $w(s)$ in (2.1) by a Dirac delta function $\delta(s-\tau)$ times a constant, which can be absorbed into the existing constant A. If we interpret τ as the average amount of time that a waste particle spends in the lake, then this seems to preserve the spirit of our model. Secondly, we assume that the probability $p_{j,i}(\tau)$ depends on the relative location of the two patches, and hence $p_{j,i}(\tau) = \beta_{|j-i|}$ for some nonnegative constants $\beta_0, \beta_1, \dots, \beta_{n-1}$ with

$$\text{(H1)} \qquad \sum_{j=0}^{n-1} \beta_j = 1 \quad \text{and} \quad \beta_j = \beta_{n-j}.$$

(It may be biologically reasonable to expect that $\beta_0 \geq \beta_1 \geq \cdots$, but this will not be necessary in our analysis, so we shall not impose this constraint.) This brings us to the following system

$$\text{(2.2)} \qquad \begin{aligned} \frac{d}{dt}u_i(t) &= r\,u_i(t)\left[1 + \gamma u_i(t) - A\sum_{j=1}^{n}\beta_{|j-i|}u_j(t-\tau)\right] \\ &\quad + d[u_{i+1}(t) - 2u_i(t) + u_{i-1}(t)], \quad i \pmod n. \end{aligned}$$

Rescaling the variable u_i by a factor $(A-\gamma)$, we get

$$\text{(2.3)} \qquad \begin{aligned} \frac{d}{dt}u_i(t) &= r\,u_i(t)\left[1 + \alpha u_i(t) - (1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}u_j(t-\tau)\right] \\ &\quad + d[u_{i+1}(t) - 2u_i(t) + u_{i-1}(t)], \quad i \pmod n. \end{aligned}$$

The reduction of the population growth rate by the accumulation of waste products in the environment was observed in the classical experiments of Gause [**17**]. In nature waste products remain in the environment for a while, and this introduces a distributed delay effect. So our assumption of a discrete delay is only an approximation of the reality. Also, we assumed that wastes are eventually removed, although in a closed laboratory system the wastes never leave (cf. MacDonald [**34**]).

It is also important to note that the motions of the waste particles are independent of one another *and* of the size of the population in each patch. (Of course, the *number* of particles is not independent of the size of the population). The result is a "competition effect" that is nonlocal in both time and space. This is where the explanation of [**7**] is inadequate. In [**7**], Britton attributes the competition to the random migration of individuals, and asserts that the competition should be measured by the frequency with which paths intersect one another. This is reasonable, but given the entire history of the population counts $u_i(s)$, $[i = 1, \dots, N,\ s \leq t]$, the paths of individuals before time t are not simply independent random walks. Nonlinearities signify interactions, and the interactions cause deviations from pure random walk behavior. For example, a particle that was present at time $t - s$ would have an increased probability of being in a patch j where $u_j(t - s)$ is large. Thus, to assess the effect of competition due to path intersections, one should be looking at the *conditional* distribution of paths given the population counts, but this seems like a complex problem. Indeed, the best approach to this model may well be through the theory of measure-valued stochastic processes, see, for example, Dawson [**9**] or Evans and Perkins [**11**]. In summary, we feel that the random walk arguments of Britton [**7**] are a major oversimplification at the probabilistic level, and a more realistic model should be developed in the future.

Finally, let us point out the symmetry of the model system (2.3) due to the ring structure of the environment. Let $\mathbf{D}_n$ be the dihedral group of order $2n$. $\mathbf{D}_n$ is generated by a rotation ψ and a reflection φ such that $\langle \psi \rangle \cong \mathbf{Z}_n$, $\langle \varphi \rangle \cong \mathbf{Z}_2$ and $\varphi\psi\varphi\psi = 1$. Define the orthogonal representation $\hat{\rho} : \mathbf{D}_n \to GL(\mathbf{R}^n)$ by

$$(\hat{\rho}(\psi)x)_j = x_{j-1}, \qquad (\hat{\rho}(\varphi)x)_j = x_{n-j}, \qquad j \pmod n, \quad x \in \mathbf{R}^n. \tag{2.4}$$

Then, we have the following

Lemma 2.1. *Suppose* (H1) *holds. Then, system* (2.3) *is equivariant with respect to the action of* $\mathbf{D}_n$ *under the representation* (2.4).

The proof of this lemma is a direct verification. For the definition of equivariance, we refer to Golubitsky, Schaeffer and Stewart [**20**], Golubitsky and Stewart [**21**], and Geba, Krawcewicz and Wu [**18**].

3. Bifurcations of equilibria. This section is concerned with the bifurcation of equilibria. Since the structure of the equilibria is independent of the delay, we only need consider system (2.3) with $\tau = 0$, i.e.,

$$\begin{aligned} \frac{d}{dt}u_i(t) &= ru_i(t)\left[1 + \alpha u_i(t) - (1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}u_j(t)\right] \\ &\quad + d[u_{i+1}(t) + u_{i-1}(t) - 2u_i(t)], \\ &\quad i = 1, 2, \ldots, n \bmod (n). \end{aligned} \tag{3.1}$$

For biological reasons, we are interested only in those equilibria located in the closed cone

$$\boldsymbol{\Omega}_+ = \{U = (u_1, u_2, \ldots, u_n)^T \in R^n;\ u_i \geq 0, i = 1, 2, \ldots, n\}.$$

It can be easily seen that $(0, 0, \ldots, 0)^T$ and $(1, 1, \ldots, 1)^T$ are the only spatially homogeneous steady equilibria of (3.1) in $\boldsymbol{\Omega}_+$. Since the linearization of (3.1) at $(0, 0, \ldots, 0)^T$ always has a positive real eigenvalue $\lambda = r > 0$, $(0, 0, \ldots, 0)^T$ is always unstable for any $r > 0$, $d \geq 0$, $\alpha > -1$ and $\beta_j \geq 0$, $j = 1, 2, \ldots, n \bmod (n)$. In what follows, we concentrate on bifurcation from the positive steady equilibrium $(1, 1, \ldots, 1)^T$, although branches of equilibria and periodic solutions can also bifurcate from $(0, 0, \ldots, 0)^T$ and other possible spatially heterogeneous equilibria.

