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CANARD CYCLE IN A SLOW-FAST BITROPHIC FOOD CHAIN MODEL IN CHEMOSTAT

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Abstract In this paper, we propose a predator-prey bitrophic food chain model with Monod type and Holling-II functional response function in the chemostat scenario. Suppose the speed of nutrition is slow and the conversion rate of predator is low, then the system can be altered to a slow-fast system. By using the geometric singular perturbation theory, we are able to prove the existence of canard cycles and the cyclicity of slow-fast cycles.

Keywords Geometric singular perturbation theory, chemostat, canard cycle, limit cycle, bifurcation theory.

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1. Introduction

A chemostat is a continuous culture system used to maintain the growth of cells or microbial communities. It is a widely-used tool in the fields of microbiology and ecology due to its ability to quantitatively describe the population dynamics of different species. In particular, lakes can be viewed as large-scale chemostats in the context of fishery resource management. Typically, the ecosystems within a lake are divided into distinct components, each with its own biological types and ecological characteristics. For instance, a lake can be divided into zones such as phytoplankton, zooplankton, benthos, and fish, with the harvest rate used to gauge the impact of fishing.

By applying dynamic analysis and numerical simulations to these models, we can predict the abundance of various organisms in lakes, the sustainability of fishery resources, and the impact of different fishery strategies. For instance, we can use models to assess the growth and mortality rates of fish at varying harvest rates, and to predict the changes in fish populations in lakes resulting from different fishery management practices. Furthermore, these models can help us evaluate the impact of nutrient limitations on ecosystems and explore ways to improve lake management to increase the sustainability of fishery resources. A chemostat model with a

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constant harvest term for fisheries resources can be described as follows:

$$\begin{aligned}\frac{dS}{dt} &= Q(S_0 - S) - \frac{f(S)}{\delta}x,\\ \frac{dx}{dt} &= f(S)x - g(x)y - Qx - K,\\ \frac{dy}{dt} &= pg(x)y - Qy,\end{aligned} \tag{1.1}$$

where S represents the substrate concentration, and x and y denote the populations of fish resources and their natural enemies, respectively. The functions $f(S)$ and $g(x)$ describe the predation abilities of species x and y, respectively. The parameter δ indicates that the growth of the fish population x is dependent on the constant consumption rate $\frac{1}{\delta}$ of nutrients from S [18]. The parameter K is used to quantify the output rate of fishery resources. In fishery resource management, a constant harvest quota is often implemented to protect the resources and ensure their sustainable development. This quota is applicable when there is a constant output, which can be influenced by the nutrient supply rate in the lake, the number of predators y, and their predation ability. Our objective is to investigate this intricate relationship.

As previously mentioned, analyzing the dynamics of model (1.1) is a compelling endeavor, yet challenging. Existing literature has shown that the dynamics of system (1.1) can differ greatly depending on the specific forms of $f(S)$ and $g(x)$. In [14], authors found the limit cycles may occur from Hopf bifurcation by simulation. In [22], authors considered the dynamics of the model, in which the functions $f(S)$ and $g(x)$ are Monod type functional response. They discussed the uniqueness of limit cycle in a triangular invariant manifold. In [17], authors studied the effects of toxins. They modified the $f(S)$ and $g(x)$ as more complicated functions, and found that it exhibits the bistability phenomenon and periodic solutions by numerical simulation. These complex phenomena reflect the complexity of such models. In [26], the authors considered models in which predators have Holling-I type functional response functions and prey group has Holling-II or Holling-I type functional response function. They proved the positive equilibrium is globally stable if it exists by Lyapunov function method. In [2], authors supposed the prey population is Holling-I type while predator population is Monod type. Then the positive equilibrium of their model could produce a stable limit cycle through supercritical Hopf bifurcation. Because there are two nonlinear functions in x equation, it is difficult to analyze the dynamics of the kind of models.

