

NONLINEAR OSCILLATIONS IN A DISCRETE DIFFUSIVE NEUTRAL LOGISTIC EQUATION

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Abstract. We consider the dynamics of a logistic neutral delay system which is continuous in time and discrete in space. Such a system models the growth of a single-species population distributed over a ring of identical patches and it allows for population dispersing from one patch to its nearest neighbors. We shall show that (i) in the case of instantaneous dispersion feedback, the dispersal in the local growth rate and the neutral term have a stabilizing effect on the population dynamics; (ii) increasing the delay in the growth phase changes the stability of a positive equilibrium and leads to a Hopf bifurcation of synchronous or phase-locked oscillations if the dispersion is small; (iii) the neutral term may bring about several global branches of phase-locked oscillations which would not occur in the absence of a neutral term, and hence the neutral term in this situation has a destabilizing influence.

1. Introduction. The purpose of this paper is to consider the dynamics of a logistic neutral delay system which is continuous in time and discrete in space. Such a system models the growth of a single-species population distributed over a ring of identical patches (islands or habitats) and it allows for population dispersing from one patch to its nearest neighbors. We shall study phase-locked oscillations in the model and draw some conclusions about the effect of dispersion as well as the delay and neutral term on population dynamics.

The role of space and dispersal in interactions among biological populations has been the subject of much theoretical and experimental work (cf. [6], [20], [28]–[31], [35], [38] and references therein). It is widely recognized that the spatial heterogeneity of environment, which leads to ecological interactions, operates in general to increase species diversity. For example, it has been asserted that in some cases dispersal can lend stability to interactions (cf. [18], [19], [35], [38], [44]) while in other cases dispersal can also give rise to instability (cf. [28], [35], [38], [44]). For the references related to this subject, we refer to [18], [27], [28], [34], [35] and [43] for the study of Lotka-Volterra models in a spatially heterogeneous environment on persistence and stability, and to [5], [7], [8], [11], [12], [17], [19], [22], [35], [38], [40], [44] and [46] for similar discussions on single-species models in a patchy environment.

Keywords. Neutral logistic equation, delayed growth response, symmetric Hopf bifurcation, stability, single species population, patchy environment, dispersal and diffusion.

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Our point of departure in this paper is the classical single-species delay logistic model. By introducing a spatially heterogeneous environment to this model, we arrive at a system which describes a population that grows and disperses in two different phases. The growth phase (or the local growth rate) is modeled by a neutral logistic equation that arises in the study of “food limited” population. The dispersal phase is modeled by a linear operator that accounts for the redistribution (or migration) of the population in its spatial habitat. There are a neutral term and time delays in the local growth rate, which could affect the stability of a positive equilibrium and give rise to Hopf bifurcations of symmetric periodic solutions which exhibit the phase-locked oscillations and synchronous oscillations (cf. [2], [4], [14], [15], [27] and [32] for the effect of delay on dynamics in other cases). We will show that (i) in the case of instantaneous dispersion feedback, the dispersal in the local growth rate and the neutral term have a stabilizing effect on the population dynamics; (ii) increasing the delay in the growth phase changes the stability of a positive equilibrium and leads to a Hopf bifurcation of synchronous as well as phase-locked oscillations if the dispersions are small; (iii) the neutral term may bring about several global branches of phase-locked oscillations which would not occur in the absence of the neutral term. In this situation, the neutral term has a destabilizing influence.

We have chosen the single species logistic equation as a beginning to an investigation of spatial heterogeneity and phase-locked oscillations for two reasons. First, it is the simplest single-species population model and contains no complex regulatory mechanisms that might obscure the effects of environmental variation. Second, there has been considerable literature, both mathematical and biological, available on the study of the logistic equation, and its dynamics are well-known, so any change of its behavior due to environmental heterogeneity will be apparent.

We emphasize that our study on single-species population dynamics in a patchy environment is limited to a theoretical aspect and we have not tried to find any experimental (or laboratory) data to fit the theory. We treat spaces as discrete ones, so only patch models are considered and dispersal is thus viewed as a between-habitat phenomenon. The continuous space diffusion model is left for a future investigation.

The remaining part of this paper is organized as follows. In Section 2, we present the model equation by introducing the discrete diffusion to a neutral logistic equation [15] which models the single-species population dynamics in a food-limited environment. The Hopf bifurcation of phase-locked oscillations as well as synchronous oscillations are considered in Section 3 in the case where the diffusion feedback in local dynamics is instantaneous. We draw some conclusions about the effect of the delay and diffusion on the stability of a positive equilibrium. Section 4 is devoted to an analysis of phase-locked oscillations when the feedback in the local dynamics is delayed. In Section 5, we deal with the global bifurcation of phase-locked oscillations in the appearance of the neutral term. In some special cases, several global branches of phase-locked and synchronous periodic solutions are obtained. Finally, in the appendix, we describe some

local and global symmetric Hopf bifurcation theorems for general neutral functional differential equations which are used in the main body of the paper.

Our study in this paper is a continuation of that initiated in [22].

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2. The model equation. Let $N(t)$ denote the numerical size of a single-species population growing in a constant homogeneous environment closed to immigration and emigration. The classical Verhulst-Pearl logistic equation, which models the dynamics of population growth, takes the following form

$$(2.1) \quad \frac{dN}{dt} = rN(t) \left[1 - \frac{N(t)}{K} \right]$$

where $r > 0$ is the intrinsic growth rate, $K > 0$ is the saturation level or the carrying capacity of the environment. The basic assumption in the equation (2.1) is that the per capita growth rate $(1/N)(dN)/(dt)$ is a linear function of the population size N . Due to its mathematical simplicity and biological clarity, this model has been widely used not only in ecology but also in biology and chemical engineering. For more details, we refer to [9], [16], [33], [36], [39] and the references therein.

In his studies, however, Nicholson [37] observed that population sizes (or densities) usually have a tendency to fluctuate around an equilibrium and in cases of convergence to a positive equilibrium, such a convergence is rarely monotonic. This observation obviously does not agree with the dynamics of the equation (2.1). To incorporate such oscillations in population model system, Hutchinson [21] therefore suggested the following modification of (2.1)

$$(2.2) \quad \frac{dN}{dt} = rN(t) \left[1 - \frac{N(t-\tau)}{K} \right], \quad \tau \in (0, \infty).$$

This equation is commonly known as the “delay-logistic” equation. The delay τ comprises various factors causing delayed growth rate response such as slow replacement of food supplies, maturation and gestation periods. The equation (2.2) has been extensively investigated and the validity of this model has been observed in several different practical situations (cf. [36]). It is proved that if $r\tau \leq 3/2$, then the unique positive equilibrium K is globally stable and the (local) asymptotic stability continues for $r\tau < \pi/2$. $r\tau = \pi/2$ is a critical value which gives rise to a Hopf bifurcation and for every $r\tau > \pi/2$, the equation (2.2) has a nonconstant periodic solution. For details, see [4], [32] and [48].

Of course, due to the complexity of biological systems and the diversity of environments in the real world, the models (2.1) and (2.2) are often unrealistic. In his

experiments on the population dynamics of *Daphnia magna*, Smith [42] observed that the per capita growth rate $(1/N)(dN)/(dt)$ is not a linear function of the density but rather a concave function. For a food-limited population, Smith argued that the term $(1 - N/K)$ should then be replaced with a term representing the proportion of “the rate of food supply not momentarily being used by the population.” Therefore

$$(2.3) \quad \frac{dN}{dt} = rN(t) \left[1 - \frac{F}{T} \right]$$

where F is the rate at which a population of density N uses food and T is the corresponding rate when the population reaches saturation level. The ratio F/T is not the same as N/K . Clearly, a growing population will use “food” faster than a saturated population. This is due to the fact that F/T , during the growth phase of a population, food is consumed both for maintenance and growth whereas when the population reaches saturation level, food is used mainly for maintenance only. Thus it is reasonable to assume that F depends on N (the size of the population being maintained) and dN/dt (the rate at which the population is growing). As a first approximation, Smith then suggested a linear function F as follows

$$F = c_1 N + c_2 \frac{dN}{dt}, \quad c_1 > 0, \quad c_2 \geq 0.$$

When saturation is attained, $dN/dt = 0$, $N = F$ and $T = K$. Thus the equation (2.1) becomes

$$(2.4) \quad \frac{dN}{dt} = rN(t) \left[1 - \frac{N(t) + c \frac{dN(t)}{dt}}{K} \right]$$

where $c = c_2/c_1 \geq 0$. Again, it is realistic to incorporate the delayed growth rate response by putting a discrete delay τ in the per capita growth rate in (2.4). This has led Gopalsamy and Zhang [15] to consider the following *neutral logistic equation* as a generalization of Hutchinson’s equation (2.2)

$$(2.5) \quad \frac{dN}{dt} = rN(t) \left[1 - \frac{N(t - \tau) + cN'(t - \tau)}{K} \right]$$

in which c is a real number and r , τ , K are as in (2.2). $cN'(t - \tau)$ is called the *neutral term*. The equation (2.5) has been studied by several authors. It is proved that the positive steady state $N(t) = K$ is stable if $0 < |cr| < 1$ and $0 < r\tau < \beta_o(1 - c^2r^2)$ where $\beta_o = \beta_o(c, \tau) \in (\pi/2, \pi)$. Consequently, the presence of the neutral term has brought about a stabilizing influence in the system (cf. [15]). The equation (2.5) and its modifications are also studied by other authors. We refer to [10], [12], [24]–[26] for the asymptotic behaviour of the solutions and [13] for the existence of $m\tau$ periodic solutions, where

$m > 0$ is an integer.