Set $x_i(t) = u_i(t) - 1$. Then, (3.1) becomes

$$\begin{aligned} \frac{d}{dt}x_i(t) &= r\,[1 + x_i(t)]\left[\alpha x_i(t) - (1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}x_j(t)\right] \\ &\quad + d[x_{i+1}(t) + x_{i-1}(t) - 2x_i(t)], \\ &\quad i = 1, 2, \ldots, n \bmod (n). \end{aligned} \tag{3.2}$$

The linearization of (3.1) at $(1,1,\dots,1)^T$ is

$$\begin{aligned}\frac{d}{dt}y_i(t) &= r\left[\alpha y_i(t) - (1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}y_j(t)\right] \\ &\quad + d[y_{i+1}(t) + y_{i-1}(t) - 2y_i(t)], \\ &\quad t \geq 0, \quad i = 1,2,\dots,n \bmod (n),\end{aligned} \tag{3.3}$$

or using matrix expression,

$$\frac{d}{dt}Y(t) = [r\alpha\,\mathrm{Id} - r(1+\alpha)\,M + d\,N]\;Y(t), \tag{3.4}$$

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

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

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

In the rest of this section, we will use $d \in [0,\infty)$ as the bifurcation parameter. For any fixed $r > 0$, $\alpha > -1$ and $\beta_j \geq 0$, $j = 1,2,\dots,n$, let

$$L(d) = r\alpha\,\mathrm{Id} - r(1+\alpha)\,M + d\,N.$$

Denote by ξ the primitive nth root of the unit in $\mathbf{C}$, i.e., $\xi = e^{i(2\pi/n)}$, and let

$$B_k = \sum_{j=0}^{n-1}\beta_j\xi^{jk}, \qquad k = 0,1,\dots,n-1.$$

Clearly, $B_k = B_{n-k}$ for $0 \leq k \leq n-1$. We have

Lemma 3.1. *Under assumption* (H1), *we have*

$$\det\,[\lambda\mathrm{Id} - L(d)] = \prod_{k=0}^{n-1}[\lambda - \lambda_k(d)]\,, \qquad \lambda \in \mathbf{C},$$

where

$$\lambda_k(d) = r\alpha - r(1+\alpha)B_k - 4d\sin^2(k\pi/n),$$
$$k = 0, 1, \dots, n-1.$$

Proof. Let

$$W_k = (1, \xi^k, \dots, \xi^{(n-1)k})^T, \qquad 0 \le k \le n-1.$$

Then, $\{W_0, W_1, \dots, W_{n-1}\}$ spans the space $\mathbf{C}^n$. Note that (H1) holds and

$$\xi^{-k} = \overline{\xi^k} = \xi^{n-k}, \qquad 0 \le k \le n-1.$$

We have, for every $j, k \in \{0, 1, \dots, n-1\}$, that

$$\begin{aligned}
(L(d)\, W_k)_j &= r\alpha\xi^{(j-1)k} + d(\xi^{(j-2)k} - 2\xi^{(j-1)k} + \xi^{jk}) \\
&\quad - r(1+\alpha)(\beta_{j-1} + \beta_{j-2}\xi^k + \cdots + \beta_0\xi^{(j-1)k} \\
&\qquad + \beta_1\xi^{jk} + \cdots + \beta_{n-j}\xi^{(n-1)k}) \\
&= \Big[r\alpha + d(\xi^{-k} - 2 + \xi^k) - r(1+\alpha)(\beta_{j-1}\xi^{-(j-1)k} \\
&\quad + \beta_{j-2}\xi^{-(j-2)k} + \cdots + \beta_0 + \beta_1\xi^k + \cdots + \beta_{n-j}\xi^{jk})\Big]\, \xi^{(j-1)k} \\
&= \left[r\alpha - r(1+\alpha)\, B_k + d\,(2\,\mathrm{Re}\,\xi^k - 2)\right] \xi^{(j-1)k} \\
&= [r\alpha - r(1+\alpha)\, B_k + 2d(\cos(2k\pi/n) - 1)]\xi^{(j-1)k} \\
&= [r\alpha - r(1+\alpha)\, B_k - 4d\sin^2(k\pi/n)]\xi^{(j-1)k} \\
&= \lambda_k(d)\xi^{(j-1)k}.
\end{aligned}$$

Thus

$$[\lambda \mathrm{Id} - L(d)]\, W_k = [\lambda - \lambda_k(d)]\, W_k,$$

and hence

$$\det\,[\lambda \mathrm{Id} - L(d)] = \prod_{k=0}^{n-1} [\lambda - \lambda_k(d)]\,.$$

This completes the proof. □

From the above lemma, we know that $L(d)$ has eigenvalues

$$\lambda_k(d) = r\alpha - 4d\sin^2\frac{k\pi}{n} - r(1+\alpha)B_k,$$
$$k = 0, 1, \dots, n-1.$$

Under assumption (H1), B_k is real and $B_{n-k} = B_k$ for $k \in \{0, 1, \ldots, n-1\}$, where $B_n = B_0$. So, each $\lambda_k(d)$ is a real number and $\lambda_k(d) = \lambda_{n-k}(d)$, $k = 0, 1, \ldots, n-1$.

It is straightforward to verify the following:

Lemma 3.2. *Let*

$$(C_k) \qquad B_k < \frac{\alpha}{1+\alpha}$$

hold for some $k \in \{1, 2, \ldots, n-1\}$. *Then for*

$$d = d_k = \frac{r\alpha - r(1+\alpha)B_k}{4\sin^2(k\pi/n)}$$

we have

$$\lambda_k(d_k) = 0 \quad \textit{and} \quad \lambda_k'(d_k) \neq 0.$$

It is naturally expected that a bifurcation of equilibria occurs near $d = d_k$. As system (3.1) is equivariant with respect to the action of $\mathbf{D}_n$ (Lemma 2.1), the associated eigenvalues are not simple and the standard steady state bifurcation theory does not apply. On the other hand, the presence of symmetry in the system suggests that the possible bifurcated equilibria possess a certain symmetry. We refer to Golubitsky, Schaeffer and Stewart [**20**] for general results.

