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Qualitative Analysis and Numerical Simulation of a Predator-Prey Model for Invertebrate Predators in Aquatic Population Ecosystem

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Abstract: The predation mechanism of invertebrates (e. g., *Tortanus dextrilobatus*) on plankton in aquatic population ecosystem is a significant research topic. In this paper, the interaction between invertebrates and plankton is simulated by a modified Leslie-Gower predator-prey model. Using the theory of reaction-diffusion equations, a priori estimate, existence, uniqueness and stability conditions of the positive steady state solution are established. Furthermore, numerical simulations are conducted to quantitatively analyze the dynamical behavior. The research shows that as long as the Allee effect constant satisfies the appropriate relationship and the growth rates of predator and prey are appropriately large, the predator and prey can not only coexist, but also the coexistence mode is unique and stable under low predation-rate. In addition, the numerical simulations show that the coexistence may be stable under high predation-rate. Meanwhile, with the increase of predation rate, the population density of predators will decrease.

Key words: predator-prey model; aquatic population ecosystem; Allee effect; Ivlev functional response; positive steady-state solutions; numerical simulation

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0 Introduction

Let's start with the following predator-prey model

$$\begin{cases} u_t - \Delta u = u(a(1-ru) - \dfrac{n_1}{u+n_2}) - p_1 uv, & (x,t) \in \Omega \times (0,\infty), \\ v_t - \Delta v = cv(1 - \dfrac{v}{u+k_1}), & (x,t) \in \Omega \times (0,\infty), \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0, x \in \partial\Omega, & t \in (0,\infty), \\ u(x,0) = u_0(x) \geqslant 0, \not\equiv 0, v(x,0) = v_0(x) \geqslant 0, \not\equiv 0, & x \in \bar{\Omega}, \end{cases} \tag{1}$$

where $\Omega \subset \mathbb{R}^n$ $(n \geqslant 1)$ is a bounded domain with smooth boundary $\partial\Omega$. In Ref. [1], the authors studied the predator-prey model (1) and gave the conditions for the steady-state bifurcation and Hopf bifurcation from the unique positive constant solution. The $n_1/(u+n_2)$ used here named additive Allee effect, where n_1 and n_2 are constants of Allee effect which describing the strength of Allee effect, refers to that the low density populations may have difficulties in finding mates, promoting reproduction, predation, environmental regulation and inbreeding, which may lead to population extinction.

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Therefore, it is significant to study the mechanism of Allee effect to avoid population extinction in low density population. Some classic studies on the impact of Allee effect on predation models can be found in Refs. [2-5]. The background and parameter meanings of this model can be found in Ref. [1] and we omit here.

It is well known that the predator-prey functional response is an important factor in predator-prey models, which profoundly affects the dynamics of predator-prey models[6-7]. The functional response $p_1 u$ in (1) is linear function and is unbounded. This deficiency reminds us that we can use the following Ivlev function, which can be written as $\phi(u)=I_{\max}(1-\mathrm{e}^{-\gamma u})$, where u is the population density of prey, γ and $I_{\max}$ are positive constants which represent the predation rate of the predator and the maximum capture rate, respectively. It is clear that the $\phi(u)$ is bounded and satisfies $\phi'(u)=I_{\max}\gamma\mathrm{e}^{-\gamma u}>0$, $\phi''(u)=-I_{\max}\gamma^2\mathrm{e}^{-\gamma u}<0$, $\lim\limits_{\gamma\to\infty}\phi(u)=I_{\max}$.

A recent experiment shows that the predation rate of *Tortanus dextrilobatus* expressed by γ can simulate the model that *Tortanus dextrilobatu*s prey on zooplankton in the San Francisco Estuary[8]. Many studies, both modeling analysis and ecological experiments, such as Refs. [8-11], show that the predation rate γ strongly affects the coexistence of predator and prey. However, there has been no research on using the Ivlev functional response to simulate predation of zooplankton in (1). For the sake of simplicity, we will take $I_{\max}=1$ in our work. By introducing the following non-dimensional variables

$$\bar{u}=aru,\quad arn_1=m,\quad arn_2=b,\quad \frac{p_1}{ar}=p,\quad car=d,\quad k_1 ar=k$$

in (1) and dropping the superscripts of u for simplicity, the predator-prey model (1) is given by the following equations

$$\begin{cases} u_t-\Delta u=u(a-u)-\dfrac{mu}{u+b}-(1-\mathrm{e}^{-\gamma u})v, & (x,t)\in\Omega\times(0,\infty),\\ v_t-\Delta v=v(c-\dfrac{dv}{u+k}), & (x,t)\in\Omega\times(0,\infty),\\ u=v=0, & x\in\partial\Omega, t\in(0,\infty),\\ u(x,0)=u_0(x)\geqslant 0,\not\equiv 0,\ v(x,0)=v_0(x)\geqslant 0,\not\equiv 0, & x\in\bar{\Omega}.\end{cases} \tag{2}$$

Here u and v are the population densities of prey and predator, a and c are the intrinsic growth rates of prey and predator, respectively. The Allee effect constants m and b satisfy $m<ab$ which is called weak additive Allee effect. $dv/(u+k)$ is a modified Leslie-Gower term[12-13]. The parameter d represents the maximum average reduction rate obtained by predators, and k represents the environmental carrying capacity of predators. For more detailed biological significance of the model, one can see Refs. [14-16]. Obviously, the corresponding steady-state problem to (2) can be written as

$$\begin{cases} -\Delta u=u(a-u)-\dfrac{mu}{u+b}-(1-\mathrm{e}^{-\gamma u})v, & x\in\Omega,\\ -\Delta v=v(c-\dfrac{dv}{u+k}), & x\in\Omega,\\ u=v=0, & x\in\partial\Omega.\end{cases} \tag{3}$$

The main purpose of this paper is to clarify the influence of weak additive Allee effect and Ivlev functional response on the positive solution of model (2). The content of this paper is arranged as follows. Section 1 introduces some preliminary results. Section 2 gives the necessary conditions and prior estimates for positive solutions of (3). Section 3 gives the sufficient conditions for the existence of positive solutions of (3). Section 4 gives the uniqueness and stability of the positive solution of (3). In Section 5, the dynamics of (2) and (3) are quantitatively analyzed by numerical simulations.

1 Preliminaries

Let $q(x)\in C^1(\bar{\Omega})$. It is well known that the following problem

$$\begin{cases} -\Delta\phi+q(x)\phi=\lambda\phi, & x\in\Omega,\\ \phi=0, & x\in\partial\Omega\end{cases} \tag{4}$$

has an infinite sequence of eigenvalues which are bounded below. Throughout this paper, we denote the first eigenvalue by $\lambda_1(q)$ and the corresponding eigenfunction does not change sign on Ω. We also denote that $\lambda_1=\lambda_1(0)$ with the corresponding eigenfunction $\Phi_1>0$, $x\in\Omega$. For more detailed information, one can see Refs. [17-19].