The equation (2.5) and all others above are modeled in a constant homogeneous environment and the spatial heterogeneity is therefore neglected. However, since all ecological systems of varying complexity exist on landscapes or seascapes, the dynamics of population and processes cannot be divorced from these spatial contexts. Following Levin [28]–[31], we therefore consider a single-species population distributed over a ring of n patches. Assume, for simplicity, that the growth of the species in each patch can be described by the model equation (2.5) and that the dispersion from one patch to the other occurs only in nearest neighbors and is proportional to the difference of population sizes between two patches. Since a portion of the population in one patch affects a portion of the population in another patch through movement of population members or transmission of signals through space, and since the physical environment varies from point to point in space, rates of population growth and interspecific interactions also vary, and, as a consequence, population density varies through space, too. Therefore, we arrive at the following system of neutral delay equations

$$\begin{aligned}
 (2.6) \quad \frac{dN_i(t)}{dt} = & rN_i(t) \left[1 - \frac{N_i(t-\tau) + cN'_i(t-\tau)}{K} \right] \\
 & - rd_1 N_i(t) \left[\frac{N_{i+1}(t-\sigma) - 2N_i(t-\sigma) + N_{i-1}(t-\sigma)}{K} \right] \\
 & + d_2(N_{i+1}(t) - 2N_i(t) + N_{i-1}(t)), \\
 & 1 \leq i \leq n, \quad (\text{mod } n)
 \end{aligned}$$

where $N_i(t)$ denotes the population size in the i -th patch, $N_{n+1}(t) = N_1(t)$, $N_0(t) = N_n(t)$, d_1 is the transfer rate at which the dispersion serves as a feedback in the localized per capita growth rate and d_2 is the transfer rate at which the dispersion affects the growth rate in each patch. d_1 may be negative and, if that occurs, the dispersion is a positive feedback to the system. The feedback can be delayed and $\sigma \geq 0$ is incorporated to reflect this delay, $d_2 \geq 0$. In the equation (2.6), we have assumed the forward and backward dispersion are the same and the anisotropy of the dispersion is neglected.

It should be mentioned that the model (2.6) ignores the consequences of structure other than space within the population modelled. This can be age structure, physiological structure, genetic or phenotypic structure. We incorporate a diffusion term in the localized per capita growth rate (i.e. d_1 may not be zero), which is not seen in the literature, by assuming that the dispersion may make a contribution to the local dynamics, at least in the “food-limited” environment situation. This is motivated by a similar consideration in [41] where the population’s per capita growth rate is assumed to be a function of a linear combination of the densities of the individual population (called the *weighted total density*) as in the predator-prey or competitive systems. Even though the system (2.6) is a much simplified model, as we will see in the subsequent

sections, the mathematical analysis of the dynamics of the model is still a problem of formidable complexity. However, the tractable analysis does give some of the implications of the dispersion and delay effect on the oscillation of population growth.

Clearly, if $N(t)$ is a solution of the neutral delayed logistic equation (2.5), then $(N(t), N(t), \dots, N(t))$ is a solution of the system (2.6). In particular, (K, K, \dots, K) is a positive (homogeneous) equilibrium of the system (2.6).

We are interested in the stability of the equilibrium (K, K, \dots, K) and in the case when there is a change of stability, we shall study the Hopf bifurcation from this equilibrium. Let $x_i(t) = N_i(t) - K$. The equation (2.6) is transformed into

$$\begin{aligned} \frac{dx_i(t)}{dt} = & -r(x_i(t) + K) \left[\frac{x_i(t - \tau) + cx'_i(t - \tau)}{K} \right] \\ & - rd_1(x_i(t) + K) \left[\frac{x_{i+1}(t - \sigma) - 2x_i(t - \sigma) + x_{i-1}(t - \sigma)}{K} \right] \\ & + d_2[x_{i+1}(t) - 2x_i(t) + x_{i-1}(t)], \\ & 1 \leq i \leq n, \pmod{n}. \end{aligned}$$

For later use, we give its linearized equation at the origin as follows:

$$\begin{aligned} \frac{dx_i(t)}{dt} = & -rx_i(t - \tau) - rcx'_i(t - \tau) - rd_1[x_{i+1}(t - \sigma) - 2x_i(t - \sigma) + x_{i-1}(t - \sigma)] \\ (2.7) \quad & + d_2[x_{i+1}(t) - 2x_i(t) + x_{i-1}(t)], \\ & 1 \leq i \leq n, \pmod{n}. \end{aligned}$$

Noting that the discrete Laplacian operator $\Delta: \mathbf{R}^n \rightarrow \mathbf{R}^n$ defined by $(\Delta x)_i = x_{i+1} - 2x_i + x_{i-1}$, $1 \leq i \leq n$, \pmod{n} , $x \in \mathbf{R}^n$, has eigenvalues $\exp(i2\pi j/n)$ and associated eigenvectors $v_j = (1, e^{i2\pi j/n}, \dots, e^{i2\pi(n-1)j/n})^T$, $0 \leq j \leq n-1$, from the analysis in the appendix, we obtain the characteristic equation of (2.7)

$$(2.8) \quad p(\lambda, \tau, \sigma, c) = \prod_{j=0}^{n-1} p_j(\lambda, \tau, \sigma, c) = 0$$

where

$$\begin{aligned} (2.9) \quad p_j(\lambda, \tau, \sigma, c) = & \lambda + r(1 + \lambda c)e^{-\lambda\tau} - rd_1 a_j e^{-\lambda\sigma} + d_2 a_j, \\ & a_j = 4 \sin^2 \frac{\pi j}{n}, \quad 0 \leq j \leq n-1. \end{aligned}$$

PROPOSITION 2.1. *Let $\phi \in C([- \max\{\sigma, \tau\}, 0]; \mathbf{R}^n)$. If $\phi(s) \in \mathbf{R}_+^n$, the positive cone in \mathbf{R}^n , for every $s \in [- \max\{\sigma, \tau\}, 0]$, then the solution $(N_i(\phi)(t))$ through $(0, \phi)$ of the equation (2.6) remains in \mathbf{R}_+^n for all $t > 0$.*

PROOF. Suppose to the contrary that $(N_i(\phi)(t)) \notin \mathbf{R}_+^n$ for some $t > 0$. Then $\bar{t} = \min\{t > 0; N_i(\phi)(t) = 0, \text{ for some } 1 \leq i \leq n\}$ and $i_0 \in \{1, 2, \dots, n\}$ exist such that $N_{i_0}(\phi)(\bar{t}) = 0$ and $N'_{i_0}(\phi)(\bar{t}) < 0$ with $N_i(\phi)(\bar{t}) \geq 0$ for all $1 \leq i \leq n$. It follows from (2.6) that

$$\frac{dN_{i_0}(\phi)(\bar{t})}{dt} = d_2[N_{i_0+1}(\phi)(\bar{t}) + N_{i_0-1}(\phi)(\bar{t})] \geq 0,$$

a contradiction to $N'_{i_0}(\phi)(\bar{t}) < 0$. This completes the proof.

3. Stability and Hopf bifurcation: Instantaneous feedback. Throughout this section, we assume that the dispersion feedback is instantaneous, i.e. $\sigma = 0$ in the equation (2.6).

Recall that in this case, we have the characteristic equation

$$(3.1) \quad p(\lambda, \tau, c) = \prod_{j=0}^{n-1} p_j(\lambda, \tau, c) = 0$$

where

$$(3.2) \quad \begin{aligned} p_j(\lambda, \tau, c) &= \lambda + r(1 + \lambda c)e^{-\lambda\tau} - (rd_1 - d_2)a_j, \\ a_j &= 4 \sin^2 \frac{\pi j}{n}, \quad 0 \leq j \leq n-1. \end{aligned}$$

We first present a result on the local asymptotic stability of the positive equilibrium (K, K, \dots, K) .

THEOREM 3.1. *Assume that $\sigma = 0$.*

- (i) *If $|rc| > 1$, the positive equilibrium (K, \dots, K) of (2.6) is not stable for all $\tau > 0$;*
- (ii) *If $|rc| < 1$ and there exist two disjoint subsets J_1 and J_2 of $\{0, 1, \dots, [n/2]\}$ such that $r \leq |(rd_1 - d_2)a_j|$ for all $j \in J_1$ and $r > |(rd_1 - d_2)a_j|$ for all $j \in J_2$, then (K, \dots, K) is stable when $\tau < \tau^* = \min_{j \in J_2} \tau_j$, where $\tau_j = \theta_j/w_j$ and*

$$(3.3) \quad \begin{aligned} w_j &= \sqrt{\frac{r^2 - (rd_1 - d_2)^2 a_j^2}{1 - r^2 c^2}} \\ \theta_j &= \cot^{-1} \left(\frac{(rd_1 - d_2)a_j - cw_j^2}{w_j(1 + c(rd_1 - d_2)a_j)} \right), \quad 0 \leq j \leq \left\lfloor \frac{n}{2} \right\rfloor; \end{aligned}$$

- (iii) *If $|rc| < 1$ and $r > |(rd_1 - d_2)a_j|$ for some $j \in \{0, 1, \dots, [n/2]\}$, then (K, \dots, K) is not stable if $\tau > \tau_j$, where τ_j is given in (ii).*

PROOF. Note that the characteristic equation at (K, \dots, K) has the forms (3.1)–(3.2). The conclusions follow directly from Theorem 4.2 of Kuang [25, Chapter 1] and Theorem 3.1 of Freedman and Kuang [10].