We now establish the following results on the existence of bifurcation of spatially periodic equilibria by degree-theoretical arguments.

Theorem 3.3. *Assume that there exists a* $k_0 \in \{1, 2, \ldots, n/2\}$ *such that* (C_{k_0}) *holds, i.e.,* $B_{k_0} < \alpha/(1+\alpha))$. *Let* k *be the greatest common divisor of* n *and* k_0, *and denote* $m = n/k$ *and* $l_0 = k_0/k$. *If*

$$(3.5) \qquad \frac{\alpha - (1+\alpha)B_j}{4\sin^2(j\pi/n)} \neq \frac{\alpha - (1+\alpha)B_{k_0}}{4\sin^2(k_0\pi/n)}$$

for $1 \leq j \leq [n/2]$ *and* $j \neq k_0$, *then* (3.1) *has a bifurcation of equilibria bifurcated from* $(1, 1, \ldots, 1)^T$ *near* $d = d_{k_0}$ *and the bifurcated equilibria satisfy*

$$(3.6) \qquad x_{j+m} = x_j, \qquad j = 1, \ldots, n.$$

Furthermore, m is the least (spatial) period of such bifurcated equilibria.

Proof. It is easy to show that

$$\mathbf{R}^n = \left\{ \sum_{j=0}^{[n/2]} (\alpha_j W_j + \overline{\alpha_j} W_{n-j})\,;\ \alpha_j \in \mathbf{C},\ 0 \le j \le [n/2] \right\}.$$

Let S_m be the subspace of $\mathbf{R}^n$ consisting of $x \in \mathbf{R}^n$ such that

$$x_j = x_{j+m}, \qquad 1 \le j \le n.$$

Then one can show that

$$S_m = \left\{ \sum_{0 \le j \le [n/2],\, k|j} (\alpha_j W_j + \overline{\alpha_j} W_{n-j})\,;\ \alpha_j \in \mathbf{C},\ 0 \le j \le [n/2],\ k|j \right\}.$$

Let $F(d) : \mathbf{R}^n \to \mathbf{R}^n$ be defined by

$$\begin{aligned}(F(d)x)_i = r\,[1 + x_i] \left[\alpha x_i - (1+\alpha) \sum_{j=1}^{n} \beta_{|j-i|} x_j \right] \\ + d\,[x_{i+1} + x_{i-1} - 2x_i], \\ 1 \le i \le n.\end{aligned}$$

Then $F(d)\,(S_m) \subseteq S_m$. Denote by $F_m(d) = F(d)|_{S_m}$ the restriction of $F(d)$ on S_m. It can be easily verified that

$$L(d)\,[\alpha_j W_j + \overline{\alpha_j} W_{n-j}] = \lambda_j(d)\,[\alpha_j W_j + \overline{\alpha_j} W_{n-j}].$$

Therefore, for the derivative $L_m(d)$ of $F_m(d)$ at the point $(1, \dots, 1)^T \in S_m$, we have

$$\det\,[\lambda I - L_m(d)] = \prod_{0 \le j \le [n/2],\, k|j} [\lambda - \lambda_j(d)].$$

So $L_m(d)$ has the eigenvalues $\{\lambda_j(d), 0 \le j \le [n/2],\, k|j\}$. At $d = d_{k_0}$ the only eigenvalue which vanishes is $\lambda_{l_0 k}(d_{k_0})$. Using Lemma 3.2, we then have

$$\text{sign}\,(\det L_m(d_{k_0} - \varepsilon)) \ne \text{sign}\,(\det L_m(d_{k_0} + \varepsilon))$$

for sufficiently small $\varepsilon > 0$. By the classical topological steady state bifurcation theory (see Demling [**10**] or Krawcewicz and Wu [**30**]), we can conclude that $d = d_{k_0}$ is a bifurcation of zeros of the parametrized mapping $F_m(d)$. This justifies the existence of a branch of equilibria which are bifurcated from $(1, \dots, 1)^T \in \mathbf{R}^n$ near $d = d_{k_0}$ and satisfy $x_j = x_{j+m}$ for $j = 1, \dots, n$.

We now use the nonresonance condition (3.5) to show that m is the least (spatial) period of the bifurcated equilibria. By way of contradiction, if $p < m$ is the minimal period, then $m = pq$ for some integer $q > 1$. The well-known implicit function theorem then implies that 0 must be an eigenvalue of $L_p(d_{k_0})$. But

$$\det L_p(d) = \prod_{0 \le j \le [n/2],\, qk|j} \lambda_j(d).$$

So under the nonresonance condition (3.5), there exists an integer $u \geq 1$ such that $k_0 = qku$. Therefore, as $n = pqk$, we know that qk is a common factor of k_0 and n, a contradiction to the definition of k as $q > 1$. This completes the proof. □

Example 3.1. Let $n = 3$, $\beta_1 = \beta_2 = \theta$ and $\beta_0 = 1 - 2\theta$, $0 \le \theta \le 1/3$. Direct calculation leads to $B_1 = B_2 = 1 - 3\theta$. So, for any fixed $\alpha \in (0, \infty)$, we have $B_1 = B_2 < \alpha/(1+\alpha)$ if $\theta > 1/(3(1+\alpha))$. Thus, (C_1) holds for $1/(3(1+\alpha)) < \theta \le 1/3$, $\alpha \in (0,\infty)$. In this case, $n = 3$ and the genericity condition (3.5) holds trivially. Therefore, by Theorem 3.3, if $1/(3(1+\alpha)) < \theta \le 1/3$ and $\alpha \in (0, \infty)$, then (3.1) has spatially heterogeneous steady state solutions bifurcating from $(1, 1, \dots, 1)^T$ when d passes through

$$d_1 = \frac{r\alpha - r(1+\alpha)B_1}{4\sin^2(\pi/3)} = \frac{r\,[3\theta(1+\alpha) - 1]}{3}.$$

Example 3.2. Let $n = 4$, $\beta_0 = 0$, $\beta_1 = \beta_2 = \beta_3 = 1/3$. Then $B_1 = B_2 = B_3 = -1/3$. Thus, for any $\alpha > -1/4$,

$$\frac{\alpha}{1+\alpha} > \frac{-1/4}{1-1/4} = -\frac{1}{3} = B_k, \qquad k = 1, 2, 3.$$

So, (C_k) holds for $k = 1, 2, 3$. Take $k_0 = 2$. A direct verification shows that the genericity condition (3.5) holds. Therefore, (3.1) has a bifurcation of equilibria bifurcating from $(1, 1, \ldots, 1)^T$ when d passes through

$$d_2 = \frac{r\alpha - r(1+\alpha)B_2}{4\sin^2(\pi/4)} = \frac{r(4\alpha+1)}{6} > 0$$

and these bifurcated equilibria have the period 2 (that is, $x_1 = x_3$, $x_2 = x_4$).

