SPATIAL PATTERN FORMATIONS IN DIFFUSIVE PREDATOR-PREY SYSTEMS WITH NON-HOMOGENEOUS DIRICHLET BOUNDARY CONDITIONS*

Yingwei Song^{1,2} and Tie Zhang^{1,†}

Abstract A reaction-diffusion predator-prey system with non-homogeneous Dirichlet boundary conditions describes the persistence of predator and prey species on the boundary. Compared with homogeneous Neumann boundary conditions, the former conditions may prompt or prevent the spatial patterns produced through diffusion-induced instability. The spatial pattern formation induced by non-homogeneous Dirichlet boundary conditions is characterized by the Turing type linear instability of homogeneous state and bifurcation theory. Furthermore, transient spatiotemporal behaviors are observed through numerical simulations.

Keywords Reaction, diffusion, predator-prey, stability, bifurcation.

MSC(2010) 35B32, 35K57, 37L10.

1. Introduction

Predator-prey interaction systems with ratio-dependent functional response have been paid great attention by both applied mathematicians and ecologists, e.g. [2, 4, 13, 16, 18, 19, 29, 32, 33, 35, 39]. Ratio-dependent functional response shows that the growth rate of capital predator should be a function of the ratio of prey to predator abundance [1, 3, 30]. Since diffusive predator-prey systems play an important role in population dynamics, the existence and non-existence of non-constant positive solutions, periodic solutions and traveling wave solutions have been investigated extensively [7, 8].

Most analyses of diffusive predator-prey systems are restricted to Neumann boundary conditions [37,40], which indicates no flux on the boundary. One interesting question is that the exterior environment is friendly and the species can move across the boundary of environment, with the number of species being constant on the boundary [10, 17, 27, 28, 31]. For example, in fish migratory behaviour [28], fishes were found to be dispersed between areas and [34] suggests an extensive

[†]Corresponding author. Email address:ztmath@163.com (T. Zhang)

 $^{^{1}\}mathrm{Department}$ of Mathematics, Northeastern University, Shenyang 110006, China

²School of Mathematical Science, Harbin Normal University, Harbin 150025, China

^{*}The authors were supported by the State Key Laboratory of Synthetical Automation for Process Industries Fundamental Research Funds (No. 2013ZCX02).

drift of cod larvae from the North Sea into coastal Skagerrak. Moreover, nonhomogeneous Dirichlet boundary value problem has attracted much attention in recent years [5,14]. In this paper, we consider the following diffusive predator-prey model with non-homogenous Dirichlet boundary conditions and ratio-dependent functional response:

$$\begin{cases} \frac{\partial u}{\partial t} - d_1 \Delta u = ug(u) - p(u)v, & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} - d_2 \Delta v = v\sigma(1 - \frac{v}{u}), & x \in \Omega, t > 0, \\ u(x,t) = v(x,t) = u^*, & x \in \partial\Omega, t > 0, \\ u(x,0) = u_0(x) \ge 0, v(x,0) = v_0(x) \ge 0, & x \in \Omega, t = 0, \end{cases}$$
(1.1)

where the habitat of both species Ω is a bounded domain in $\mathbb{R}^N (N \geq 1)$ with a smooth boundary $\partial\Omega$; u(x,t) and v(x,t) represent the densities of prey and predator at the location x and time t, respectively, and d_1 , d_2 are the rescaled diffusion coefficient for the prey and the predator, respectively, the parameter σ is the intrinsic growth rate of predator, typically it admits that the carrying capacity of predator is proportional to the densities of prey. Moreover, p, g are assumed to satisfy the following hypotheses:

- (a1) $p \in C^1(\overline{\mathbb{R}^+})$, p(0) = 0; p(u) > 0 for u > 0 and $p_u(u) > 0$ for $u \ge 0$, moreover, there exists N > 0, such that $p_u(u) \le N$ for all u > 0;
- (a2) $g \in C^1(\overline{\mathbb{R}^+})$, there exists K > 0, such that for any u > 0, $u \neq K$, g(u)(u K) < 0 and g(K) = 0; $g_u(u) \leq -\widehat{g}$, where $\widehat{g} > 0$, u > 0.

The condition (a1) on the functional response p(u) includes the classical Leslie-Gower type, Holling-Tanner type, Sigmodial type and Ivlev type. Here ug(u) is the net growth rate of the prey, the prey u has a growth which is reflected from the assumption (a2). Note that (1.1) has a unique constant positive equilibrium $e^* = (u^*, v^*)$ under assumptions (a1) and (a2), where u^* satisfies $g(u^*) = p(u^*)$, and non-homogeneous Dirichlet boundary conditions $u(x,t) = v(x,t) = u^*$ indicate that species are free to penetrate and cross borders. In some cases, the number of predators is the same as the number of prey on the boundary.