Now we consider the following boundary value problem

$$\begin{cases} -\Delta u+q(x)u=au-u^2, & x\in\Omega,\\ u=0, & x\in\partial\Omega.\end{cases}$$

According to Ref. [20], if $a\leqslant\lambda_1(q)$, then u=0 is the unique non-negative solution of this problem, and it has a unique positive solution if $a>\lambda_1(q)$. In particular, if $q(x)\equiv 0$ and $a>\lambda_1$, then it has a unique positive solution, denoted by $\theta_{[a]}$, which is monotonically increasing with respect to a. And then, for the boundary value problem

$$\begin{cases} -\Delta u = u(a-u) - \dfrac{mu}{u+b}, & x\in\Omega, \\ u=0, & x\in\partial\Omega, \end{cases} \tag{5}$$

using the upper and lower solution method, it has a unique positive solution $\tilde{u}$ which satisfies $\tilde{u}\leqslant\theta_{[a]}\leqslant a$ when $m<b^2$ and $a>\lambda_1+m/b$. We remark here that the condition $a>\lambda_1+m/b$ can meet the requirements of the condition of weak additive Allee effect, i.e., $m<ab$. Finally, consider the following boundary value problem

$$\begin{cases} -\Delta v = v(c-hv), & x\in\Omega, \\ v=0, & x\in\partial\Omega. \end{cases} \tag{6}$$

It has a unique positive solution, denoted by $\theta_{[c,h]}$, if $c>\lambda_1$. Moreover, $\theta_{[c,h]}\leqslant c/h$ and is monotonically decreasing with respect to h. Especially, when $h=k/d$, denote the unique positive solution by $\tilde{v}$, that is $\tilde{v}=\theta_{[c,d/k]}$.

According to (5) and (6), (3) has a unique semi-trivial solution $(\tilde{u},0)$ if $m<b^2$ and $a>\lambda_1+m/b$, and has a unique semi-trivial solution $(0,\tilde{v})=(0,\theta_{[c,d/k]})$ and $\theta_{[c,d/k]}\leqslant ck/d$ if $c>\lambda_1$.

Lemma 1[21-22] Let $q(x)\in C(\bar{\Omega}), M-q(x)>0$ with the constant M, $\lambda_1(q(x))$ be the principal eigenvalue of (4). We have the following statements:

(a) $r[(M-\Delta)^{-1}(M-q(x))]>1$ if $\lambda_1(q(x))<0$,

(b) $r[(M-\Delta)^{-1}(M-q(x))]<1$ if $\lambda_1(q(x))>0$,

(c) $r[(M-\Delta)^{-1}(M-q(x))]=1$ if $\lambda_1(q(x))=0$.

Lemma 2[22] Let $u(x), v(x)\in C^1(\bar{\Omega})$ satisfy

$$u(x)>0,\ x\in\Omega,\ u|_{\partial\Omega}=0;\ v|_{\partial\Omega}>0,\ \frac{\partial u}{\partial n}|_{\partial\Omega}<0.$$

Then there exists $\varepsilon>0$ such that $u+\varepsilon v>0$ for any $x\in\Omega$.

2 Necessary Conditions and Prior Estimates

In this section, we use the upper and lower solution method and the strong maximum principle to establish the necessary condition and a priori estimate of positive solutions of (3).

Theorem 1 If (3) has a positive solution, then $a>\lambda_1$, $c>\lambda_1$.

Proof Let (u,v) be a positive solution of (3). Multiply both sides of the first equation of (3) by Φ_1 and integrate on Ω, we can get

$$\int_\Omega (a-\lambda_1)\Phi_1 u\mathrm{d}x = \int_\Omega \Big(u+\frac{m}{u+b}+\frac{(1-\mathrm{e}^{-\gamma u})v}{u}\Big)\Phi_1 u\mathrm{d}x>0.$$

This implies that $a>\lambda_1$. The inequality $c>\lambda_1$ can be obtained by the second equation of (3) similarly.

Remark 1 Theorem 1 shows that when the growth rate of predator or prey is low, at least one species is extinct in (3).

Theorem 2 Suppose that $m<b^2, a>\lambda_1+m/b$ and (u,v) is a positive solution of (3). Then

$$0<u\leqslant\tilde{u}\leqslant\theta_{[a]}\leqslant a,\ \tilde{v}\leqslant v\leqslant\theta_{[c,d/(a+k)]}\leqslant\frac{c(a+k)}{d}.$$

Proof The above two inequalities are proved in the same way, and we only prove the second inequality. According to the second equation of (3) we have

$$-\Delta v = v\Big(c-\frac{dv}{u+k}\Big)\geqslant v\Big(c-\frac{dv}{k}\Big),$$

$$-\Delta v = v\Big(c-\frac{dv}{u+k}\Big)\leqslant v\Big(c-\frac{dv}{a+k}\Big).$$

If (u,v) is a positive solution of (3), according to Theorem 1 we have $c>\lambda_1$. Then

$$-\Delta v = v\Big(c-\frac{dv}{k}\Big), v|_{\partial\Omega}=0 \text{ and } -\Delta v = v\Big(c-\frac{dv}{a+k}\Big), v|_{\partial\Omega}=0$$

have a unique positive solution $\tilde{v}$, $\theta_{[c,d/(a+k)]}$, respectively. Thus $\tilde{v}\leqslant v\leqslant\theta_{[c,d/(a+k)]}$ can be obtained from upper-lower solution method and uniqueness of $\theta_{[c,d/(a+k)]}$. The inequality $\theta_{[c,d/(a+k)]}\leqslant c(a+k)/d$ can be obtained from the nature of $\theta_{[c,d/(a+k)]}$.

3 Existence of Positive Steady-State Solutions

In this section, we establish the existence of positive solution of (3) by using the degree theory. In order to apply the degree theory, we make the following definitions:

$$X=C_0^1(\bar{\Omega})=:\{u\in C^1(\bar{\Omega}): u=0, x\in\partial\Omega\},$$

$$K=\{u\in C_0^1(\bar{\Omega}): u\geqslant 0, x\in\bar{\Omega}\},$$

$$E=X\times X,\ W=K\times K,$$

$$D=\{(u,v)\in W: u<a+1, v<\frac{c(a+k)}{d}+1\}.$$

Using Lemma 2, we can get

1) $\bar{W}_{(0,0)}=K\times K,\ S_{(0,0)}=\{(0,0)\}$,

2) $\bar{W}_{(\tilde{u},0)}=X\times K,\ S_{(\tilde{u},0)}=X\times\{0\}$,

3) $\bar{W}_{(0,\tilde{v})}=K\times X,\ S_{(0,\tilde{v})}=\{0\}\times X$.

Lemma 3[22] For the mapping $\phi_t(x)$: $\bar{\Omega}\times[0,1]\to\mathbb{R}^n$. Suppose that $\phi_t(x)$ is continuous on $\bar{\Omega}\times[0,1]$ and $\phi_t(x)\in C^1(\Omega)$ for any $t\in[0,1]$. If $y_0\notin\phi_t(\partial\Omega)$ for any $t\in[0,1]$, then the topological degree $\deg(\phi_t,\Omega,y_0)$ does not depend on t.

Lemma 4[22] Let $I-F'(y)$ be invertible on $\bar{W}_y$.

(i) If $F'(y)$ has α-property, then $\mathrm{index}_W(F,y)=0$;

(ii) If $F'(y)$ has no α-property, then $\text{index}_W(F,y)=(-1)^\sigma$, where σ is the sum of the algebraic multiplicities of the eigenvalues of $F'(y)$ which are larger than one.

