

HOPF BIFURCATION IN A PREDATOR-PREY MODEL WITH MEMORY EFFECT AND INTRA-SPECIES COMPETITION IN PREDATOR

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Abstract This paper investigates the spatiotemporal dynamics of a reaction diffusion predator-prey model that incorporates memory delay and intra-species competition in predator. We provide rigorous results of the model including the local stability of positive equilibrium, the existence and the property of Hopf bifurcation. We show that increasing the intra-species competition is not beneficial to the stability of the positive equilibrium. Moreover, we obtain that the stable region of the positive equilibrium will decrease with the increase of memory-based diffusion coefficient when it larger than the critical value. In addition, the memory delay may also affect the stability of the positive equilibrium. When the memory delay crosses the critical value, the stable positive equilibrium becomes unstable, and the stably inhomogeneous periodic solutions appears. These results indicate that the memory delay and intra-species competition play an important role in the spatiotemporal dynamics of predator-prey model.

Keywords Predator-prey, delay, memory effect, Hopf bifurcation, inhomogeneous periodic solutions, intra-species competition.

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1. Introduction

The predator-prey model mainly describes the relationship between two populations, in which one population takes the other population as food [7, 10, 27, 28]. It is one of the important research contents of biological mathematics. Many scholars have studied different type predator-prey models to explore the law of population development [8, 9, 12, 17, 25, 26, 29]. In nature, the intra-species competition in predators exists widely, and Crowley-Martin functional response reflects this effect [4]. It is with the following form

$$\eta(U, V) = \frac{CU}{A_1 + B_1U + C_1V + B_1C_1UV},$$

where A_1 is a positive constant, and C , B_1 , C_1 represent capture rate, handling time and magnitude of interference among predators [4, 16], respectively.

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The work about predator-prey model with Crowley-Martin functional response can refer to [3, 11, 15, 18, 24]. In [16], J. Tripathi et al. proposed the following model

$$\begin{cases} \frac{dU}{dT} = U \left(A - BU - \frac{CV}{A_1 + B_1U + C_1V + B_1C_1UV} \right), \\ \frac{dV}{dT} = V \left(\frac{FU}{A_1 + B_1U + C_1V + B_1C_1UV} - D - EV \right). \end{cases} \quad (1.1)$$

All parameters are positive. $U(T)$ and $V(T)$ represent the prey and predator's population densities. A and A/B represent growth rate and maximum environmental capacity of prey. The term $D + EV$ represents the death rate of predator. Especially, D is the natural mortality of predator and E is the magnitude of intra-species competition in predator. J. Tripathi et al. [16] mainly studied the local and global stability of equilibrium, Hopf bifurcation and the effect of time delay on the model (1.1). In [24], the author studied the effect of self-diffusion and time delay on the model (1.1), and showed Turing instability of positive equilibrium and the homogeneous periodic solutions induced by time delay.

In the natural world, the smart predators may have memory effect and cognitive behavior [6]. For example, the migration of blue whales depends on memory [1, 5]. Another example, animals in polar regions usually determine their spatial movement by judging footprints, which record the history of species distribution and movement, involving time delay [21]. Obviously, highly developed animals can even remember the historically spatial distribution of species. Much progress has been made in implicitly integrating spatial cognition or memory [13, 14, 21]. Some scholars have studied the population models with memory effect [2, 19–23]. For example, Shi et al. proposed a single specie model with spatial memory by introducing an additional delayed diffusion term [21]. Q. An et al. studied the local stability and Hopf bifurcation in a memory-based reaction-diffusion equation [2]. Song et al. studied the Turing-Hopf bifurcation in the general reaction-diffusion equation with memory-based diffusion [23]. Song et al. [22] obtained a computing method of the normal forms for the Hopf bifurcations in the diffusive predator-prey model with memory effect. These works showed the stably inhomogeneous periodic solutions induced by the memory effect.

Motivated by the above work, we will study the effect of spatial-memory delay in predator on the model (1.1), as follow

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d_1 \Delta u + u \left(1 - u - \frac{\alpha v}{1 + au + bv + cuv} \right), \\ \frac{\partial v(x, t)}{\partial t} = -d \nabla(v \nabla u(t - \tau)) + d_2 \Delta v + v \left(\frac{\beta u}{1 + au + bv + cuv} - s - ev \right), \quad x \in \Omega, \quad t > 0 \\ \frac{\partial u(x, t)}{\partial \bar{\nu}} = \frac{\partial v(x, t)}{\partial \bar{\nu}} = 0, \quad x \in \partial\Omega, \quad t > 0 \\ u(x, \theta) = u_0(x, \theta) \geq 0, v(x, \theta) = v_0(x, \theta) \geq 0, \quad x \in \bar{\Omega}, \theta \in [-\tau, 0], \end{cases} \quad (1.2)$$

where $U = Au/B$, $V = v$, $T = t/A$, $a = \frac{AB_1}{A_1B}$, $b = \frac{C_1}{A_1}$, $c = \frac{AB_1C_1}{A_1B}$, $\alpha = \frac{C}{AA_1}$, $s = \frac{D}{A}$, $e = \frac{E}{A}$, $\beta = \frac{F}{A_1B}$. d_1 and d_2 are self-diffusion coefficients of prey and predator. $-d \nabla(v \nabla u(t - \tau))$ represents the memory effect of predator. d and τ are the memory-based diffusion coefficient and the averaged memory period of predator. The boundary condition is Newman type. The aim of this paper is to study the

effect of the memory effect on the model (1.2), from the perspective of stability and Hopf bifurcation.

The paper is arranged as follows. In Sec. 2, the stability of coexisting equilibrium and existence of Hopf bifurcation are considered. In Sec. 3, the property of Hopf bifurcation is studied. In Sec. 4, some numerical simulations are given. In Sec. 5, a short conclusion is obtained.