When ug(u) is of a logistic growth on the prey, the kinetics of system (1.1) with Leslie-Gower type functional response has a globally asymptotically stable equilibrium [22]. For the kinetics of system (1.1) with logistic growth on the prey and Holling-Tanner type functional response, a complete dynamical analysis can be obtained in [6, 11, 20, 24, 25, 39]. With homogeneous Neumann boundary conditions and under suitable conditions, there is a positive steady state solution which indicates that the predator and prey species coexist see [9, 12, 26] and the references therein. In these work, specific forms of function g(u) were used. For system (1.1) with homogeneous Neumann boundary conditions, Ko [21] investigated the existence and non-existence of non-constant positive solutions under some conditions. In [38], Wang studied a diffusive plant-herbivore system with homogeneous and non-homogeneous Dirichlet boundary conditions, which shows more richer dynamical behaviors.

Our purpose here is to investigate the spatiotemporal dynamics of system (1.1). We identify an explicit difference of the stability of equilibrium e^* between nonhomogeneous Dirichlet boundary conditions and homogeneous Neumann boundary conditions for $p(u^*)$ in some ranges. The paper is organized as follows. In Section 2, we study the linear stability and instability of the positive spatially homogeneous steady state of system (1.1). The difference between the former boundary conditions and the latter boundary conditions on the stability of system (1.1) is discussed. We investigate the occurrence of steady state bifurcation and Hopf bifurcation in Section 3. Some numerical results are given in Section 4.

2. The stability of the unique constant steady state solution

For such diffusive predator-prey model (1.1), it is normal to obtain the existence and boundedness of the unique solution by using the maximum principle and the comparison principle [23, 41]. It is clear that $e^* = (u^*, v^*)$ is the only constant positive equilibrium of system (1.1). In this section, we discuss the stability of the unique constant steady state.

Linearizing the reaction-diffusion system (1.1) about $e^* = (u^*, v^*)$ gives

$$\begin{pmatrix} \phi_t \\ \psi_t \end{pmatrix} = L \begin{pmatrix} \phi \\ \psi \end{pmatrix} = D \begin{pmatrix} \Delta \phi \\ \Delta \psi \end{pmatrix} + J \begin{pmatrix} \phi \\ \psi \end{pmatrix},$$

where

$$\boldsymbol{D} = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}, \ \boldsymbol{J} = \begin{pmatrix} A(u^*, v^*) & B(u^*, v^*) \\ C(u^*, v^*) & D(u^*, v^*) \end{pmatrix},$$

then

$$L := \begin{pmatrix} d_1 \Delta + A(u^*, v^*) & B(u^*, v^*) \\ C(u^*, v^*) & d_2 \Delta + D(u^*, v^*) \end{pmatrix},$$

where

$$A(u^*, v^*) = g(u^*) + u^* g_u(u^*) - p_u(u^*) v^* := M, \ B(u^*, v^*) = -p(u^*),$$

$$C(u^*, v^*) = \sigma, \ D(u^*, v^*) = -\sigma.$$
(2.1)

Let μ_i be the sequence of eigenvalues of $-\Delta$ with Dirichlet boundary conditions such that $0 < \mu_1 \leq \mu_2 \leq \ldots$ and $\lim_{t \to \infty} \mu_i = \infty$ and ϕ_i be the normalized eigenfunctions corresponding to μ_i . After Fourier series expansions, the eigenvalues of L are determined by the characteristic equation:

$$Det(\delta I - \mathbf{J}_i) = \delta^2 - tr(\mathbf{J}_i)\delta + det(\mathbf{J}_i), \quad i = 1, 2, \cdots$$
(2.2)

where

$$\mathbf{J}_{i} := \begin{pmatrix} -d_{1}\mu_{i} + A(u^{*}, v^{*}) & B(u^{*}, v^{*}) \\ C(u^{*}, v^{*}) & -d_{2}\mu_{i} + D(u^{*}, v^{*}) \end{pmatrix},$$

and

$$Tr(\mathbf{J}_i) = -\mu_i(d_1 + d_2) + A(u^*, v^*) + D(u^*, v^*),$$

$$Det(\mathbf{J}_i) = d_1 d_2 \mu_i^2 - \mu_i(d_2 A(u^*, v^*) + d_1 D(u^*, v^*)) + det \mathbf{J}_i$$

Therefore, all the eigenvalues of the operator L can be the union of the eigenvalues of J_i for $i \ge 1$.

Denote

$$T_i = Tr(J_i) = M - \sigma - \mu_i (d_1 + d_2), \qquad (2.3)$$

$$D_i = Det(\mathbf{J}_i) = d_1 d_2 \mu_i^2 - \mu_i (d_2 M - d_1 \sigma) - M \sigma + p(u^*) \sigma.$$
(2.4)

The linear stability of the steady state $e^* = (u^*, v^*)$ of system (1.1) is determined by the eigenvalues of the characteristic equation (2.3) and (2.4), if $T_i < 0$ and $D_i > 0$ for all $i = 1, 2, 3, \dots$, then $e^* = (u^*, v^*)$ is locally asymptotically stable. Otherwise, $e^* = (u^*, v^*)$ is unstable [36, 42].