Lemma 5 Let $m<b^2$, $a>\lambda_1+m/b$. Then all eigenvalues of J_0 are greater than 0. Here J_0 is the linearization operator of (5) at $\tilde{u}$, i.e.,

$$J_0=-\Delta-(a-2\tilde{u}-\frac{mb}{(\tilde{u}+b)^2}).$$

Proof By $m<b^2$, $a>\lambda_1+m/b$, we have $\tilde{u}$ is a unique positive solution of (5). Thus

$$\lambda_1(-a+\tilde{u}+\frac{m}{\tilde{u}+b})=0.$$

According to $m<b^2$, we have

$$\tilde{u}>\frac{m\tilde{u}}{(\tilde{u}+b)^2}=\frac{m}{\tilde{u}+b}-\frac{mb}{(\tilde{u}+b)^2},$$

It means that $\tilde{u}+mb/(\tilde{u}+b)^2>m/(\tilde{u}+b)$. By the nature of principle eigenvalue, there holds

$$\lambda_1(-a+2\tilde{u}+\frac{mb}{(\tilde{u}+b)^2})>\lambda_1(-a+\tilde{u}+\frac{m}{\tilde{u}+b})=0.$$

The proof is completed.

According to Theorem 2, we have any nonnegative solution of (3) belongs to D. Then there exists a positive constant M, such that

$$u(a-u-\frac{m}{u+b}-\frac{(1-e^{-\gamma u})v}{u})+Mu\geqslant 0,$$
$$v(c-\frac{dv}{u+k})+Mv\geqslant 0,\ (u,v)\in\bar{D}.$$

Define mapping $F: E\to E$ as

$$F(u,v)=(-\Delta+M)^{-1}\begin{pmatrix} u(a-u-\frac{m}{u+b}-\frac{(1-e^{-\gamma u})v}{u})+Mu \\ v(c-\frac{dv}{u+k})+Mv \end{pmatrix}. \quad (7)$$

Then it is a compact operator and $F: D\to W$. Thus $F(u,v)=(u,v)$ if and only if (u,v) is a solution of (3).

For any $t\in[0,1]$, we also define

$$F_t(u,v)=(-\Delta+M)^{-1}\begin{pmatrix} tu(a-u-\frac{m}{u+b}-\frac{(1-e^{-\gamma u})v}{u})+Mu \\ tv(c-\frac{dv}{u+k})+Mv \end{pmatrix}.$$

Clearly, $F_t(u,v): [0,t]\times D\to W$ is a positive compact operator and $F_1=F$.

Lemma 6 Let $m<b^2, a>\lambda_1+m/b$. We have the following statements:

(i) $\deg_W(I-F,D)=1$,

(ii) If $c\neq\lambda_1$, then $\text{index}_W(F,(0,0))=0$,

(iii) If $c>\lambda_1$, then $\text{index}_W(F,(\tilde{u},0))=0$,

(iv) If $c<\lambda_1$, then $\text{index}_W(F,(\tilde{u},0))=1$.

Proof (i) It is clear that F has no fixed point on $\partial\Omega$. For any $t\in[0,1]$, the fixed point of F_t is equivalent to the solution of boundary value problem

$$\begin{cases} -\Delta u=tu(a-u-\frac{m}{u+b}-\frac{(1-e^{-\gamma u})v}{u}), & x\in\Omega, \\ -\Delta v=tv(c-\frac{dv}{u+k}), & x\in\Omega, \\ u=v=0, & x\in\partial\Omega. \end{cases}$$

According to Theorem 2, the fixed point of F_t satisfies $u\leqslant a, v\leqslant c(a+k)/d$ for any $t\in[0,1]$. Thus $\deg_W(I-F_t,D)$ does not depend on t from homotopic invariant property and

$$\deg_W(I-F,D)=\deg_W(I-F_1,D)$$
$$=\deg_W(I-F_0,D).$$

By the above boundary value problem has a unique solution (0, 0) as $t=0$, we have

$$\deg_W(I-F_0,D)=\text{index}_W(F_0,(0,0)).$$

Notice $\bar{W}_{(0,0)}\setminus S_{(0,0)}=\{K\times K\}\setminus\{(0,0)\}$. Denote $L_1=F_0'(0,0)$. Then

$$L_1=(-\Delta+M)^{-1}\begin{pmatrix} M & 0 \\ 0 & M \end{pmatrix}.$$

By $\lambda_1(0)=\lambda_1>0$ and Lemma 1, $r(L_1)<1$. It can derive that $I-L_1$ is invertible on $\bar{W}_{(0,0)}$ and L_1 has no α-property on $\bar{W}_{(0,0)}$. According to Lemma 4, we have

$$\deg_W(I-F,D)=\text{index}_W(F_0,(0,0))=1.$$

(ii) Let $L_2=F'(0,0)$. Then

$$L_2=(-\Delta+M)^{-1}\begin{pmatrix} a-\frac{m}{b}+M & 0 \\ 0 & c+M \end{pmatrix}.$$

At first, we will show that $I-L_2$ is invertible on $\bar{W}_{(0,0)}=K\times K$. If it is not true, then there is $(\xi,\eta)\in\bar{W}_{(0,0)}$ and $(\xi,\eta)\neq(0,0)$ such that $L_2(\xi,\eta)^T=(\xi,\eta)^T$, i.e.,

$$\begin{cases} -\Delta\xi=(a-\frac{m}{b})\xi, & x\in\Omega, \\ \xi=0, & x\in\partial\Omega. \end{cases}$$

If $\xi>0$, then $a-m/b=\lambda_1$, this is contrary to $a>m/b+\lambda_1$. Thus $\xi\equiv 0$. Similarly, $\eta\equiv 0$. This is a contradiction with $(\xi,\eta)\neq(0,0)$. Then $I-L_2$ is invertible on $\bar{W}_{(0,0)}$.

Now we claim that L_2 has α-property on $\bar{W}_{(0,0)}$. By $a>m/b+\lambda_1$ and Lemma 1,

$$r_1=r[(-\Delta+M)^{-1}(a-\frac{m}{b}+M)]$$
$$=r[(-\Delta+M)^{-1}(M-(-a+\frac{m}{b}))]>1.$$

Notice that r_1 is the principal eigenvalue of the operator $(-\Delta+M)^{-1}(a-m/b+M)$, and the corresponding eigenfunction is $\phi_1>0,\ x\in\Omega$. Take $t_1=1/r_1$, then $0<t_1<1$ and $(\phi_1,0)\in\bar{W}_{(0,0)}\setminus S_{(0,0)}$. Thus we have

$$(I-t_1L_2)(\phi_1,0)^{\mathrm{T}}=\begin{pmatrix}\phi_1-t_1(-\Delta+M)^{-1}(a-\dfrac{m}{b}+M)\phi_1\\0\end{pmatrix}=\begin{pmatrix}0\\0\end{pmatrix}\in S_{(0,0)}.$$

Therefore, L_2 has α-property. By Lemma 4, we have $\mathrm{index}_W(F,\ (0,0))=0$.

(iii) Obviously, (3) has a semi-trivial solution $(\tilde{u},0)$. Notice that $\bar{W}_{(\tilde{u},0)}=X\times K,\ \ S_{(\tilde{u},0)}=X\times\{0\}$, we have $\bar{W}_{(\tilde{u},0)}\setminus S_{(\tilde{u},0)}=X\times\{K\setminus\{0\}\}$. Let $L_3=F'(\tilde{u},0)$. There holds

$$L_3=(-\Delta+M)^{-1}\begin{pmatrix}a-2\tilde{u}-\dfrac{mb}{(\tilde{u}+b)^2}+M & -(1-\mathrm{e}^{-\gamma\tilde{u}})\eta\\0 & c+M\end{pmatrix}.$$

Assume that there exists $(\xi,\eta)\in\bar{W}_{(\tilde{u},0)}$ and $(\xi,\eta)\neq(0,0)$ such that $L_3(\xi,\eta)^{\mathrm{T}}=(\xi,\eta)^{\mathrm{T}}$. Then

$$\begin{cases}-\Delta\xi=(a-2\tilde{u}-\dfrac{mb}{(\tilde{u}+b)^2})\xi-(1-\mathrm{e}^{-\gamma\tilde{u}})\eta, & x\in\Omega,\\-\Delta\eta=c\eta, & x\in\Omega,\\\xi=\eta=0, & x\in\partial\Omega.\end{cases}$$

By $c>\lambda_1$, we have $\eta\equiv0$ in K. If $\xi\not\equiv0$, then the above boundary value problem can be written as

$$\begin{cases}-\Delta\xi=(a-2\tilde{u}-\dfrac{mb}{(\tilde{u}+b)^2})\xi, & x\in\Omega,\\\xi=0, & x\in\partial\Omega.\end{cases}$$

According to J_0 is invertible (see Lemma 5), we have $\xi\equiv0$. This contradiction leads to $I-L_3$ being invertible on $\bar{W}_{(\tilde{u},0)}$.