2. Stability analysis

Lemma 2.1. *The model (1.2) always has two boundary equilibrium $(0, 0)$ and $(K, 0)$. If $\beta > e + ae + s + as$, then the model (1.2) has at least one positive equilibrium.*

Proof. The positive equilibrium of (1.2) is the positive root of the following equations

$$\begin{cases} 1 - u - \frac{\alpha v}{1 + au + bv + cuv} = 0, \\ \frac{\beta u}{1 + au + bv + cuv} - s - eu = 0. \end{cases} \quad (2.1)$$

Multiply the first equation by βu , the second equation by αv , and then add them. We can obtain $v = \frac{u\beta(1-u)}{(s+eu)\alpha}$. Substitute it into the first equation, we can obtain that u is the positive root of the following equation

$$f(u) = c\beta u^3 + u^2(-ae\alpha + b\beta - c\beta) + u(-e\alpha - as\alpha - b\beta + \alpha\beta) - s\alpha = 0.$$

To ensure v is positive, u should fall into $(0, 1)$. By direct calculation, $f(0) = -s\alpha < 0$, and $f(1) = \alpha(\beta - e - ae - s - as)$. If $\beta > e + ae + s + as$, then $f(1) > 0$ which implies $f(u) = 0$ has at least one positive root fall into $(0, 1)$. Hence, the model (1.2) has at least one positive equilibrium. $\square$

In the following, we just suggest the model (1.2) has a positive equilibrium $E_*(u_*, v_*)$. In particular, the model (1.2) may has one, two or three positive equilibria. Then we can use the same method to study the property for different positive equilibria. Linearize system (1.2) at $E_*(u_*, v_*)$

$$\frac{\partial u}{\partial t} \begin{pmatrix} u(x, t) \\ u(x, t) \end{pmatrix} = J_1 \begin{pmatrix} \Delta u(t) \\ \Delta v(t) \end{pmatrix} + J_2 \begin{pmatrix} \Delta u(t - \tau) \\ \Delta v(t - \tau) \end{pmatrix} + L \begin{pmatrix} u(x, t) \\ v(x, t) \end{pmatrix}, \quad (2.2)$$

where

$$J_1 = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}, \quad J_2 = \begin{pmatrix} 0 & 0 \\ -dv_* & 0 \end{pmatrix}, \quad L = \begin{pmatrix} \alpha_1 & \alpha_2 \\ \beta_1 & \beta_2 \end{pmatrix},$$

and

$$\begin{aligned} \alpha_1 &= u_* \left(\frac{v_*(a + cv_*)\alpha}{(1 + au_* + bv_* + cu_*v_*)^2} - 1 \right), \quad \alpha_2 = -\frac{u_*(1 + au_*)\alpha}{(1 + au_* + bv_* + cu_*v_*)^2} < 0, \\ \beta_1 &= v_* \left(\frac{\beta + bv_*\beta}{(1 + au_* + bv_* + cu_*v_*)^2} - e \right), \quad \beta_2 = -\frac{u_*(b + cu_*)v_*\beta}{(1 + au_* + bv_* + cu_*v_*)^2} < 0. \end{aligned}$$

The characteristic equations are

$$\lambda^2 + \kappa_n \lambda + \nu_n + \varrho_n e^{-\lambda \tau} = 0, \quad n \in \mathbb{N}_0, \quad (2.3)$$

where

$$\begin{aligned} \kappa_n &= -\alpha_1 - \beta_2 + (d_1 + d_2)\mu_n, \quad \nu_n = -\alpha_2\beta_1 + \alpha_1\beta_2 - (d_2\alpha_1 + d_1\beta_2)\mu_n + d_1d_2\mu_n^2, \\ \varrho_n &= -dv_*\alpha_2\mu_n, \quad \mu_n = \frac{n^2}{l^2}. \end{aligned}$$

2.1. $\tau = 0$

The characteristic equations (2.3) are

$$\lambda^2 + \kappa_n \lambda + \nu_n + \varrho_n = 0, \quad n \in \mathbb{N}_0, \quad (2.4)$$

where $\nu_n + \varrho_n = \alpha_1\beta_2 - \alpha_2\beta_1 - (d_2\alpha_1 + dv_*\alpha_2 + d_1\beta_2)\mu_n + d_1d_2\mu_n^2$. Make the following hypothesis

$$(\mathbf{H}_1) \quad \alpha_1 < \min\{-\beta_2, \frac{\alpha_2}{\beta_2}\beta_1, -\frac{1}{d_2}(dv_*\alpha_2 + d_1\beta_2)\}.$$

Under the hypothesis $(\mathbf{H}_1)$, we can easily obtain $\kappa_n < 0$ and $\nu_n + \varrho_n > 0$ for $n \in \mathbb{N}_0$, which means Eq. (2.4) all have roots with negative real parts. Then $E_*(u_*, v_*)$ is locally asymptotically stable for system (1.2) with $\tau = 0$.

2.2. $\tau > 0$

In the following, we assume $(\mathbf{H}_1)$ holds. Let $i\omega$ ($\omega > 0$) be a solution of Eq. (2.3), then

$$-\omega^2 + \kappa_n i\omega + \nu_n + \varrho_n(\cos\omega\tau - i\sin\omega\tau) = 0.$$

We can obtain $\cos\omega\tau = \frac{\omega^2 - \nu_n}{\varrho_n}$, $\sin\omega\tau = \frac{\kappa_n \omega}{\varrho_n} > 0$ under hypothesis $(\mathbf{H}_1)$. It leads to

$$\omega^4 + (\kappa_n^2 - 2\nu_n)\omega^2 + \nu_n^2 - \varrho_n^2 = 0. \quad (2.5)$$

Let $p = \omega^2$, then (2.5) becomes

$$p^2 + (\kappa_n^2 - 2\nu_n)p + \nu_n^2 - \varrho_n^2 = 0, \quad (2.6)$$

and the roots of (2.6) are $p_n^\pm = \frac{1}{2}[-(\kappa_n^2 - 2\nu_n) \pm \sqrt{(\kappa_n^2 - 2\nu_n)^2 - 4(\nu_n^2 - \varrho_n^2)}]$. By direct computation, we have

$$\begin{cases} \kappa_n^2 - 2\nu_n = \alpha_1^2 + 2\alpha_2\beta_1 + \beta_2^2 - 2(d_1\alpha_1 + d_2\beta_2)\mu_n + (d_1^2 + d_2^2)\mu_n^2, \\ \nu_n - \varrho_n = \alpha_1\beta_2 - \alpha_2\beta_1 - (d_2\alpha_1 + d_1\beta_2 - dv_*\alpha_2)\mu_n + d_1d_2\mu_n^2, \end{cases}$$

and $\nu_n + \varrho_n > 0$ under hypothesis $(\mathbf{H}_1)$. Define

$$\begin{cases} z_\pm = \frac{d_2\alpha_1 + d_1\beta_2 - dv_*\alpha_2 \pm \sqrt{(d_2\alpha_1 + d_1\beta_2 - dv_*\alpha_2)^2 - 4d_1d_2(\alpha_1\beta_2 - \alpha_2\beta_1)}}{2d_1d_2}, \\ d_* = \frac{d_2\alpha_1 + d_1\beta_2}{v_*\alpha_2} - \frac{2\sqrt{d_1d_2(\alpha_1\beta_2 - \alpha_2\beta_1)}}{v_*\alpha_2}, \\ \mathbb{M} = \{n | \mu_n \in (z_-, z_+), \quad n \in \mathbb{N}_0\}, \\ \mathbb{M}_1 = \{n | \kappa_n^2 - 2\nu_n < 0, \quad (\kappa_n^2 - 2\nu_n)^2 - 4(\nu_n^2 - \varrho_n^2) > 0, \quad n \in \mathbb{N}_0\}. \end{cases}$$

Then we can obtain that

$$\begin{cases} \nu_n - \varrho_n \geq 0, & \text{for } d \leq d_*, n \in \mathbb{N}_0, \\ \nu_n - \varrho_n \geq 0, & \text{for } d > d_*, n \notin \mathbb{M}, \\ \nu_n - \varrho_n < 0, & \text{for } d > d_*, n \in \mathbb{M}. \end{cases} \quad (2.7)$$

The existence of purely imaginary roots of Eq. (2.3) can be divided into the following three cases.