4. Hopf bifurcations. This section deals with the Hopf bifurcation of system (2.3). As mentioned in the previous section, $(0, 0, \ldots, 0)^T$ and $(1, 1, \ldots, 1)^T$ are the only spatially homogeneous steady equilibria of system (2.3) in the positive orthant, and $(0, 0, \ldots, 0)^T$ is always unstable for any $\tau \geq 0$, $r > 0$, $d \geq 0$, $\alpha > -1$ and $\beta_j \geq 0$, $j = 1, 2, \ldots, n \bmod (n)$. We will concentrate on Hopf bifurcation from the positive steady equilibrium $(1, 1, \ldots, 1)^T$.

Set $z_i(t) = u_i(t) - 1$. Then, (2.3) becomes

$$\begin{aligned} \frac{d}{dt}z_i(t) =& r\,[1 + z_i(t)]\left[\alpha z_i(t) - (1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}z_j(t-\tau)\right] \\ &+ d\,[z_{i+1}(t) + z_{i-1}(t) - 2z_i(t)], \\ &\qquad i = 1, 2, \ldots, n \mod (n). \end{aligned} \tag{4.1}$$

So, the linearization of (2.3) at $(1, 1, \ldots, 1)^T$ is

$$\begin{aligned} \frac{d}{dt}x_i(t) =& r\left[\alpha x_i(t) - (1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}x_j(t-\tau)\right] \\ &+ d\,[x_{i+1}(t) + x_{i-1}(t) - 2x_i(t)], \\ &\qquad i = 1, 2, \ldots, n \mod (n). \end{aligned} \tag{4.2}$$

In Section 3, we have seen that (4.2) only has real eigenvalues when $\tau = 0$, 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 determine whether or not and when Hopf bifurcation occurs when we increase τ. The spatial-temporal patterns of the bifurcating solutions will also be considered.

Normalizing the delay by $y_i(t) = x_i(\tau t)$, (4.2) becomes

$$\begin{aligned}\frac{d}{dt}y_i(t) &= r\tau\left[\alpha y_i(t) - (1+\alpha)\sum_{j=1}^{n}\beta_{|j-i|}y_j(t-1)\right] \\ &\quad + d\tau\left[y_{i+1}(t) + y_{i-1}(t) - 2y_i(t)\right], \\ &\quad i = 1,2,\ldots,n \quad \bmod (n),\end{aligned} \tag{4.3}$$

or using matrix expression

$$\frac{d}{dt}Y(t) = (\tau\alpha r\,\mathrm{Id} + \tau d\,N)\,Y(t) - \tau r(1+\alpha)\,MY(t-1),$$

where Id, M and N are as in Section 3.

For fixed $r > 0$, $\alpha > -1$ and $d \geq 0$, let

$$\mathbf{\Lambda}_\tau(\lambda) := (\lambda - \tau r\alpha)\,\mathrm{Id} + e^{-\lambda}\tau r(1+\alpha)\,M - \tau\,dN.$$

Denote by A the generator of the semigroup generated by the solutions of (4.3). Then, λ is an eigenvalue of A if and only if

$$\det \mathbf{\Lambda}_\tau(\lambda) = 0. \tag{4.4}$$

The following lemma is an analogue of Lemma 3.1.

Lemma 4.1. *Under* (H1), *we have*

$$\det \mathbf{\Lambda}_\tau(\lambda) = \prod_{k=0}^{n-1} q_k(\tau,\lambda)$$

where

$$\begin{aligned}q_k(\tau,\lambda) &= \lambda - \tau r\alpha + e^{-\lambda}\tau r(1+\alpha)B_k \\ &\quad + 4\tau d\sin^2(k\pi/n), \qquad k = 0,1,\ldots,n-1, \\ B_k &= \sum_{j=0}^{n-1}\beta_j\xi^{jk}, \qquad k = 0,1,\ldots,n-1, \\ \xi &= e^{i(2\pi/n)}.\end{aligned}$$

The proof is similar to that of Lemma 3.1 and thus is omitted.

Lemma 4.2. *The following statements hold:*

(i) *The equation*

$$q_k(\tau, \lambda) = 0 \tag{4.5_k}$$

has purely imaginary roots λ *for some* $\tau > 0$ *if and only if*

$$|B_k| > \frac{|r\alpha - 4d\sin^2(k\pi/n)|}{r(1+\alpha)} \tag{A_k}$$

holds.

(ii) *For each* $k \in \{0, 1, \ldots, n-1\}$ *satisfying* (A_k), *the least positive* τ *for* (4.5_k) *to have purely imaginary roots and the corresponding pair* $\pm i\omega_k$ *of the purely imaginary roots are given by*

$$\begin{cases} \tau_k = \dfrac{\omega_k}{B_k r(1+\alpha)\sin\omega_k}, \\ \omega_k = \begin{cases} \arccos \dfrac{r\alpha - 4d\sin^2(k\pi/n)}{rB_k(1+\alpha)} & \text{if } B_k > 0, \\ 2\pi - \arccos \dfrac{r\alpha - 4d\sin^2(k\pi/n)}{rB_k(1+\alpha)} & \text{if } B_k < 0. \end{cases} \end{cases} \tag{4.6_k}$$

Proof. Substituting $\lambda = i\omega$ into (4.5_k), we get

$$i\omega - \tau r\alpha + e^{-i\omega}\tau r(1+\alpha)B_k + 4\tau d\sin^2(k\pi/n) = 0.$$