REMARK 3.1. If $d_1 = 0$ (i.e. there is no feedback in the local dynamics) and $c = 0$ (i.e. no neutral term), then we have from (3.3)

$$w_j = \sqrt{r^2 - d_2^2 a_j^2}, \quad \theta_j = \cot^{-1} \left[-\frac{d_2 a_j}{\sqrt{r^2 - d_2^2 a_j^2}} \right]$$

and hence $\theta_j/w_j \geq \pi/2r$. By (ii), (K, \dots, K) is stable if $r\tau < \pi/2$. This implies that for the delay logistic system with discrete diffusion, dispersion cannot change the stability of the local dynamics. This generalizes a result in [22].

REMARK 3.2. Let $b_j = (rd_1 - d_2)a_j$, $J_1 = \{1, 2, \dots, [n/2]\}$ and $J_2 = \{0\}$. It follows from (ii) that if

$$(3.4) \quad r \leq |b_j| \quad \text{for } 1 \leq j \leq \left[\frac{n}{2} \right],$$

$$(3.5) \quad \tau \leq \tau_0 = \frac{\sqrt{1 - r^2 c^2}}{r} \cot^{-1} \left(-\frac{rc}{\sqrt{1 - r^2 c^2}} \right),$$

then (K, \dots, K) is stable. Note that (3.5) allows us to choose $r, c > 0$ so that we still could have the stability in case $r\tau > \pi/2$. However, this is impossible when $c = 0$ (i.e. the neutral term does not appear). The condition (3.4) can be satisfied by increasing the dispersals. Therefore, the dispersals as well as the neutral term here exhibit a stabilizing influence on the population dynamics (see also Gopalsamy and Zhang [15] and Kuang [25]).

From Theorem 3.1, if $|rc| > 1$, (K, \dots, K) is always unstable. In what follows, we therefore assume $|rc| < 1$.

We fix a, r, d_1 and d_2 , regard the delay τ as a parameter and consider the Hopf bifurcation in the equation (2.6). We find that when the dispersion is small, there are phase-locked oscillations on the population growth, as the following theorem shows.

THEOREM 3.2. Assume that $\sigma = 0$, $|rc| < 1$ and $|(rd_1 - d_2)a_j| < r$ for some $j \in \{0, 1, \dots, [n/2]\}$. Let

$$(3.6) \quad \beta_j = \sqrt{\frac{r^2 - (rd_1 - d_2)^2 a_j^2}{1 - r^2 c^2}},$$

$$(3.7) \quad \tau_j = \beta_j^{-1} \cot^{-1} \left[\frac{(rd_1 - d_2)a_j - c\beta_j^2}{\beta_j(1 + c(rd_1 - d_2)a_j)} \right].$$

Then $\tau = \tau_j$ is a Hopf bifurcation point of phase-locked oscillations for the equation (2.6). More precisely, there exists a sequence of p_k -periodic solutions $N^k(t)$ of (2.6) with $\tau = \tau^k$ such that

$$\tau^k \rightarrow \tau_j, \quad p_k \rightarrow 2\pi/\beta_j, \quad N^k(t) \rightarrow (K, \dots, K)$$

uniformly for $t \in \mathbf{R}$ as $k \rightarrow \infty$ and

$$N_{i-1}^k(t) = N_i^k(t - p_k j/n), \quad 1 \leq i \leq n, \quad (\text{mod } n), \quad k \geq 1, \quad t \in \mathbf{R}.$$

PROOF. Recall that $p_j(\lambda) = \lambda + (r + rc\lambda)e^{-\lambda\tau} - (rd_1 - d_2)a_j$. Let $\lambda = i\beta$, $\beta > 0$, and set $p_j(i\beta) = 0$. Separating the real parts and imaginary parts gives

$$(3.8) \quad \begin{cases} r \cos \beta\tau + rc\beta \sin \beta\tau = (rd_1 - d_2)a_j \\ rc\beta \cos \beta\tau - r \sin \beta\tau = -\beta. \end{cases}$$

Squaring them and solving for $\cos \beta\tau$ in (3.8) yield

$$(3.9) \quad \begin{cases} r^2 + r^2c^2\beta^2 = (rd_1 - d_2)^2a_j^2 + \beta^2 \\ \sin \beta\tau = \frac{\beta(r + rc(rd_1 - d_2)a_j)}{r^2(1 + c^2\beta^2)} \\ \cos \beta\tau = -\frac{rc\beta^2 - r(rd_1 - d_2)a_j}{r^2(1 + c^2\beta^2)}. \end{cases}$$

Therefore, by (3.6)

$$\beta = \beta_j = \sqrt{\frac{r^2 - (rd_1 - d_2)^2a_j^2}{1 - r^2c^2}}$$

satisfies $p_j(i\beta_j) = 0$ and solving for τ in (3.9) gives τ_j in (3.7).

On the other hand, differentiating $p_j(\lambda) = 0$ with respect to τ , we get

$$(3.10) \quad \frac{d\lambda}{d\tau} = \frac{\lambda(rc\lambda + r)e^{-\lambda\tau}}{1 + [rc - \tau(rc\lambda + r)]e^{-\lambda\tau}}.$$

Note that $(r + rc\lambda)e^{-\lambda\tau} = (rd_1 - d_2)a_j - \lambda$. It follows from (3.10) and (3.9) that

$$(3.11) \quad \begin{aligned} & \text{Sign} \left\{ \frac{d}{d\tau} (\text{Re } \lambda) \right\} \Big|_{\substack{\lambda = i\beta_j \\ \tau = \tau_j}} \\ &= \text{Sign} \left\{ \text{Re} \left(\frac{d\lambda}{d\tau} \right)^{-1} \right\} \Big|_{\substack{\lambda = i\beta_j \\ \tau = \tau_j}} \\ &= \text{Sign} \left\{ \text{Re} \left[\frac{e^{\lambda\tau} + rc}{\lambda(rc\lambda + r)} - \frac{\tau}{\lambda} \right] \right\} \Big|_{\substack{\lambda = i\beta_j \\ \tau = \tau_j}} \\ &= \text{Sign} \left\{ \text{Re} \frac{e^{\lambda\tau}}{\lambda(rc\lambda + r)} + \text{Re} \frac{rc}{\lambda(rc\lambda + r)} \right\} \Big|_{\substack{\lambda = i\beta_j \\ \tau = \tau_j}} \end{aligned}$$

$$\begin{aligned}
 &= \text{Sign} \left\{ \text{Re} \frac{1}{\lambda((rd_1 - d_2)a_j - \lambda)} + \text{Re} \frac{rc}{\lambda(rc\lambda + r)} \right\} \Big|_{\lambda=i\beta_j} \\
 &= \text{Sign} \left\{ \text{Re} \frac{-i[(rd_1 - d_2)a_j + i\beta_j]}{\beta_j[(rd_1 - d_2)^2 a_j^2 + \beta_j^2]} + \text{Re} \frac{-rci(r - irc\beta_j)}{\beta_j[r^2 + r^2 c^2 \beta_j^2]} \right\} \\
 &= \text{Sign} \left\{ \frac{1}{(rd_1 - d_2)^2 a_j^2 + \beta_j^2} - \frac{r^2 c^2}{r^2 + r^2 c^2 \beta_j^2} \right\} \\
 &= \text{Sign} \left\{ \frac{1 - r^2 c^2}{r^2 + r^2 c^2 \beta_j^2} \right\} = 1 > 0.
 \end{aligned}$$

This implies that $\text{deg}_B(p_j(\cdot, \tau_j + \varepsilon), \Omega) \neq \text{deg}_B(p_j(\cdot, \tau_j - \varepsilon), \Omega)$ for some small $\varepsilon > 0$, where $\Omega = \{x + iy; 0 < x < \delta, \beta_j - \delta < y < \beta_j + \delta\}$ and $\delta > 0$ is a sufficiently small number. Consequently, the theorem follows from Theorem A in the appendix.

Let $d_1 = d_2 = 0$ in (2.6). Then all the local dynamics are identical, and are described by the neutral delay logistic equation (2.5). Recall that

$$\tau_0 = \frac{\sqrt{1 - r^2 c^2}}{r} \cot^{-1} \left(-\frac{rc}{\sqrt{1 - r^2 c^2}} \right).$$

It follows from Theorem 3.2 that $\tau = \tau_0$ is a local Hopf bifurcation point for the equation (2.5). This leads to a branch of *synchronous oscillations* in (2.6).

COROLLARY 3.3. *Assume that $\sigma = 0$ and $|rc| < 1$. Then $\tau = \tau_0$ is a Hopf bifurcation point of synchronous oscillations for the equation (2.6). More precisely, there exists a sequence of p_k -periodic solutions $N^k(t) = (n^k(t), \dots, n^k(t))$ of (2.6) with $\tau = \tau^k$ such that $n^k(t)$ is a p_k -periodic solution for (2.5) and*

$$\tau^k \rightarrow \tau_0, \quad p_k \rightarrow 2\pi\sqrt{1 - r^2 c^2}/r, \quad n^k(t) \rightarrow K$$

uniformly for $t \in \mathbf{R}$ as $k \rightarrow \infty$.

