

HOPF BIFURCATION AND PATTERN FORMATION IN A DELAYED DIFFUSIVE LOGISTIC MODEL WITH SPATIAL HETEROGENEITY

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ABSTRACT. In this paper, we study the Hopf bifurcation and spatiotemporal pattern formation of a delayed diffusive logistic model under Neumann boundary condition with spatial heterogeneity. It is shown that for large diffusion coefficient, a supercritical Hopf bifurcation occurs near the non-homogeneous positive steady state at a critical time delay value, and the dependence of corresponding spatiotemporal patterns on the heterogeneous resource function is demonstrated via numerical simulations. Moreover, it is proved that the heterogeneous resource supply contributes to the increase of the temporal average of total biomass of the population even though the total biomass oscillates periodically in time.

1. Introduction. In recent years, the effects of spatial heterogeneity on the population dynamics draw a lot of attention [3–6, 10, 19–22, 24, 25, 27, 31, 32], as the resource distribution which significantly affects the population biomass is restricted by some spatial factors such as climate, topography, etc. Hence it is more realistic to consider heterogeneous resource supply in the biological modeling. A prototypical reaction-diffusion model with logistic growth and spatial heterogeneous resource

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is in the following form [27]:

$$\begin{cases} u_t(x, t) = d\Delta u(x, t) + u(x, t)(m(x) - u(x, t)), & x \in \Omega, t > 0, \\ \partial_\nu u(x, t) = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x), & x \in \Omega, \end{cases} \quad (1)$$

where $u(x, t)$ represents the population density at location x and at time t and $d > 0$ is the diffusion coefficient; the spatial domain Ω is a region in \mathbb{R}^N for $N \geq 1$; and the function $m(x)$ is the carrying capacity, or equivalently, the resource supply of the species, which is related to spatial location and reflects the influence of environment on the species. Here $\partial_\nu u(x, t) = \nabla u(x, t) \cdot \nu$ where ν is the unit outer normal vector at $x \in \partial\Omega$, so a no-flux boundary condition is imposed so the system is a closed one. System (1) admits a unique positive spatially non-homogeneous steady state which is globally asymptotically stable [5, 27].

It is known that historical information may significantly impact the dynamics of population system because of the maturation time for reproduction or other time delays in biological process, hence the logistic equation with time delay (also called Hutchinson equation) has been proposed as a more realistic model [23]. Combining with the spatial movement of population, the reaction-diffusion logistic equation with time delay has been proposed to consider the evolution of population distribution. Dynamics of such equation under the Neumann boundary condition was studied in [14, 29, 41], and the Dirichlet boundary value problem of a delayed diffusive logistic model has been considered in, for example, [2, 9, 34, 36, 40]. In general, the time delay leads to occurrence of Hopf bifurcations, and the positive steady state loses its stability and temporally oscillatory patterns arise. In these previous works, only homogeneous resource supply is assumed. Under homogeneous Neumann boundary condition, the unique positive steady state is constant and the stable bifurcating periodic orbit is spatially homogeneous. In this work, we introduce a time delay into the model with spatial heterogeneity (1), which describes a more realistic growth scenario. More precisely, we propose a diffusive logistic model with heterogeneous resource supply and delay effect as follows:

$$\begin{cases} u_t(x, t) = d\Delta u(x, t) + u(x, t)(m(x) - u(x, t - \tau)), & x \in \Omega, t > 0, \\ \partial_\nu u(x, t) = 0, & x \in \partial\Omega, t > 0, \\ u(x, t) = u_0(x, t), & x \in \Omega, t \in [-\tau, 0]. \end{cases} \quad (2)$$

Here $\tau > 0$ represents the time delay and $u_0 \in \mathcal{C} := C([-\tau, 0], Y)$ with $Y = L^2(\Omega)$ is the initial condition. By taking the transform:

$$\lambda = \frac{1}{d}, \quad \tilde{t} = \frac{t}{\lambda}, \quad \tilde{\tau} = \frac{\tau}{\lambda},$$

and dropping tilde, we obtain the following system:

$$\begin{cases} u_t(x, t) = \Delta u(x, t) + \lambda u(x, t)(m(x) - u(x, t - \tau)), & x \in \Omega, t > 0, \\ \partial_\nu u(x, t) = 0, & x \in \partial\Omega, t > 0, \\ u(x, t) = u_0(x, t), & x \in \Omega, t \in [-\tau, 0]. \end{cases} \quad (3)$$

When $m(x)$ is a positive constant K , Eq. (3) is the classic delayed diffusive logistic model which has been thoroughly studied in [29, 39, 41] and the references therein. The results show that there is a threshold value $\tau_0 = \pi/(2\lambda K)$ at which the system undergoes a supercritical Hopf bifurcation, then the positive constant steady state loses its stability and a stable spatially homogeneous periodic orbit arises when

$\tau > \tau_0$. It is clear that the delay τ plays a critical role in the destabilization of the constant steady state. However, when $m(x)$ is not constant, Eq. (3) admits a spatially non-homogeneous steady state denoted by $u_\lambda(x)$ whose stability is more difficult to determine.

Define $\bar{m} := \frac{1}{|\Omega|} \int_\Omega m(x)dx$ with $|\Omega|$ being the Lebesgue measure of Ω , which biologically means the average resource. In this paper, under some mild conditions on the resource function $m(x)$, we prove the following main results regarding Eq. (3) when $\lambda \in (0, \lambda_*)$ with λ_* defined in Lemma 2.1 of this paper:

1. there exists an infinite sequence $\{\tau_{n\lambda}\}_{n=0}^\infty$ with $\tau_{n\lambda} \rightarrow \frac{\pi/2+2n\pi}{\lambda\bar{m}}$ as $\lambda \rightarrow 0^+$ such that the positive steady state of Eq. (3) is locally asymptotically stable when $\tau \in (0, \tau_{0\lambda})$, and it is unstable when $\tau \in (\tau_{0\lambda}, \infty)$;
2. a supercritical Hopf bifurcation occurs at $\tau = \tau_{n\lambda}$ for (3) near the spatially non-homogeneous steady state u_λ and all bifurcating periodic orbits are locally asymptotically stable on the center manifold. Especially, there exists a $\epsilon > 0$ such that a locally stable spatially non-homogeneous periodic orbit arises near u_λ for $\tau \in (\tau_{0\lambda}, \tau_{0\lambda} + \epsilon)$;
3. the spatial heterogeneity increases the temporal average of total biomass when the population is oscillating in time: any periodic solution $u(x, t)$ of (3) satisfies that $\bar{u} > \int_\Omega m(x)dx$ where $\bar{u} := \frac{1}{T} \int_s^{s+T} \int_\Omega u(x, t)dxdt$ is the temporal average of the population total biomass and $\int_\Omega m(x)dx$ is the total resource. Also the time-dependent total biomass shows a temporal oscillation and it is possible that sometimes the total biomass is below the total resource $\int_\Omega m(x)dx$.

The existence and uniqueness of the positive steady state $\theta(x, d)$ of Eq. (2) for any $d > 0$ has been established in [27, Theorem 1], and it is known that the positive steady state is spatially non-homogeneous. Moreover, when $d \rightarrow \infty$, it is shown in [27] that $\theta(x, d) \rightarrow \bar{m}$. In [22, Proposition 3.1], a more precise asymptotic estimate of $\theta(x, d)$ for large d is obtained and the estimate is useful for determining the stability of $u_\lambda(x)$ (which is equivalent to $\theta(x, d)$) with respect to (3). On the other hand, for Eq. (1) which is the case of $\tau = 0$ of Eq. (2), it was shown in [27] that the population biomass satisfies $\int_\Omega \theta(x, d)dx > \int_\Omega m(x)dx$, while, when the resource supply is a constant \bar{m} , the population biomass is equal to $\int_\Omega m(x)dx$. It implies that the heterogeneity of resource leads to the increase of population biomass. Our result 3 above shows the same phenomenon still occurs when a time delay exists in the biological process. The population now oscillates over time, but the temporal average of population biomass is still greater than the total resource. Such results also hold for more general diffusive logistic type model with heterogeneous growth rate and carrying capacity [10], and ecological experiments have been carried out to verify it in [42]. Other than the scalar equation (1), the effect of spatial heterogeneity on the competition of two species is investigated in [19–22, 25, 27]. The method we use here for Neumann boundary value problem with heterogeneous resource function is similar to earlier work for Dirichlet boundary value problem with homogeneous resource function [2, 9, 16, 17, 34, 36, 37, 40], as the steady states in both cases are spatially non-homogeneous. That approach is powerful but also limited as it requires a precise profile of the steady state. Hence the stability/instability of positive steady state for large λ is still not known, as the profile of positive steady state is not clear in that case and thus the current method cannot be applied.

After the completion of initial draft of this paper, we learned that in a recent work [8], the Hopf bifurcation in a reaction-diffusion-advection logistic model with time delay and spatial heterogeneous resource has been proved by using a similar approach as ours. In this paper, we also investigate the effect of heterogeneous resource function on the spatiotemporal patterns generated by (3) with numerical simulations. In particular when $m(x)$ is spatially periodic or monotone function, the resulting spatiotemporal patterns are strikingly distinctive.