In order to overcome the technological difficulty, Kooi [18] introduced the geometric singular perturbation theory established by Fenichel [10–13] in chemostat food chain model. They considered the model with Holling-I type for prey population and Holling-II type for predator population (Mass Balance model). They also supposed the flow rate is very slow, and the gains and losses of predators are small enough relative to prey, then the system can be deduced as a slow-fast model. They found the global dynamics are determined by the slow manifold of the system totally. However, the global dynamics and bifurcation of both prey and predator populations with Holling-II functional response functions are still open. Another successful application of geometric singular perturbation theory to chemostat model is Poggiale et al. [23]. They proposed a four-dimensional model with viruses, susceptible bacteria, infectious bacteria and nutrients. They first reduced the model to two two-dimensional invariant submanifolds, which can intersect in some parameters ranges. Then they obtained the global stability of positive equilibrium, and pointed that the system may generate limit cycle under certain condition by simulation. More food chain models in chemostat can refer to [16, 19] and references therein.

The food chain models with nonlinear functional response in chemostat always have high dimensions, which lead to complicated dynamics. The geometric singular perturbation theory established by Fenichel is often employed to reduce the dimensions [10–13]. Meanwhile, the theory can be used to prove the persistence of compact normally hyperbolic critical manifolds under small perturbations, the existence and the fibrotic properties of centrally stable and unstable manifolds. Recently, this method was extended to study the dynamics of non-hyperbolic points by means of blow-up technique in phase plane [3,4,6,8], Krupa [20], Szmolyan [21], Wechselberger [25], and some interesting results were obtained, such as relaxation oscillation, canard explosion and so on. To study the cyclicity of period solution of slow-fast system, Dumortier and Roussarie developed the theory of slow divergence integra [9]. De Maesschalck, Dumortier and Roussarie [8], Zhang [24], Ruan [15] and Ai [1] developed the entry-exit function in two or more dimensional systems independently.

In the paper, we will analyze a food chain model with constant harvesting rate and discuss the cyclicity of limit cycle bifurcated by limit period set in view of above mentioned theory. The paper is organized as follows. In Section 2, a chemostat food chain model with Monod type functional response function and constant harvesting rate is proposed. After a topological transformation, the model is equivalent to a planar system. Under some assumption, the model can be changed to a slow-fast system. In section 3, the existence condition of canard slow-fast cycle is given. In section 4, we will discuss the cyclicity of slow-fast cycle. A brief discussion and a summary of the findings in the study are provided in the last section, and provide the biological explanation.

2. Model description

In the section, we will present our model with Monod type. Suppose $S(t)$, $X(t)$ and $Y(t)$ are the concentration of microorganisms, densities of preys and predators, respectively. In our model, we also include a constant harvest term K for the prey population. Based on above assumptions, we will consider the model as follows:

$$\begin{aligned}
\frac{dS}{dt} &= Q(S_0 - S) - \frac{\mu S X}{\delta(c+S)},\\
\frac{dX}{dt} &= \frac{\mu S X}{c+S} - \frac{\alpha X Y}{b+X} - QX - K,\\
\frac{dY}{dt} &= p\frac{\alpha X Y}{b+X} - QY,
\end{aligned} \tag{2.1a}$$

where S_0 is the initial nutrient density, μ and α are the maximal growth rates of microorganisms and predators, c and b are the Michaelis-Menten (or half-saturation) constants of microorganisms and predators. Q is the dilution rate, p is conversion rate and δ is yield constant reflecting the conversion of nutrition to organism. Taking a simple transform by $X = \delta x, Y = \delta p y$ and denote $k = \frac{K}{\delta}$, $S = s$, then the system

(2.1a) is changed as

$$
\begin{aligned}
\frac{ds}{dt} &= Q(S_0 - s) - \frac{\mu s x}{c+s},\\
\frac{dx}{dt} &= -Qx - k + \frac{\mu s x}{c+s} - \frac{p\alpha\delta x y}{b+\delta x},\\
\frac{dy}{dt} &= -Qy + \frac{p\alpha\delta x y}{b+\delta x}.
\end{aligned}
\tag{2.1b}
$$