Case 1: $d < d_*$. For $n \in \mathbb{M}_1$, Eq. (2.3) has two pairs of purely imaginary roots $\pm i\omega_n^\pm$ at $\tau_n^{j,\pm}$ for $j \in \mathbb{N}_0$. Otherwise, Eq. (2.3) does not have characteristic roots with zero real parts.

Case 2: $d = d_*$. For $n \in \mathbb{M}_1$, Eq. (2.3) has two pairs of purely imaginary roots $\pm i\omega_n^\pm$ at $\tau_n^{j,\pm}$ for $j \in \mathbb{N}_0$ and $\mu_n \neq z_+ = z_-$, and a pair of purely imaginary roots $\pm i\omega_n^\pm$ at $\tau_n^{j,+}$ for $j \in \mathbb{N}_0$ and $\mu_n = z_+ = z_-$. Otherwise, Eq. (2.3) does not have characteristic roots with zero real parts.

Case 3: $d > d_*$. For $n \in \mathbb{M}$, Eq. (2.3) has a pair of purely imaginary roots $\pm i\omega_n^\pm$ at $\tau_n^{j,+}$ for $j \in \mathbb{N}_0$ and $n \in \mathbb{M}$. For $n \in \mathbb{M}_1 \setminus \mathbb{M}$, then Eq. (2.3) has two pairs of purely imaginary roots $\pm i\omega_n^\pm$ at $\tau_n^{j,\pm}$ for $j \in \mathbb{N}_0$, $\mu_n \neq z_\pm$, and a pair of purely imaginary roots $\pm i\omega_n^\pm$ at $\tau_n^{j,+}$ for $j \in \mathbb{N}_0$, $\mu_n = z_+$ or z_- . Otherwise, Eq. (2.3) does not have characteristic roots with zero real parts.

Where

$$\omega_n^\pm = \sqrt{p_n^\pm}, \quad \tau_n^{j,\pm} = \frac{1}{\omega_n^\pm} \arccos\left(\frac{(\omega_n^\pm)^2 - \nu_n}{\varrho_n}\right) + 2j\pi. \quad (2.8)$$

Define

$$\begin{aligned} \mathbb{S} = & \{\tau_n^{j,+} | n \in \mathbb{M} \text{ or } \mu_n = z_\pm, j \in \mathbb{N}_0\} \\ & \bigcup \{\tau_n^{j,\pm} | n \in \mathbb{M}_1 \setminus \mathbb{M}, \mu_n \neq z_+, \mu_n \neq z_-, j \in \mathbb{N}_0\}. \end{aligned}$$

We have the following lemma.

Lemma 2.2. Assume $(\mathbf{H}_1)$ holds. Then $\operatorname{Re}(\frac{d\lambda}{d\tau})|_{\tau=\tau_n^{j,+}} > 0$, $\operatorname{Re}(\frac{d\lambda}{d\tau})|_{\tau=\tau_n^{j,-}} < 0$ for $\tau_n^{j,\pm} \in \mathbb{S}$ and $j \in \mathbb{N}_0$.

Proof. By (2.3), we have

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{2\lambda + \kappa_n}{\varrho_n \lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda}.$$

Then

$$\begin{aligned} \left[\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right]_{\tau=\tau_n^{j,\pm}} &= \operatorname{Re}\left[\frac{2\lambda + \kappa_n}{\varrho_n \lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda}\right]_{\tau=\tau_n^{j,\pm}} \\ &= \left[\frac{1}{\kappa_n^2 \omega^2 + (\nu_n - \omega)^2} (2\omega^2 + \kappa_n^2 - 2\nu_n)\right]_{\tau=\tau_n^{j,\pm}} \\ &= \pm \left[\frac{1}{\kappa_n^2 \omega^2 + (\nu_n - \omega)^2} \sqrt{(\kappa_n^2 - 2\nu_n)^2 - 4(\nu_n^2 - \varrho_n^2)}\right]_{\tau=\tau_n^{j,\pm}}. \end{aligned}$$

Therefore $\operatorname{Re}(\frac{d\lambda}{d\tau})|_{\tau=\tau_n^{j,+}} > 0$, $\operatorname{Re}(\frac{d\lambda}{d\tau})|_{\tau=\tau_n^{j,-}} < 0$. $\square$

Denote $\tau_* = \min\{\tau_n^{0,\pm} | \tau_n^{0,\pm} \in \mathbb{S}\}$. We have the following theorem.

Theorem 2.1. Assume $(\mathbf{H}_1)$ holds, then the following statements are true for system (1.2).

- (i) $E_*(u_*, v_*)$ is locally asymptotically stable for $\tau > 0$ when $\mathbb{S} = \emptyset$.
- (ii) $E_*(u_*, v_*)$ is locally asymptotically stable for $\tau \in [0, \tau_*)$ when $\mathbb{S} \neq \emptyset$.
- (iii) $E_*(u_*, v_*)$ is unstable for $\tau \in (\tau_*, \tau_* + \varepsilon)$ for some $\varepsilon > 0$ when $\mathbb{S} \neq \emptyset$.
- (iv) Hopf bifurcation occurs at (u_*, v_*) when $\tau = \tau_n^{j,+}$ ($\tau = \tau_n^{j,-}$), $j \in \mathbb{N}_0$, $\tau_n^{j,\pm} \in \mathbb{S}$.