As mentioned in Section 3, B_k is real for $k = 0, 1, \ldots, n-1$. We thus have

$$\begin{cases} \omega = \tau r(1+\alpha)B_k \sin\omega, \\ r\alpha - 4d\sin^2(k\pi/n) = r(1+\alpha)B_k\cos\omega. \end{cases} \tag{4.7_k}$$

Conclusion (i) follows immediately from the above equations. Since we only need to solve for $\omega > 0$ and $\tau > 0$, and since the function $\omega/(\sin\omega)$ is increasing in $(0, \pi)$ and decreasing in $(-\pi, 0)$, we can easily see that the least positive solution of (4.7_k) for τ is given by (4.6_k). This completes the proof. □

By Lemma 4.2, for each $k \in \{0, 1, \ldots, n-1\}$ satisfying (A_k), (4.6_k) determines the least positive τ_k such that (4.5_k) has a pair of purely imaginary roots at $\tau = \tau_k$. Hence, by Lemma 4.1, the characteristic equation (4.4) has purely imaginary roots at $\tau = \tau_k$. Since $\sin^2((n-k)\pi/n) = \sin^2(k\pi/n)$ and $B_{n-k} = B_k$ for $k = 0, 1, \ldots, n-1$, by Lemma 4.1, the purely imaginary roots of (4.4) at $\tau = \tau_k$ have even multiplicity except for $k = 0$, or $k = n/2$ (when n is even). Thus, the standard Hopf bifurcation theorem is not applicable in the cases $k \neq 0$ and $k \neq n/2$ (when n is even). In what follows, we are going to use the symmetric topological bifurcation theory developed in Geba, Krawcewicz and Wu [**18**] and Krawcewicz and Wu [**28,29**] to establish the existence of the local Hopf bifurcation of periodic solutions of (2.3). Examples will also be given to show that both cases $k = 0$ and $k \neq 0$ could happen, corresponding to synchronous oscillations and discrete waves.

We first introduce the *symmetric Hopf bifurcation theory* developed by Geba, Krawcewicz and Wu [**18**] and Krawcewicz and Wu [**28,29**] based on an equivariant degree theory. Let N be a given positive integer and C_τ denote the Banach space of all continuous functions from $[-\tau, 0]$ into $\mathbf{R}^N$ with the supremum norm. Consider the following one parameter family of retarded equations

$$\dot{x} = f(x_t, \mu), \tag{4.8}$$

where $x \in \mathbf{R}^N$, $\mu \in \mathbf{R}$, $f : C_\tau \times \mathbf{R} \to \mathbf{R}^N$ is a continuously differentiable compact mapping satisfying the following conditions

(P_1) there exists an orthogonal representation $\rho : \mathbf{Z}_n \to GL(\mathbf{R}^N)$ of $\mathbf{Z}_n$ on $\mathbf{R}^N$ such that

$$f(\rho(r)\phi, \mu) = \rho(r) f(\phi, \mu), \qquad \phi \in C_\tau,\ \mu \in \mathbf{R},\ r \in \mathbf{Z}_n,$$

where $\rho(r)\phi \in C_\tau$ is defined as $(\rho(r)\phi)(\theta) = \rho(r)\phi(\theta)$ for $\theta \in [-\tau, 0]$.

(P_2) $f(0, \mu) = 0$ for all $\mu \in \mathbf{R}$, and $D\bar{f}(0,0) : \mathbf{R}^N \to \mathbf{R}^N$ is an isomorphism, where $\bar{f}$ denotes the restriction of f to $\mathbf{R}^N \times \mathbf{R}$, and $D\bar{f}(0,0)$ denotes the derivative of $\bar{f}$ with respect to the first variable x, evaluated at $(0,0)$.

Moreover, for any continuous $x : \mathbf{R} \to \mathbf{R}^N$ and $t \in \mathbf{R}$, $x_t \in C_\tau$ is defined as $x_t(s) = x(t+s)$ for $s \in [-\tau, 0]$.

Let $\mathbf{C}^N := \mathbf{R}^N + i\mathbf{R}^N$ and $\{\varepsilon_1, \ldots, \varepsilon_N\}$ denote the standard basis of $\mathbf{R}^N$. For any $\lambda \in \mathbf{C}$ and $1 \le j \le N$, define $e^{\lambda \cdot}\varepsilon_j : [-\tau, 0] \to \mathbf{C}^N$ by

$$e^{\lambda \cdot}\varepsilon_j(\theta) = e^{\lambda\theta}\varepsilon_j, \qquad \theta \in [-\tau, 0].$$

Let $\Delta_\mu(\lambda) : \mathbf{C}^N \to \mathbf{C}^N$ be defined by

$$\Delta_\mu(\lambda) = \lambda I - Df(0,\mu)(e^{\lambda \cdot} I)$$

where

$$Df(0,\mu)(e^{\lambda \cdot} I) = (\, Df(0,\mu)(e^{\lambda \cdot}\varepsilon_1), \ldots, Df(0,\mu)(e^{\lambda \cdot}\varepsilon_N)).$$

Denote by

$$\mathbf{C}^N = \mathbf{C}_0^N \bigoplus \mathbf{C}_1^N \bigoplus \cdots \bigoplus \mathbf{C}_{n-1}^N$$

the isotypical decomposition of the $\mathbf{Z}_n$-action on $\mathbf{C}^N$, where $\mathbf{C}_r^N$, $0 \le r \le n-1$, is the direct sum of all one-dimensional $\mathbf{Z}_n$-irreducible subspace V of $\mathbf{C}^N$ such that the restricted action of $\mathbf{Z}_n$ on V is isomorphic to the $\mathbf{Z}_n$-action on $\mathbf{C}$ defined by

$$\rho_r(e^{i(2\pi j/n)})\, z = e^{i(2\pi r j/n)}\, z, \qquad z \in \mathbf{C}, \quad 0 \le j \le n-1.$$