Add all equations in (2.1b), we obtain $\frac{d(s+x+y)}{dt} = QS_0 - k - Q(s+x+y)$ and $s+x+y \to S_0 - \frac{k}{Q} := \Lambda$ as $t \to \infty$. Therefore, it is natural to study the behavior of system (2.1b) on the plane $s+x+y=\Lambda$. By using $s = \Lambda - x - y$, the system (2.1b) is reduced to

$$
\begin{aligned}
\frac{dx}{dt} &= -Qx - k + \frac{\mu(\Lambda - x - y)x}{c+\Lambda - x - y} - \frac{p\alpha\delta x y}{b+\delta x},\\
\frac{dy}{dt} &= -Qy + \frac{p\alpha\delta x y}{b+\delta x}.
\end{aligned}
\tag{2.1c}
$$

For mathematical simplicity, we first nondimensionalize model (2.1c) with the scaling as $x = \frac{k}{\mu}X, y = \frac{k}{\mu}Y, t = \frac{1}{\mu}T, m_1 = \frac{\Lambda\mu}{k}, m_2 = \frac{(c+\Lambda)\mu}{k}, \tilde{a} = \frac{kp\alpha\delta}{b\mu^2}, \hat{b} = \frac{k\delta}{b\mu}, \tilde{m} = \frac{Q}{\mu}$. Notice $m_1 < m_2$, and $x+y-m_2 < x+y-m_1 = \frac{k}{\mu}(X+Y-\Lambda) < 0$. To avoid the redundancy of symbols, we still denote $(X,Y,T) = (x,y,t)$, then the system (2.1c) takes the form

$$
\begin{aligned}
\frac{dx}{dt} &= -1 + \frac{x(x+y-m_1)}{x+y-m_2} - \frac{\tilde{a}xy}{\hat{b}x+1} - \tilde{m}x,\\
\frac{dy}{dt} &= -\tilde{m}y + \frac{\tilde{a}xy}{\hat{b}x+1}.
\end{aligned}
\tag{2.1d}
$$

From the first expression of (2.1d), $\frac{dx}{dt} < -1 - \tilde{m}x + \frac{(x+y-m_2)x}{x+y-m_2} - \frac{\tilde{a}xy}{\hat{b}x+1} = -1 + x - \tilde{m}x - \frac{\tilde{a}xy}{\hat{b}x+1} < 0$. Hence, if $x < 1$, the x population will continue to decrease until extinction. This situation is mathematically trivial. In fact, in population dynamics, we have the so-called "enrichment effect", which means that if the size of a population decreases below a certain threshold, the population will not be sustainable. Therefore, we always assume $x > 1$ in the following discussion.

In chemostat, to ensure the full use of nutrition, we assume the speed of nutrition is very slow, that is Q is smaller than other parameters. Meanwhile, the conversion rate p is small because the growth of per-capita $y(t)$ needs quite a few microorganisms, so we introduce a small positive parameter ϵ satisfying $0 < \epsilon \ll 1$. Let $\tilde{a} = \epsilon a, \tilde{m} = \epsilon m$, then the system (2.1d) becomes

$$
\begin{aligned}
\frac{dx}{dt} &= -1 + \frac{x(x+y-m_1)}{x+y-m_2} - \frac{\epsilon a x y}{\hat{b}x+1} - \epsilon m x,\\
\frac{dy}{dt} &= \epsilon\left(\frac{axy}{\hat{b}x+1} - my\right).
\end{aligned}
\tag{2.2a}
$$

Let $\tau = \epsilon t$, then the layer system is obtained by setting $\epsilon = 0$ in system (2.2a):

$$
\begin{aligned}
\frac{dx}{dt} &= \frac{x(x+y-m_1)}{x+y-m_2} - 1,\\
\frac{dy}{dt} &= 0,
\end{aligned}
\tag{2.2b}
$$

and the reduced system is obtained by some way:

$$\begin{aligned} 0 &= \frac{x(x+y-m_1)}{x+y-m_2} - 1, \\ \frac{dy}{d\tau} &= \frac{axy}{\hat{b}x+1} - my. \end{aligned} \tag{2.2c}$$