3. Property of Hopf bifurcation

In this section, we give the normal form of Hopf bifurcation by the work [22], which is given in the Appendix A with the detail computation. The normal form is

$$\dot{z} = Bz + \frac{1}{2} \begin{pmatrix} B_1 z_1 \varepsilon \\ \bar{B}_1 z_2 \varepsilon \end{pmatrix} + \frac{1}{3!} \begin{pmatrix} B_2 z_1^2 z_2 \varepsilon \\ \bar{B}_2 z_1 z_2^2 \varepsilon \end{pmatrix} + O(|z|\varepsilon^2 + |z|^4), \quad (3.1)$$

where

$$B_1 = 2i\tilde{\omega}\psi^T \phi, \quad B_2 = B_{21} + \frac{3}{2}(B_{22} + B_{23}).$$

By coordinate transformation $z_1 = \omega_1 - i\omega_2$, $z_2 = \omega_1 + i\omega_2$, and $\omega_1 = \rho \cos \xi$, $\omega_2 = \rho \sin \xi$, the normal form (3.1) can be rewritten as

$$\dot{\rho} = K_1 \varepsilon \rho + K_2 \rho^3 + O(\rho \varepsilon^2 + |(\rho, \varepsilon)|^4), \quad (3.2)$$

where $K_1 = \frac{1}{2}\text{Re}(B_1)$, $K_2 = \frac{1}{3!}\text{Re}(B_2)$.

By the work [22], we have the following theorem.

Theorem 3.1. *If $K_1 K_2 < 0 (> 0)$, the Hopf bifurcation is supercritical (subcritical), and the bifurcating periodic orbits is stable (unstable) for $K_2 < 0 (> 0)$.*

4. Numerical simulations

In this section, we give some numerical simulations by Matlab. Fix the following parameters

$$\alpha = 0.4, \quad a = 0.5, \quad b = 0.2, \quad c = 0.5, \quad \beta = 1.75, \quad s = 0.05, \quad d_1 = 0.1, \quad d_2 = 0.2, \quad l = 2. \quad (4.1)$$

We give the unique positive equilibrium with the intra-species competition parameter e in the Fig. 1. We can see that increasing the intra-species competition parameter e is beneficial to the prey. But the predators will increase first and then decrease.

To consider the effect of the intra-species competition parameter e and the memory-based diffusion coefficient d on the stability of the positive equilibrium, we give the bifurcation diagrams in Fig. 2 and 3. From Fig. 2, we can see that increasing the intra-species competition parameter e is not beneficial to the stability of the positive equilibrium. From Fig. 3, we can see that the positive equilibrium is always stable when d is less than the critical value. But when d crosses the critical value, the stable region of the positive equilibrium will decrease with the increase of parameter d and the inhomogeneous periodic solutions appear.

If we choose $e = 0.1$ and $d = 1.5 > d_* \approx 1.1627$, then $(u_*, v_*) \approx (0.0758, 5.3258)$ is the unique positive equilibrium and $(\mathbf{H}_1)$ holds. By direct calculation, we have

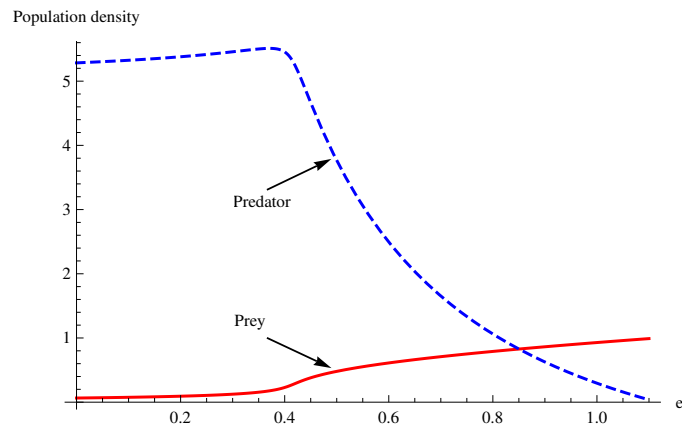


Figure 1. The population densities of prey and predator with parameter e .

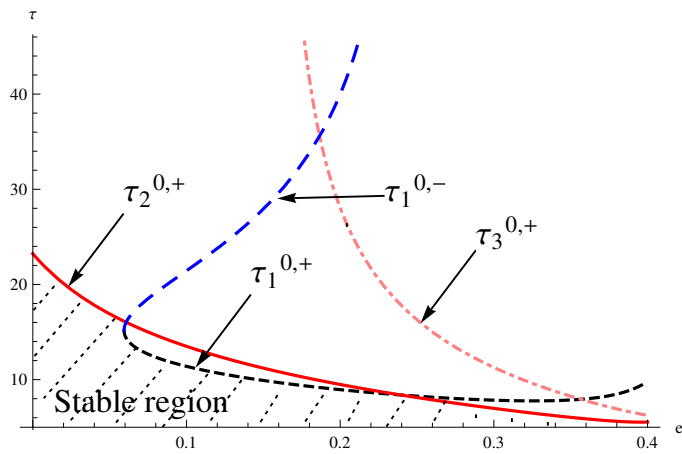


Figure 2. Bifurcation diagram of system (1.2) with parameter e when $d = 1.5$.

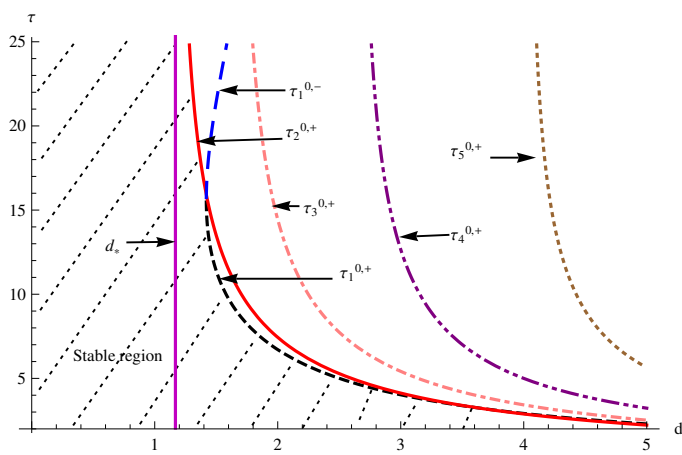


Figure 3. Bifurcation diagram of system (1.2) with parameter d when $e = 0.1$.

$\mathbb{M}_1 = \{1\}$, $\mathbb{M} = \{2\}$, $\tau_* = \tau_1^{0,+} \approx 11.3928 < \tau_2^{0,+} \approx 13.4977 < \tau_1^{0,-} \approx 21.4421$ and $K_1 \approx 0.0191 > 0$, $K_2 \approx -0.5741 < 0$ when $\tau = \tau_*$. Then (u_*, v_*) is locally asymptotically stable for $\tau \in [0, \tau_*)$ (Fig. 4), and is unstable for $\tau > \tau_*$. Then, the stable bifurcating periodic orbits with mode-1 is exists for $\tau > \tau_*$ (Fig. 5). This means that the delay in averaged memory period of predator can affect the stability of (u_*, v_*) , and induce the spatial inhomogeneous periodic oscillation of prey and predator's density under some parameters.