By Lemma 1 and $c>\lambda_1$, we also have

$$r_2=r[(-\Delta+M)^{-1}(c+M)]=r[(-\Delta+M)^{-1}(M-(-c))]>1.$$

Notice that r_2 is the principal eigenvalue of $(-\Delta+M)^{-1}(c+M)$ and the corresponding eigenfunction $\phi_2>0$. Take $t_2=1/r_2$, then $t_2\in[0,1]$. Thus $(0,\phi_2)\in\bar{W}_{(\tilde{u},0)}\setminus S_{(\tilde{u},0)}$, and

$$(I-t_2L_3)(0,\phi_2)^{\mathrm{T}}=\begin{pmatrix}t_2(-\Delta+M)^{-1}(1-\mathrm{e}^{-\gamma\tilde{u}})\phi_2\\0\end{pmatrix}\in S_{(\tilde{u},0)}.$$

It shows L_3 has α-properties. According to Lemma 4, there holds $\mathrm{index}_W(F,\ (\tilde{u},0))=0$.

(iv) It follows from the proof of (iii) that L_3 is invertible on $\bar{W}_{(\tilde{u},0)}$.

Now we claim L_3 has no α-properties on $\bar{W}_{(\tilde{u},0)}$. If it is not true, then there exist $0<t<1$ and $(\phi_3,\phi_4)\in\bar{W}_{(\tilde{u},0)}\setminus S_{(\tilde{u},0)}$ such that $(I-tL_3)(\phi_3,\phi_4)^{\mathrm{T}}\in S_{(\tilde{u},0)}$. Thus

$$\phi_4-t(-\Delta+M)^{-1}(c+M)\phi_4=0.$$

Notice that $\phi_4\in K\setminus\{0\}$, then $1/t$ is one eigenvalue of the $(-\Delta+M)^{-1}(c+M)$. On the other hand, by $c<\lambda_1$ and Lemma 1 we have $r_2=r[((-\Delta+M)^{-1})(c+M))]<1$, which is a contradiction.

According to L_3 has no α-property on $\bar{W}_{(\tilde{u},0)}$ and Lemma 4, we have

$$\mathrm{index}_W(F,(\tilde{u},0))=(-1)^{\sigma},$$

where σ is the sum of the algebraic multiplicities of the eigenvalues of L_3 which are larger than one.

Assume that $1/\mu>1$ is the eigenvalue of L_3, and the corresponding eigenfunction is $(\xi,\eta)^{\mathrm{T}}$. Then $L_3(\xi,\eta)^{\mathrm{T}}=(1/\mu)(\xi,\eta)^{\mathrm{T}}$. This can be written as

$$\begin{cases}-\Delta\xi+M\xi=\mu((a-2\tilde{u}-\dfrac{mb}{(\tilde{u}+b)^2}+M)\xi-(1-\mathrm{e}^{-\gamma\tilde{u}})\eta), & x\in\Omega,\\-\Delta\eta+M\eta=\mu(c+M)\eta, & x\in\Omega,\\\xi=\eta=0, & x\in\partial\Omega.\end{cases}$$

If $\eta\not\equiv0$, then the inequality

$$0\geqslant\lambda_1(M(1-\mu)-\mu c)>\lambda_1(-c)=\lambda_1-c$$

holds from the second equation of the above boundary value problem. This is a contradiction with $c<\lambda_1$. Thus $\eta\equiv0$. So $\xi\not\equiv0$. Then from the first equation of the above boundary value problem we have

$$0\geqslant\lambda_1(M(1-\mu)-\mu(a-2\tilde{u}-\frac{mb}{(\tilde{u}+b)^2}))>\lambda_1(-a+\tilde{u}+\frac{m}{\tilde{u}+b})=0.$$

This is an obvious contradiction. Therefore, L_3 has no eigenvalue greater than one, that is $\sigma=0$ and then

$$\mathrm{index}_W(F,\ (\tilde{u},0))=1.$$

It is similar to Lemma 6 that we can get Lemma 7.

Lemma 7 Let $c>\lambda_1$.

(i) If $a>\lambda_1(\gamma\tilde{v})+m/b$, then $\mathrm{index}_W(F,\ (0,\tilde{v}))=0$,

(ii) If $a<\lambda_1(\gamma\tilde{v})+m/b$, then $\mathrm{index}_W(F,\ (0,\tilde{v}))=1$,

where $\tilde{v}$ and F are given by (6) and (7), respectively.

Theorem 3 If $m<b^2,\ a>\lambda_1(\gamma\tilde{v})+m/b,\ \ c>\lambda_1$, then (3) has at least one positive solution.

Proof From the additivity of the degree, combining Lemma 6 and Lemma 7 we have

$$\begin{aligned}1&=\deg(I-F,D)\\&\neq\mathrm{index}_W(F,\ (0,0))+\mathrm{index}_W(F,\ (\tilde{u},0))+\mathrm{index}_W(F,\ (0,\tilde{v}))\\&=0+0+0.\end{aligned}$$

Therefore, (3) has at least one positive solution.

Remark 2 Theorem 3 shows that predator and prey can coexist as long as the Allee effect constant satisfies the appropriate conditions and the growth rates of predator and prey are appropriately large.

4 Uniqueness and Stability

In this section, we use the stability theory of linear operators to discuss uniqueness and stability of positive steady-state solutions. First, the following Lemma 8 is given.

Lemma 8 Let $m<b^2, a>\lambda_1+m/b, c>\lambda_1$. There exists a constant $\delta>0$ small enough, such that any positive solution of (3) is nondegenerate and linearly stable when $\gamma<\delta$ (if the positive solution exists).

Proof Assume that it is not true. For $\{\gamma_i\}_{i=1}^{\infty}$ with $\gamma_i\to 0$, there exists a sequence of positive solutions $\{(u_i,v_i)\}_{i=1}^{\infty}$ of (3), which are degenerate or unstable.