In [26], a two-patch logistic population model with a single delay was considered. In that work, the dispersal coefficients are chosen to resemble the Neumann or Dirichlet boundary condition, and the resource function can also be homogeneous or non-homogeneous. The existence of Hopf bifurcation and locally stable periodic orbits is proved under these conditions. Our work here can also be viewed as a continuous counter part for the non-homogeneous case in that paper.

This paper is organized as follows. In Section 2, we study the stability and Hopf bifurcation of the positive steady state through analyzing the corresponding eigenvalue problem. By using some specific function $m(x)$, we perform the simulations for system (2) in Section 3. Finally, we conclude our results and discuss some future work in Section 4. Here, we want to introduce some notations in this paper. The Lebesgue space of integrable functions defined on a spatial domain Ω which is bounded and smooth is denoted by $L^2(\Omega)$ and we use H^k, H_0^k to denote the real-valued Sobolev space in which the functions have k th order weak derivative based on $L^2(\Omega)$ space. Denote $X = H^2(\Omega) \cap H_0^1(\Omega)$ and $Y = L^2(\Omega)$. For a space Z , we define its complexification is $Z_{\mathbb{C}} \triangleq Z \oplus iZ = \{x_1 + ix_2 : x_1, x_2 \in Z\}$. The Banach space of continuous and differentiable mappings from $(-\tau, 0]$ into Y is denoted by $\mathcal{C} = C((-\tau, 0], Y)$ and $\mathcal{C}^1 = C^1((-\tau, 0], Y)$ respectively, and the complex-valued Hilbert space $Y_{\mathbb{C}}$ has the inner product: $\langle u, v \rangle = \int_{\Omega} \bar{u}(x)v(x)dx$.

2. Stability and Hopf bifurcation. In this section, we investigate the stability of the unique positive non-homogeneous steady state $u_{\lambda}(x)$ (for the convenience of writing, we will use u_{λ} in the rest part of this paper) of Eq. (3) by studying the associated eigenvalue problem. Here we assume that the non-homogeneous resource function $m(x)$ satisfies

$$(H) \quad m(x) \in C^{\alpha}(\bar{\Omega}) \text{ for } \alpha \in (0, 1), m(x) \text{ is non-constant and } \int_{\Omega} m(x)dx \geq 0.$$

Firstly, the steady state of Eq. (3) satisfies the following elliptic boundary value problem:

$$\begin{cases} \Delta u(x) + \lambda u(x)(m(x) - u(x)) = 0, & x \in \Omega, \\ \partial_{\nu} u(x) = 0, & x \in \partial\Omega. \end{cases} \quad (4)$$

For the following analysis, we decompose the spaces X, Y as follows,

$$X = K \oplus X_1, \quad Y = K \oplus Y_1,$$

where

$$K = \text{Span}\{1\}, \quad X_1 = \left\{ y \in X : \int_{\Omega} y(x)dx = 0 \right\}, \quad Y_1 = \left\{ y \in Y : \int_{\Omega} y(x)dx = 0 \right\}.$$

For the existence, uniqueness and asymptotic profile of the positive steady state solution, the following results have been given in [22, Proposition 3.1]:

Lemma 2.1. *Suppose that $m(x)$ satisfies (H), then there exists a $\lambda_* > 0$ depending on $m(x)$ such that, for $\lambda \in (0, \lambda_*)$, Eq. (4) has a unique positive solution with the*

following form:

$$u_\lambda = \bar{m} + \lambda(\rho_m(x) + C(m)) + \lambda^2(\gamma_m(x) + K(m)) + o(\lambda^2), \tag{5}$$

where $o(\lambda^2)$ is taken in $L^\infty(\Omega)$. Here $\rho_m(x)$ satisfies

$$\begin{cases} \Delta\rho_m(x) + \bar{m}(m(x) - \bar{m}) = 0, & x \in \Omega, \\ \int_\Omega \rho_m(x)dx = 0, \\ \partial_\nu\rho_m(x) = 0, & x \in \partial\Omega, \end{cases} \tag{6}$$

$\gamma_m(x)$ is the unique solution of

$$\begin{cases} \Delta\gamma_m(x) + (m(x) - 2\bar{m})(\rho_m(x) + C(m)) = 0, & x \in \Omega, \\ \int_\Omega \gamma_m(x)dx = 0, \\ \partial_\nu\gamma_m(x) = 0, & x \in \partial\Omega, \end{cases} \tag{7}$$

and $C(m)$, $K(m)$ are constants defined by

$$C(m) = \frac{1}{\bar{m}^2|\Omega|} \int_\Omega |\nabla\rho_m|^2(x)dx, \tag{8}$$

and

$$K(m) = \frac{1}{\bar{m}^2|\Omega|} \int_\Omega (m(x) - 3\bar{m})\rho_m^2(x)dx. \tag{9}$$

The following analysis is always based on the assumption that $0 < \lambda < \lambda_*$ and λ_* is sufficiently small. Let u_λ be the unique positive steady state of Eq. (3) for $0 < \lambda < \lambda_*$ and linearize Eq. (3) at u_λ , we have

$$\begin{cases} \varphi_t(x, t) = \Delta\varphi(x, t) + \lambda[m(x) - u_\lambda]\varphi(x, t) - \lambda u_\lambda\varphi(x, t - \tau), & x \in \Omega, t > 0, \\ \partial_\nu\varphi(x, t) = 0, & x \in \partial\Omega, t > 0. \end{cases} \tag{10}$$

Define a linear operator $A(\lambda) : \mathcal{D}(A(\lambda)) \rightarrow Y_{\mathbb{C}}$ by

$$A(\lambda)\varphi := \Delta\varphi + \lambda[m(x) - u_\lambda]\varphi, \tag{11}$$

where $\mathcal{D}(A(\lambda)) = X_{\mathbb{C}}$. From [39, Theorem 3.1.5], the semigroup induced by the solution of Eq. (10) has an infinitesimal generator $A_\tau(\lambda)$ given by

$$A_\tau(\lambda)\phi = \dot{\phi}$$

with

$$\mathcal{D}(A_\tau(\lambda)) = \{\phi \in \mathcal{C}_{\mathbb{C}} \cap \mathcal{C}_{\mathbb{C}}^1 : \dot{\phi}(0) = A(\lambda)\phi(0) - \lambda u_\lambda\phi(-\tau)\}.$$

Then, the spectrum of $A_\tau(\lambda)$ is

$$\sigma(A_\tau(\lambda)) = \{\mu \in \mathbb{C} : \Lambda(\lambda, \mu, \tau)\psi = 0, \text{ for some } \psi \in X_{\mathbb{C}} \setminus \{0\}\} \tag{12}$$

with

$$\Lambda(\lambda, \mu, \tau) := A(\lambda) - \lambda u_\lambda e^{-\mu\tau} - \mu. \tag{13}$$

Then, through analyzing the spectrum of $A_\tau(\lambda)$, we investigate the stability of the positive non-homogeneous steady state u_λ and Hopf bifurcation of system (3) with τ considered as the bifurcation parameter. Firstly, we have the following results for the spectrum of $A_\tau(\lambda)$ and the stability of the steady state u_λ of system (3) when $\tau = 0$.

Theorem 2.2. For $\lambda \in (0, \lambda_*)$,

- (i) all the eigenvalues of $A_\tau(\lambda)$ have negative real parts when $\tau = 0$. Therefore, the steady state u_λ is locally asymptotically stable when $\tau = 0$;
(ii) for any $\tau > 0$, $0 \notin \sigma(A_\tau(\lambda))$.

Proof. When $\tau = 0$, the stability of u_λ is determined by the eigenvalues of $A_\tau(\lambda)$ when $\tau = 0$. By the fact that u_λ satisfies

$$\Delta u_\lambda + \lambda(m(x) - u_\lambda)u_\lambda = A(\lambda)u_\lambda = 0,$$

we know that 0 is the principal eigenvalue of $A(\lambda)$ and u_λ is its corresponding eigenfunction. On the other hand, the principal eigenvalue of $A(\lambda)$ can be expressed through the variational method, thus we have

$$0 = \mu_1 = \inf_{0 \neq y \in X_C} \frac{-\int_\Omega |\nabla y|^2 + \lambda \int_\Omega (m(x) - u_\lambda)y^2}{\int_\Omega y^2}.$$

Similarly, for $A_\tau(\lambda)$ when $\tau = 0$, we have

$$\Delta y + \lambda(m(x) - 2u_\lambda)y = \tilde{\mu}, \text{ for some } y \in X_C \setminus \{0\},$$

and the principal eigenvalue is

$$\tilde{\mu}_1 = \inf_{0 \neq y \in X_C} \frac{-\int_\Omega |\nabla y|^2 + \lambda \int_\Omega (m(x) - 2u_\lambda)y^2}{\int_\Omega y^2}. \quad (14)$$

Comparing $\tilde{\mu}_1$ with μ_1 , we conclude that $\tilde{\mu}_1 < \mu_1 = 0$. Therefore, all eigenvalues of $A_\tau(\lambda)$ are negative when $\tau = 0$, thus we know that u_λ is locally asymptotically stable when $\tau = 0$.