Clearly, $\Delta_\mu(\lambda)\mathbf{C}_r^N \subset \mathbf{C}_r^N$ for $0 \le r \le n-1$. So, we can define

$$\Delta_{\mu,r}(\lambda) := \Delta_\mu(\lambda)|_{\mathbf{C}_r^N}, \qquad 0 \le r \le n-1.$$

We further assume

(P_3) there exist ε_0, δ_0 and $\omega_0 > 0$ such that

(i) $\det \Delta_0(u+iv) = 0$ with $(u,v) \in \partial\Omega$ if and only if $u = 0$ and $v = \omega_0$, where $\Omega = (0, \varepsilon_0) \times (\omega_0 - \varepsilon_0, \omega_0 + \varepsilon_0)$;

(ii) $\det \Delta_\mu(i\omega) = 0$ with $(\mu, \omega) \in [-\delta_0, \delta_0] \times [\omega_0 - \varepsilon_0, \omega_0 + \varepsilon_0]$ if and only if $\mu = 0$ and $\omega = \omega_0$;

(iii) $\det \Delta_{\pm\delta_0}(\lambda) \ne 0$ for $\lambda \in \partial\Omega$.

Theorem 4.3. *Assume* (P$_1$)–(P$_3$) *are satisfied and*

$$\deg_B(\det \Delta_{-\delta_0,r}(\cdot), \Omega) \ne \deg_B(\det \Delta_{\delta_0,r}(\cdot), \Omega)$$

for some $r \in \{0, 1, \ldots, n-1\}$, *where* $\deg_B$ *denotes the Brouwer degree. Then there exists a sequence of triples* $\{(x^{(k)}, \mu^{(k)}, \omega^{(k)})\}_{k=1}^{\infty}$ *such that*

(i) $\mu^{(k)} \to 0$, $\omega^{(k)} \to \omega_0$, $x^{(k)}(t) \to 0$ *uniformly for* $t \in \mathbf{R}$ *as* $k \to \infty$;

(ii) $x^{(k)}$ *is a* $(2\pi/\omega_k)$*-periodic solution of* (4.8) *with* $\mu = \mu_k$ *for* $k = 1, 2, \ldots$;

(iii) $\rho(e^{i(2\pi/n)})x^{(k)}(t) = x^{(k)}(t - (2\pi/\omega_k)(r/n))$ *for* $t \in \mathbf{R}$ *and* $k = 1, 2, \ldots$.

Remark 4.4. The above result is taken from Krawcewicz and Wu [**29**]. Symmetric Hopf bifurcations have been extensively investigated in the literature. A general result of analytic nature was obtained by Golubitsky and Stewart [**21**] for ordinary differential equations. Similar results were obtained and global continuation was described by Fiedler [**12**] for parabolic differential equations. We refer to the monograph of Golubitsky, Schaeffer and Stewart [**20**] and the paper of Fiedler [**12**] for a detailed account of the subject. Theorem 4.3 was established in Krawcewicz and Wu [**29**] by using equivariant degree-theoretical arguments and is of topological nature. In particular, one does not need non-resonance condition, dimension restrictions on some fixed point subspaces and maximality assumptions on a certain isotropy group. The drawback, however, is that we do not know if the symmetry described by (iii) exactly corresponds to the isotropy group of the bifurcated periodic solutions and that we cannot describe the asymptotic form as well as the stability of the obtained periodic solutions. Also, we cannot show if the bifurcations are supercritical or subcritical.

We now turn to (4.2) and the corresponding subrepresentation $\hat{\rho} : \mathbf{Z}_n \to GL(\mathbf{R}^n)$ defined in Lemma 2.1. In this situation, we have

$$\mathbf{C}_r^N = \{(1, \xi^r, \ldots, \xi^{(n-1)r})^T x;\ x \in \mathbf{R}\}, \qquad 0 \le r \le n-1$$

with $\xi = e^{i(2\pi/n)}$ and (iii) of Theorem 4.3 becomes

$$x_{j-1}^{(k)}(t) = x_j^{(k)}\left(t - \frac{2\pi}{\omega_k}\frac{r}{n}\right), \qquad t \in \mathbf{R},\ k = 1, 2, \ldots .$$

(P_1) of Theorem 4.3 is clearly satisfied by (4.1). For (P_3), we need the following

Lemma 4.5. *For each $k \in \{0, 1, \ldots, n-1\}$ satisfying (A_k), there exist δ_k and a continuously differentiable $\lambda : (\tau_k - \delta_k, \tau_k + \delta_k) \to \mathbf{C}$ such that*

$$q_k(\tau, \lambda(\tau)) = 0 \quad \textit{for} \quad \tau \in (\tau_k - \delta_k, \tau_k + \delta_k),$$
$$\lambda(\tau_k) = i\omega_k$$

and

$$\frac{d}{d\tau}(\mathrm{Re}\,\lambda(\tau))\Big|_{\tau=\tau_k} = \frac{1}{\tau_k}\frac{\omega_k^2}{\left(1 - \tau_k r\alpha + 4d\tau_k \sin^2(k\pi/n)\right)^2 + \omega_k^2} \neq 0.$$

The proof is a direct application of the implicit function theorem, and hence is omitted.

Remark 4.6. Lemma 4.5 implies that for each $k \in \{0, 1, \ldots, n-1\}$ satisfying (A_k), we have

$$\deg_B(q_k(\tau_k - \varepsilon, \cdot), \Omega) \neq \deg_B(q_k(\tau_k + \varepsilon, \cdot), \Omega)$$

for sufficiently small $\varepsilon > 0$, where $\deg_B$ is the Brouwer degree and

$$\Omega = (0, \varepsilon) \times (\omega_k - \varepsilon, \omega_k + \varepsilon).$$

We will also need the following condition which implies (P_2) for (4.1):

(H2) $r(1+\alpha)B_k - r\alpha + 4d\sin^2(k\pi/n) \neq 0, \qquad k \in \{0, 1, \ldots, n-1\}.$

That is, we will consider the values of parameters at which equilibrium bifurcation does not take place.