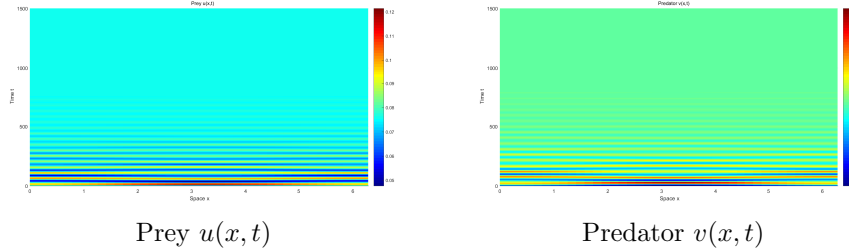


Figure 4. The numerical simulations of system (1.2) with $e = 0.1$ and $\tau = 10$. The coexisting equilibrium (u_*, v_*) is stable.

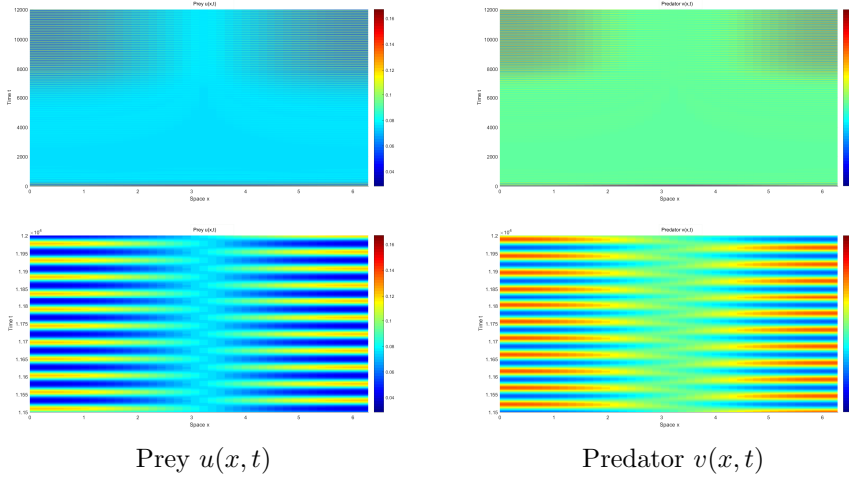


Figure 5. The numerical simulations of system (1.2) with $e = 0.1$ and $\tau = 12$. The coexisting equilibrium (u_*, v_*) is unstable and there exists a spatially inhomogeneous periodic solution with mode-1 spatial pattern.

If we choose $e = 0.3$ and $d = 1.5 > d_* \approx 1.1627$, then $(u_*, v_*) \approx (0.1244, 5.4576)$ is the unique positive equilibrium and $(\mathbf{H}_1)$ holds. By direct calculation, we have $\mathbb{M} = \{1, 2, 3\}$, $\mathbb{M}_1 \setminus \mathbb{M} = \emptyset$, $\tau_* = \tau_2^{0,+} \approx 6.981 < \tau_1^{0,+} \approx 7.8421 < \tau_3^{0,+} \approx 11.2804$ and $K_1 \approx 0.0600 > 0$, $K_2 \approx -0.5118 < 0$ when $\tau = \tau_*$. Then (u_*, v_*) is locally asymptotically stable for $\tau \in [0, \tau_*)$ (Fig. 6), and is unstable for $\tau > \tau_*$. Then, the stable bifurcating periodic orbits with mode-2 is exists for $\tau > \tau_*$ (Fig. 7).

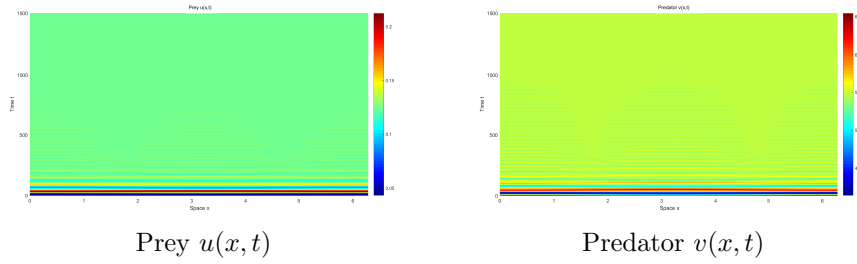


Figure 6. The numerical simulations of system (1.2) with $e = 0.3$ and $\tau = 6.5$. The coexisting equilibrium (u_*, v_*) is stable.

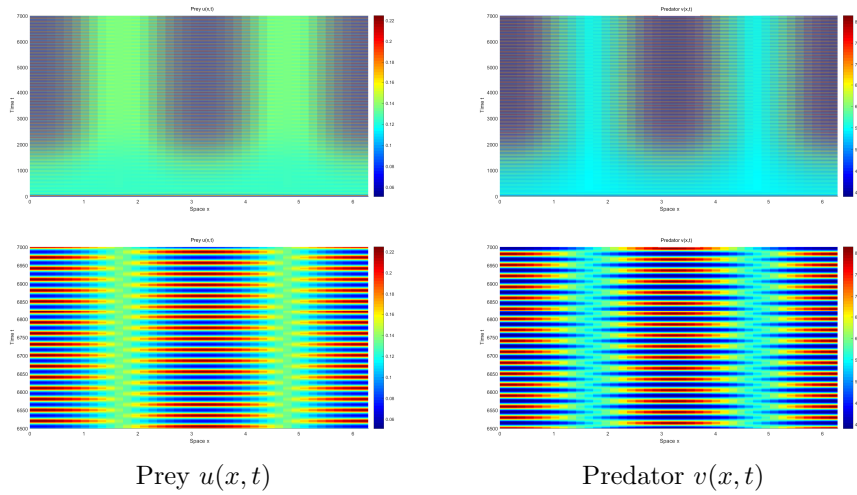


Figure 7. The numerical simulations of system (1.2) with $e = 0.3$ and $\tau = 7.2$. The coexisting equilibrium (u_*, v_*) is unstable and there exists a spatially inhomogeneous periodic solution with mode-2 spatial pattern.