Next, we prove $0 \notin \sigma(A_\tau(\lambda))$ for any $\tau > 0$ and $\lambda \in (0, \lambda^*)$ by contradiction. Assuming that $0 \in \sigma(A_\tau(\lambda))$, we substitute $\mu = 0$ into Eq. (12) and obtain

$$(\Delta + \lambda(m(x) - 2u_\lambda))\tilde{y} = 0, \text{ for some } \tilde{y} \in X_C \setminus \{0\}. \quad (15)$$

However, by (14), we know that the principal eigenvalue of the operator $\Delta + \lambda(m(x) - 2u_\lambda)$ is $\tilde{\mu}_1 < 0$, so there exists no \tilde{y} such that Eq. (15) holds. This is a contradiction to $0 \in \sigma(A_\tau(\lambda))$. \square

Secondly, we study the situation that $A_\tau(\lambda)$ has a pair of purely imaginary eigenvalues $\mu = \pm i\omega$ ($\omega > 0$) for some $\tau > 0$, which is a necessary condition for the Hopf bifurcation. For that purpose, we substitute $\mu = i\omega$ into Eq. (12) and obtain

$$\Delta \psi + \lambda(m(x) - u_\lambda)\psi - \lambda u_\lambda e^{-i\theta}\psi - i\omega\psi = 0, \text{ for some } \psi \in X_C \setminus \{0\} \quad (16)$$

with $\theta := \omega\tau$. For further study, we give the following lemma first.

Lemma 2.3. *For $\lambda \in (0, \lambda_*)$, if there exist some $(\omega, \theta, \psi) \in \mathbb{R}^+ \times \mathbb{R} \times X_C \setminus \{0\}$ solving Eq. (16), then ω/λ is uniformly bounded.*

Proof. By Eq. (16), we have

$$\begin{aligned} & \langle [\Delta + \lambda(m(x) - u_\lambda) - \lambda u_\lambda e^{-i\theta} - i\omega] \psi, \psi \rangle \\ &= \langle A(\lambda)\psi, \psi \rangle - \lambda e^{i\theta} \langle u_\lambda \psi, \psi \rangle - i\omega \langle \psi, \psi \rangle = 0. \end{aligned} \quad (17)$$

Since $A(\lambda)$ is self-adjoint, then $\langle A(\lambda)\psi, \psi \rangle$ is real. Separating the real and imaginary parts of Eq. (17), we have

$$\omega \langle \psi, \psi \rangle = \lambda \sin(\theta) \int_\Omega u_\lambda |\psi|^2 dx.$$

Since $|\sin(\theta)| \leq 1$ and there exists $M > 0$ such that $|u_\lambda| = |\bar{m} + \lambda(\rho_m + C(m)) + o(\lambda)| \leq M$, we obtain

$$\frac{|\omega|}{\lambda} = \frac{\sin(\theta) \int_\Omega u_\lambda |\psi|^2 dx}{\|\psi\|_{Y_C}^2} \leq M.$$

Thus, we proved the boundedness of ω/λ . □

For $\lambda \in (0, \lambda_*)$, we have the following results about the existence of the triple $(\omega, \theta, \psi) \in \mathbb{R}^+ \times \mathbb{R} \times X_C \setminus \{0\}$ satisfying Eq. (16). Let

$$\psi = \beta + \lambda z, \quad \beta > 0, \quad \text{with } \|\psi\|_{Y_C} = 1, \quad \omega = \lambda h. \tag{18}$$

Substituting (18) and $u_\lambda = \bar{m} + \lambda \xi$ with $\xi := (\rho_m(x) + C(m)) + \lambda(\gamma_m(x) + K(m)) + o(\lambda)$ into Eq. (16), we get

$$\begin{aligned} g_1(z, \beta, \theta, h, \lambda) &:= \Delta z + (m(x) - (\bar{m} + \lambda \xi))(\beta + \lambda z) \\ &\quad - (\bar{m} + \lambda \xi)e^{-i\theta}(\beta + \lambda z) - ih(\beta + \lambda z) = 0, \tag{19} \\ g_2(\beta, z, \lambda) &:= (\beta^2 - 1) + \lambda^2 \|z\|_{Y_C} = 0. \end{aligned}$$

We define $G(z, \beta, \theta, h, \lambda) := (g_1, g_2)$ from $(X_1)_C \times \mathbb{R}^3 \times \mathbb{R}$ to $(Y_1)_C \times \mathbb{R}$. When $\lambda \rightarrow 0$, the limiting equation of (19) is

$$\begin{aligned} g_1(z, \beta, \theta, h, 0) &= \Delta z + \beta(m(x) - \bar{m}) - \beta \bar{m} e^{-i\theta} - ih\beta = 0, \tag{20} \\ g_2(\beta, z, 0) &= \beta^2 - 1 = 0, \end{aligned}$$

and by the second equation, immediately we have $\beta = 1$. Substituting $\beta = 1$ into the first equation of (20) and integrating it over Ω , we obtain

$$\bar{m} e^{-i\theta} + ih = 0.$$

Hence the solution set of Eq. (20) is

$$\Sigma = \left\{ (z, \beta, \theta, h) = \left(\rho_m, 1, \frac{\pi}{2} + 2n\pi, \bar{m} \right), \quad n \in \mathbb{N} \cup \{0\} \right\},$$

where ρ_m is the unique solution of Eq. (6). By the periodicity of θ , we can always set $\theta \in [0, 2\pi)$, under which Eq. (20) has a unique solution given by

$$(z_0, \beta_0, \theta_0, h_0) = \left(\rho_m, 1, \frac{\pi}{2}, \bar{m} \right). \tag{21}$$

By the implicit function theorem, the existence of the solution of $G(z, \beta, \theta, h, \lambda) = 0$ for small λ can be shown as follows.

Theorem 2.4. For $\lambda \in (0, \lambda_*)$,

- (i) there exists a unique continuously differentiable map $W_\lambda := (z_\lambda, \beta_\lambda, \theta_\lambda, h_\lambda)$ from $(0, \lambda_*)$ to $(X_1)_C \times \mathbb{R}^3$ satisfying $W_0 = (z_0, \beta_0, \theta_0, h_0)$ defined in (21) such that $G(W_\lambda, \lambda) = 0$;
- (ii) the eigenvalue problem

$$\Lambda(\lambda, i\omega, \tau)\psi = 0, \quad \tau > 0, \psi \in X_C \setminus \{0\}$$

with Λ defined in (13) has non-trivial solutions, that is, $i\omega \in \sigma(A_\tau(\lambda))$ if and only if

$$\begin{aligned} \omega = \omega_\lambda &:= \lambda h_\lambda, \quad \tau = \tau_{n\lambda} := \frac{\theta_\lambda + 2n\pi}{\omega_\lambda} (n \in \mathbb{N} \cup \{0\}), \\ \psi &= r\psi_\lambda \quad \text{with } \psi_\lambda := \beta_\lambda + \lambda z_\lambda, \end{aligned}$$

where r is a nonzero constant and $(z_\lambda, \beta_\lambda, h_\lambda, \theta_\lambda) = W_\lambda$ is defined in part (i).

Proof. We define $T = (T_1, T_2) : (X_1)_{\mathbb{C}} \times \mathbb{R}^3 \mapsto Y_{\mathbb{C}} \times \mathbb{R}$ by

$$T := D_{(z, \beta, \theta, h)} G(W_0, 0).$$

Therefore we have

$$\begin{aligned} T_1(\chi, \kappa, \vartheta, \epsilon) &= \Delta \chi + (m(x) - \bar{m})\kappa + \bar{m}\vartheta - i\epsilon, \\ T_2(\kappa) &= 2\kappa. \end{aligned}$$

It can be verified that T is bijective from $(X_1)_{\mathbb{C}} \times \mathbb{R}^3$ to $(Y_1)_{\mathbb{C}} \times \mathbb{R}$, thus by the implicit function theorem, there exists a continuously differentiable mapping $W_\lambda : (0, \lambda_*) \rightarrow (X_1)_{\mathbb{C}} \times \mathbb{R}^3$ such that $G(W_\lambda, \lambda) = 0$ with $W_0 = (z_0, \beta_0, \theta_0, h_0)$ as $\lambda \rightarrow 0$.