PROOF. Note that $\beta_0 = r/\sqrt{1 - r^2 c^2}$. The proof then follows from Theorem 3.2 by letting $d_1 = d_2 = 0$.

Note that $a_j = 4 \sin^2 \pi j/n \geq 0$. If $d_1/d_2 > 1/r$, then $(rd_1 - d_2)a_j$ increases with j . This implies that if $(rd_1 - d_2)a_j < r$ for some $j \in \{1, \dots, [n/2]\}$, then $(rd_1 - d_2)a_l < r$ for all $0 \leq l \leq j$. By Theorem 3.2, we have also bifurcation points τ_l other than τ_j , where $1 \leq l < j$, τ_j is given by (3.6)–(3.7) with j replaced by l . Moreover, the crossing number at each bifurcation point is always -1 . Theorem B in the appendix implies the following simple observation:

THEOREM 3.4. *Assume $\sigma = 0$ and $|rc| < 1$. If $|(rd_1 - d_2)a_j| < r$ for some $j \in \{1, \dots, [n/2]\}$. Then there undergoes a global Hopf bifurcation at each $\tau = \tau_l, 1 \leq l \leq j$, such that*

every branch of phase-locked solutions of (2.6) in $C^1(S^1; \mathbf{R}^n) \times (0, \infty) \times (0, \infty)$, bifurcating from each $(0, \tau_l, w_l)$ with τ_l defined by (3.7) and $w_l = 2\pi/\beta_l$, does not terminate at $(0, \tau_m, \beta_m)$ with $m \neq l$.

4. Stability and Hopf bifurcation: Delayed feedback. In this section we consider the case where the dispersion feedback in the local dynamics is delayed, i.e. $\sigma > 0$. We regard σ as a parameter.

Note that in this case, we have

$$(4.1) \quad p_j(\lambda, \sigma) = \lambda + r(1 + \lambda c)e^{-\lambda\tau} - rd_1 a_j e^{-\lambda\sigma} + d_2 a_j$$

where a_j is as in (3.2).

We first obtain the following result on the asymptotic stability of the equilibrium (K, \dots, K) .

THEOREM 4.1. *Assume that (iii) of Theorem 3.1 hold. If $0 < |rd_1| < d_2$ and the equation*

$$(4.2) \quad (r^2 d_1^2 - d_2^2) a_j^2 - r^2 = y[(1 + r^2 c^2)y + 2cry \cos y\tau - 2r \sin y\tau] \\ + 2d_2 a_j (r \cos y\tau + yrc \sin y\tau)$$

has no positive solution y for every $j \in \{1, \dots, [n/2]\}$, then (K, \dots, K) is asymptotically stable for (2.6) with any $\sigma \geq 0$ and $\tau < \tau^*$, where τ^* is given by (ii) of Theorem 3.1.

PROOF. We show that for every $\sigma \geq 0$, all roots of $p_j(\lambda, \tau)$ have negative real parts. To see this, let $P(\lambda) = \lambda + r(1 + \lambda c)e^{-\lambda\tau} + d_2 a_j$ and $Q(\lambda) = -rd_1 a_j$, $1 \leq j \leq [n/2]$. We have

- (i) $\overline{P(-iy)} = P(iy)$ and $\overline{Q(-iy)} = Q(iy)$ for every real y ;
- (ii) $P(0) + Q(0) = r - (rd_1 - d_2)a_j > 0$ since $|rd_1| < d_2$;
- (iii) $p_j(\lambda, 0) = \lambda + r(1 + \lambda c) - (rd_1 - d_2)a_j$ has all roots of negative real parts for $\tau < \tau^*$ by Theorem 3.1;
- (iv) $F(y) = |P(iy)|^2 - |Q(iy)|^2$ has neither positive nor negative zeros, since the right-hand side of (4.2) is an even function of y .

Note that $Q(\lambda)$ is a non-zero constant function. $Q(\lambda)$ and $P(\lambda)$ have no common imaginary zeros. By a result of Cooke and van den Driessche [3] (see also Freedman and Kuang [10]), $p_j(\lambda, \tau)$ has only roots with negative real parts when $\tau < \tau^*$ and the asymptotic stability of (K, \dots, K) follows.

This completes the proof.

REMARK 4.1. The assumption that the equation (4.2) has no positive solutions seems a complicated condition. However, we can show that if

$$(4.3) \quad \tau d_2 a_j (\tau - 2c) + 2\tau \leq \frac{(1 - rc)^2}{r}, \quad cd_2 a_j < 1,$$

then (4.2) has no positive solutions. Indeed, under (4.3) and $|rd_1| < d_2$, for all $y > 0$

$$\begin{aligned}
& y[(1+c^2r^2)y+2ycr\cos y\tau+(2d_2a_jrc-2r)\sin\tau y]+2d_2a_jr\cos y\tau \\
& \geq y^2[1+c^2r^2-2rc+(2d_2a_jrc-2r)\tau]+2rd_2a_j\cos y\tau \\
& = y^2[(1-rc)^2+2r\tau(cd_2a_j-1)]+2rd_2a_j\cos y\tau \\
& > 2rd_2a_j \geq 0,
\end{aligned}$$

while the left hand side of (4.2) is negative, implying that (4.2) has no positive solutions. Theorem 4.1 seems to indicate that the delay in the dispersion feedback may not have destabilizing influence.

To obtain Hopf bifurcation, we now assume that the equation (4.2) has at least one positive solution for some $j \in \{1, \dots, [n/2]\}$. Let us denote this solution by y_j . Then

$$(r\cos y_j\tau + y_jrc\sin y_j\tau + d_2a_j)^2 + (y_j - r\sin y_j\tau + y_jrc\cos y_j\tau)^2 = r^2d_1^2a_j^2.$$

This implies that there exists a unique $\theta_j \in (0, 2\pi]$ such that

$$(4.4) \quad \begin{cases} d_2a_j + r\cos y_j\tau + y_jrc\sin y_j\tau = rd_1a_j\cos\theta_j \\ y_j - r\sin y_j\tau + y_jrc\cos y_j\tau = -rd_1a_j\sin\theta_j. \end{cases}$$

Define

$$(4.5) \quad \sigma_j = \frac{\theta_j}{y_j}.$$

It follows from (4.4) that $p_j(iy_j, \sigma_j) = 0$, i.e. iy_j is a purely imaginary root of $p_j(\lambda, \sigma)$ with $\sigma = \sigma_j$. This leads us to the following Hopf bifurcation of phase-locked oscillations.

THEOREM 4.2. *Assume that there exists $j \in \{1, \dots, [n/2]\}$ such that (4.2) has a positive solution y_j . If y_j satisfies*

$$(4.6) \quad (1+r^2c^2)y_j - r(1-cy_j^2 + (c-1)d_2a_j)\sin y_j\tau \neq r[1-2c-cd_2a_j]y_j\cos y_j\tau,$$

then σ_j is a Hopf bifurcation point of phase-locked oscillations, where σ_j is defined by (4.5).

PROOF. By Theorem A in the appendix, we need only to check that

$$\frac{d}{d\sigma}(\operatorname{Re} \lambda) \Big|_{\substack{\lambda=iy_j \\ \sigma=\sigma_j}} \neq 0$$

where λ is a root of $p_j(\lambda, \sigma) = 0$.

To see this, let us differentiate $p_j(\lambda, \sigma) = 0$ with respect to σ (by viewing λ as a function of σ). It follows that

$$(4.7) \quad \frac{d\lambda}{d\sigma} = \frac{-\lambda rd_1a_j e^{-\lambda\sigma}}{1+rce^{-\lambda\tau} - r(1+\lambda c)e^{-\lambda\tau} + \sigma rd_1a_j e^{-\lambda\sigma}}.$$

Note that $p_j(\lambda, \sigma) = 0$ is equivalent to

$$(4.8) \quad r(1 + \lambda c)e^{-\lambda\tau} = -(\lambda + d_2 a_j) + rd_1 a_j e^{-\lambda\sigma}.$$

Combining (4.7) and (4.8), we obtain

$$(4.9) \quad \begin{aligned} \left(\frac{d\lambda}{d\sigma}\right)^{-1} &= \frac{1 + rce^{-\lambda\tau} + (\lambda + d_2 a_j) - rd_1 a_j e^{-\lambda\sigma} + \sigma rd_1 a_j e^{-\lambda\sigma}}{-\lambda rd_1 a_j e^{-\lambda\sigma}} \\ &= \frac{(1 + d_2 a_j + \lambda) + rce^{-\lambda\tau}}{-\lambda rd_1 a_j e^{-\lambda\sigma}} + \frac{1 - \sigma}{\lambda}. \end{aligned}$$