5. Conclusion

In this paper, we consider a predator-prey model with memory effect and intra-species competition in predator. We mainly study the local stability of the positive equilibrium and the Hopf bifurcation by using the memory delay as parameter. Through central manifold theorem and normal form method, we consider the direction of Hopf bifurcation and stability of bifurcating periodic solutions. By the numerical simulations, we obtain that increasing the intra-species competition is not beneficial to the stability of the positive equilibrium. And the stable region of the positive equilibrium will decrease with the increase of memory-based diffusion coefficient d when d larger than the critical value. In addition, the memory delay may also affect the stability of the positive equilibrium. When the memory delay crosses the critical value, the stable positive equilibrium becomes unstable, and the stably inhomogeneous periodic solutions appears. Particularly, we observe the stably inhomogeneous periodic solutions with mode-1 and mode-2 by numerical simulations, which are not often seen in the predator-prey models without memory effect.

A. Computation of normal form

In this section, we use the algorithm in [22] to compute the normal form of Hopf bifurcation. We denote the critical value of Hopf bifurcation as $\tilde{\tau}$ and Eq. (2.3) has a pair of purely imaginary roots $\pm i\omega_n$. Let $\bar{u}(x, t) = u(x, \tau t) - u_*$ and $\bar{v}(x, t) = v(x, \tau t) - v_*$. Drop the bar, (1.2) can be written as

$$\begin{cases} \frac{\partial u}{\partial t} = \tau [d_1 \Delta u + (u + u_*) \left(1 - (u + u_*) - \frac{\alpha(v + v_*)}{1 + a(u + u_*) + b(v + v_*) + c(u + u_*)(v + v_*)} \right)], \\ \frac{\partial v}{\partial t} = \tau [-d \nabla((v + v_*) \nabla(u(t - 1) + u_*)) + d_2 \Delta v \\ + (v + v_*) \left(\frac{\beta(u + u_*)}{1 + a(u + u_*) + b(v + v_*) + c(u + u_*)(v + v_*) - s - e(u + u_*)} \right)]. \end{cases} \quad (\text{A.1})$$

Define the real-valued Sobolev space

$$\mathbb{X} = \left\{ U = (u, v)^T \in W^{2,2}(0, l\pi)^2, \left(\frac{\partial u}{\partial x}, \frac{\partial v}{\partial x} \right) \Big|_{x=0, l\pi} = 0 \right\},$$

the inner product

$$[U, V] = \int_0^{l\pi} U^T V dx, \quad \text{for } U, V \in \mathbb{X},$$

and $\mathbb{C} = C([-1, 0]; \mathbb{X})$. Set $\tau = \tilde{\tau} + \varepsilon$, where ε is small perturbation. Then system (A.1) is rewritten as

$$\frac{dU(t)}{dt} = d(\varepsilon) \Delta(U_t) + L(\varepsilon)(U_t) + F(U_t, \varepsilon), \quad (\text{A.2})$$

where for $\varphi = (\varphi_1, \varphi_2)^T \in \mathbb{C}$, $d(\varepsilon) \Delta$, $L(\varepsilon) : \mathbb{C} \rightarrow \mathbb{X}$, $F : \mathbb{C} \times \mathbb{R}^2 \rightarrow \mathbb{X}$. They are defined as

$$\begin{aligned} d(\varepsilon) \Delta(\varphi) &= d_0 \Delta(\varphi) + F^d(\varphi, \varepsilon), \quad L(\varepsilon)(\varphi) = (\tilde{\tau} + \varepsilon) A \varphi(0), \\ F(\varphi, \varepsilon) &= (\tilde{\tau} + \varepsilon) \begin{pmatrix} f(\phi^{(1)}(0) + u_*, \phi^{(2)}(0) + v_*) \\ g(\phi^{(1)}(0) + u_*, \phi^{(2)}(0) + v_*) \end{pmatrix} - L(\varepsilon)(\varphi), \end{aligned}$$

and

$$\begin{aligned} d_0 \Delta(\varphi) &= \tilde{\tau} J_1 \varphi_{xx}(0) + \tilde{\tau} J_2 \varphi_{xx}(-1), \\ F^d(\varphi, \varepsilon) &= -d(\tilde{\tau} + \varepsilon) \begin{pmatrix} 0 \\ \phi_x^{(1)}(-1) \phi_x^{(2)}(0) + \phi_{xx}^{(1)}(-1) \phi^{(2)}(0) \end{pmatrix} \\ &\quad + \varepsilon \begin{pmatrix} d_1 \phi_{xx}^{(1)}(0) \\ -dv_* \phi_{xx}^{(1)}(-1) + d_2 \phi_{xx}^{(2)}(0) \end{pmatrix}. \end{aligned}$$

Denote $L_0(\varphi) = \tilde{\tau} A \varphi(0)$, and rewrite (A.2) as

$$\frac{dU(t)}{dt} = d_0 \Delta(U_t) + L_0(U_t) + \tilde{F}(U_t, \varepsilon), \quad (\text{A.3})$$

where $\tilde{F}(\varphi, \varepsilon) = \varepsilon A\varphi(0) + F(\varphi, \varepsilon) + F^d(\varphi, \varepsilon)$. The characteristic equation for the linearized equation $\frac{dU(t)}{dt} = d_0\Delta(U_t) + L_0(U_t)$ is $\tilde{\Gamma}_n(\lambda) = \det(\tilde{M}_n((\lambda)))$, where

$$\tilde{M}_n((\lambda)) = \lambda I_2 + \tilde{\tau}\mu_n D_1 + \tilde{\tau}e^{-\lambda}\mu_n D_2 - \tilde{\tau}A. \quad (\text{A.4})$$

The eigenvalue problem

$$-z(x)'' = \nu z(x), \quad x \in (0, l\pi); \quad z(0)' = z(l\pi)' = 0,$$

has eigenvalues μ_n and normalized eigenfunctions

$$z_n(x) = \frac{\cos \frac{nx}{l}}{\|\cos \frac{nx}{l}\|_{2,2}} = \begin{cases} \frac{1}{l\pi}, & n = 0, \\ \frac{\sqrt{2}}{l\pi} \cos \frac{nx}{l}, & n \neq 0. \end{cases} \quad (\text{A.5})$$

Set $\beta_n^{(j)} = z_n(x)e_j$, $j = 1, 2$, where $e_1 = (1, 0)^T$ and $e_2 = (0, 1)^T$. Define $\eta_n(\theta) \in BV([-1, 0], \mathbb{R}^2)$, such that

$$\int_{-1}^0 d\eta^n(\theta)\phi(\theta) = L_0^d(\varphi(\theta)) + L_0(\varphi(\theta)), \quad \varphi \in C,$$