Case I: $M \leq 0$

Theorem 2.1. Suppose that $d_1, d_2 > 0$ and Ω is a bounded domain with smooth boundary. If $M \leq 0$, then the constant positive equilibrium solution (u^*, v^*) of system (1.1) is locally asymptotically stable.

Proof. It is easy to find $T_i < 0, i = 1, 2, 3, \cdots$ for $M \leq 0$ from (2.3) and $D_i > 0, i = 1, 2, 3, \cdots$ for $M \leq 0$ from (2.4), which implies the desired conclusion. \Box

Remark 2.1. In fact, compared with homogenous Neumann boundary conditions, the stability of $e^* = (u^*, v^*)$ does not change for $M \leq 0$, see [21], but it is very different for M > 0.

Case II: M > 0

Now we study the stability change of $e^* = (u^*, v^*)$ when M > 0.

Lemma 2.1. If

(A1) $\sigma > M - \mu_1(d_1 + d_2),$

then $T_i < 0$ for all $i = 1, 2, 3, \cdots$.

Proof. From (2.3), $T_i < T_1$ for $i = 2, 3, \dots$. If $\sigma > M - \mu_1(d_1 + d_2)$, then $T_1 < 0$. Thus we have $T_i < 0$ for all $i = 1, 2, 3, \dots$

Based on Lemma 2.3, we further justify the sign of D_i for all $i = 1, 2, 3, \cdots$. To simplify, we denote $\widetilde{M} = \frac{(d_2M + d_1\sigma)^2}{4d_1d_2\sigma} > 0$, then $\widetilde{M} > M > 0$.

Theorem 2.2. Let $M, d_1, d_2 > 0$ and Ω be a bounded domain with smooth boundary. Suppose (A1) holds. If $p(u^*) > \widetilde{M}$, then the constant positive equilibrium (u^*, v^*) of system (1.1) is locally asymptotically stable.

Proof. Note that $D_i = d_1 d_2 \mu_i^2 - \mu_i (d_2 A(u, v) + d_1 D(u, v)) + det J$ can be regarded as a quadratic polynomial of μ_i with the discriminant

$$\zeta(D_i) := (d_2 A(u^*, v^*) + d_1 D(u^*, v^*))^2 - 4d_1 d_2 det(\mathbf{J}_{(u^*, v^*)})$$

Spatial pattern formations in diffusive predator-prey systems

$$= (d_2 M - d_1 \sigma)^2 - 4d_1 d_2 [p(u^*) - M]\sigma, \qquad (2.5)$$

conditions $p(u^*) > \widetilde{M} > 0$ implies that $\zeta(D_i) < 0$. Combined with the condition (A1), (u^*, v^*) is locally asymptotically stable for (1.1).

Remark 2.2. Here we show that if $\sigma > M - \mu_1(d_1 + d_2)$ and $p(u^*) > M$, the coexistent equilibrium of system (1.1) with non-homogeneous Dirichlet boundary conditions is locally asymptotically stable for $i = 1, 2, 3, \cdots$. The stability of the coexistence equilibrium to the diffusive predator-prey system (1.1) with Neumann boundary conditions can be founded in [21].

Theorem 2.3. Let $M, d_1, d_2 > 0$ and Ω be a bounded domain with smooth boundary. Suppose (A1) holds, if $\overline{M} < p(u^*) < M$, then the constant positive equilibrium (u^*, v^*) of system (1.1) is locally asymptotically stable, where $\overline{M} = \frac{(M-d_1\mu_1)(d_2\mu_1+\sigma)}{\sigma}$.

Proof. In order to determine the sign of D_i in (2.4), we need to consider the term of $-M\sigma + p(u^*)\sigma$. If $p(u^*) < M$, one can easily see that $-M\sigma + p(u^*)\sigma < 0$ and $\zeta(D_i) > 0$. We recall from Lemma 2.3, if $\sigma > M - \mu_1(d_1 + d_2)$, then $T_i < 0$. Note $D_1 = d_1 d_2 \mu_1^2 - \mu_1(d_2 M + d_1 \sigma) + (p(u^*) - M)\sigma$, if $p(u^*) > \frac{(M - d_1 \mu_1)(d_2 \mu_1 + \sigma)}{\sigma} = \overline{M}$, then $D_1 > 0$ and $D_i > 0, i = 2, 3, \cdots$. Hence the constant positive equilibrium (u^*, v^*) of system (1.1) is locally asymptotically stable.

Remark 2.3. Theorem 2.6 shows that if $\sigma > M - \mu_1(d_1 + d_2)$ and $\overline{M} < p(u^*) < M$, the coexistence equilibrium of system (1.1) with non-homogeneous Dirichlet boundary conditions is locally asymptotically stable. Compared with Neumann boundary conditions, when $\overline{M} < p(u^*) < M$, it is easy to check that $D_0 < 0$, then there exists at least some *i* such that $D_i < 0$, the constant positive equilibrium $e^* = (u^*, v^*)$ is unstable. The change of boundary conditions alters the stable possibility of $e^* = (u^*, v^*)$.