Now we suppose there are μ_i and (ξ_i,η_i), which satisfy $\mathrm{Re}(\mu_i)\leqslant 0$ and $\|\xi_i\|_{L^2}^2+\|\eta_i\|_{L^2}^2=1$, such that

$$L_{(u_i,v_i)}(\xi_i,\eta_i)^{\mathrm{T}}=\mu_i(\xi_i,\eta_i)^{\mathrm{T}},$$

where $L_{(u_i,v_i)}$ is the linearization operator of (3) at (u_i,v_i), i.e.,

$$\begin{cases}-\Delta\xi_i-(a-2u_i)\xi_i+\dfrac{mb}{(u_i+b)^2}\xi_i \\ \quad +\gamma_i v_i\mathrm{e}^{-\gamma_i u_i}\xi_i+(1-\mathrm{e}^{-\gamma_i u_i})\eta_i=\mu_i\xi_i, & x\in\Omega, \\ -\Delta\eta_i-(c-\dfrac{2dv_i}{u_i+k})\eta_i-\dfrac{dv_i^2}{(u_i+k)^2}\xi_i=\mu_i\eta_i, & x\in\Omega, \\ \xi_i=\eta_i=0, & x\in\partial\Omega.\end{cases}\tag{8}$$

Obviously, $(u_i,v_i)\to(\tilde{u},v^*)$ as $\gamma_i\to 0$, where v^* is a unique positive solution of the boundary value problem

$$\begin{cases}-\Delta v=v(c-\dfrac{dv}{\tilde{u}+k}), & x\in\Omega, \\ v=0, & x\in\partial\Omega.\end{cases}$$

Multiplying ξ_i and η_i both sides of the first and second equations in (8), respectively, then integrating on Ω and adding the results, we can get

$$\begin{aligned}\mu_i=&\int_\Omega[|\nabla\xi_i|^2+|\nabla\eta_i|^2]\mathrm{d}x \\ &+\int_\Omega[|\xi_i|^2(2u_i-a+\frac{mb}{(u_i+b)^2}+\gamma_i v_i\mathrm{e}^{-\gamma_i u_i})+(1-\mathrm{e}^{-\gamma_i u_i})\eta_i\bar{\xi}_i]\mathrm{d}x \\ &-\int_\Omega[|\eta_i|^2(c-\frac{2dv_i}{u_i+k})+\frac{dv_i^2}{(u_i+k)^2}\xi_i\bar{\eta}_i]\mathrm{d}x.\end{aligned}$$

Note that $\mathrm{Re}(\mu_i)\leqslant 0$, $\|\xi_i\|_{L^2}^2+\|\eta_i\|_{L^2}^2=1$ and u_i, v_i are both bounded according to Theorem 2. Thus $\{\mu_i\}_{i=1}^{\infty}$ is also bounded. Suppose $\mu_i\to\mu$, $\mathrm{Re}(\mu)\leqslant 0$ (take subsequences if necessary). By L^p estimates for (8), both ξ_i and η_i are also bounded in $W^{2,p}(\Omega)$ for $\forall p>n$. So there exists a convergent subsequence of (ξ_i,η_i), which is still denoted by (ξ_i,η_i) for the sake of convenience, such that $\xi_i\to\xi$, $\eta_i\to\eta$ in $W^{1,p}(\Omega)$. Taking the limit in (8) with respect to $\gamma_i\to 0$, then (μ,ξ,η) satisfies

$$\begin{cases}-\Delta\xi-a\xi+2\tilde{u}\xi+\dfrac{mb}{(\tilde{u}+b)^2}\xi=\mu\xi, & x\in\Omega, \\ -\Delta\eta-c\eta+\dfrac{2dv^*}{\tilde{u}+k}\eta-\dfrac{dv^{*2}}{(\tilde{u}+k)^2}\xi=\mu\eta, & x\in\Omega, \\ \xi=\eta=0, & x\in\partial\Omega,\end{cases}\tag{9}$$

under the condition of weak convergence. According to the regularity theory, (ξ,η) is a pair of classical solution of (9). It means that μ is a real number and $\mu\leqslant 0$.

If $\xi\not\equiv 0$, then μ is an eigenvalue of the problem

$$\begin{cases}-\Delta\phi-a\phi+2\tilde{u}\phi+\dfrac{mb}{(\tilde{u}+b)^2}\phi=\mu\phi, & x\in\Omega, \\ \phi=0, & x\in\partial\Omega.\end{cases}$$

Combining with Lemma 5, there holds

$$0\geqslant\mu\geqslant\lambda_1(-a+2\tilde{u}+\frac{mb}{(\tilde{u}+b)^2})>\lambda_1(-a+\tilde{u}+\frac{mb}{(\tilde{u}+b)^2})=0,$$

which is a contradiction. Thus $\xi\equiv 0$ and (9) can be written as

$$\begin{cases}-\Delta\eta-c\eta+\dfrac{2dv^*}{\tilde{u}+k}\eta=\mu\eta, & x\in\Omega, \\ \eta=0, & x\in\partial\Omega.\end{cases}$$

Similarly, if $\eta\not\equiv 0$, then

$$0\geqslant\mu\geqslant\lambda_1(-c+\frac{2dv^*}{\tilde{u}+k})>\lambda_1(-c+\frac{dv^*}{\tilde{u}+k})=0,$$

also a contradiction. So $(\xi,\eta)=(0,0)$, which is a new contradiction with $\|\xi_i\|_{L^2}^2+\|\eta_i\|_{L^2}^2=1$.

Theorem 4 Let $m<b^2$, $a>\lambda_1(\gamma\tilde{v})+m/b$, $c>\lambda_1$, and δ be a positive constant small enough, then (3) has a unique non-degenerate and linearly stable positive solution if $\gamma<\delta$.

Proof By Theorem 3 and Lemma 8, the existence of positive solution is clear. So we only show the rest of this Theorem.

At first, it is easy to verify that both trivial solution $(0,0)$ and semi-trivial solutions $(\tilde{u},0)$, $(0,\tilde{v})$ are all non-degenerate, linearly stable and isolated. According to the compactness theory[23], (3) has at most a finite number of positive solutions, which are recorded as $\{(u_i,v_i)\,|\,i=1,2,\cdots,k\}$. It is similar to the proof of Lemma 8 that $I-F'(u_i,v_i)$ is invertible on $\bar{W}_{(u_i,v_i)}$. Notice that $\bar{W}_{(u_i,v_i)}=X\times X=S_{(u_i,v_i)}$, we have $\bar{W}_{(u_i,v_i)}\setminus S_{(u_i,v_i)}=\varnothing$. Thus $F'(u_i,v_i)$ has no α-property.

Furthermore, $F'(u_i,v_i)$ has no eigenvalue which is greater than 1. According to Lemma 4, $\mathrm{index}_W(F,$

$(u_i, v_i)) = 1$. From the additivity of degree and combining Lemma 6 and Lemma 7, we have

$$\begin{aligned} 1 &= \deg_W(I-F, D) \\ &= \sum_{i=1}^{k} \text{index}_W(F, (u_i, v_i)) \ + \text{index}_W(F, (0,0)) \\ &\quad + \text{index}_W(F, (\tilde{u}, 0)) + \text{index}_W(F, (0, \tilde{v})) \\ &= k + 0 + 0 + 0 = k. \end{aligned}$$

It follows that $k = 1$. The uniqueness of the positive solution is obtained.

Remark 3 Theorem 4 shows that, as long as the Allee effect constant satisfies the appropriate relationship and the growth rate of predator and prey is appropriately large, the predator and prey not only coexist, but also the coexistence mode generated by low predator efficiency is stable.