Therefore, from (4.9),

$$\begin{aligned} &\text{Sign}\left(\frac{d}{d\sigma}(\text{Re } \lambda)\right)\Bigg|_{\substack{\lambda = iy_j \\ \sigma = \sigma_j}} = \text{Sign}\left(\text{Re } \frac{d\lambda}{d\sigma}\right)\Bigg|_{\substack{\lambda = iy_j \\ \sigma = \sigma_j}} \\ &= \text{Sign}\left(\text{Re}\left(\frac{d\lambda}{d\sigma}\right)^{-1}\right)\Bigg|_{\substack{\lambda = iy_j \\ \sigma = \sigma_j}} \\ &= \text{Sign}\left(\text{Re}\left\{\frac{(1 + d_2 a_j + \lambda) + rce^{-\lambda\tau}}{-\lambda rd_2 a_j e^{-\lambda\sigma}} + \frac{1 - \sigma}{\lambda}\right\}\right)\Bigg|_{\substack{\lambda = iy_j \\ \sigma = \sigma_j}} \\ &= \text{Sign}\left(\text{Re}\frac{1 + d_2 a_j + \lambda + rce^{-\lambda\tau}}{-\lambda rd_2 a_j e^{-\lambda\tau}}\right)\Bigg|_{\substack{\lambda = iy_j \\ \sigma = \sigma_j}} \\ &= \text{Sign}\left(\text{Re}\frac{1 + d_2 a_j + iy_j + rce^{-iy_j\tau}}{-iy_j rd_1 a_j e^{-i\theta_j}}\right) \\ &= \text{Sign}\left\{-\text{Re}\frac{(1 + d_2 a_j)e^{i\theta_j}}{iy_j rd_1 a_j} - \text{Re}\frac{rce^{(\theta_j - y_j\tau)i}}{iy_j rd_1 a_j e^{i\theta_j}} - \text{Re}\frac{1}{rd_1 a_j} e^{i\theta_j}\right\} \\ &= \text{Sign}\left\{\text{Re}\frac{i(1 + d_2 a_j)e^{i\theta_j}}{y_j rd_1 a_j} + \text{Re}\frac{irce^{(\theta_j - y_j\tau)i}}{y_j rd_1 a_j} - \frac{\cos \theta_j}{rd_1 a_j}\right\} \\ &= \text{Sign}\left\{-\frac{(1 + d_2 a_j) \sin \theta_j - rc \sin(\theta_j - y_j\tau) - y_j \cos \theta_j}{y_j rd_1 a_j}\right\} \neq 0, \end{aligned}$$

whenever

$$(4.10) \quad (1 + d_2 a_j) \sin \theta_j \neq rc \sin(\theta_j - y_j\tau) - y_j \cos \theta_j.$$

A direct calculation, by noting that θ_j satisfies (4.4), shows that (4.6) and (4.10) are equivalent. This proves the theorem.

REMARK 4.2. The conditions given by (4.2) and (4.6) are usually difficult to verify. However, we do have some solutions $y_j > 0$ to (4.2) and (4.6) in some special cases. Take $c = 0$ and $d_2 = 0$, for example. Then (4.2) and (4.6) simplify to

$$(4.11) \quad r^2(d_1^2 a_j^2 - 1) = y(y - 2r \sin y\tau),$$

$$(4.12) \quad y_j - r \sin y_j \tau \neq r y_j \cos y_j \tau .$$

Define $f(y) = r^2(d_1^2 a_j^2 - 1)/y$ and $g(y) = y - 2r \sin y \tau$, $y > 0$. If $d_1^2 a_j^2 > 1$ and $2r\tau \leq 1$. Then $f(y)$ is decreasing and $g(y)$ is increasing. It follows that there exists a unique $y_j > 0$ such that $f(y_j) = g(y_j)$. This $y_j > 0$ gives a positive solution to (4.11).

On the other hand, note that if $r \leq 1/2$,

$$\frac{r}{1 - r \cos y_j \tau} \leq \frac{r}{1 - r} \leq 1 \quad \text{and} \quad \frac{y_j}{\sin y_j} > 1 .$$

So y_j satisfies (4.12). Therefore, if

$$d_1^2 a_j^2 > 1, \quad 2r\tau \leq 1 \quad \text{and} \quad r \leq \frac{1}{2}$$

then $y_i > 0$ exists such that both (4.11) and (4.12) are satisfied. For the general case, when the coefficients are specified we may use the computer to verify (4.2) and (4.6).

5. Global Hopf bifurcation: Neutral term effect. We now consider the global aspects of phase-locked as well as synchronous oscillations in the system (2.6). For simplicity, we only deal with the case where $\sigma = 0$.

In order to examine local bifurcation points, we shall regard $\alpha = rc < 1$ as a parameter. Recall that we have the j -th characteristic equation as follows

$$(5.1) \quad \begin{aligned} p_j(\lambda, \alpha) &= \lambda + (r + \alpha\lambda)e^{-\lambda\tau} - b_j = 0, \\ b_j &= (rd_1 - d_2)a_j, \quad j \in \left\{ 0, 1, 2, \dots, \left[\frac{n}{2} \right] \right\}. \end{aligned}$$

We look for purely imaginary roots of (5.1) for a fixed $1 \leq j \leq [n/2]$.

Let $\lambda = i\beta$, $\beta > 0$, be a root of $p_j(\lambda, \alpha)$, i.e. $p_j(i\beta, \alpha) = 0$. Separating the real and imaginary parts, respectively, we get

$$(5.2) \quad \begin{aligned} b_j \cos \beta\tau + \beta \sin \beta\tau &= r, \\ \beta \cos \beta\tau - b_j \sin \beta\tau &= -\alpha\beta. \end{aligned}$$

Squaring both sides of (5.2) and adding them yield

$$(5.3) \quad \alpha = \frac{\sqrt{\beta^2 + b_j^2 - r^2}}{\beta} < 1$$

if $b_j^2 < r^2$. Also, solving for $\cos \beta\tau$ and $\sin \beta\tau$ in (5.2) gives us

$$(5.4) \quad \tan \beta\tau = -\frac{\beta(r + \alpha b_j)}{\alpha\beta^2 - r b_j}.$$

Substituting (5.3) into (5.4), we then obtain

$$(5.5) \quad \tan \beta\tau = \frac{\beta r + b_j \sqrt{\beta^2 + b_j^2 - r^2}}{r b_j - \beta \sqrt{\beta^2 + b_j^2 - r^2}}.$$

Let

$$f(\beta) = \frac{\beta r + b_j \sqrt{\beta^2 + b_j^2 - r^2}}{r b_j - \beta \sqrt{\beta^2 + b_j^2 - r^2}}, \quad \beta \geq \sqrt{r^2 - b_j^2}.$$

Assume $b_j > 0$. It follows that $f'(\beta) > 0$ for all $\beta \geq \sqrt{r^2 - b_j^2}$ and hence $z = f(\beta)$ is an increasing function. Note that $f(\sqrt{r^2 - b_j^2}) = \sqrt{r^2 - b_j^2}/b_j > 0$ and $\lim_{\beta \rightarrow \infty} f(\beta) = 0$, $\lim_{\beta \rightarrow r^-} f(\beta) = +\infty$ and $\lim_{\beta \rightarrow r^+} f(\beta) = -\infty$. We have infinitely many solutions for β to the equation (5.5), which correspond to the β -coordinates of the intersection points of two graphs $z = \tan \beta\tau$ and $z = f(\beta)$.

Let $0 < r\tau < \pi/2$. Then we have solutions β_m to the equation (5.5) as follows:

$$(5.6) \quad \frac{(2m-1)\pi}{2\tau} < \beta_m < \frac{m\pi}{\tau}, \quad m = 1, 2, 3, \dots$$

More generally, if there is a positive integer N such that $(N-1)\pi/\tau < r \leq (2N-1)\pi/2\tau$, then

$$(5.7) \quad \frac{[2(N+m)-3]\pi}{2\tau} < \beta_m < \frac{[N+m-2]\pi}{\tau}, \quad m = 1, 2, \dots$$

exist as solutions to the equation (5.4) and if $(N-q-1)\pi/\tau < \sqrt{r^2 - b_j^2} \leq (N-q)\pi/\tau$ for some positive integer q , then

$$(5.8) \quad \frac{(N-l-1)\pi}{\tau} < \beta_{-l} < \frac{(2N-2l-1)\pi}{2\tau}, \quad 1 \leq l \leq q$$

also exist as solutions other than β_m to the equation (5.6). Thus, we get α values from (5.3) as follows:

$$(5.9) \quad \alpha_m = \frac{\sqrt{\beta_m^2 + b_j^2 - r^2}}{\beta_m}, \quad m = -q, -q+1, \dots, -1, 1, 2, \dots$$

This leads us to the following local bifurcation result.

THEOREM 5.1. *Assume $0 < b_j < r$ for some $j \in \{1, 2, \dots, [n/2]\}$. If*

$$(5.10) \quad (N-1)\pi < r\tau \leq \frac{(2N-1)\pi}{2}$$

for some integer $N > 0$, then $(0, \alpha_m, \beta_m)$, $m = -q, -q+1, \dots, -1, 1, 2, \dots$, with $\alpha_m < 1$ are all local bifurcation points of phase-locked oscillations for (2.6).