At here, we investigate the unstability for the positive equilibrium $e^* = (u^*, v^*)$ with hypothesis $\zeta(D_i) > 0$. Solving $D_i = 0$ for σ gives the critical point of neutral stability:

$$\sigma = \sigma(\mu_i) = \frac{d_1 d_2 \mu_i^2 - d_2 M \mu_i}{M - p(u^*) - d_1 \mu_i}.$$
(2.6)

Since

$$\frac{d\sigma}{d\mu_i} = \frac{-d_2[d_1\mu_i - (M - p(u^*))]^2 + d_2[M - p(u^*)][-p(u^*)]}{[d_1\mu_i - (M - p(u^*))]^2},$$

where $p(u^*) > M$, $\sigma(\mu_i)$ is increasing with respect to μ_i for $0 < \mu_i < \overline{\mu_i}$ and decreasing for $\mu_i > \overline{\mu_i}$, with $\overline{\mu_i} = \frac{\sqrt{[M-p(u^*)][-p(u^*)]} + [M-p(u^*)]}{d_1}$. At this critical wave number $\overline{\mu_i}$,

$$\sigma(\overline{\mu_i}) = \max\{\sigma(\mu_i), i = 1, 2, \cdots n\}.$$

Theorem 2.4. Let $M, d_1, d_2 > 0$ and Ω be a bounded domain with smooth boundary. Suppose that (A1) holds and $M < p(u^*) < \widetilde{M}$.

1 If

$$\sigma > \sigma(\overline{\mu_i}),$$

then the constant equilibrium (u^*, v^*) is locally asymptotically stable for system (1.1).

169

2 If

$$0 < \sigma < \sigma(\overline{\mu_i}),$$

then the constant equilibrium (u^*, v^*) is unstable for system (1.1).

Proof. If $p(u^*) < \widetilde{M}$, then $\zeta(D_i) > 0$. Note that $p(u^*) > M$ and

$$\frac{\partial D_i}{\partial \sigma} = d_1 \mu_i + p(u^*) - M > 0.$$
(2.7)

So, for $i \in N$, if

$$\sigma > \sigma(\overline{\mu_i}),\tag{2.8}$$

then $D_i > 0$ for all $i = 1, 2 \cdots$. So the constant positive equilibrium solution (u^*, v^*) of system (1.1) is locally asymptotically stable. Moreover, if

$$0 < \sigma < \sigma(\overline{\mu_i}),\tag{2.9}$$

then there exists at least one *i* as $D_i < 0$, then the constant positive equilibrium solution (u^*, v^*) of system (1.1) is unstable.

3. Steady state bifurcation and Hopf bifurcation

In this section we consider non-constant steady state solutions of (1.1) bifurcating from the positive constant equilibrium (u^*, v^*) , using the predator intrinsic growth coefficient σ as the main bifurcation parameter while $d_1 > 0$, $d_2 > 0$, $\sigma > 0$ and Ω are fixed. It is clear that the positive constant coexistence steady state (u^*, v^*) exists and the precise stability information of (u^*, v^*) is determined by the trace and determinant of $\mathbf{J}_i (i \ge 0)$, which are defined in (2.3) and (2.4). From Theorem 2.8, the steady state bifurcation occurs at $\sigma = \sigma(\overline{\mu_i})$. Take σ as the main parameter, we try to find the steady state bifurcation values σ^S and Hopf bifurcation values σ^H . For simplicity, we rewrite formula (2.3) and (2.4) as

$$T(\sigma, q) = -\sigma - q(d_1 + d_2) + M, \tag{3.1}$$

$$D(\sigma, q) = d_1 d_2 q^2 - d_2 M q + [d_1 q - M + p(u^*)]\sigma.$$
(3.2)

Then the sets $\aleph = \{(\sigma, q) \in R_+ : T(\sigma, q) = 0\}$ and $\Re = \{(\sigma, q) \in R_+ : D(\sigma, q) = 0\}$ are potential Hopf bifurcation and steady state bifurcation curves sets. The studies in [15,36,42] show that the geometric properties of \aleph and \Re play an important role in the bifurcation analysis of system (1.1).

3.1. Steady state bifurcation

In this subsection, we explore the occurrence of steady state bifurcation at the steady state (u^*, v^*) . Applying the abstract bifurcation theorem in [42], we know that a steady state bifurcation occurs if there exists a critical value σ^S for some integer $i \geq 1$, at which

(S1)
$$D_i(\sigma^S) = 0, T_i(\sigma^S) \neq 0$$
, and $D_j(\sigma^S) \neq 0$, for $j \neq i$;
(S2) $\frac{\partial D_i}{\partial \sigma}|_{\sigma^S} \neq 0$.