Next we prove the uniqueness of W_λ . Assume that there exists another continuously differentiable mapping $W^\lambda := (z^\lambda, \beta^\lambda, \theta^\lambda, h^\lambda)$ with $\theta^\lambda \in [0, 2\pi)$, $h^\lambda > 0$ such that $G(W^\lambda, \lambda) = 0$, then we need to show that $W^\lambda \rightarrow W_0$ as $\lambda \rightarrow 0$ in the norm of $(X_1)_{\mathbb{C}} \times \mathbb{R}^3$ by the implicit function theorem. First, the boundedness of the sequences $\{\beta^\lambda\}$, $\{\theta^\lambda\}$ and $\{h^\lambda\}$ can be easily obtained from the definition of W^λ and Lemma 2.3. In the following, we will prove the boundedness of the z^λ . From the first equation of Eq. (19), we have

$$\|z^\lambda\|_{Y_{\mathbb{C}}}^2 \leq \frac{1}{\lambda_2} \left| \langle [(m(x) - u_\lambda) - u_\lambda e^{-i\theta^\lambda} - ih^\lambda](\beta^\lambda + \lambda z^\lambda), z^\lambda \rangle \right|,$$

where λ_2 is the second eigenvalue of $-\Delta$ on $H^1(\Omega)$. The boundedness of $m(x)$, $\{h^\lambda\}$ and u_λ implies that there exists a constant $M_1 > 0$ such that

$$\frac{1}{\lambda_2} \left\| (m(x) - u_\lambda) - u_\lambda e^{-i\theta^\lambda} - ih^\lambda \right\|_\infty \leq M_1,$$

then we have

$$\|z^\lambda\|_{Y_{\mathbb{C}}}^2 \leq M_1 |\beta^\lambda| \|z^\lambda\|_{Y_{\mathbb{C}}} + \lambda M_1 \|z^\lambda\|_{Y_{\mathbb{C}}}^2. \quad (22)$$

We can choose a proper M_1 such that $\lambda M_1 < 1/2$, then Eq. (22) implies that

$$\|z^\lambda\|_{Y_{\mathbb{C}}}^2 \leq 2M_1 |\beta^\lambda|.$$

Hence, $\{z^\lambda\}$ is bounded in $Y_{\mathbb{C}}$ when $\lambda \in (0, \lambda_*]$. Since the operator $\Delta : (X_1)_{\mathbb{C}} \mapsto (Y_1)_{\mathbb{C}}$ has a bounded inverse, by applying Δ^{-1} on $g_1(z^\lambda, \beta^\lambda, h^\lambda, \theta^\lambda, \lambda) = 0$, we find that $\{z^\lambda\}$ is also bounded in $X_{\mathbb{C}}$, and hence $\{W^\lambda : \lambda \in (0, \lambda_*]\}$ is precompact in $Y_{\mathbb{C}} \times \mathbb{R}^3$. Therefore, there is a subsequence $\{W^{\lambda_j} := (z^{\lambda_j}, \beta^{\lambda_j}, h^{\lambda_j}, \theta^{\lambda_j})\}$ such that

$$W^{\lambda_j} \rightarrow W^0, \quad \lambda_j \rightarrow 0 \text{ as } j \rightarrow \infty.$$

By taking the limit of the equation $G(W^{\lambda_j}, \lambda_j) = 0$ as $j \rightarrow \infty$, we have that $G(W^0, 0) = 0$. Also, we know that $G(z, \beta, h, \theta, 0) = 0$ has a unique solution given by $(z, \beta, h, \theta) = W_0$, thus $W^0 = W_0$. Hence, $W^\lambda \rightarrow W_0$ as $\lambda \rightarrow 0$ in the norm of $X_{\mathbb{C}} \times \mathbb{R}^3$. This proves part (i), and part (ii) is immediately observed from part (i). \square

Remark 2.5. The results in Theorem 2.4 are for Eq. (3) which has a rescaling in time $\tilde{\tau} = \tau/\lambda$. Therefore, if we go back to the real time scale that is the original system (2), the critical value for Eq. (2) satisfies

$$\tau_{n\lambda} = \frac{\lambda(\theta_\lambda + 2n\pi)}{\omega_\lambda} = \frac{\theta_\lambda + 2n\pi}{h_\lambda}, \text{ and } \lim_{\lambda \rightarrow 0} \tau_{n\lambda} = \frac{\pi + 4n\pi}{2\bar{m}},$$

which we will use in the numerical simulations.

Next we demonstrate that a Hopf bifurcation indeed occurs at $\tau_{n\lambda} = (\theta_\lambda + 2n\pi)/\omega_\lambda$ in system (3) by verifying the transversality condition.

Lemma 2.6. For $\lambda \in (0, \lambda_*)$, we have

- (i) $A_\tau(\lambda)$ has a simple eigenvalue $\mu(\tau) = a(\tau) + ib(\tau)$ satisfying $a(\tau_{n\lambda}) = 0$, $b(\tau_{n\lambda}) = \omega_\lambda$ when τ is near $\tau_{n\lambda}$;
- (ii) $\text{Re} \left(\frac{d\mu}{d\tau}(\tau_{n\lambda}) \right) > 0$.

Proof. As for part (i), the proof is similar to that in [36, Theorem 3.5] which is omitted here. Now we give the proof for part (ii). Applying the implicit function theorem, we obtain that there exist a neighborhood $O \times D \times H \subset \mathbb{R} \times \mathbb{C} \times X_{\mathbb{C}}$ of $(\tau_\lambda, i\omega_\lambda, \psi_\lambda)$ and a continuous differential function $(\mu, \psi) : O \rightarrow D \times H$ such that, for each $\tau \in O$, $\mu(\tau)$ is the only eigenvalue of $A_\tau(\lambda)$ with associated eigenfunction $\psi(\tau)$ and the following equalities hold:

$$\mu(\tau_{n\lambda}) = i\omega_\lambda, \psi(\tau_{n\lambda}) = \psi_\lambda,$$

$$\Lambda(\lambda, \mu(\tau), \tau) = [\Delta + \lambda(m(x) - u_\lambda) - \lambda u_\lambda e^{-\mu(\tau)\tau} - \mu(\tau)] \psi(\tau) = 0, \tau \in O. \tag{23}$$

Differentiating Eq. (23) with respect to τ at $\tau = \tau_{n\lambda}$, we get

$$\Lambda(\lambda, i\omega_\lambda, \tau_{n\lambda}) \frac{d\psi(\tau_{n\lambda})}{d\tau} + \lambda u_\lambda e^{-i\theta_\lambda} \left(\frac{d\mu(\tau_{n\lambda})}{d\tau} + i\omega_\lambda \right) \psi_\lambda - \frac{d\mu(\tau_{n\lambda})}{d\tau} \psi_\lambda = 0. \tag{24}$$

Multiplying Eq. (24) by ψ_λ and integrating over Ω , we have

$$\frac{d\mu(\tau_{n\lambda})}{d\tau} = \frac{i\lambda\omega_\lambda e^{-i\theta_\lambda} \int_\Omega u_\lambda \psi_\lambda^2 dx}{\int_\Omega \psi_\lambda^2 dx - \lambda\tau_{n\lambda} e^{-i\theta_\lambda} \int_\Omega u_\lambda \psi_\lambda^2 dx}. \tag{25}$$

We define

$$S_{n\lambda} = \int_\Omega \psi_\lambda^2 dx - \lambda\tau_{n\lambda} e^{-i\theta_\lambda} \int_\Omega u_\lambda \psi_\lambda^2 dx. \tag{26}$$

When $\lambda \rightarrow 0$, we obtain that

$$\lim_{\lambda \rightarrow 0} u_\lambda = \bar{m}, \lim_{\lambda \rightarrow 0} \theta_\lambda = \frac{\pi}{2}, \lim_{\lambda \rightarrow 0} \psi_\lambda = 1, \lim_{\lambda \rightarrow 0} \lambda\tau_{n\lambda} = \frac{\pi/2 + 2n\pi}{\bar{m}}, \tag{27}$$

so

$$\lim_{\lambda \rightarrow 0} S_{n\lambda} = 1 + i \left(\frac{\pi}{2} + 2n\pi \right) \neq 0.$$

By the continuity with respect to λ , we know $S_{n\lambda} \neq 0$ in a small neighborhood of $\lambda = 0$. We continue the calculation of Eq. (25) and have

$$\frac{d\mu(\tau_{n\lambda})}{d\tau} = \frac{1}{|S_{n\lambda}|^2} \left(i\lambda\omega_\lambda e^{-i\theta_\lambda} \int_\Omega \psi_\lambda^2 dx - i\lambda^2\tau_{n\lambda}\omega_\lambda \left| \int_\Omega u_\lambda \psi_\lambda^2 dx \right|^2 \right). \tag{28}$$

Therefore,

$$\text{Re} \left(\frac{d\mu(\tau_{n\lambda})}{d\tau} \right) = \frac{\lambda\omega_\lambda \sin(\theta_\lambda) \int_\Omega \psi_\lambda^2 dx}{|S_{n\lambda}|^2}.$$

Since $\lim_{\lambda \rightarrow 0} \sin \theta_\lambda \int_\Omega \psi_\lambda^2 dx = 1 > 0$, for $\lambda \in (0, \lambda_*)$, we also can attain that $\sin \theta_\lambda \int_\Omega \psi_\lambda^2 dx > 0$. Hence, by the positiveness of ω_λ , we have $\text{Re} \left(\frac{d\mu(\tau_{n\lambda})}{d\tau} \right) > 0$. \square

By Theorem 2.4 and Lemma 2.6, we have the following results for the stability and Hopf bifurcation of u_λ which is the positive steady state solution of (3).