$C = C([-1, 0], \mathbb{R}^2)$, $C^* = C([0, 1], \mathbb{R}^{2*})$, and

$$\langle \psi(s), \varphi(\theta) \rangle = \psi(0)\varphi(0) - \int_{-1}^0 \int_0^\theta \psi(\xi - \theta) d\eta^n(\theta) \varphi(\xi) d\xi, \quad \psi \in C^*, \varphi \in C. \quad (\text{A.6})$$

Let $\Lambda = \{i\tilde{\omega}, -i\tilde{\omega}\}$, the eigenspace P , and corresponding adjoint space P^* . Decompose $C = P \oplus Q$, where $Q = \{\varphi \in C : \langle \psi, \varphi \rangle = 0, \forall \psi \in P^*\}$. Choose $\Phi(\theta) = (\phi(\theta), \bar{\phi}(\theta))$, $\Psi(\theta) = \text{col}(\psi^T(s), \bar{\psi}^T(s))$, where

$$\begin{aligned} \phi(\theta) &= \phi e^{i\tilde{\omega}\theta} := \begin{pmatrix} \phi_1(\theta) \\ \phi_2(\theta) \end{pmatrix}, \quad \psi(s) = \psi e^{-i\tilde{\omega}s} := \begin{pmatrix} \psi_1(s) \\ \psi_2(s) \end{pmatrix}, \\ \phi &= \begin{pmatrix} 1 \\ (i\tilde{\omega} + d_1\mu_n - \alpha_1)/\alpha_2 \end{pmatrix}, \quad \psi = M \begin{pmatrix} 1 \\ \alpha_2/(i\tilde{\omega} + d_2\mu_n - \beta_2) \end{pmatrix}, \end{aligned}$$

and

$$M = \left(\frac{\alpha_1 + \beta_2 - d_1\mu_n - d_2\mu_n - de^{-i\tilde{\omega}}e^{-i\tilde{\omega}\tilde{\tau}}v_*\alpha_2\mu_n\tilde{\tau} - 2i\tilde{\omega}}{\beta_2 - d_2\mu_n - i\tilde{\omega}} \right)^{-1}.$$

Then $\phi(\theta)$ and $\psi(s)$ are the bases of P and P^* , respectively. And such that $\langle \phi, \psi \rangle = I_2$.

By direct computation, we have

$$\begin{aligned} f_{20} &= \begin{pmatrix} f_{20}^{(1)} \\ f_{20}^{(2)} \end{pmatrix}, \quad f_{11} = \begin{pmatrix} f_{11}^{(1)} \\ f_{11}^{(2)} \end{pmatrix}, \quad f_{02} = \begin{pmatrix} f_{02}^{(1)} \\ f_{02}^{(2)} \end{pmatrix}, \\ f_{30} &= \begin{pmatrix} f_{30}^{(1)} \\ f_{30}^{(2)} \end{pmatrix}, \quad f_{21} = \begin{pmatrix} f_{21}^{(1)} \\ f_{21}^{(2)} \end{pmatrix}, \quad f_{12} = \begin{pmatrix} f_{12}^{(1)} \\ f_{12}^{(2)} \end{pmatrix}, \quad f_{03} = \begin{pmatrix} f_{03}^{(1)} \\ f_{03}^{(2)} \end{pmatrix}, \end{aligned}$$

where

$$\left\{ \begin{aligned} f_{20}^{(1)} &= \frac{2v_*(1+bv_*)(a+cv_*)\alpha}{(1+au_*+bv_*+cu_*v_*)^3} - 2, \quad f_{11}^{(1)} = -\frac{(1+bv_*-cu_*v_*+a(u_*+2bu_*v_*))\alpha}{(1+au_*+bv_*+cu_*v_*)^3}, \\ f_{02}^{(1)} &= \frac{2u_*(1+au_*)(b+cu_*)\alpha}{(1+au_*+bv_*+cu_*v_*)^3}, \quad f_{30}^{(1)} = -\frac{6v_*(1+bv_*)(a+cv_*)^2\alpha}{(1+au_*+bv_*+cu_*v_*)^4}, \\ f_{21}^{(1)} &= \frac{2(a^2(u_*+2bu_*v_*)+cv_*(2+2bv_*-cu_*v_*))+a(1-b^2v_*^2+2bcu_*v_*^2))\alpha}{(1+au_*+bv_*+cu_*v_*)^4}, \\ f_{12}^{(1)} &= \frac{2(b^2(v_*+2au_*v_*)+cu_*(2+2au_*-cu_*v_*))+b(1-a^2u_*^2+2acu_*^2v_*))\alpha}{(1+au_*+bv_*+cu_*v_*)^4}, \\ f_{03}^{(1)} &= -\frac{6u_*(1+au_*)(b+cu_*)^2\alpha}{(1+au_*+bv_*+cu_*v_*)^4}, \quad f_{20}^{(2)} = -\frac{2v_*(1+bv_*)(a+cv_*)\beta}{(1+au_*+bv_*+cu_*v_*)^3}, \\ f_{11}^{(2)} &= \frac{(1+bv_*-cu_*v_*+a(u_*+2bu_*v_*))\beta}{(1+au_*+bv_*+cu_*v_*)^3} - e, \quad f_{02}^{(2)} = -\frac{2u_*(1+au_*)(b+cu_*)\beta}{(1+au_*+bv_*+cu_*v_*)^3}, \\ f_{21}^{(2)} &= -\frac{2(a^2(u_*+2bu_*v_*)+cv_*(2+2bv_*-cu_*v_*))+a(1-b^2v_*^2+2bcu_*v_*^2))\beta}{(1+au_*+bv_*+cu_*v_*)^4}, \\ f_{12}^{(2)} &= -\frac{2(b^2(v_*+2au_*v_*)+cu_*(2+2au_*-cu_*v_*))+b(1-a^2u_*^2+2acu_*^2v_*))\beta}{(1+au_*+bv_*+cu_*v_*)^4}, \\ f_{30}^{(2)} &= \frac{6v_*(1+bv_*)(a+cv_*)^2\beta}{(1+au_*+bv_*+cu_*v_*)^4}, \quad f_{03}^{(2)} = \frac{6u_*(1+au_*)(b+cu_*)^2\beta}{(1+au_*+bv_*+cu_*v_*)^4}. \end{aligned} \right.$$