Let $S = \{(x,y) \in R^2 | y = m_1 - x - \frac{m_2-m_1}{x-1}\}$ be the critical manifold. By direct calculation, $y'(x) = \frac{m_2-m_1}{(x-1)^2} - 1$, $y''(x) = -\frac{2(m_2-m_1)}{(x-1)^3}$, we obtain S has a unique extreme point $M(x_M, y_M) = (1+\sqrt{m_2-m_1}, m_1 - 1 - 2\sqrt{m_2-m_1})$, which is also the unique maximum point when $m_1 > -1 + 2\sqrt{m_2}$ as shown in Fig (1)(Left),the shape of S is hyperbola. Consider the constraint of model in biological meaning, we only discuss the property in the region $D = \{(x,y)|0 < x+y \leq \Lambda, x > 1\}$. In order to $y_M > 0$, we always assume $m_2 < (m_1+1)^2/4$, i.e.

$$m_1 - 1 > 2\sqrt{m_2 - m_1} > 0. \tag{2.3}$$

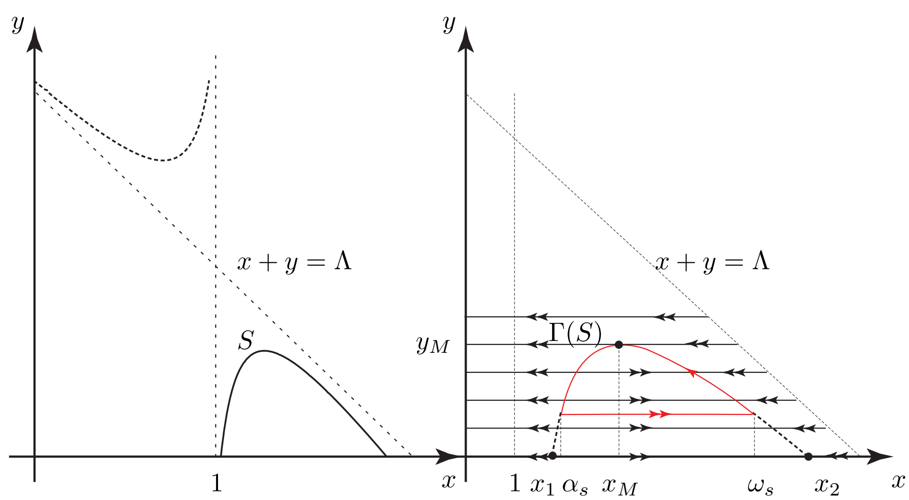

Figure 1. The critical manifold S and the limit period cycle $\Gamma(S)$. Left: S shape. Right: Slow-fast dynamics and Canard cycle without head.

3. The boundary equilibria of system (2.2a)

We first discuss existence of the equilibria of system (2.2a). When $y = 0$, there are two boundary equilibria $E_1 = (x_1^\epsilon, 0), E_2 = (x_2^\epsilon, 0)$, where the x_1^ϵ and x_2^ϵ are the roots of the following equation:

$$(1-\epsilon m)x^2 - (1 + m_1 - \epsilon m m_2)x + m_2 = 0, \tag{3.1}$$

and

$$\begin{aligned} x_1^\epsilon &= \frac{1 + m_1 - \epsilon m m_2 - \sqrt{\Delta}}{2(1-\epsilon m)} = x_1 + O(\epsilon), \\ x_2^\epsilon &= \frac{1 + m_1 - \epsilon m m_2 + \sqrt{\Delta}}{2(1-\epsilon m)} = x_2 + O(\epsilon), \end{aligned}$$

where

$$x_1 = \frac{1}{2}\left(m_1 + 1 - \sqrt{(m_1+1)^2 - 4m_2}\right),$$
$$x_2 = \frac{1}{2}\left(m_1 + 1 + \sqrt{(m_1+1)^2 - 4m_2}\right).$$