Theorem 2.7. *Suppose that $m(x)$ satisfies (H), then for each $\lambda \in (0, \lambda_*)$,*

- (i) *there exists an infinite sequence $\tau_{n\lambda} > 0$ defined in Theorem 2.4 such that all the eigenvalues of $A_\tau(\lambda)$ have negative real parts when $\tau \in (0, \tau_{0\lambda})$, $A_\tau(\lambda)$ has a pair of purely imaginary eigenvalues $\pm i\omega_\lambda$ ($\omega_\lambda > 0$) when $\tau = \tau_{n\lambda}$, and $A_\tau(\lambda)$ has $2(n+1)$ eigenvalues with positive real parts when $\tau \in (\tau_{n\lambda}, \tau_{(n+1)\lambda})$;*
- (ii) *the unique positive steady state u_λ of Eq. (3) is locally asymptotically stable when $\tau \in (0, \tau_{0\lambda})$, and it is unstable when $\tau \in (\tau_{0\lambda}, +\infty)$;*
- (iii) *a Hopf bifurcation occurs at $\tau = \tau_{n\lambda}$ for (3) so that there is a continuous family of periodic orbits of (3) in form of $\{(\tau_n(s), u_n(x, t, s), T_n(s)) : s \in (0, \delta_1)\}$ so that $u_n(x, t, s)$ is a $T_n(s)$ -periodic solution of (3) with $\tau = \tau_n(s)$, and $\tau_n(0) = \tau_{n\lambda}$, $\lim_{s \rightarrow 0^+} u_n(x, t, s) = u_\lambda(x)$ and $\lim_{s \rightarrow 0^+} T_n(s) = 2\pi/\omega_\lambda$.*

Next, by applying the method of Faria [11, 12], the normal form of system (3) can be computed to determine the direction of the Hopf bifurcation proved in Theorem 2.7 and the stability of the periodic orbits.

Theorem 2.8. *Suppose that $m(x)$ satisfies (H), for each $\lambda \in (0, \lambda_*)$, the Hopf bifurcation of the steady state u_λ of Eq. (3) at $\tau = \tau_{n\lambda}$ defined in Theorem 2.4 is supercritical, and the bifurcating periodic orbits are stable on the center manifold. Especially, there exists $\epsilon > 0$ such that system (3) has a stable periodic orbit when $\tau \in (\tau_{0\lambda}, \tau_{0\lambda} + \epsilon)$.*

Proof. In Theorem 2.7, we obtain conditions under which system (3) undergoes a Hopf bifurcations near the positive steady state u_λ at $\tau = \tau_{n\lambda}$. By letting $U(t) = u(\cdot, t) - u_\lambda$ and $U_t = U(t + a) \in \mathcal{C} = C([- \tau, 0], Y_{\mathbb{C}})$, $\alpha = \tau - \tau_{n\lambda}$ and $t \rightarrow t/\tau$, for each $\lambda \in (0, \lambda_*)$, we translate the steady state and parameter τ to the origin, then $\alpha = 0$ is the Hopf bifurcation value now.

Then we rewrite Eq. (3) as follows:

$$\frac{dU(t)}{dt} = \tau_{n\lambda} \Delta U_t(0) + L_0(U_t) + F(U_t, \alpha),$$

where

$$\begin{aligned} L_0(\varphi) &= \lambda \tau_{n\lambda} ((m(x) - u_\lambda)\varphi(0) - u_\lambda \varphi(-1)), \\ F(\varphi, \alpha) &= \alpha \Delta \varphi(0) + L_\alpha(\varphi) - \lambda(\tau_{n\lambda} + \alpha)\varphi(0)\varphi(-1), \end{aligned}$$

where $L_\alpha(\varphi) = \lambda \alpha ((m(x) - u_\lambda)\varphi(0) - u_\lambda \varphi(-1))$. And the Taylor expansion of $F(U_t, \alpha)$ is

$$F(U_t, \alpha) = \frac{1}{2!} F_2(U_t, \alpha) + \frac{1}{3!} F_3(U_t, \alpha) + h.o.t.$$

with

$$\begin{aligned} F_2(U_t, \alpha) &= 2! \alpha ((\Delta + \lambda(m(x) - u_\lambda)U_t(0) - \lambda u_\lambda U_t(-1))), \\ F_3(U_t, \alpha) &= -3! \lambda \alpha U_t(0)U_t(-1). \end{aligned}$$

By following the computing procedure of normal form in [12], the bifurcation direction and the stability of the bifurcating periodic orbits can be determined by the following two numbers:

$$K_1 = \mathcal{R}e(A_1), \quad K_2 = \mathcal{R}e(A_2),$$

where

$$A_1 := \frac{i\omega_\lambda}{S_{n\lambda}} \langle \psi_\lambda, \psi_\lambda \rangle, \quad A_2 := \frac{1}{4}(C_1 + C_2),$$

with

$$C_1 := \frac{8i\lambda^2\tau_{n\lambda}}{\omega_\lambda} \left[\frac{1}{S_{n\lambda}^2} \mathcal{R}e(e^{i\theta_\lambda})e^{-i\theta_\lambda} \langle \psi_\lambda, \psi_\lambda^2 \rangle \langle \psi_\lambda, |\psi_\lambda|^2 \rangle \right. \\ \left. - \frac{1}{|S_{n\lambda}|^2} \left(2(\mathcal{R}e(e^{i\theta_\lambda}))^2 |\langle \psi_\lambda, |\psi_\lambda|^2 \rangle|^2 + \frac{1}{3} |\langle \psi_\lambda, \bar{\psi}_\lambda^2 \rangle|^2 \right) \right],$$

$$C_2 := -\frac{2\lambda\tau_{n\lambda}}{S_{n\lambda}} [\langle \psi_\lambda, (h_{20}(-1) + h_{20}(0)e^{i\theta_\lambda})\psi_\lambda \rangle + \langle \psi_\lambda, (h_{11}(-1) + h_{11}(0)e^{i\theta_\lambda})\psi_\lambda \rangle].$$

Here h_{20} , h_{11} are the solutions of the following equations, respectively,

$$\begin{cases} \dot{h}_{20}(s) - 2i\theta_{n\lambda}h_{20}(s) = -2\lambda\tau_{n\lambda}e^{-i\theta_\lambda} \left[\frac{\langle \psi_\lambda, \psi_\lambda^2 \rangle \psi_\lambda e^{i\theta_\lambda s}}{S_{n\lambda}} + \frac{\langle \bar{\psi}_\lambda, \psi_\lambda^2 \rangle \bar{\psi}_\lambda e^{-i\theta_\lambda s}}{\bar{S}_{n\lambda}} \right], \\ \dot{h}_{20}(0) - \tau_{n\lambda} [A(\lambda)h_{20}(0) - \lambda u_\lambda h_{20}(-1)] = -2\lambda\tau_{n\lambda}e^{-i\theta_\lambda} \psi_\lambda^2, \end{cases}$$

and

$$\begin{cases} \dot{h}_{11}(s) = -4\lambda\tau_{n\lambda} \mathcal{R}e(e^{i\theta_\lambda}) \left[\frac{\langle \psi_\lambda, |\psi_\lambda|^2 \rangle \psi_\lambda e^{i\theta_\lambda s}}{S_{n\lambda}} + \frac{\langle \bar{\psi}_\lambda, |\psi_\lambda|^2 \rangle \bar{\psi}_\lambda e^{-i\theta_\lambda s}}{\bar{S}_{n\lambda}} \right], \\ \dot{h}_{11}(0) - \tau_{n\lambda} [A(\lambda)h_{11}(0) - \lambda u_\lambda h_{11}(-1)] = -4\lambda\tau_{n\lambda} \mathcal{R}e(e^{i\theta_\lambda}) |\psi_\lambda|^2, \end{cases}$$

where $\theta_{n\lambda} := \theta_\lambda + 2n\pi$ and $A(\lambda)$, $S_{n\lambda}$ are defined in (11) and (26), respectively. Then, by taking the limits of K_1 and K_2 when $\lambda \rightarrow 0$ and using (27), we have the following results:

$$K_1 = \mathcal{R}e(A_1) = \omega_\lambda \mathcal{R}e \left(\frac{i\langle \psi_\lambda, \psi_\lambda \rangle}{S_{n\lambda}} \right),$$

where

$$\lim_{\lambda \rightarrow 0} \mathcal{R}e \left(\frac{i\langle \psi_\lambda, \psi_\lambda \rangle}{S_{n\lambda}} \right) = \frac{\pi/2 + 2n\pi}{1 + (\pi/2 + 2n\pi)^2} > 0.$$

Thus, we have $K_1 > 0$. And

$$\begin{aligned} \lim_{\lambda \rightarrow 0} K_2 &= \lim_{\lambda \rightarrow 0} \mathcal{R}e \left(\frac{1}{4}(C_1 + C_2) \right) \\ &= \frac{1}{15\bar{m}^2\theta_{n\lambda}|1 + i\theta_{n\lambda}|^4} (-3\theta_{n\lambda}^3 + 13\theta_{n\lambda}^2 - 39\theta_{n\lambda} + 1) < 0. \end{aligned}$$

According to [12, Theorem 3.2], $K_1 > 0$ and $K_2 < 0$ imply that a supercritical Hopf bifurcation occurs here for Eq. (3) and the bifurcating periodic orbits are locally asymptotically stable on the center manifold. The first bifurcating periodic orbit is stable in the small neighborhood of the bifurcation point $\tau_{0\lambda}$. \square

Finally, we show that the spatial heterogeneity increases the population size, which has been proved for the case that the solution of system (3) converges to the steady state without time delay in [27, Theorem 1.2]. When the time delay is incorporated in the model, it also can be proved that, compared to the constant resource supply case (i.e. $m(x) = \bar{m}$), the temporal average of total biomass increases in the situation that a stable spatially non-homogeneous periodic orbit arises in Eq. (3) when $\tau > \tau_{0\lambda}$ because of the non-homogeneous resource distribution.