Now we claim that there exists some $i \ge 1$, such that $\sigma_i^S = \sigma^S(\mu_i) = \frac{d_1 d_2 \mu_i^2 - d_2 M \mu_i}{M - p(u^*) - d_1 \mu_i}$ is a steady state bifurcation value. From $D_i(\sigma) = 0$, we can obtain that $\sigma = \sigma_i^S = \frac{d_1 d_2 \mu_i^2 - d_2 M \mu_i}{M - p(u^*) - d_1 \mu_i}$, Then $T_j(\sigma^S) \neq 0$, $D_j(\sigma^S) \neq 0$ for $j \neq i$.

Next we verify $\frac{\partial D_i}{\partial \sigma}|_{\sigma_i^S} = d_1 \mu_i + p(u^*) - M \neq 0.$

Assume $\frac{\partial D_i}{\partial \sigma}|_{\sigma_i^S} = 0$, it is easy to see that $d_1\mu_i - M + p(u^*) = 0$, which implies that $D_i(\sigma_i^S) = d_2\mu_i[d_1\mu_i - M] = -d_2\mu_ip(u^*) < 0$. Indeed one has $D_i(\sigma_i^S) = 0$, therefore $\frac{\partial D_i}{\partial \sigma}|_{\sigma_i^S} \neq 0$. Summarizing the discussions above, we obtain the main result of this section on the global bifurcation of steady state solutions:

Theorem 3.1. Assume that $M, d_1, d_2 > 0$ and all eigenvalues μ_i are simple for $i \ge 1$. If $M < p(u^*) < \widetilde{M}$ and there exists some $i \ge 1$ such that

$$\sigma_i^S = \sigma^S(\mu_i) = \frac{d_1 d_2 \mu_i^2 - d_2 M \mu_i}{M - p(u^*) - d_1 \mu_i},$$
(3.3)

then there exists a branch of non-constant positive solutions of system (1.1) bifurcating from (u^*, v^*) when $\sigma = \sigma_i^S$, where μ_i satisfies that $\mu_1 < \mu_2 < \cdots < M/d_1$ to make sure that $\sigma_i > 0$.

3.2. Hopf bifurcation

In this subsection, we analyze the properties of Hopf bifurcations for (1.1). To identify Hopf bifurcation values σ^{H} , we recall the following sufficient condition from [42]: $(T_i(\sigma) \text{ and } D_i(\sigma) \text{ are defined in (3.1) and (3.2)}).$

(H1) : There exists $i \ge 1$ such that

$$T_i(\sigma^H) = 0, \quad D_i(\sigma^H) > 0 \quad \text{and} \quad T_j(\sigma^H) \neq 0, \quad D_j(\sigma^H) \neq 0 \quad \text{for} \quad j \neq i$$

for the unique pair of complex eigenvalues near the imaginary axis $\alpha(\sigma) \pm i\beta(\sigma)$,

$$\alpha'(\sigma^H) \neq 0$$
 and $\beta(\sigma^H) > 0$.

Firstly $\sigma_i^H = \sigma^H(\mu_i) = M - \mu_i(d_1 + d_2)$ is a Hopf bifurcation point since $T_i(\sigma_i^H) = 0$, and $T_j(\sigma_i^H) \neq 0$ for any $j \neq i$. Next we verify that $D_i(\sigma_i^H) > 0$. In fact, from $d_1 > 0, d_2 > 0$ and $M(p(u^*) - M) > 0$, we denote μ_{\pm} be the two roots of $-d_1\mu_i^2 - [2d_1M + (d_1 + d_2)p(u^*)]\mu_i + M(p(u^*) - M) = 0$, then $\mu_- < 0 < \mu_+$. Therefore, for any $\sigma \in (0, \sigma_1(\overline{\mu_i}))$, if μ_i satisfy

$$\mu_i < \mu_+, \tag{3.4}$$

then

$$D_i(\sigma_i^H) = d_1 d_2 \mu_i^2 - d_2 M \mu_i + [d_1 \mu_i - M + p(u^*)][M - (d_1 + d_2)\mu_i]$$
(3.5)
= $-d_1 \mu_i^2 - [2d_1 M + (d_1 + d_2)p(u^*)]\mu_i + M(p(u^*) - M) > 0.$

Finally $D_j(\sigma_i^H) \neq 0$ if $\sigma_i^H \neq \sigma_j^S$, which also implies that a Hopf bifurcation point and a steady state bifurcation point do not overlap.

Summarizing our analysis above and applying Theorem 2.1 in [42], we obtain the following results on the Hopf bifurcations:

Theorem 3.2. Assume that $M, d_1, d_2 > 0$, all eigenvalues μ_i are simple for $i \ge 1$ and μ_i satisfies condition (3.4). Let $\sigma_i^H = M - \mu_i(d_1 + d_2)$, $i \ge 1$. If $M < p(u^*) < \widetilde{M}$, then Hopf bifurcation occurs at $\sigma = \sigma_i^H$ and there exists a branch of nonconstant solutions of system (1.1) bifurcating from (u^*, v^*) for $\sigma = \sigma_i^H$, where $\sigma_1^H > \sigma_2^H > \cdots > 0$.