5 Numerical Simulations

In this section, some numerical simulations for (2) and (3) in one-dimensional $\Omega = (0, 2\pi)$ will be carried out to verify the qualitative results of this paper. The algorithm used here is Pdepe in MATLAB. The initial value is taken as

$$(u_0(x), v_0(x)) = h(2|\sin x|, |\sin(x/2)|), \quad (10)$$

where h is a positive constant. The principal eigenvalue of $-\mathrm{d}^2/\mathrm{d}x^2$ under the homogeneous Dirichlet boundary conditions is $\lambda_1 = 0.25$ when $\Omega = (0, 2\pi)$[24]. By the property of the principal eigenvalue we have

$$\lambda_1(\gamma\tilde{v}) \leqslant \lambda_1\left(\frac{\gamma c(a+k)}{d}\right) = 0.25 + \frac{\gamma c(a+k)}{d},$$

and

$$a > \lambda_1(\gamma\tilde{v}) + m/b \text{ only if } a > \lambda_1 + \gamma c(a+k)/d + m/b.$$

(i) Existence of steady-state solutions

As is well known, when the solution of (2) does not change with time, it is called the steady-state solution of (2), which is the solution of (3). The other remark here is that the weak Allee effect constant relationship $m < ab$ can be satisfied when $a > \lambda_1 + m/b$. A large number of numerical simulations are consistent with Theorem 3. Some examples are provided in the following statements, where the parameters are given by

$$h = 0.1, \quad k = 0.8, \quad b = 0.5, \quad d = 0.3, \quad m = 0.2, \quad \gamma = 0.6.$$

Let $a = 0.1 < \lambda_1 + m/b, c = 0.2 < \lambda_1$. (3) has a unique solution $(0, 0)$, which is shown in Fig. 1.

Let $a = 0.7 > \lambda_1 + m/b, c = 0.2 < \lambda_1$. (3) has a unique semi-trivial solution $(u, 0)$, which is shown in Fig. 2.

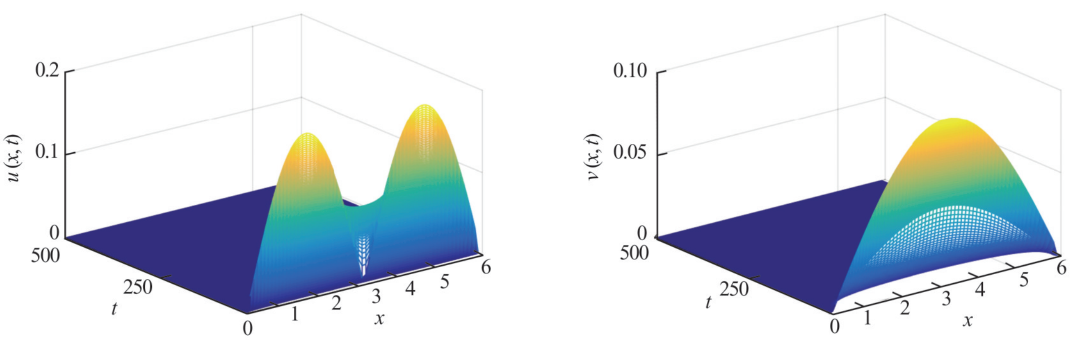

Fig. 1 Steady-state solution (0, 0)

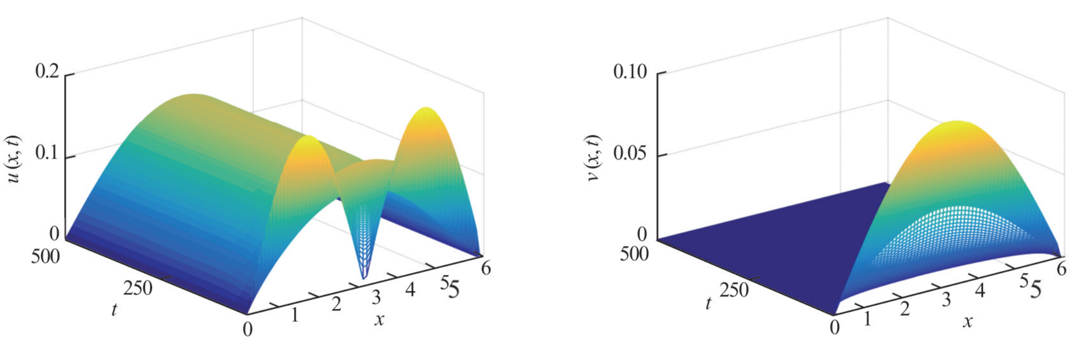

Fig. 2 Steady-state solution (*u*, 0)

Let $a=0.1<\lambda_1+m/b$, $c=0.6>\lambda_1$. (3) has a unique semi-trivial solution $(0, v)$, which is shown in Fig. 3.

Let $a=3>\lambda_1+\gamma c(a+k)/d+m/b$, $c=0.3>\lambda_1$, (3) has a positive solution (u, v), which is shown in Fig. 4.

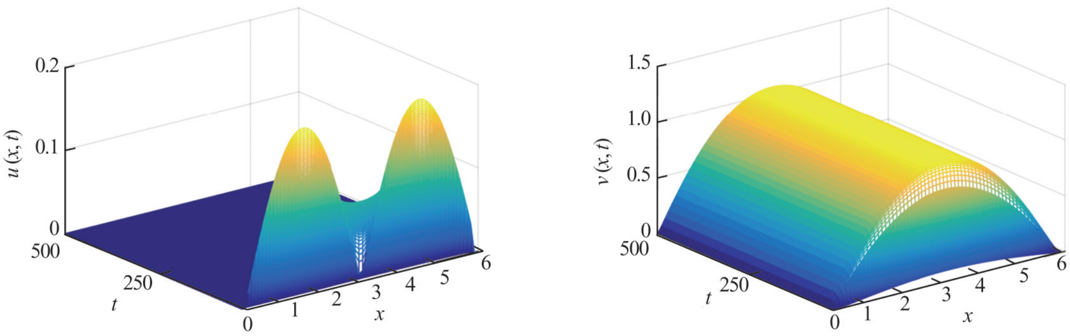

Fig. 3 Steady-state solution (0, *v*)

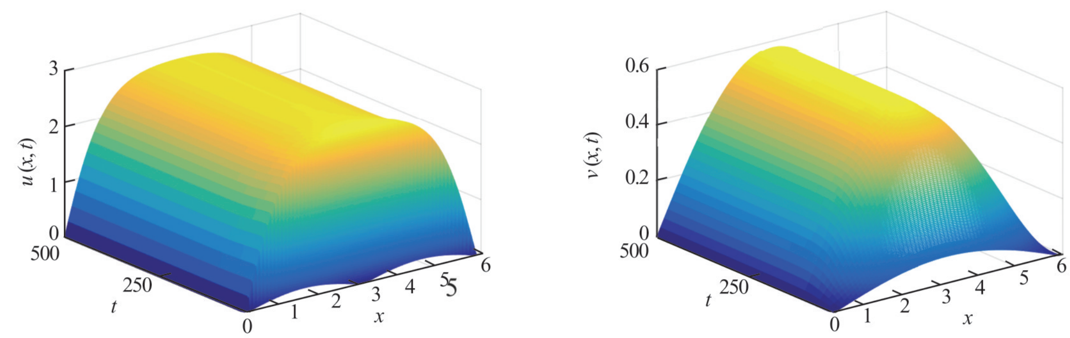

Fig. 4 Steady-state solution (*u*, *v*)

(ii) Influence of γ on the positive steady-state solutions

A large number of numerical simulations will verify the existence of steady-state solution when γ is sufficiently small. One of examples is shown in Fig. 5, which is consistent with the existence of positive solution in Theorem 4, where the parameters take

$$h=0.1,\ k=0.8,\ b=0.5,\ d=0.3,\ m=0.2,\ a=1,\ c=0.3,\ \gamma=0.000\,1. \tag{11}$$

Furthermore, a large number of numerical simulations show that predator and prey density decrease with the increase of predation rate γ. One of the examples is shown in Fig. 6, where $\gamma=0.001$, 0.1, 1, 2, 2.8 and the other parameters are given by (11).