Definition 2.9. Suppose that $u(x, t)$ is a time-periodic solution of Eq. (3) with period T , then $\bar{u}(t) := \int_\Omega u(x, t) dx$ is the total biomass of the population at time t , and the temporal average of total biomass is defined as

$$\bar{u} := \frac{1}{T} \int_s^{s+T} \int_\Omega u(x, t) dx dt.$$

Note that $\tilde{u}(t)$ is still a time-periodic function of time t , while \bar{u} is a positive constant. Here we assume that $m(x)$ satisfies a stronger condition:

(H') $m(x) \in C^\alpha(\bar{\Omega})$ for $\alpha \in (0, 1)$, $m(x)$ is non-constant and $m(x) \geq 0$ for all $x \in \bar{\Omega}$.

Then, we have the following result:

Theorem 2.10. *Assume that $m(x)$ satisfies (H'), and suppose that $u(x, t)$ is a time-periodic solution of Eq. (3) with period T . Then*

$$\bar{u} > \int_{\Omega} m(x) dx.$$

Proof. Because $u(x, t)$ satisfies Eq. (3), we have

$$\int_{\Omega} u_t(x, t) \varphi(x, t) dx = \int_{\Omega} \Delta u(x, t) \varphi(x, t) dx + \lambda \int_{\Omega} u(x, t) [m(x) - u(x, t - \tau)] \varphi(x, t) dx \quad (29)$$

for any $\varphi(x, t) \in W^{1,2}(\Omega)$ and $t > 0$. By using the Maximum Principle [33] and a similar argument as the one in [15, Lemma 1], the positiveness of the periodic solution $u(x, t)$ can be obtained. We choose the test function φ in Eq. (29) to be $\varphi = 1/u$. Integrating the both sides of Eq. (29) in one temporal period $[s, s + T]$, we have

$$\frac{1}{T} \int_s^{s+T} \int_{\Omega} \frac{u_t}{u} dx dt = \frac{1}{T} \int_s^{s+T} \int_{\Omega} \frac{\Delta u}{u} dx dt + \frac{\lambda}{T} \int_s^{s+T} \int_{\Omega} [m(x) - u(t - \tau)] dx dt. \quad (30)$$

From Fubini Theorem, the left side of Eq. (30) can be computed as

$$\begin{aligned} \frac{1}{T} \int_s^{s+T} \int_{\Omega} \frac{u_t}{u} dx dt &= \frac{1}{T} \int_{\Omega} \int_s^{s+T} \frac{u_t}{u} dt dx \\ &= \frac{1}{T} \int_{\Omega} [\ln(u(x, s + T)) - \ln(u(x, s))] dx = 0. \end{aligned}$$

Then, by applying the Neumann boundary condition and direct calculation, we have

$$\frac{1}{T} \int_s^{s+T} \int_{\Omega} u(x, t) dx dt = \frac{1}{\lambda T} \int_s^{s+T} \int_{\Omega} \frac{|\nabla u(x, t)|^2}{u^2(x, t)} dx dt + \int_{\Omega} m(x) dx > \int_{\Omega} m(x) dx, \quad (31)$$

where the fact that

$$\frac{1}{T} \int_s^{s+T} \int_{\Omega} u(x, t) dx dt = \frac{1}{T} \int_s^{s+T} \int_{\Omega} u(x, t - \tau) dx dt$$

is used. Also, the last inequality in (31) holds for the reason that $u(x, t)$ is non-constant. The conclusion is inferred by (31). \square

Remark 2.11. From Theorem 2.10, we have $\bar{u} > \int_{\Omega} m(x) dx$ for a time periodic solution $u(x, t)$ of Eq. (3), which means that the temporal average of total biomass with heterogeneous resource supply is always greater than that of the constant case (i.e. $m(x) = \bar{m}$). In other words, the spatial heterogeneity will benefit the temporal average of population size. However, $\tilde{u}(t) > \int_{\Omega} m(x) dx$ is not always true, and $\tilde{u}(t)$ is a time-periodic function and oscillates around $\int_{\Omega} m(x) dx$, which will be shown by the numerical simulations in Section 3.

3. Pattern formation: Numerical simulations. In this part, we investigate the effect of $m(x)$ on the profile of the non-homogeneous steady state and the structure of the spatial periodic solutions of Eq. (3) which is equivalent to the original system (2) under a rescaling in time which is supposed to simplify the theoretical analysis. In order to preserve the real time scale, we carry out the simulations for the original system (2), and the critical value for stability switch will be $\tau_{0\lambda} = \frac{\pi}{2\bar{m}} + o(\lambda)$ according to Remark 2.5. The numerical simulations are performed on a one-dimensional spatial domain $(0, 2\pi)$, and two classes of $m(x)$ are considered: (i) $m(x)$ is monotone in x ; (ii) $m(x)$ is periodic in x .

3.1. Non-homogeneous steady states. From (5) in Lemma 2.1, the profile of the steady state $u_\lambda(x)$ of Eq. (3) has the following form:

$$u_\lambda(x) = \bar{m} + \lambda(\rho_m(x) + C(m)) + \lambda^2(\gamma_m(x) + K(m)) + o(\lambda^2),$$

with $\rho_m(x)$, $C(m)$, $\gamma_m(x)$ and $K(m)$ satisfying Eq. (6), (8), (7) and (9) respectively. Since we assume that λ is sufficiently small, thus u_λ can be interpreted as a perturbation of the constant \bar{m} which is the average resource. But the spatial variation of $m(x)$ affects the profile of u_λ in the order λ through the term $\rho_m(x) + C(m)$. Note that the steady state of Eq. (2) is equivalent to that of Eq. (3) in the sense that $\lambda = 1/d$.

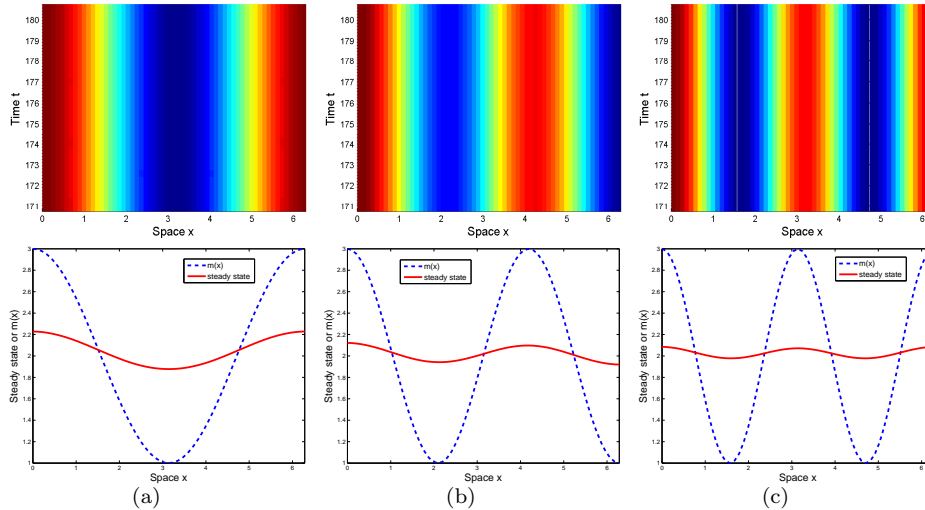


FIGURE 1. The non-homogeneous steady states of Eq (2) when $m(x)$ is a cosine function: (a) $m(x) = \cos(x) + 2$; (b) $m(x) = \cos(1.5x) + 2$; (c) $m(x) = \cos(2x) + 2$. Here $d = 2$ (which is equivalent to $\lambda = 0.5$), $\tau = 0.71 < \tau_{0\lambda} \approx 0.785$ and initial value $u_0 = 2$ for all three cases, and the solution converges to the non-homogeneous steady state.