Now we can employ Theorem 4.3 to obtain

Theorem 4.7. *Assume that* (H1) *and* (H2) *are satisfied, and (A_{k_0}) holds for some $k_0 \in \{0, 1, \ldots, n-1\}$. Then, there exists a sequence of triples $\{(u^{(l)}, \tau^{(l)}, \omega^{(l)})\}$ such that*

(i) $\tau^{(l)} \to \tau^* = \tau_{k_0}$, $\omega^{(l)} \to \omega_{k_0}$ *as* $l \to \infty$ *and*

$$u^{(l)} = (u_1^{(l)}(t), u_2^{(l)}(t), \ldots, u_n^{(l)}(t))^T \longrightarrow (1, 1, \ldots, 1)^T$$
$$\textit{uniformly for} \quad t \in R \quad \textit{as } l \to \infty.$$

(ii) $u^{(l)} = (u_1^{(l)}(t), u_2^{(l)}(t), \ldots, u_n^{(l)}(t))^T$ *is a* $(2\pi/\omega^{(l)})$*-periodic solution of* (2.3) *with* $\tau = \tau^{(l)}$ *for* $l = 1, 2, \ldots$.

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

Remark 4.8. Note that if $k_0 = 0$, then, from (iii) of Theorem 4.7, we have

$$u_{j-1}^{(l)}(t) = u_j^{(l)}(t) \quad \text{for } t \in R, \quad j = 1, 2, \ldots, n \mod (n)$$
$$\text{and } l = 1, 2, \ldots ,$$

which means that the sequence of the bifurcated periodic solutions $\{u^{(l)}(t)\}$ of (2.3) are spatially homogeneous (such periodic solutions are called synchronous oscillations). If $k_0 \neq 0$, then each $u^{(l)}$, $l = 1, 2, \ldots$, is a spatially heterogeneous periodic solution of (2.3) which is called a discrete wave or phase-locked oscillation in the literature. (See Alexander and Auchmuty [**3**], Krawcewicz and Wu [**29**], and Wu and Krawcewicz [**38**]).

Remark 4.9. We only consider the subrepresentation $\hat{\rho} : \mathbf{Z}_n \to GL(\mathbf{R}^n)$, and we detect synchronous oscillations and phase-locked oscillations. By considering the (full) representation $\hat{\rho} : \mathbf{D}_n \to GL(\mathbf{R}^n)$, we should be able to detect other bifurcations (standing waves and mirror reflection waves) as the monograph by Golubitsky, Schaeffer and Stewart [**20**] shows (for ordinary differential equations).

In the remainder of this section, we are going to give some numerical examples which exhibit the complexity of the dynamics and spatial-temporal patterns of the considered system.

First, note that if $\alpha \in (-1, -1/2]$, then

$$\frac{\left|r\alpha - 4d\sin^2(k\pi/n)\right|}{r(1+\alpha)} \geq \frac{|\alpha|}{1+\alpha} \geq 1.$$

By the definition of B_k, we can easily verify that $|B_k| \leq 1 = B_0$. So, (A_k) cannot hold for any $k \in \{0, 1, \dots, n-1\}$, and thus no Hopf bifurcation can occur in this case. (Actually, it can be easily shown that if $\alpha \in (-1, -1/2]$, then the equilibrium $(1, 1, \dots, 1)^T$ of (2.3) is asymptotically stable for all $\tau > 0$.) So, in the sequel we only need to consider the case where $\alpha \in (-1/2, \infty)$.

Example 4.1. Let $n = 3$, $d = s\,r$, $\beta_1 = \beta_2 = 0$, $\beta_0 = 1$. Then $B_0 = B_1 = B_2 = 1$. Fix $\alpha \in (-1/2, \infty)$. Note that (A_0) holds and that (H2) is satisfied. Since

$$\frac{|r\alpha - 4d\sin^2(k\pi/3)|}{r(1+\alpha)}\bigg|_{k=1} = \frac{|\alpha - 3s|}{1+\alpha} \longrightarrow \frac{|\alpha|}{1+\alpha} < 1 \quad \text{as } s \to 0^+,$$

we have $|\alpha - 3\,s(\alpha)|/(1+\alpha) < 1 = B_1$ for sufficiently small $s = s(\alpha) > 0$. Thus (A_1) also holds for sufficiently small $s = s(\alpha) > 0$. Now

$$\frac{\alpha - 3\,s(\alpha)}{1+\alpha} < \frac{\alpha}{1+\alpha}$$

implies that

$$0 < \arccos\frac{\alpha}{1+\alpha} = \omega_0 < \omega_1 = \arccos\frac{\alpha - 3\,s(\alpha)}{1+\alpha} < \pi,$$

and hence

$$\tau_0 = \frac{1}{r(1+\alpha)}\frac{\omega_0}{\sin\omega_0} < \frac{1}{r(1+\alpha)}\frac{\omega_1}{\sin\omega_1} = \tau_1.$$

So, when $s > 0$ is sufficiently small, synchronous oscillations occur first as one increases $\tau > 0$ to $\tau_0 > 0$, and then there come discrete waves when one further increases $\tau > 0$ to $\tau_1 > \tau_0$.

On the other hand, if $s > 0$ is sufficiently large, then $|\alpha - 3s|/(1+\alpha) > 1$, and hence (A_1) does not hold. Therefore, only synchronous oscillations occur in this case.

Remark 4.10. The results of Example 4.1 can be easily extended to general dimension n. Thus, we can conclude that in the case where $\alpha > -1/2$ and the nonlocal effect is ignored ($\beta_j = 0$ for $j = 1, 2, \ldots, n-1$), only synchronous oscillations can bifurcate from the positive equilibrium if the diffusion is large, but both synchronous oscillations and phase-locked oscillations can bifurcate if the diffusion is small. In the latter case, phase-locked oscillations always appear after synchronous oscillations as one increases $\tau > 0$.