PROOF. It suffices to show that

$$\frac{d}{d\sigma} \operatorname{Re} \lambda \Big|_{\substack{\lambda=i\beta_m \\ \alpha=\alpha_m}} \neq 0$$

for each m . To see this, we differentiate both sides of $(\lambda - b_j)e^{\lambda\tau} + r + \alpha\lambda = 0$ with respect to α and obtain

$$(5.11) \quad \frac{d\lambda}{d\alpha} = -\frac{\lambda}{e^{\lambda\tau} + (\lambda - b_j)\tau e^{\lambda\tau} + \alpha}.$$

Setting $p_j(\lambda, \alpha) = 0$ implies that $(\lambda - b_j)e^{\lambda\tau} = -r - \alpha\lambda$. Substituting this into (5.11) gives

$$(5.12) \quad \left(\frac{d\lambda}{d\alpha}\right)^{-1} = -\frac{e^{\lambda\tau}}{\lambda} - \frac{\alpha - r\tau}{\lambda} + \alpha\tau.$$

Consequently, using (5.2) in the last step, we have

$$\begin{aligned} (5.13) \quad & \operatorname{Sign} \frac{d}{d\alpha} (\operatorname{Re} \lambda) \Big|_{\substack{\lambda=i\beta_m \\ \alpha=\alpha_m}} \\ &= \operatorname{Sign} \operatorname{Re} \frac{d\lambda}{d\alpha} \Big|_{\substack{\lambda=i\beta_m \\ \alpha=\alpha_m}} = \operatorname{Sign} \operatorname{Re} \left(\frac{d\lambda}{d\alpha}\right)^{-1} \Big|_{\substack{\lambda=i\beta_m \\ \alpha=\alpha_m}} \\ &= \operatorname{Sign} \operatorname{Re} \left(-\frac{e^{\lambda\tau}}{\lambda} + \alpha\tau - \frac{\alpha - r\tau}{\lambda}\right) \Big|_{\substack{\lambda=i\beta_m \\ \alpha=\alpha_m}} = \operatorname{Sign} \left(\alpha\tau - \operatorname{Re} \frac{e^{\lambda\tau}}{\lambda}\right) \Big|_{\substack{\lambda=i\beta_m \\ \alpha=\alpha_m}} \\ &= \operatorname{Sign} \left(\alpha_m\tau - \frac{\sin \beta_m\tau}{\beta_m}\right) = \operatorname{Sign} \left(\frac{\alpha_m b_j + r}{b_j^2 + \beta_m^2} + \alpha_m\tau\right) = 1 \neq 0, \end{aligned}$$

as desired. This completes the proof.

To study the global Hopf bifurcation, we choose any $0 < k < 1$ and let $|\alpha| < k$ and investigate the equation on the region $D := \{x \in \mathbf{R}_+^n; 0 < |x| < K/k\}$, where $|x| = \max_{1 \leq i \leq n} \{|x_i|\}$ for $x \in \mathbf{R}^n$.

We need the following lemma concerning the periods of periodic solutions to the equation (2.6).

LEMMA 5.2. *For any integer $m > 0$, the equation (2.6) has no nonconstant $2\tau/m$ -periodic positive solution $\{x_i(t)\}_{i=1}^n$ with $x_{i-1}(t) = x_i(t - \tau/m)$ in D .*

PROOF. It suffices to show that the lemma holds for $m = 1, 2$. In the following we only give the proof for $m = 1$. The case $m = 2$ can be treated analogously.

By way of contradiction, we suppose that $x(t) = \{x_i(t)\}_{i=1}^n$ is a nonconstant 2τ -periodic positive solution of (2.6) with $x_{i-1}(t) = x_i(t - \tau)$. Then $x_{i+1}(t) = x_i(t - \tau)$, $x_{i+1}(t - \tau) = x_i(t)$ and $x_{i-1}(t - \tau) = x_i(t)$. Let $y_i(t) = x_i(t - \tau)$. We have

$$x_{i+1}(t) - 2x_i(t) + x_{i-1}(t) = 2(y_i(t) - x_i(t))$$

and

$$(5.14) \quad \begin{cases} x'_i = rx_i \left[1 - \frac{y_i + 2d_1(y_i - x_i)}{K} + c \left(1 - \frac{y_i}{K} \right)' \right] + 2d_2(y_i - x_i) \\ y'_i = ry_i \left[1 - \frac{x_i + 2d_1(x_i - y_i)}{K} + c \left(1 - \frac{x_i}{K} \right)' \right] + 2d_2(x_i - y_i). \end{cases}$$

Put

$$u(t) = 1 - \frac{x_i(t)}{K} \quad \text{and} \quad v(t) = 1 - \frac{y_i(t)}{K}$$

and $\delta_i = 2d_i$, $i = 1, 2$. The equation (5.14) becomes an implicit differential equation of u and v

$$\begin{cases} u' = r(u-1)[v - \delta_1(u-v) + cv'] + \delta_2 K(u-v) \\ v' = r(v-1)[u - \delta_1(v-u) + cu'] + \delta_2 K(v-u) \end{cases}$$

which, by solving for u' and v' , leads to an ordinary differential system

$$(5.15) \quad \begin{cases} u' = \frac{r(u-1)[f(u, v) + cr(v-1)f(v, u) + g(v, u)] + g(u, v)}{1 - r^2 c^2 (u-1)(v-1)} \\ v' = \frac{r(v-1)[f(v, u) + cr(u-1)f(u, v) + g(u, v)] + g(v, u)}{1 - r^2 c^2 (u-1)(v-1)}, \end{cases}$$

where

$$\begin{aligned} f(u, v) &= v - \delta_1(u - v), & g(u, v) &= \delta_2 K(u - v), \\ (u, v) &\in \{(u, v) \in \mathbf{R}^2; |x - 1| < 1/k, |y - 1| < 1/k\}. \end{aligned}$$

Note that (5.15) is symmetric about u and v . The diagonal $\Delta \cong \{(u, v) \in \mathbf{R}^2; |u - 1| < 1/k, u = v\}$ is invariant under the system (5.15) of ordinary differential equations. Since any autonomous one-dimensional ordinary differential equation has no non-constant periodic solutions, $(u(t), v(t)) \notin \Delta$ for all t . Without loss of generality, we assume that

$$(5.16) \quad u(t) < v(t) \quad \text{for all } t \in \mathbf{R}.$$

Replacing t by $t - \tau$ in (5.16), we get

$$(5.17) \quad u(t - \tau) < v(t - \tau) \quad \text{for all } t \in \mathbf{R}.$$

On the other hand, we have

$$v(t - \tau) = 1 - \frac{y_i(t - \tau)}{k} = 1 - \frac{x_i(t)}{k} = u(t),$$

$$u(t-\tau) = 1 - \frac{x_i(t-\tau)}{k} = 1 - \frac{y_i(t)}{k} = v(t).$$

Consequently, (5.17) implies that $v(t) < u(t)$ for all $t \in \mathbf{R}$, which contradicts (5.16). This completes the proof.

We now state and prove the following global bifurcation theorem.

THEOREM 5.3. *Assume n is even and $0 < (rd_1 - d_2) < r/4$. Suppose that there exists a positive integer N satisfying (5.10). Let q be an integer such that*

$$\frac{(N-q-1)\pi}{\tau} < \sqrt{r^2 - b_{n/2}^2} \leq \frac{(N-q)\pi}{\tau}.$$

Then for each integer m such that

$$-q \leq m \leq 1 - N + \frac{\tau}{\pi} \sqrt{\frac{r^2 - b_{n/2}^2}{1 - k^2}},$$

at least one of the following conclusions holds:

- (i) For any $c \in (0, \alpha_m/r)$, the system (2.6) has a p -periodic solution $\{N_i(t)\}_{i=1}^n$ with $\tau/(N+m-1) \leq p \leq 2\tau/(2(N+m)-3)$ and satisfying

$$N_{i-1}(t) = N_i(t-p/2), \quad i = 1, 2, \dots, n;$$

- (ii) For any $c \in (\alpha_m/r, k/r)$, the conclusion in (i) holds;

- (iii) For any $A \in (0, K)$, there exists a $c_A > 0$ and a p -periodic solution $\{N_i(t)\}_{i=1}^n$ to (2.6) with $c = c_A$, with period $p > 0$ as in (i) and satisfying

$$N_{i-1}(t) = N_i(t-p/2), \quad \max_{\substack{1 \leq i \leq n \\ t \in \mathbf{R}}} |N_i(t)| = A, \quad i = 1, 2, \dots, n;$$

- (iv) For any $A \in (K, K/k)$, the conclusion in (iii) holds;

where α_m is given by (5.9).

PROOF. We choose $j = n/2$. Then by (3.2), $a_{n/2} = 4$ and $b_j = 4(rd_1 - d_2) < r$. It follows that, from (5.3) and (5.7)–(5.8), β_m and β_{-l} exist to the equation (5.5), where $1 \leq l \leq q$ and

$$m \leq 1 - N + \frac{\tau}{\pi} \sqrt{\frac{r^2 - b_{n/2}^2}{1 - k^2}}$$

and the locations of β_m, β_{-l} are estimated by (5.7) and (5.8). Let α_m be any α_m given by (5.9). By Theorem 5.1, $(0, \alpha_m, \beta_m)$ is a bifurcation point with $n/2$ -th crossing number $\gamma_{n/2}(\alpha_m, \beta_m) < 0$. Consequently, the assertion of Theorem B in the appendix implies that each bifurcating branch \mathcal{C}_m from $(0, \alpha_m, \beta_m)$ of phase-locked periodic solutions continues to the boundary ∂G , where

$$G := \{(N(pt), \alpha, p); N(pt) \in D \text{ is a 1-periodic solution of (2.6), } 0 < \alpha < k\} \\ \subset H^1(S^1; \mathbf{R}^n) \times (0, k) \times (0, \infty).$$

Note that by Lemma 5.2, (2.6) has no nonconstant $2\tau/m$ -periodic phase-locked solutions in D with $N_{i-1}(t) = N_i(t - \tau/m)$. Every bifurcating branch \mathcal{C}_m has the property

$$\{p; (N(pt), \alpha, p) \in \mathcal{C}_m\} \subset \left[\frac{\tau}{N+m-1}, \frac{2\tau}{2(N+m)-3} \right], \quad \text{if } m \geq 1$$

or

$$\{p; (N(pt), \alpha, p) \in \mathcal{C}_m\} \subset \left[\frac{2\tau}{2N-2m-1}, \frac{\tau}{N-m-1} \right], \quad \text{if } m \leq -1.$$

This implies that each \mathcal{C}_m contains a least one point from ∂G with $\alpha = k$, or $\alpha = 0$, or $N(pt) \in \partial D$. Consequently, at least one of (i)–(iv) holds. This completes the proof.