In Figure 1, the resource function $m(x)$ is a cosine function with $\bar{m} = 2$ for several different periods. According to Theorem 2.4 and Remark 2.5, the first Hopf bifurcation point for Eq. (2) is $\tau_{0\lambda} \approx \frac{\pi}{2\bar{m}} \approx 0.785$ when λ is small. Simulations of solutions of (2) are shown in Figure 1 when $\tau = 0.73 < \tau_{0\lambda}$, and the solutions

converge to the steady state. In each group, the top figure is the graph of $u(x, t)$ in two-dimensional space (x, t) with color showing the value of $u(x, t)$, and the bottom one is the profile of the steady state $u_\lambda(x)$ and corresponding resource function $m(x)$. Comparing the profile of the steady state and the resource function (see the lower figures in all groups), we can see that the steady state $u_\lambda(x)$ has the exactly same maximum and minimum points as the resource function $m(x)$ even though their amplitudes are different. This shows that the population distribution roughly matches the distribution of food resource, but not in the more restrictive sense of ideal-free distribution in biology [7, 13]. Here the matching is achieved as the chosen resource function $m(x)$ satisfies the homogeneous Neumann boundary condition. In the next two examples (i.e. the sine and linear function cases), the maximum and minimum points of steady states do not always match with the ones of resource functions.

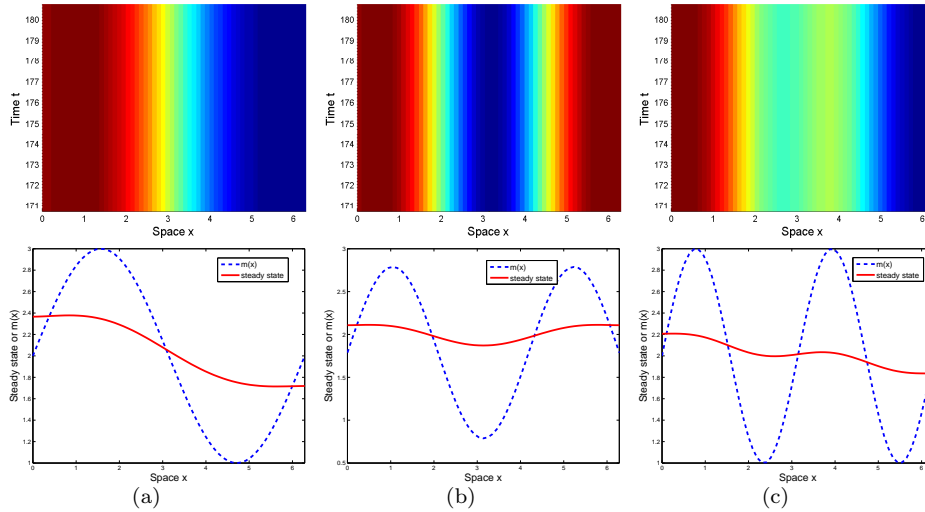


FIGURE 2. The non-homogeneous steady states of Eq. (2) when $m(x)$ is a sine function: (a) $m(x) = \sin(x) + 2$; (b) $m(x) = \sin(1.5x) + 1.788$; (c) $m(x) = \sin(2x) + 2$. The parameters are the same as in Figure 1, and here $\tau = 0.73 < \tau_{0\lambda} \approx 0.785$. The solution converges to the non-homogeneous steady state for each case.

In Figure 2, the resource functions are sine functions with $\bar{m} = 2$ and the critical value of stability switch again is $\tau_{0\lambda} \approx 0.785$ for all cases. By taking $\tau = 0.71 < \tau_{0\lambda}$, the solutions of system (2) also converge to the stable non-homogeneous steady state. The situation here is different from the case that $m(x)$ is a cosine function. The individuals still show the tendency of aggregating to where the food resources is relatively rich, but this trend is influenced by the boundary condition. Here the interior local maximum or minimum points of $u_\lambda(x)$ still matches with the ones of $m(x)$, but $u_\lambda(x)$ achieves local maximum/minimum on the boundary which are not extreme points of $m(x)$. On the other hand, the two local maximum/minimum points of $m(x)$ closest to boundary are not local maximum/minimum points of

$u_\lambda(x)$. Indeed the positive steady states shown in Figure 2 aggregates to the left side in the sense that

$$\hat{u}_\lambda(x) := \frac{1}{x} \int_0^x u_\lambda(y)dy \geq \bar{u}_\lambda := \frac{1}{2\pi} \int_0^{2\pi} u_\lambda(y)dy, \quad x \in [0, 2\pi],$$

as the resource function $m(x)$ also satisfies $\hat{m}(x) \geq \bar{m}$ for every $x \in [0, 2\pi]$. We can also observe from Figures 1 and 2 that $u_\lambda(x)$ inherits the symmetry property that $m(x)$ satisfies. That is, if $m(x)$ is “even” in x in the sense $m(2\pi - x) = m(x)$, so is $u_\lambda(x)$; and if $m(x)$ is “odd” in x in the sense $m(2\pi - x) = -m(x)$, so is $u_\lambda(x)$.

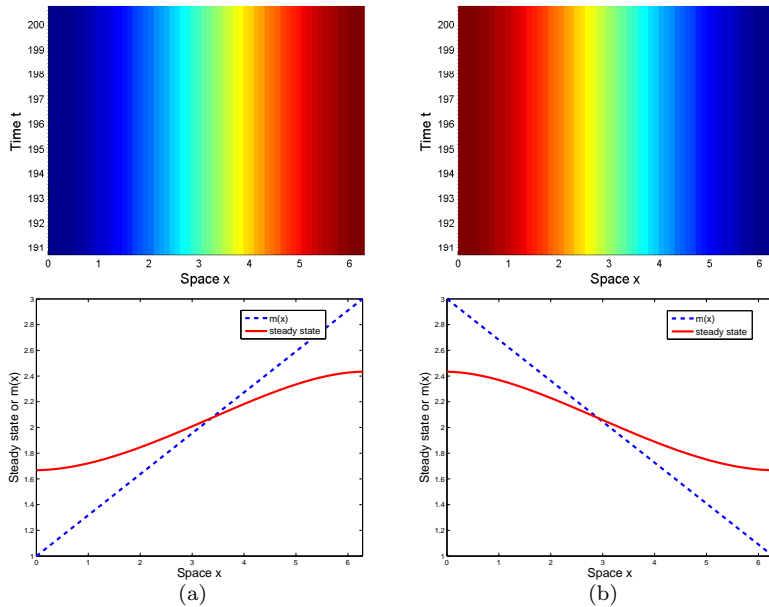


FIGURE 3. The non-homogeneous steady states of Eq. (2) when $m(x)$ is a monotone linear function: (a) $m(x) = 1 + x/\pi$; (b) $m(x) = 3 - x/\pi$. Here $d = 2$ and $\tau = 0.73 < \tau_{0\lambda}$. The solution converges to the positive monotone steady state.

Finally, in Figure 3, simulations of increasing and decreasing linear function cases are exhibited. We still have $\tau_{0\lambda} \approx 0.785$ here. One can observe that the positive steady state inherits the odd symmetry and monotone properties of $m(x)$.

3.2. Spatiotemporal patterns. In this subsection we demonstrate the spatially non-homogeneous periodic orbits which bifurcate from the non-homogeneous steady state of system (2) through a supercritical Hopf bifurcation. By Theorem 2.4 and Remark 2.5, the first Hopf bifurcation value is $\tau_{0\lambda} = \frac{\pi}{2\bar{m}} + o(\lambda)$. In all of the following figures, we set the parameters as $d = 2, \tau = 0.82 > \tau_{0\lambda} \approx 0.785$ with $\bar{m} = 2$ in all the cases. In each group, the top figure is the graph of $u(x, t)$ in two-dimensional space (x, t) with color showing the value of $u(x, t)$, and the bottom figure shows the oscillation of the total biomass $\tilde{u}(t) = \int_\Omega u(x, t)dx$, and comparison with temporal average of total biomass \bar{u} and corresponding total resource $\int_\Omega m(x)dx$.