4. Conclusions and numerical simulations



Figure 1. The *u*-component and *v*-component of a numerical solution of system (1.1) with non-homogeneous Dirichlet boundary conditions. Parameter values: $p = 0.3, a = 0.1, b = 0.3 \times 10^{-14}, d_1 = 1000, d_2 = 0.1$ and the initial condition: $(u_0(x), v_0(x)) = (0.0185 + 0.005 \sin(4x), 0.0185 + 0.003 \sin(6x))$. The positive equilibrium (u^*, v^*) is stable and the solution converges to $(u^*, v^*) = (0.0185, 0.0185)$.



Figure 2. The *u*-component and *v*-component of a numerical solution of system (1.1) with homogeneous Neumann boundary conditions. Parameter values: $p = 0.3, a = 0.1, b = 0.3 \times 10^{-14}, d_1 = 1000, d_2 = 0.1$ and initial condition: $(u_0(x), v_0(x)) = (0.0185 + 0.005 \sin(4x), 0.0185 + 0.003 \sin(6x))$. When only the boundary conditions are changed and the same parameters and initial value are kept the same as in Figure 1, the solution does not converge to $(u^*, v^*) = (0.0185, 0.0185)$.

In this paper, we discuss a diffusive predator-prey model with ratio-dependent functional response subject to non-homogeneous Dirichlet boundary conditions. We consider the case of linear functional response g(u) = p - bu and Holling-Tanner type $p(u) = \frac{u}{u+a}$, where g(u) and p(u) satisfy (a1)-(a2). From Theorems 2.1, 2.4, 2.6, 2.8, 3.1 and 3.2, we obtain a complete picture of the dynamics of system (1.1). Furthermore, we use some numerical simulations to illustrate our analytical results. Three sets of parameter were used: (i) $p = 0.3, a = 0.1, b = 0.3 \times 10^{-14}, \sigma = 0.001, d_1 = 1000, d_2 = 0.1$; (ii) $p = 0.8, a = 0.1, b = 0.3, d_1 = 1, d_2 = 0.7$; (iii) $p = 0.8, a = 0.1, b = 0.3, d_1 = 1, d_2 = 0.7$; (iii) $p = 0.8, a = 0.1, b = 0.3, d_1 = 0.02, d_2 = 0.001$.

With parameter set (i), (A1) and $\overline{M} < p(u^*) < M$ hold, (u^*, v^*) of system (1.1) with non-homogeneous Dirichlet boundary conditions is locally asymptotically stable, as is shown in Figure 1, which confirms the analysis of Theorem 2.6. When



Figure 3. The *u*-component and *v*-component of a numerical solution of system (1.1) with parameter values: $\sigma = 0.065, p = 0.8, a = 0.1, b = 0.3, d_1 = 1, d_2 = 0.7$ and the initial condition: $(u_0(x), v_0(x)) = (0.2598 + 0.005 \sin(4x), 0.2598 + 0.003 \sin(6x))$. Since $\sigma = 0.065 > \sigma(\overline{\mu_i}) = 0.064$, the positive equilibrium $(u^*, v^*) = (0.2598, 0.2598)$ is stable.



Figure 4. The *u*-component and *v*-component of a numerical solution of system (1.1) with parameter values: $\sigma = 0.063, p = 0.8, a = 0.1, b = 0.3, d_1 = 1, d_2 = 0.7$ and the initial condition: $(u_0(x), v_0(x)) = (0.2598 + 0.005 \sin(4x), 0.2598 + 0.003 \sin(6x))$. Since $\sigma = 0.063 < \sigma(\overline{\mu_i}) = 0.064$, steady state bifurcation occurs resulting non-constant steady states.



Figure 5. The *u*-component and *v*-component of a numerical solution of system (1.1) with parameter values: $\sigma = 0.51, p = 0.8, a = 0.1, b = 0.3, d_1 = 0.002, d_2 = 0.001$ and the initial condition: $(u_0(x), v_0(x)) = (0.2598 + 0.005 \sin(4x), 0.2598 + 0.003 \sin(6x))$. Since $\sigma = 0.51 > \sigma_1^H = 0.4427$, the positive equilibrium (u^*, v^*) is stable and the solution converges to $(u^*, v^*) = (0.2598, 0.2598)$.

 $\sigma > M - \mu_1(d_1 + d_2)$ and $\overline{M} < p(u^*) < M$, (u^*, v^*) of system (1.1) with homogeneous Neumann boundary conditions becomes unstable, see Figure 2. As shown in Figure 1 and Figure 2, under the same parameters and initial value, compared the former conditions with the latter conditions, the change of boundary conditions alters the stability of (u^*, v^*) .