Remark 4.11. In Wu and Krawcewicz [**38**], the following system

$$(4.9) \quad \begin{aligned} \frac{d}{dt}x_i(t) = r x_i(t)\left[1 - \frac{x_i(t-\tau)}{K}\right] \\ + d[x_{i+1}(t-\sigma) - 2x_i(t-\sigma) + x_{i-1}(t-\sigma)] \\ i = 1, 2, \ldots, n \quad \bmod (n) \end{aligned}$$

was studied. It was observed that for $(4.9)_{\sigma=0}$, small d induces while large d prevents phase-locked oscillations. Note that when $\beta_0 = 1$, $\beta_j = 0$ for $j = 1, 2, \ldots, n-1$ and $\alpha = 0$, system (2.1) reduces to $(4.9)_{\sigma=0}$, and the conclusions of Remark 4.10 coincide with their results. Thus, we have extended their results to a larger class of systems ($\alpha \in (-1/2, \infty)$ instead of $\alpha = 0$) where both instantaneous and delayed intra-competition (local interaction) are present.

The following example exhibits the impact of nonlocal interaction in accordance with the dispersion.

Example 4.2. Let $n = 3$, $\beta_1 = \beta_2 = \theta$, $\beta_0 = 1 - 2\theta$, $0 \le \theta \le 1/3$ and $d = s\,r$. Then, $B_0 = 1$, and $B_1 = B_2 = 1 - 3\theta$. Fix $\alpha \in (-1/2, \infty)$; then (A_0) holds for all $\theta \in [0, 1/3]$. Now,

$$\left.\frac{|r\alpha - 4d\sin^2(k\pi/3)|}{r(1+\alpha)}\right|_{k=1} = \frac{|\alpha - 3s|}{1+\alpha}.$$

For fixed $\theta = \theta(\alpha) \ge 0$ which is sufficiently small, we have

$$\frac{|\alpha|}{1+\alpha} < |1 - 3\theta| < 1,$$

and hence

$$\frac{|\alpha - 3s|}{1+\alpha} < |1 - 3\theta|$$

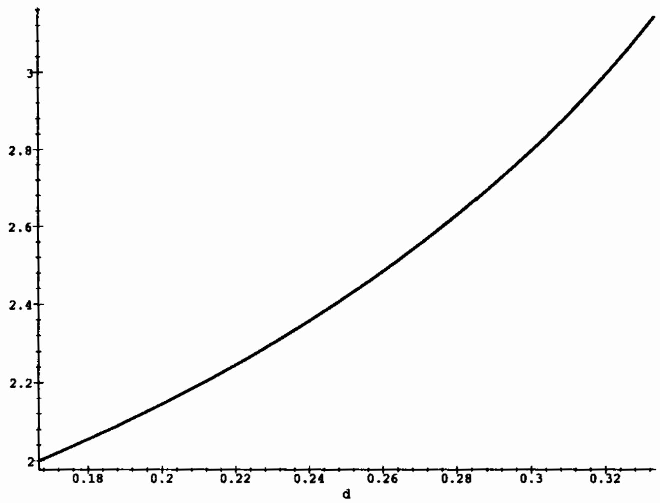

FIGURE 1. Consider the case where $n = 3$, $\beta_1 = \beta_2 = \theta$, $\beta_0 = 1 - 2\theta$, $d = s$, $\alpha = 1$, $r = 1$, $\theta = 1/4$. In this case $d_1 = 1/6$, and the curve $\tau = \tau(d)$ defined on $(1/6, 1/6 + \varepsilon_0)$ for some small $\varepsilon_0 > 0$ is given by

$$\tau = \frac{2\omega_1}{\sin \omega_1}, \qquad \omega_1 = \arccos(2 - 6d).$$

Near the curve one has the coexistence of spatially heterogeneous equilibria and phase-locked oscillations.

for sufficiently small $s = s(\alpha, \theta) > 0$ which means that (A_1) and (A_2) hold, and

$$\frac{|\alpha - 3s|}{1 + \alpha} \geq |1 - 3\theta|$$

for large $s > 0$ which means that (A_1) and (A_2) do not hold. We thus know that when the nonlocal interaction exists but is small ($\beta_1 = \beta_2 = \theta$ sufficiently small), the conclusions in Remark 4.10 remain valid.

On the other hand, for fixed $\alpha \in (-1/2, \infty)$ and $s > 0$ with $\alpha - 3s \neq 0$, (A_1) and (A_2) cannot hold for θ close to $1/3$. Note that as $\theta = 1/3$, $\beta_1 = \beta_2 = \beta_0 = 1/3$. This implies that nearly identical nonlocal effect among patches may prevent phase-locked oscillations.

We conclude this paper by demonstrating the coexistence of equilibrium bifurcations and Hopf bifurcations of phase-locked oscillations. Consider Example 4.2 again. For simplicity, let $r = 1$. By the result in Example 3.1, if

$$1 - 3\theta < \frac{\alpha}{1+\alpha}, \tag{4.10}$$

then an equilibrium bifurcation takes place at

$$d(= s) = d_1 = \frac{\alpha - (1+\alpha)(1-3\theta)}{3}. \tag{4.11}$$

One can easily show by the global bifurcation theorem (Theorem 29.1 of Deimling [10]) that this bifurcation takes place in the direction of increasing d. Therefore, there exists $\varepsilon_0 > 0$ such that for each $d \in (d_1, d_1 + \varepsilon_0)$ system (2.3) has a spatially heterogeneous equilibrium near the positive spatially homogeneous equilibrium. For each such fixed $d(= s) \in (d_1, d_1 + \varepsilon_0)$, if

$$\alpha > 3s \tag{4.12}$$

then

$$|1 - 3\theta| = 1 - 3\theta > \frac{\alpha - 3s}{1+\alpha} = \frac{|\alpha - 3s|}{1+\alpha}.$$

Consequently, Example 4.2 shows that a Hopf bifurcation of phase-locked oscillations of (2.3) occurs at

$$\tau = \tau_1 = \frac{\omega_1}{(1-3\theta)(1+\alpha)\sin\omega_1}, \tag{4.13}$$

where

$$\omega_1 = \arccos\frac{\alpha - 3s}{(1-3\theta)(1+\alpha)}. \tag{4.14}$$

Clearly, (4.13) and (4.14) give a curve $\tau = \tau(s)$ $(= \tau(d))$ for $s\,(= d) \in (d_1, d_1 + \varepsilon_0)$ near which both phase-locked oscillations and spatially heterogeneous equilibria coexist. See Figure 1.

Acknowledgment. The authors are grateful to the referees for their valuable comments and suggestions.

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