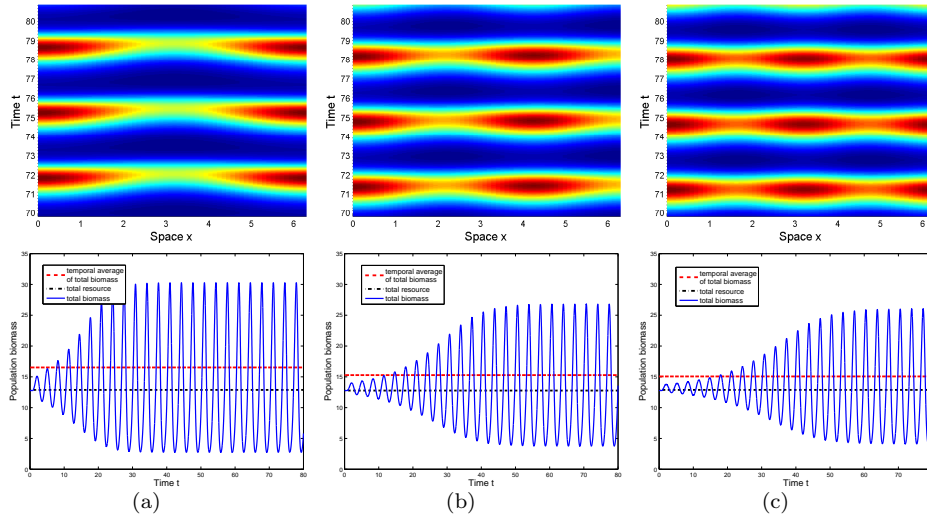


FIGURE 4. The periodic orbits induced by Hopf bifurcation near the non-homogeneous steady state of Eq. (2) for case that $m(x)$ is cosine function: (a) $m(x) = \cos(x) + 2$; (b) $m(x) = \cos(1.5x) + 2$; (c) $m(x) = \cos(2x) + 2$. Here $d = 2$, and $\tau = 0.82 > \tau_{0\lambda} \approx 0.785$.

In Figure 4, we use the same resource functions as the ones in Figure 1, but with a larger delay $\tau = 0.82$ which is greater than the first Hopf bifurcation value $\tau_{0\lambda}$. Compared with Figure 1, the solutions now show a temporal oscillation with a spatial profile (same number of peaks) consistent with the spatial non-homogeneous steady state. The bottom row verifies the result in Theorem 2.10 that the temporal average of total biomass of the population is greater than the total resource. However, because of the oscillation of the population density in time, the total biomass $\tilde{u}(t)$ is also a time-periodic function and it goes below the total resource for some interval in each period. Figures 5 and 6 show the periodic orbits of system (2) when $m(x)$ are sine and linear functions, respectively. From these figures, the same conclusion can be drawn that the periodic orbits have the same spatial structure with the corresponding steady states. Because the periodicity both in space and time, so the spot patterns can be observed. In Figure 5 (a), (c) and Figure 6, the spatiotemporal patterns are not spatially symmetric, which also inherits from the steady state profile.

4. Discussion. In consideration of the spatial movement of species in the realistic biological systems, the reaction-diffusion logistic model is widely employed to describe the evolution of spatial distribution of the population. However this model is often not sufficient to explain the heterogeneous distribution of the species in space. So some revisions of the diffusive models are needed to fit the actual situation. One of them is to introduce the advection term or use nonlinear diffusion instead of only using the simplest diffusion (see [18, 28, 30, 35, 38] and the references therein). Another mechanism is the aggregation of the population which is proposed by Britton [1] who argue that there are some reasons for individuals to group together, for example, the aggregation of bees or ants for social work, or the herd behavior which

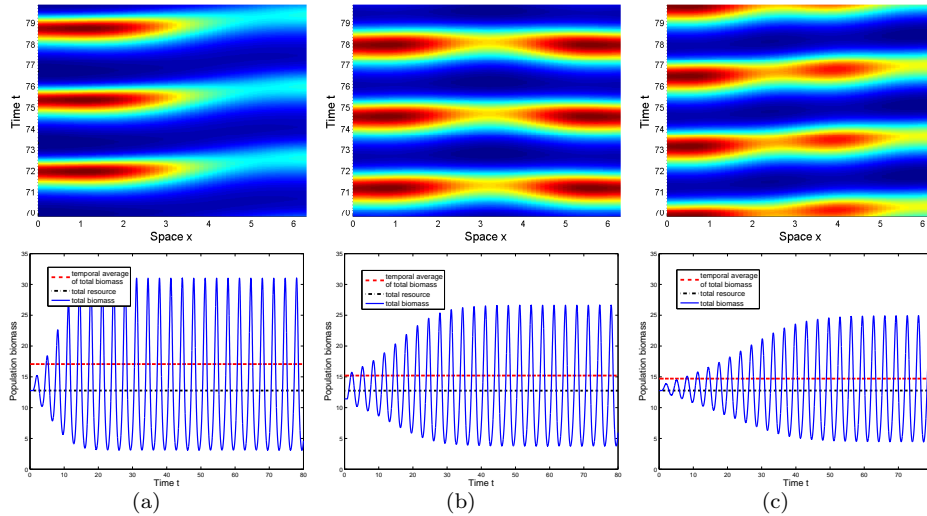


FIGURE 5. The periodic orbits induced by Hopf bifurcation near the non-homogeneous steady state of Eq. (2) for case that $m(x)$ is sine function: (a) $m(x) = \sin(x) + 2$; (b) $m(x) = \sin(1.5x) + 1.788$; (c) $m(x) = \sin(2x) + 2$. Here $d = 2$, and $\tau = 0.82 > \tau_{0\lambda} \approx 0.785$.

is well known for herds to prevent the predation. Therefore, nonlocal models are established in order to describe the aggregation occurring in some species, which admits spatially non-homogeneous steady states and thus can illustrate the heterogeneous distribution of the species. In [3,27], the authors give a new mechanism for the spatial heterogeneity of population due to the non-homogeneous carrying capacity which is largely determined by the distribution of resource. The results show that the heterogeneity of resource will lead to the increase of population biomass and the non-homogeneous distribution of population [27], which means that the spatial patterns will arise in such models.

The time delay is embraced into population models or other biological systems on account of the dependence on the historical information of the systems. And it is well known that time delay is an important mechanism inducing the temporal patterns due to the occurrence of Hopf bifurcation. Therefore, a delayed reaction-diffusion logistic model with heterogeneous carrying capacity in a bounded habitat is investigated under the homogeneous Neumann boundary condition in the present paper. By taking time delay as parameter, there is a threshold value $\tau_{0\lambda} \approx \pi/(2\lambda\bar{m})$ such that the non-constant steady state of system (3) loses its stability and the system undergoes a supercritical Hopf bifurcation, thus spatiotemporal patterns arise through self-organization (see Figures 4, 5, 6). Also, through the simulations in Section 3, we can observe that the food resource distribution has profound impact on the structure of the steady state, and there is a significant aggregation tendency toward the high density region of resource. And such tendency is also influenced by the Neumann boundary condition (see Figures 2 and 5 for the case that $m(x)$ being a sine function). Moreover, we proved that the spatial heterogeneity of the resource increases the temporal average of total biomass of the population when it

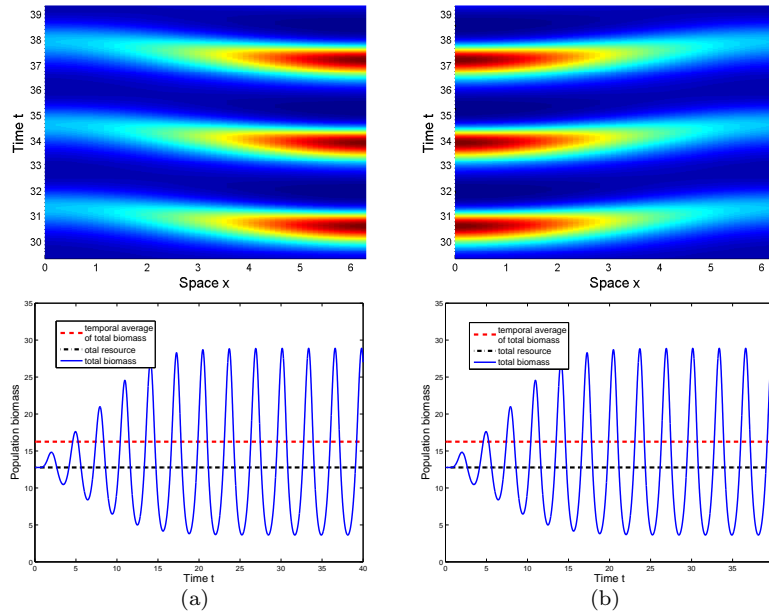


FIGURE 6. The periodic orbits induced by Hopf bifurcation near the non-homogeneous steady state of Eq. (2) for case that $m(x)$ is monotone linear function: (a) $m(x) = 1 + x/\pi$; (b) $m(x) = 3 - x/\pi$. Here $d = 2$, and $\tau = 0.82 > \tau_{0\lambda} \approx 0.785$.

oscillates periodically in time. This is in accordance with the result of the situation that the population converges to the steady state, which shows the robustness of such result.

There are still a lot of open questions for future investigations. Because of the limitation of the analytic method which requires the concrete form of the steady state, the existence of Hopf bifurcation is only proved when the diffusion coefficient is sufficiently large in this paper. The numerical simulations show that the Hopf bifurcation occurs for a wide range of diffusion coefficient, and we conjecture that system (2) undergoes Hopf bifurcation for all $d > 0$. Therefore, new methods need to be developed to study the Hopf bifurcation for such general case. On the other hand, the model can be refined to relate to the practical situation. For example, we may consider the distributed delay or nonlocal delay effect in stead of the discrete delay considered here.

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