Let us now consider the global Hopf bifurcation of synchronous oscillations, i.e. bifurcation of periodic solutions of the form $N(t) = (n(t), n(t), \dots, n(t))$. We need only to study the Hopf bifurcation for the scalar logistic equation (2.5). The characteristic equation for the linearized equation at K of (2.5) reads

$$(5.18) \quad p(\lambda, \alpha) = \lambda + (r + \alpha\lambda)e^{-\lambda\tau} = 0,$$

where $\alpha = rc < 1$. We again use α as a bifurcation parameter.

As before, we first look at local bifurcation points. It follows that $p(\lambda, \alpha) = 0$ has purely imaginary roots $i\beta$ where each β is a solution of the equation

$$(5.19) \quad \tan \beta\tau = -\frac{r}{\sqrt{\beta^2 - r^2}}.$$

We can also estimate the locations of β by viewing the solution β of (5.19) as the intersection points of two graphs $z = \tan \beta\tau$ and $z = -r/\sqrt{\beta^2 - r^2}$. If $r < \pi/2\tau$, then we have

$$(5.20) \quad \frac{(2m-1)\pi}{2\tau} < \beta_m < \frac{m\pi}{\tau}, \quad m = 1, 2, \dots$$

and

$$(5.21) \quad \alpha_m = \frac{\sqrt{\beta_m^2 - r^2}}{\beta_m}, \quad m = 1, 2, \dots$$

A calculation similar to that of (5.13) shows that each $(0, \alpha_m, \beta_m)$ is a local bifurcation point and their crossing numbers are all of the same sign.

We need a similar result concerning the periods of periodic solutions to (2.5).

LEMMA 5.4. For each integer $m > 0$ and constant $0 < k < 1$, the equation (2.5) has no nonconstant $2\tau/m$ -periodic solution $N(t) \in (0, K/k)$.

PROOF. It suffices to show the lemma for $m = 1$. Suppose that $N(t)$ is a nonconstant 2τ -periodic solution of (2.5) with $N(t) \in (0, K/k)$. Let $M(t) = N(t - \tau)$. We have

$$(5.22) \quad \begin{cases} N'(t) = rN(t) \left[1 - \frac{M(t) + cM'(t)}{K} \right] \\ M'(t) = rM(t) \left[1 - \frac{N(t) + cN'(t)}{K} \right]. \end{cases}$$

Put

$$u(t) = 1 - \frac{N(t)}{K} \quad \text{and} \quad v(t) = 1 - \frac{M(t)}{K}.$$

Then (5.21) simplifies to

$$\begin{cases} u'(t) = r(u-1)[v + cv'] \\ v'(t) = r(v-1)[u + cu'] \end{cases}.$$

An argument similar to that in the proof of Lemma 5.2 now leads to a contradiction. This completes the proof.

We now obtain the following global result for the equation (2.5).

THEOREM 5.5. Let $\sqrt{3}/2 < k < 1$ be given. Assume that $\pi\sqrt{1-k^2} \leq r\tau < \pi/2$. Then there exist (α_m, β_m) given by (5.20) and (5.21), $m = 1, 2, \dots, q$, such that at least one of (i)–(iv) below holds for the equation (2.5):

- (i) For any $c \in (0, \alpha_m/r)$, (2.5) has a p -periodic positive solution $N(t)$ with period $\tau/m \leq p \leq 2\tau/(2m-1)$;
- (ii) For any $c \in (\alpha_m/r, k/r)$, the conclusion in (i) holds;
- (iii) For any $A \in (0, K)$, there is a $c_A > 0$ such that a positive p -periodic solution $N(t)$ to (2.5) with $c = c_A$ exists, with period p as in (i) and $\max_{t \in \mathbf{R}} N(t) = A$;
- (iv) For any $A \in (K, K/k)$, the conclusion in (iii) holds;

where q is an integer satisfying

$$\frac{r\tau}{\pi\sqrt{1-k^2}} - 1 < q \leq \frac{r\tau}{\pi\sqrt{1-k^2}}.$$

Consequently, the above bifurcating periodic solutions $N(t)$ to (2.5) give rise to a global Hopf bifurcation of synchronous oscillations $(N(t), \dots, N(t))$ in (2.6).

PROOF. The proof is similar to that of Theorem 5.3. We therefore omit it.

REMARK 5.1. It is well-known (by a result of Wright [48]) that the unique positive equilibrium K of (2.2) is globally stable under the condition $r \leq 3/2\tau$. However, Theorem

5.5 shows that when the neutral term appears, the system (2.5) may have periodic solutions. This implies, in another aspect, that the *neutral term* can have a destabilizing effect on population dynamics.

Theorem 5.5 has the following corollary.

COROLLARY 5.6. *Let $0 < k < 1$ be given as in Theorem 5.5 and $\pi\sqrt{1-k^2} \leq r\tau \leq 3/2$. Then at least one of the following statements holds for each $m \geq 1$ as in Theorem 5.5:*

- (i) *For any $\alpha_m/r < c < 1/r$, the neutral logistic equation (2.5) possesses a periodic solution;*
- (ii) *For any $0 < A < K$, there exists a number $0 < c_A < 1/r$ such that the neutral logistic equation (2.5) with $c = c_A$ has a periodic solution $N(t)$ with $\max_{t \in \mathbf{R}} |N(t) + K| = A$;*
- (iii) *For any $K < A < K/k$, the conclusion in (ii) holds;*

where

$$\alpha_m = \sqrt{\beta_m^2 - r^2} / \beta_m$$

and β_m is given by (5.19)–(5.20).

PROOF. Note that the equation (2.5) reduces to (2.2) when $c = 0$ and by Remark 5.1, the equation (2.2) has no nonconstant periodic solutions. This excludes the alternative (i) in Theorem 5.5 and the conclusion follows.

6. Appendix. In this appendix, we describe two results regarding the existence and global continuation of symmetric periodic solutions of neutral functional differential equations.

Let $\tau \geq 0$ be a given constant and $C = C([-\tau, 0]; \mathbf{R}^n)$ the Banach space of bounded continuous functions from $[-\tau, 0] \rightarrow \mathbf{R}^n$ equipped with the supnorm $\|\cdot\|$. As usual, for $x \in C([-\tau, 0]; \mathbf{R}^n)$ and $t \geq 0$, define $x_t \in C$ by $x_t(s) = x(t+s)$, $s \in [-\tau, 0]$.

We consider the following neutral functional differential equation

$$(6.1) \quad \frac{d}{dt} [x(t) - b(x_t, \alpha)] = F(x_t, \alpha),$$

where $x \in \mathbf{R}^n$, $\alpha \in \mathbf{R}$, $b, F: C \times \mathbf{R} \rightarrow \mathbf{R}^n$ are continuously differentiable and satisfy

- (A1) $F: C \times \mathbf{R} \rightarrow \mathbf{R}^n$ is completely continuous and there exists a constant $k \in [0, 1)$ such that $|b(\phi, \alpha) - b(\psi, \alpha)| \leq k\|\phi - \psi\|$ for all $\phi, \psi \in C$, $\alpha \in \mathbf{R}$.
- (A2) There exists a real orthogonal representation $\rho: \mathbf{Z}_n \rightarrow O(\mathbf{R}^n)$ of \mathbf{Z}_n on \mathbf{R}^n such that $b(\rho(\gamma)\phi, \alpha) = \rho(\gamma)b(\phi, \alpha)$, $F(\rho(\gamma)\phi, \alpha) = \rho(\gamma)F(\phi, \alpha)$ for all $\phi \in C$, $\alpha \in \mathbf{R}$ and $\gamma \in \mathbf{Z}_n$, where $\rho(\gamma)\phi \in C$ is defined by $(\rho(\gamma)\phi)(s) = \rho(\gamma)\phi(s)$ for all $s \in [-\tau, 0]$.
- (A3) $F(0, \alpha) = 0$ for all $\alpha \in \mathbf{R}$ and there exists $\alpha_0 \in \mathbf{R}$ such that $D_x \bar{F}(0, \alpha_0): \mathbf{R}^n \rightarrow \mathbf{R}^n$ is an isomorphism, where $\bar{F}: \mathbf{R}^n \times \mathbf{R} \rightarrow \mathbf{R}^n$, the restriction of F on $\mathbf{R}^n \times \mathbf{R}$, is defined by $\bar{F}(x, \alpha) = F(\bar{x}, \alpha)$, $x \in \mathbf{R}^n$, $\alpha \in \mathbf{R}$, \bar{x} is the constant map from $[-\tau, 0]$

into \mathbf{R}^n with the value $x \in \mathbf{R}^n$ and $D_x \bar{F}(0, \alpha_0)$ denotes the derivative of \bar{F} with respect to x at $(0, \alpha_0)$.