Obviously, the discriminant of equation (3.1) $\Delta = 4(-1+\epsilon m)m_2 + (1+m_1-\epsilon m m_2)^2 = m_1^2 + 2(1-\epsilon m m_2)m_1 + 1 + 2(\epsilon m - 2)m_2 + \epsilon^2 m^2 m_2^2$ is a quadratic equation for m_1. The constant term $\epsilon^2 m^2 m_2^2 + 2(\epsilon m - 2)m_2 + 1 > 0$ if $m_2 > m_{22}$ or $0 < m_2 < m_{21}$, and $\epsilon^2 m^2 m_2^2 + 2(\epsilon m - 2)m_2 + 1 < 0$ if $m_{21} < m_2 < m_{22}$, where $m_{21} = \frac{-\epsilon m + 2 - 2\sqrt{1-\epsilon m}}{\epsilon^2 m^2}, m_{22} = \frac{-\epsilon m + 2 + 2\sqrt{1-\epsilon m}}{\epsilon^2 m^2}$. Meanwhile, we can get $\Delta > 0 \Leftrightarrow m_1 > -1 + \epsilon m m_2 + 2\sqrt{m_2 - \epsilon m m_2}$. When $\Delta > 0$, there are two boundary singular points. Notice ϵ is infinite small, so both of the equilibria are positive if they exist by Vieta's formulas.

Suppose $E_i = (x_i^\epsilon, 0), (i = 1, 2)$ is an arbitrary equilibrium of the system (2.2a), then the Jacobian matrix at E_i is

$$\begin{pmatrix} \frac{(1-\epsilon m)x^2 + 2m_2(\epsilon m - 1)x + m_1 m_2 - \epsilon m m_2^2}{(x-m_2)^2} & x\left(-\frac{\epsilon a}{1+\hat{b}x} + \frac{m_1 - m_2}{(x-m_2)^2}\right) \\ 0 & \epsilon\left(\frac{ax}{1+\hat{b}x} - m\right) \end{pmatrix}.$$

Therefore, the eigenvalues are $\lambda_1 = \frac{(1-\epsilon m)x^2 + 2m_2(\epsilon m - 1)x + m_1 m_2 - \epsilon m m_2^2}{(x-m_2)^2}$, $\lambda_2 = \epsilon(\frac{ax}{1+\hat{b}x} - m)$. The sign of λ_1 is decided by the numerator $(1-\epsilon m)x^2 + 2m_2(\epsilon m - 1)x + m_1 m_2 - \epsilon m m_2^2 := \tilde{\lambda}_1 + O(\epsilon)$. For E_1,

$$\begin{aligned} \tilde{\lambda}_1 &= -2m_2^2 + 2m_1 m_2 - \left(m_1 - 2m_2\sqrt{m_2(m_2 - m_1)} + 1\right) \\ &= \sqrt{m_2(m_2 - m_1)}\left(2m_2 - m_1 - 2\sqrt{m_2(m_2 - m_1)}\right). \end{aligned}$$

According to the assumption in Remark 2.3, we can get $\tilde{\lambda}_1 > 0$. In view of $0 < \epsilon \ll 1$, $\lambda_1 > 0$ at equilibrium E_1. With the same discussion, we can also get $\lambda_1 < 0$ at E_2. In the paper, we aim to the existence and cyclicity of canard cycles, so we always suppose $x_1^\epsilon < \frac{\tilde{m}}{a - \hat{b}\tilde{m}} < x_2^\epsilon$. Therefore, we obtain the conclusion as follows:

Lemma 3.1. *If $m_1 > -1 + \epsilon\tilde{m}m_2 + 2\sqrt{m_2 - \epsilon\tilde{m}m_2}$ and $0 < \epsilon \ll 1$, there exist two boundary equilibria E_1 and E_2 of system (2.2a). Moreover, if $x_1^\epsilon < \frac{m}{a - \hat{b}m} < x_2^\epsilon$, both E_1 and E_2 are hyperbolic saddles.*