In addition, our numerical simulations show that under appropriate parameters, (3) has still the positive steady-state solution even if the γ is large, which needs to be theoretically proved in future research. One example is shown in Fig. 7, where the parameters take

$$h=0.1,\ k=0.8,\ b=0.5,\ d=4,\ m=0.2,\ a=3.2,\ c=2.8,\ \gamma=3\,000. \tag{12}$$

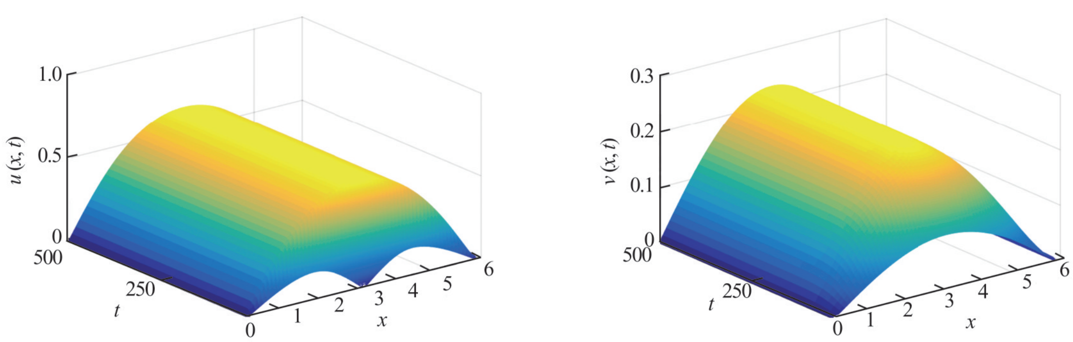

Fig. 5 Existence of steady-state solutions, $\gamma=0.000\,1$

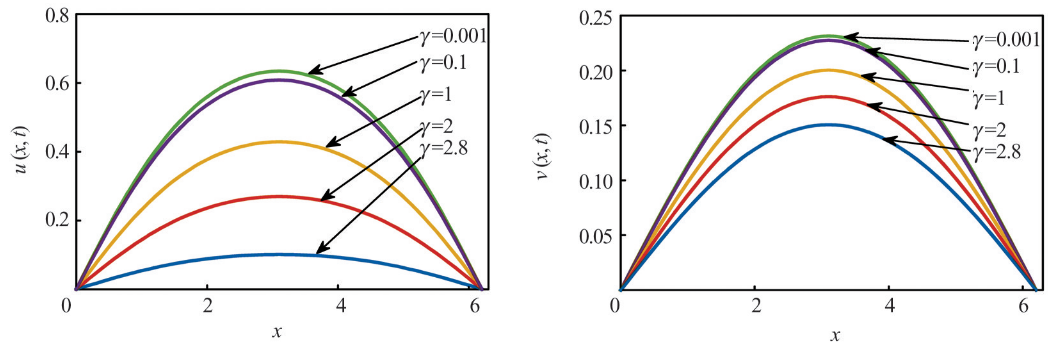

Fig. 6 Existence of steady-state solutions, $\gamma = 0.001,\ 0.1,\ 1,\ 2$ and 2.8

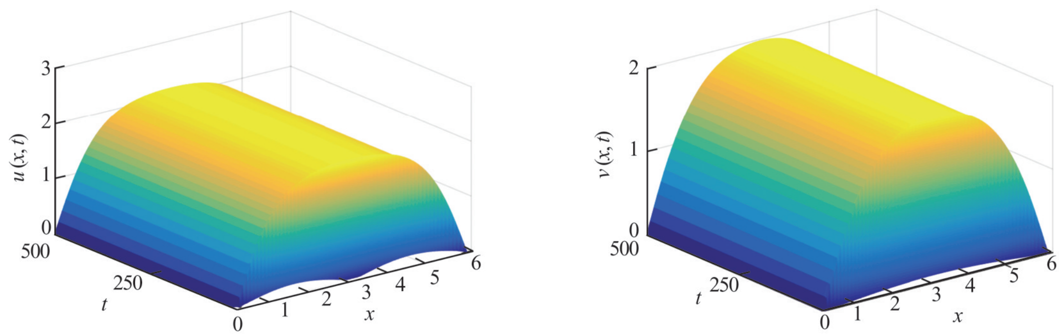

Fig. 7 Existence of steady-state solutions, $\gamma = 3\ 000$

(iii) Influence of γ on the stability of positive steady-state solutions

We change the initial value parameter h to simulate the disturbance of the initial value. For the convenience of discussion, the maximum norm of u with respect to x (denote it by $\| u \|$) is plotted by Pdepe. If u and v do not change with initial values after a long period of time, then u and v are stable. Otherwise, the steady-state solution is unstable. In fact, a large number of numerical simulations show that a positive steady-state solution is stable regardless of whether the γ is large or small.

For example, let $\gamma = 0.000\ 1$ and $h = 0.1$, 0.4, 0.8, 1.2, the other parameters are given by (11), see Fig. 8. This shows that the positive solution is stable, which is consisted with the stability of positive solution in Theorem 4.

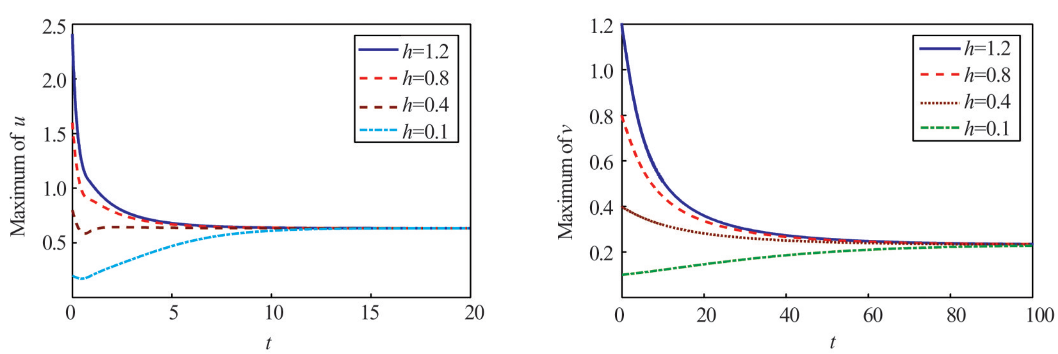

Fig. 8 Stability of steady-state solutions, $\gamma = 0.000\ 1$

Let $\gamma = 3\ 000$ and $h = 0.1$, 0.4, 0.8, 1.2, the other parameters are given by (12), see Fig. 9. This shows that the positive solution is also stable, but the theoretical proof of this conclusion needs to be studied further.