We call $(0, \alpha)$ a stationary solution and $(0, \alpha_0)$ a nonsingular stationary solution. The characteristic equation of (6.1) at $(0, \alpha)$ is given by

$$(6.2) \quad \det_{\mathbf{C}} \Delta_{\alpha}(\lambda) = 0,$$

where $\Delta(\lambda)$ is an $n \times n$ complex matrix defined by

$$\begin{aligned} \Delta_{\alpha}(\lambda) &:= \lambda[\text{Id} - D_{\phi} b(0, \alpha)(e^{\lambda} \text{Id})] - D_{\phi} F(0, \alpha)(e^{\lambda} \text{Id}): \mathbf{C}^n \rightarrow \mathbf{C}^n, \\ D_{\phi} b(0, \alpha)(e^{\lambda} \text{Id}) &= (D_{\phi} b(0, \alpha)(e^{\lambda} \varepsilon_1), \dots, D_{\phi} b(0, \alpha)(e^{\lambda} \varepsilon_n)), \\ D_{\phi} F(0, \alpha)(e^{\lambda} \text{Id}) &= (D_{\phi} F(0, \alpha)(e^{\lambda} \varepsilon_1), \dots, D_{\phi} F(0, \alpha)(e^{\lambda} \varepsilon_n)), \\ e^{\lambda} \varepsilon_j(s) &= e^{\lambda s} \varepsilon_j, \quad s \in [-\tau, 0], \end{aligned}$$

and $\{\varepsilon_1, \dots, \varepsilon_n\}$ is the standard basis of \mathbf{R}^n and $\mathbf{C}^n = \mathbf{R}^n + i\mathbf{R}^n$.

A solution $\lambda \in \mathbf{C}$ to the equation (6.2) is called a characteristic value of the stationary solution $(0, \alpha)$. The point $(0, \alpha)$ is called a center of (6.1) if (6.2) has a pair of purely imaginary characteristic values and it is said to be an isolated center if there is no other center in some neighborhood of $(0, \alpha)$ in $\mathbf{R}^n \times \mathbf{R}$.

We also make the following assumption:

(A4) $(0, \alpha_0)$ is an isolated center of (6.1).

By (A4), there exist constants $\beta_0 > 0$ and $\delta > 0$ such that $\det_{\mathbf{C}} \Delta_{\alpha_0}(i\beta_0) = 0$ and if $0 < |\alpha - \alpha_0| < \delta$, then $i\mathbf{R} \cap \{\lambda \in \mathbf{C}; \det_{\mathbf{C}} \Delta_{\alpha}(\lambda) = 0\} = \emptyset$.

Choose now constants $b = b(\alpha_0, \beta_0) > 0$ and $c = c(\alpha_0, \beta_0) > 0$ such that the closure of $\Omega = (0, b) \times (\beta_0 - c, \beta_0 + c) \subset \mathbf{R}^2$ contains no other zero of $\det_{\mathbf{C}} \Delta_{\alpha_0}(\lambda)$. Note that $\det_{\mathbf{C}} \Delta_{\alpha}(\lambda)$ is analytic in $\lambda \in \Omega$ and continuous in $\alpha \in [\alpha_0 - \delta, \alpha_0 + \delta]$, $\det_{\mathbf{C}} \Delta_{\alpha_0 \pm \delta}(\lambda) \neq 0$ for $\lambda \in \partial\Omega$.

The real orthogonal representation ρ of \mathbf{Z}_n induces a unitary representation, again denoted by ρ , on \mathbf{C}^n . Let us identify $\mathbf{Z}_n = \{\gamma \in \mathbf{C}; \gamma^n = 1\}$ and let $\gamma_n = e^{i2\pi/n}$. Put $T_n = \rho(\gamma_n): \mathbf{R}^n \rightarrow \mathbf{R}^n$ and denote by $\sigma(T_n) \in \mathbf{C}$ the spectrum of T_n .

Define a subset of integers $J = \{j \in \{0, 1, \dots, n-1\}; e^{i2\pi j/n} \in \sigma(T_n)\}$. We have the following isotypical decomposition of \mathbf{C}^n

$$\mathbf{C}^n = \bigoplus_{j \in J} \mathbf{C}_j^n,$$

where \mathbf{C}_j^n , $j \in J$ is the direct sum of all one-dimensional \mathbf{Z}_n -irreducible subrepresentation spaces V of \mathbf{C}^n such that each restricted representation $\rho|_V$ is isomorphic to the irreducible representation of \mathbf{Z}_n on \mathbf{C} given by

$$\rho(e^{i2\pi j/n})z = e^{i2\pi j/n} z, \quad z \in \mathbf{C}, \quad j \in J.$$

Note that b and F are \mathbf{Z}_n -equivariant by (A2). Thus $\Delta_{\alpha}(\lambda): \mathbf{C}^n \rightarrow \mathbf{C}^n$ is \mathbf{Z}_n -equivariant for all $\alpha \in \mathbf{R}$ and $\lambda \in \mathbf{C}$ with $\text{Re } \lambda \geq 0$. Therefore, $\Delta(\lambda)\mathbf{C}_j^n \subset \mathbf{C}_j^n$ for each $j \in J$. This gives for each $j \in J$ a map

$$\Delta_{\alpha,j}(\lambda) = \Delta_{\alpha}(\lambda)|_{\mathcal{C}_j^n}, \quad j \in J.$$

Recall that $\det_{\mathcal{C}} \Delta_{\alpha_0 \pm \delta}(\lambda) \neq 0$ for $\lambda \in \partial\Omega$. We have $\det_{\mathcal{C}} \Delta_{\alpha_0 \pm \delta,j}(\lambda) \neq 0$ for $\lambda \in \partial\Omega$ and $j \in J$. Consequently, we obtain a well-defined number

$$c_j(\alpha_0, \beta_0) = \det_B(\det_{\mathcal{C}} \Delta_{\alpha_0 - \delta,j}(\cdot), \Omega) - \det_B(\det_{\mathcal{C}} \Delta_{\alpha_0 + \delta,j}(\cdot), \Omega)$$

for each $j \in J$, where \det_B denotes the classical Brouwer degree. We will call $\Delta_{\alpha,j}(\lambda) = 0$ the j -th characteristic equation and $c_j(\alpha_0, \beta_0)$ the j -th crossing number of (α_0, β_0) .

We can now state a local symmetric Hopf bifurcation theorem.

THEOREM A. *Assume that (A1)–(A4) hold. If there exists a $j \in J$ such that $c_j(\alpha_0, \beta_0) \neq 0$, then (α_0, β_0) is a bifurcation point. More precisely, there is a sequence of triples $\{(x_k, \alpha_k, \beta_k)\}_k^\infty$ such that*

- (i) $(x_k, \alpha_k, \beta_k) \rightarrow (0, \alpha_0, \beta_0)$ uniformly for $t \in \mathbf{R}$ as $k \rightarrow \infty$;
- (ii) $x_k(t)$ is a $2\pi/|\beta_k|$ -periodic solution of (1) with $\alpha = \alpha_k, k = 1, 2, \dots$;
- (iii) $\rho(e^{i2\pi/n})x_k(t) = x_k(t + 2\pi j / (\beta_k n))$ for $t \in \mathbf{R}, k = 1, 2, \dots$.

For a global bifurcation theorem, we need the following assumptions:

- (A5) $\bar{F}(x, \alpha) = 0$ with $x \in \mathbf{R}^n$ such that $\rho(e^{i2\pi/n})x = x$ if and only if $x = 0$. Moreover, $D_x \bar{F}(0, \alpha) \in GL(\mathbf{R}^n)$ for every $\alpha \in \mathbf{R}$.
- (A6) The set $\{\alpha \in \mathbf{R}; \text{ the stationary solution } (0, \alpha) \text{ has purely imaginary characteristic values}\}$ is discrete.

For every $j \in J$, denote by \mathcal{S}^j the closure in $H^1(S^1; \mathbf{R}^n) \times \mathbf{R}^2$ of the set consisting of (z, α, p) such that $x(t) = z(t/p)$ is a p -periodic solution of (6.1) with $\rho(e^{i2\pi/n})z(t) = z(t + j/n)$. Put

$$M = \{(0, \alpha, p); \alpha \in \mathbf{R}, p > 0\} \subset H^1(S^1; \mathbf{R}^n) \times \mathbf{R}^2.$$

The global Hopf bifurcation theorem can be stated as follows:

THEOREM B. *Let (A1), (A2), (A5) and (A6) hold. If there exists an integer j such that \mathcal{S}^j has a bounded connected component \mathcal{C}^j , then $\mathcal{C}^j \cap M$ is a finite set and*

$$\sum_{(0, \alpha, p) \in \mathcal{C}^j \cap M} c_j\left(\alpha, \frac{2\pi}{p}\right) = 0.$$

Theorems A and B are proved in Xia [49] by using the equivariant degree for set-condensing mappings. They can also be proved by first using the symmetry condition (iii) in Theorem A and then applying the S^1 -degree developed in [23]. For details, see [47].

In our applications to system (2.6), Z_n acts linearly on \mathbf{R}^n by

$$(\rho(e^{i2\pi/n})x)_i = x_{i-1}, \quad 1 \leq i \leq n, \quad (\text{mod } n), \quad x \in \mathbf{R}^n$$

and the associated mappings b and F are equivariant with respect to this action.

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