We can computation the following parameters

$$\begin{aligned} A_{20} &= f_{20}\phi_1(0)^2 + f_{02}\phi_2(0)^2 + 2f_{11}\phi_1(0)\phi_2(0) = \bar{A}_0 2, \\ A_{11} &= 2f_{20}\phi_1(0)\bar{\phi}_1(0) + 2f_{02}\phi_2(0)\bar{\phi}_2(0) + 2f_{11}(\phi_1(0)\bar{\phi}_2(0) + \bar{\phi}_1(0)\phi_2(0)), \\ A_{21} &= 3f_{30}\phi_1(0)^2\bar{\phi}_1(0) + 3f_{03}\phi_2(0)^2\bar{\phi}_2(0) + 3f_{21}(\phi_1(0)^2\bar{\phi}_2(0) + 2\phi_1(0)\bar{\phi}_1(0)\phi_2(0)) \\ &\quad + 3f_{12}(\phi_2(0)^2\bar{\phi}_1(0) + 2\phi_2(0)\bar{\phi}_2(0)\phi_1(0)), \end{aligned} \quad (\text{A.7})$$

$$A_{20}^d = -2d\tau \begin{pmatrix} 0 \\ \phi_1(0)(-1)\phi_2(0)(0) \end{pmatrix} = \bar{A}_{02}^d, \quad A_{11}^d = -2d\tau \begin{pmatrix} 0 \\ 2\text{Re}[\phi_1(-1)\bar{\phi}_2(0)] \end{pmatrix},$$

and $\tilde{A}_{j_1 j_2} = A_{j_1 j_2} - 2\mu_n A_{j_1 j_2}^d$ for $j_1, j_2 = 0, 1, 2$, $j_1 + j_2 = 2$. In addition, $h_{0,20}(\theta) = \frac{1}{i\pi}(\tilde{M}_0(2i\tilde{\omega}))^{-1}A_{20}e^{2i\tilde{\omega}\theta}$, $h_{0,11}(\theta) = \frac{1}{i\pi}(\tilde{M}_0(0))^{-1}A_{11}$, $h_{2n,20}(\theta) = \frac{1}{2i\pi}(\tilde{M}_{2n}(2i\tilde{\omega}))^{-1}\tilde{A}_{20}e^{2i\tilde{\omega}\theta}$, $h_{2n,11}(\theta) = \frac{1}{i\pi}(\tilde{M}_{2n}(0))^{-1}\tilde{A}_{11}$.

$$S_2(\phi(\theta), h_{n,q_1 q_2}(\theta)) = 2\phi_1 h_{n,q_1 q_2}^{(1)} f_{20} + 2\phi_2 h_{n,q_1 q_2}^{(2)} f_{02} + 2(\phi_1 h_{n,q_1 q_2}^{(2)} + \phi_2 h_{n,q_1 q_2}^{(1)}) f_{11},$$

$$S_2(\bar{\phi}(\theta), h_{n,q_1 q_2}(\theta)) = 2\bar{\phi}_1 h_{n,q_1 q_2}^{(1)} f_{20} + 2\bar{\phi}_2 h_{n,q_1 q_2}^{(2)} f_{02} + 2(\bar{\phi}_1 h_{n,q_1 q_2}^{(2)} + \bar{\phi}_2 h_{n,q_1 q_2}^{(1)}) f_{11},$$

$$S_2^{d,1}(\phi(\theta), h_{0,11}(\theta)) = -2d\tilde{\tau} \begin{pmatrix} 0 \\ \phi_1(-1)h_{0,11}^{(2)}(0) \end{pmatrix},$$

$$S_2^{d,1}(\bar{\phi}(\theta), h_{0,11}(\theta)) = -2d\tilde{\tau} \begin{pmatrix} 0 \\ \bar{\phi}_1(-1)h_{0,20}^{(2)}(0) \end{pmatrix},$$

$$\begin{aligned}
S_2^{d,1}(\phi(\theta), h_{2n,11}(\theta)) &= -2d\tilde{\tau} \begin{pmatrix} 0 \\ \phi_1(-1)h_{2n,11}^{(2)}(0) \end{pmatrix}, \\
S_2^{d,1}(\bar{\phi}(\theta), h_{2n,20}(\theta)) &= -2d\tilde{\tau} \begin{pmatrix} 0 \\ \bar{\phi}_1(-1)h_{2n,20}^{(2)}(0) \end{pmatrix}, \\
S_2^{d,2}(\phi(\theta), h_{2n,11}(\theta)) &= -2d\tilde{\tau} \begin{pmatrix} 0 \\ \phi_1(-1)h_{2n,11}^{(2)}(0) \end{pmatrix} - 2d\tilde{\tau} \begin{pmatrix} 0 \\ \phi_2(0)h_{2n,11}^{(1)}(-1) \end{pmatrix}, \\
S_2^{d,2}(\bar{\phi}(\theta), h_{2n,20}(\theta)) &= -2d\tilde{\tau} \begin{pmatrix} 0 \\ \bar{\phi}_1(-1)h_{2n,20}^{(2)}(0) \end{pmatrix} - 2d\tilde{\tau} \begin{pmatrix} 0 \\ \bar{\phi}_2(0)h_{2n,20}^{(1)}(-1) \end{pmatrix}, \\
S_2^{d,3}(\phi(\theta), h_{2n,11}(\theta)) &= -2d\tilde{\tau} \begin{pmatrix} 0 \\ \phi_2(0)h_{2n,11}^{(1)}(-1) \end{pmatrix}, \\
S_2^{d,3}(\bar{\phi}(\theta), h_{2n,20}(\theta)) &= -2d\tilde{\tau} \begin{pmatrix} 0 \\ \bar{\phi}_1(0)h_{2n,20}^{(2)}(-1) \end{pmatrix}.
\end{aligned}$$

Then we have

$$\begin{aligned}
B_{21} &= \frac{3}{2l\pi} \psi^T A_{21}, \\
B_{22} &= \frac{1}{l\pi} \psi^T (S_2(\phi(\theta), h_{0,11}(\theta)) + S_2(\bar{\phi}(\theta), h_{0,20}(\theta))) \\
&\quad + \frac{1}{2l\pi} \psi^T (S_2(\phi(\theta), h_{2n,11}(\theta)) + S_2(\bar{\phi}(\theta), h_{2n,20}(\theta))), \\
B_{23} &= -\frac{1}{l\pi} \mu_n \psi^T (S_2^{d,1}(\phi(\theta), h_{0,11}(\theta)) + S_2^{d,1}(\bar{\phi}(\theta), h_{0,20}(\theta))) \\
&\quad + \frac{1}{2l\pi} \psi^T \sum_{j=1,2,3} b_{2n}^{(j)} (S_2^{d,j}(\phi(\theta), h_{2n,11}(\theta)) + S_2^{d,j}(\bar{\phi}(\theta), h_{2n,20}(\theta))),
\end{aligned}$$

where $b_{2n}^{(1)} = -\mu_n$, $b_{2n}^{(2)} = -2\mu_n$, $b_{2n}^{(3)} = -4\mu_n$.

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