With parameter set (ii), (A1) and $M < p(u^*) < \widetilde{M}$ hold, there is one steady state bifurcation value $\sigma_1^S = 0.064$. When $\sigma = 0.065$, i.e., $\sigma > \sigma_1^S = 0.064$, (u^*, v^*) is stable for system (1.1) (see Figure 3). When $\sigma = 0.063$, i.e., $\sigma < \sigma_1^S = 0.064$, (u^*, v^*) is unstable and steady state bifurcation occurs, as shown in Figure 4, which illustrates Theorem 2.8 and Theorem 3.1. We fix $p = 0.8, a = 0.1, b = 0.3, d_1 =$ $1, d_2 = 0.7$ and consider σ as the bifurcation parameter, note that (u^*, v^*) is stable,



Figure 6. The *u*-component and *v*-component of a numerical solution of system (1.1) with parameter values: $\sigma = 0.4426, p = 0.8, a = 0.1, b = 0.3, d_1 = 0.002, d_2 = 0.001$ and the initial condition: $(u_0(x), v_0(x)) = (0.2598 + 0.1 \sin(x), 0.2598 + 0.1 \sin(x))$. Since $\sigma = 0.4426$ is near the Hopf bifurcation value $\sigma_1^H = 0.4427$, the solution converges to a spatially non-homogeneous periodic orbit.

if $\sigma > 0.064$ and becomes unstable if $\sigma \in (0, 0.064)$. Choosing $\sigma = 0.063 < \sigma_1^S = 0.064$, our numerical simulation confirms that (u^*, v^*) becomes unstable. Moreover, simulation suggests that there is one spatially non-homogeneous steady state and it is stable, the solution with $\sigma = 0.063 < \sigma_1^S$ converges to one spatially non-homogeneous steady state, see Figure 4.

With parameter set (iii), $M < p(u^*) < M$ holds, there are 25 Hopf bifurcation values. When $\sigma = 0.51$, i.e. $\sigma > \sigma_1^H = 0.4427$, (u^*, v^*) is stable for system (1.1), see Figure 5. When $\sigma < \sigma_1^H$, (u^*, v^*) is unstable, for σ decreases the first bifurcation point encountered is σ_1^H , and Hopf bifurcation occurs, and spatially non-homogeneous periodic orbit exists, which illustrates Theorem 3.2. Choose $\sigma =$ 0.4426 which is near the Hopf bifurcation value $\sigma_1^H = 0.4427$, as is shown in Figure 6, the solution converges to a spatially non-homogeneous periodic orbit.

Remark 4.1. Since T_0 and D_0 are strictly greater or less than zero, there is no spatially homogeneous Hopf/steady state bifurcation considered in the paper. But we obtain spatially non-homogeneous Hopf bifurcation, also as shown in Figure 5, Figure 6.

Acknowledgements

The authors are grateful to the anonymous referees for their useful suggestions which improve the contents of this article.

References

- R. Arditi and L. R. Ginzburg, Coupling in predator-prey dynamics: Ratiodependence, Journal of Theoretical Biology, 1989, 139(3), 311–326.
- [2] R. Arditi, L. R. Ginzburg and H. R. Akcakaya, Variation in plankton densities among lakes: a case for ratio-dependent models, The American Naturalist, 1991, 138(5), 1287–1296.
- [3] R. Arditi, N. Perrin and H. Saiah, Functional responses and heterogeneities: an experimental test with cladocerans, Oikos., 1991, 60(1), 69–75.
- [4] R. Arditi and H. Saiah, Empirical evidence of the role of heterogeneity in ratiodependent consumption, Ecology, 1992, 73(5), 1544–1551.

- H. Beirao da Veiga, On the global regularity for singular p-systems under nonhomogeneous dirichlet boundary conditions, Journal of Mathematical Analysis and Applications, 2013, 398, 527–533.
- [6] P. A. Braza, The bifurcation structure of the holling-tanner model for predatorprey interactions using two-timing, SIAM J. Appl. Math., 2003, 63(3), 889–904.
- [7] R. S. Cantrell and C. Cosner, Spatial Ecology via Reaction-Diffusion Equations, Academic Press, New York, 2003.
- [8] C. Chen and L. Hung, Nonexistence of traveling wave solutions, exact and semi-exact traveling wave solutions for diffusive lotka-volterra systems of three competing species, Comm. Pure Appl Anal., 2017, 15(4), 1451–1469.
- [9] S. Chen, J. Shi and J. Wei, Global stability and hopf bifurcation in a delayed diffusive leslie-gower predator-prey system, International Journal of Bifurcation and Chaos, 2012. 10.1142/S0218127412500617.
- [10] L. Ciannelli, M. Hunsicker, M. Hidalgo et al., Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes, Mar Ecol Prog Ser., 2013, 480, 227–243.
- [11] J. B. Collings, Bifurcation and stability analysis of a temperature-dependent mite predator-prey interaction model incorporating a prey refuge, Bull. Math. Biol., 1995, 57(1), 63–76.
- [12] Y. Du and S. B. Hsu, A diffusive predator-prey model in heterogeneous environment, Journal of Differential Equations, 2004, 203(2), 331–364.
- [13] A. P. Gutierrez, Physiological basis of ratio-dependent predator-prey theory: the metabolic pool model as a paradigm, Ecology, 1992, 73(5), 1552–1563.
- [14] J. Ha and S. Nakagiri, Damped sine-gordon equations with non-homogeneous dirichlet boundary conditions, Journal of Mathematical Analysis and Applications, 2001, 263(2), 708–720.
- [15] M. Han, Bifurcation theory and methods of dynamical systems, Science Press, Beijing, 1995.
- [16] M. P. Hassell, The dynamics of arthropod predator-prey systems, Monogr. Popul. Biol., 1978, 65(13), 1–237.
- [17] L. Hauser and G. R. Carvalho, Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts, Fish Fish., 2010, 9(4), 333–362.
- [18] C. S. Holling, The functional response of predators to prey density and its role in mimicry and population regulation, Mem. Ent. Soc. Can., 1965, 97(45), 1–60.
- [19] C. S. Holling, The functional response of invertebrate predators to prey density, Mem. Ent. Soc. Can., 1966, 98(48), 1–86.
- [20] S. B. Hsu and T. W. Huang, Global stability for a class of predator-prey systems, SIAM J. Appl. Math., 1995, 55(3), 763–783.
- [21] W. Ko and K. Ryu, Non-constant positive steady-states of a diffusive predatorprey system in homogeneous environment, J. Math. Anal. Appl., 2007, 327, 539–549.
- [22] A. Korobeinikov, A lyapunov function for leslie-gower predator-prey models, Appl. Math. Lett., 2001, 14(6), 697–699.