4. Existence of canard cycles

In the section, we will study the local behavior of system (2.2a). First, we give the existence condition of the positive equilibrium $E^*(x^*, y^*)$. For system (2.2a), the equilibrium $E^*(x^*, y^*)$ is satisfied with $x^* = \frac{m}{a - \hat{b}m} > 0$ when $a - \hat{b}m > 0$, and y^* is the root of the following equation

$$\begin{aligned} &\epsilon\tilde{m}(y^*)^2 + (1 - (1 - 2\epsilon\tilde{m})x^* - \epsilon\tilde{m}m_2)y^* \\ &-[(1-\epsilon\tilde{m})(x^*)^2 - (1 + m_1 - \epsilon\tilde{m}m_2)x^* + m_2] = 0. \end{aligned} \tag{4.1}$$

This is a quadratic equation of y^*. When $0 < \epsilon \le 1$, the discriminant of (4.1) is always greater than zero, which means there are two real roots of (4.1). Meanwhile, the coefficient of y^* is less than zero if $x^* > 1$. By Vieta's formulas, there are two positive equilibria of system (2.2a) if and only if the constant term of equation (4.1) is greater than zero. In fact, we can notice that the part of this constant term inside the square brackets is exactly the equation satisfied by the boundary equilibrium point, so to make the constant term of equation (4.1) greater than 0, we only need the horizontal coordinate of the positive equilibrium point to lie between the horizontal coordinates of the boundary equilibrium point, that is $x_1^\epsilon < x^* < x_2^\epsilon$. In view of above discussion, we can obtain

Lemma 4.1. *Suppose $x_1^\epsilon < x^* < x_2^\epsilon$, the system (2.2a) has a unique positive equilibrium $E^*(x^*, y^*)$ in the region $D = \{(x, y)|x > 1, 0 < x+y < \Lambda\}$, where x^*, y^* are satisfied with $x^* = \frac{m}{a-\hat{b}m}$ and (4.1).*

Remark 4.1. In Fig. (1)(Left), there is one intersection point at most of y-isoclinic line and critical manifold when $x > 1$, which is not contradictory with the conclusion that the system (4.1) has two real roots, because the asymptotic line of hyperbolic curve will change when parameters perturbations happen, but the y-isoclinic line is still the straight line $x^* = \frac{m}{a-\hat{b}m}$. Therefore, there maybe two intersection points with x-isoclinic line. The larger one is above the line $x + y = \Lambda$ and the smaller is below it. We only need to consider the smaller one.

In the paper, we focus on the Hopf bifurcation and canard explosion phenomenon. Canard explosion is process that a series of canard cycles generated by Hopf bifurcation become relaxation oscillation cycles. For our system, Hopf bifurcation maybe occur near by the fold point M. To study this process, we denote $\alpha = x_M, \beta = y_M$. we translate (x_M, y_M) to the origin by letting $x = x-\alpha, y = y-\beta$, then the system (2.2a) can be changed as

$$\begin{aligned}\frac{dx}{dt} &= -c_{01}y + c_{20}x^2 + c_{30}x^3 + O(x)^4 + \epsilon(c_\epsilon + c_{\epsilon 10}x + O(x)^2),\\ \frac{dy}{dt} &= \epsilon(d_0 + d_{10}x + d_{20}x^2 + d_{01}y + O(x,y)^3),\end{aligned} \tag{4.2}$$

where

$$\begin{aligned}
c_{01} &= \frac{\alpha(m_2-m_1)}{(\alpha+\beta-m_2)^2}, & c_{20} &= \frac{(\beta-m_2)(m_1-m_2)}{(\alpha+\beta-m_2)^3},\\
c_{30} &= \frac{(\beta-m_2)(m_2-m_1)}{(\alpha+\beta-m_2)^4}, & c_\epsilon &= -\frac{\alpha\beta a}{1+\alpha\hat{b}} - \alpha m,\\
c_{\epsilon 10} &= -\frac{\beta a + m(1+\alpha\hat{b})^2}{(1+\alpha\hat{b})^2}, & &\\
d_0 &= \beta\left(\frac{\alpha a}{1+\alpha\hat{b}} - m\right), & d_{10} &= \frac{a\beta}{(1+\alpha\hat{b})^2},\\
d_{20} &= -\frac{\beta a\hat{b}}{(1+\alpha\hat{b})^3}, & d_{01} &= \frac{\alpha a}{1+\alpha\hat{b}} - m.
\end{aligned}$$