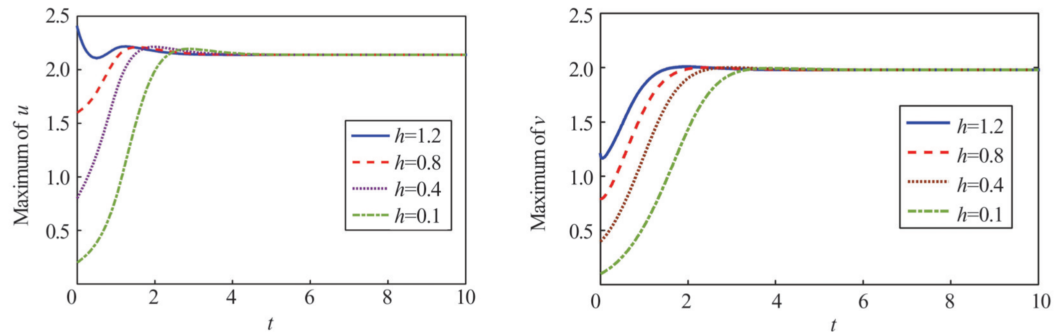

Fig. 9 Stability of steady-state solutions, $\gamma = 3\ 000$

6 Conclusion

We simulate the interaction between invertebrates and plankton using a modified Leslie-Gower predator-prey model with the Ivlev type functional response function, which is used to describe the fact that Tortanus dextrilubatus prey on zooplankton. Meanwhile, we also focus on the Allee effect in the model. Our research shows that under the Allee effect, predators and prey can coexist. Specifically, the growth rates of predators and prey can control the uniqueness of the coexistence pattern, which is consistent with the actual situation. We employ some numerical simulations primarily to verify the rationality of the conditions in this article, such as Lemma 8 and Theorem 4, etc. At the same time, we also verify the stability of the steady-state solutions by making small perturbations to the initial values. In a sense, these studies only provide a framework for model dynamics, and there are still some things that have not been studied, such as simulating the non-enclosure of habitats using Neumann boundary conditions, then the properties of constant and non-constant solutions of the model will be an interesting problem. In fact, more complex coexistence patterns of predator-prey systems can be examined through Turing pattern and Hopf bifurcation.

References

[1] Zhang C H, Yang W B. Dynamic behaviors of a predator-prey model with weak additive Allee effect on prey[J]. *Nonlinear Analysis*: *Real World Applications*, 2020, **55**: 103137.

[2] Aguirre P, González-Olivares E, Sáez E. Three limit cycles in a Leslie-Gower predator-prey model with additive Allee effect[J]. *SIAM Journal on Applied Mathematics*, 2009, **69** (5): 1244-1262.

[3] Cai Y L, Banerjee M, Kang Y, *et al*. Spatiotemporal complexity in a predator: Prey model with weak Allee effects[J]. *Mathematical Biosciences and Engineering*, 2014, **11**(6): 1247-1274.

[4] Pal P J, Mandal P K. Bifurcation analysis of a modified Leslie-Gower predator-prey model with Beddington-DeAngelis functional response and strong Allee effect[J]. *Mathematics and Computers in Simulation*, 2014, **97**: 123-146.

[5] Yang W S, Li Y Q. Dynamics of a diffusive predator-prey model with modified Leslie-Gower and Holling-type III schemes[J]. *Computers* & *Mathematics with Applications*, 2013, **65**(11): 1727-1737.

[6] Yang W B. Analysis on existence of bifurcation solutions for a predator-prey model with herd behavior[J]. *Applied Mathematical Modelling*, 2018, **53**: 433-446.

[7] Li S B, Wu J H, Dong Y Y. Uniqueness and stability of a predator-prey model with C-M functional response[J]. *Computers* & *Mathematics with Applications*, 2015, **69**(10): 1080-1095.

[8] Hooff R C, Bollens S M. Functional response and potential predatory impact of *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco Estuary[J]. *Marine Ecology Progress Series*, 2004, **277**: 167-179.

[9] Wang X C, Wei J J. Dynamics in a diffusive predator-prey system with strong Allee effect and Ivlev-type functional response[J]. *Journal of Mathematical Analysis and Applications*, 2015, **422**(2): 1447-1462.

[10] Wang H L, Wang W M. The dynamical complexity of a Ivlev-type prey-predator system with impulsive effect[J]. *Chaos*, *Solitons* & *Fractals*, 2008, **38**(4): 1168-1176.

[11] Wang X C, Wei J J. Diffusion-driven stability and bifurcation in a predator-prey system with *Ivlev-type functional response*[J]. *Applicable Analysis*, 2013, **92**(4): 752-775.

[12] Li S B, Wu J H, Nie H. Steady-state bifurcation and Hopf bifurcation for a diffusive Leslie-Gower predator-prey model [J]. *Computers* & *Mathematics with Applications*, 2015, **70**

(12): 3043-3056.

[13] Zhou J, Shi J P. The existence, bifurcation and stability of positive stationary solutions of a diffusive Leslie-Gower predator – prey model with Holling-type II functional responses[J]. *Journal of Mathematical Analysis and Applications*, 2013, **405**(2): 618-630.

[14] Cai Y L, Zhao C D, Wang W M, *et al*. Dynamics of a Leslie-Gower predator-prey model with additive Allee effect[J]. *Applied Mathematical Modelling*, 2015, **39**(7): 2092-2106.

[15] Yang L, Zhong S M. Dynamics of a diffusive predator-prey model with modified Leslie-Gower schemes and additive Allee effect[J]. *Computational and Applied Mathematics*, 2015, **34**(2): 671-690.

[16] Ma Z P. Spatiotemporal dynamics of a diffusive Leslie-Gower prey-predator model with strong Allee effect[J]. *Nonlinear Analysis*: *Real World Applications*, 2019, **50**: 651-674.

[17] Wang L J, Jiang H L. Properties and numerical simulations of positive solutions for a variable-territory model[J]. *Applied Mathematics and Computation*, 2014, **236**: 647-662.

[18] Cano-Casanova S. Existence and structure of the set of positive solutions of a general class of sublinear elliptic non-classical mixed boundary value problems[J]. *Nonlinear Analysis*: *Theory*, *Methods* & *Applications*, 2002, **49**(3): 361-430.

[19] Blat J, Brown K J. Global bifurcation of positive solutions in some systems of elliptic equations[J]. *SIAM Journal on Mathematical Analysis*, 1986, **17**(6): 1339-1353.

[20] Ye Q X, Li Z Y, Wang M X, *et al*. *Introduction to Reaction-Diffusion Equation*[M]. Beijing: Science Press, 2013(Ch).

[21] Pao C V. *Nonlinear Parabolic and Elliptic Equations*[M]. Cham: Springer-Verlag, 1992.

[22] Wang M X. *Nonlinear Elliptic Equation*[M]. Beijing: Science Press, 2007(Ch).

[23] Du Y H, Lou Y. Some uniqueness and exact multiplicity results for a predator-prey model[J]. *Transactions of the American Mathematical Society*, 1997, **349**(6): 2443-2475.

[24] Wang L J, Jiang H L. The multiplicity and uniqueness of positive solutions for a competition model with diffusion[J]. *Journal of Wuhan University* (*Natural Science Edition*), 2015, **61**(4): 308-314(Ch).

水生种群生态系统中具有无脊椎捕食者的捕食食饵模型定性分析与数值模拟

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摘要：无脊椎动物（例如溞溏水蚤）对水生种群生态系统中浮游生物的捕食机制是一个重要的研究课题。本文采用改进的Leslie-Gower捕食-食饵模型模拟了无脊椎动物和浮游生物之间的相互作用。利用反应扩散方程理论，建立了正稳态解的先验估计、存在性、惟一性和稳定性条件。此外，利用数值模拟定量分析了模型动力学行为。研究表明，只要Allee效应常数满足适当的关系、捕食者和食饵的生长速度适当大，捕食者和食饵不仅可以共存，而且在低捕食率下共存模式是惟一且稳定的。此外，数值模拟表明，在高捕食率下，也可能共存。同时，随着捕食率的增加，捕食者的种群密度会减小。

关键词：捕食-食饵模型；水生种群生态系统；Allee效应；Ivlev型功能反应函数；正稳态解；数值模拟

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