- [23] Y. Lou and W. Ni, Diffusion, self-diffusion and cross-diffusion, J. Differential Equations, 1996, 131, 79–131.
- [24] R. M. May, Limit cycles in predator-prey communities, Science, 1972, 177, 900–902.
- [25] R. M. May, Stability and Complexity in Model Ecosystems, Academic Press, New York, 1973.
- [26] R. Peng and M. Wang, Positive steady sates of the holling-tanner prey-predator model with diffusion, Proceedings of the Royal Society of Edinburgh, 2005, 135(1), 149–164.
- [27] H. Reiss, G. Hoarau and M. Dickey-Collas, Genetic population structure of marine fish: mismatch between biological and fisheries management units, Fish Fish., 2009, 10(4), 361–395.
- [28] D. Robichaud and G. Rose, Migratory behaviour and range in atlantic cod: inference from a century of tagging, Fish Fish., 2004, 5(3), 185–214.
- [29] E. Saez and E. Gonzalez-Olivares, Dynamics of a predator-prey model, Siam Journal on Applied Mathematics, 1999, 59(5), 1867–1878.
- [30] T. Saha and C. Chakrabarti, Dynamical analysis of a delayed ratio-dependent holling-tanner predator-prey model, Journal of Mathematical Analysis and Applications, 2009, 358(2), 389–402.
- [31] D. E. Schindler, H. Ray and C. Brandon, Population diversity and the portfolio effect in an exploited species, Nature, 2010, 465(7298), 609–612.
- [32] S. M. Sohel Rana, Bifurcations and chaos control in a discrete-time predatorprey system of leslie type, Journal of Applied Analysis and Computation, 2019, 9(1), 31–44.
- [33] J. Song, M. Hu and Y. Bai, Dynamic analysis of a non-autonomous ratiodependent predator-prey model with additional food, Journal of Applied Analysis and Computation, 2018, 8(6), 1893–1909.
- [34] N. Stenseth, P. Jorde and K. Chan, Ecological and genetic impact of atlantic cod larval drift in the skagerrak, Proc Roy Soc Biol., 2006, 273(1590), 1085–1092.
- [35] J. T. Tanner, The stability and the intrinsic growth rates of prey and predator populations, Ecology, 1975, 56(4), 855–867.
- [36] J. Wang, J. Shi and J. Wei, Dynamics and pattern formation in a diffusive predator-prey system with strong allee effect in prey, J. Differential Equations, 2011, 251(4), 1276–1304.
- [37] J. Wang, J. Shi and J. Wei, Global bifurcation analysis and pattern formation in homogeneous diffusive predator-prey systems, J. Differential Equations, 2016, 260(4), 3495–3523.
- [38] L. Wang, J. Watmough and F. Yu, Bifurcation analysis and transient spatiotemporal dynamics for a diffusive plant-herbivore system with dirichlet boundary conditions, Mathematical Biosciences and Engineering, 2015, 12(4), 699– 715.
- [39] D. J. Wollkind, J. B. Collings and J. A. Logan, Metastability in a temperaturedependent model system for predator-prey mite outbreak interactions on fruit trees, Bull. Math. Biol., 1988, 50(4), 379–409.

- [40] S. Wu, J. Wang and J. Shi, Dynamics and pattern formation of a diffusive predator-prey model with predator-taxis, Math. Models. Methods. Appl. Sci., 2018, 28(11), 2275–2312.
- [41] Y. Yamada, Stability of steady states for prey-predator diffusion equations with homogeneous dirichlet conditions, SIAM J. Math. Anal., 1990, 21(2), 327–345.
- [42] F. Yi, J. Wei and J. Shi, Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator-prey system, J. Diff. Eqs., 2009, 246(4), 1944–1977.