Make a change of variables as follows: $x = \frac{\sqrt{d_{10}}\sqrt{c_{01}}}{c_{20}}X, y = \frac{d_{10}}{c_{20}}Y, = \frac{1}{\sqrt{d_{10}}\sqrt{c_{01}}}T$, and still denote (X,Y,T) by (x,y,t), then the system (4.2) can be written as

$$\begin{aligned}\frac{dx}{dt}&=-yh_1(x,y,\lambda)+x^2h_2(x,y\lambda)+\epsilon h_3(x,y,\lambda),\\ \frac{dy}{dt}&=\epsilon\left(xh_4(x,y,\lambda)-\lambda h_5(x,y,\lambda)+yh_6(x,y,\lambda)\right),\end{aligned}\tag{4.3}$$

where

$$h_1(x,y,\lambda)=1, \qquad h_2(x,y,\lambda)=1+\frac{\sqrt{c_{01}}c_{30}\sqrt{d_{10}}}{c_{20}^2}x,$$

$$h_3(x,y,\lambda)=\frac{c_\epsilon c_{20}}{c_{01}d_{10}}+\frac{c_{\epsilon 10}}{\sqrt{c_{01}}\sqrt{d_{10}}}x, \quad h_4(x,y,\lambda)=1+\frac{\sqrt{c_{01}}d_{20}}{c_{20}\sqrt{d_{10}}}x,$$

$$h_5(x,y,\lambda)=1, \qquad h_6(x,y,\lambda)=\frac{d_{01}}{\sqrt{c_{01}}\sqrt{d_{10}}}, \qquad \lambda=-\frac{d_0c_{20}}{\sqrt{c_{01}}d_{10}^{\frac{3}{2}}}.$$

Obviously, $\lambda=0$ is equal to $m=\frac{\alpha a}{1+\alpha\hat{b}}$.

$$d_{10}|_{\lambda=0}=\frac{\beta a}{(1+\alpha\hat{b})^2},\ d_{20}|_{\lambda=0}=-\frac{\beta a\hat{b}}{(1+\alpha\hat{b})^3},\ d_{01}|_{\lambda=0}=0.$$

By direct calculation,

$$\begin{aligned}a_1&=\frac{\partial h_3}{\partial x}|_{(0,0,0)}=\frac{(\alpha+\beta+\alpha^2\hat{b})\sqrt{a}(\alpha+\beta-m_2)}{(1+\alpha\hat{b})\sqrt{\alpha\beta(m_2-m_1)}},\\ a_2&=\frac{\partial h_1}{\partial x}|_{(0,0,0)}=0,\\ a_3&=\frac{\partial h_2}{\partial x}|_{(0,0,0)}=\frac{\alpha\sqrt{\beta a}(\alpha+\beta-m_2)}{(1+\alpha\hat{b})(m_2-\beta)\sqrt{\alpha(m_2-m_1)}},\\ a_4&=\frac{\partial h_4}{\partial x}|_{(0,0,0)}=\frac{\alpha\hat{b}\sqrt{\beta a}(\alpha+\beta-m_2)^2}{(1+\alpha\hat{b})(m_2-\beta)\sqrt{\alpha(m_2-m_1)}},\\ a_5&=h_6(0,0,0)=0,\end{aligned}$$

and

$$\begin{aligned}A&=-a_2+3a_3-2a_4-2a_5\\ &=\frac{\alpha\sqrt{\beta a}\,(\alpha+\beta-m_2)\left(\hat{b}\,(\alpha-2\beta+2m_2)+3\right)}{\left(\alpha\hat{b}+1\right)^2\sqrt{\alpha\,(m_2-m_1)}\,(m_2-\beta)}\\ &<0.\end{aligned}$$

Next, we will show the sign of A is defined. First recall $\alpha=x_M,\beta=y_M$, and all parameters mentioned in model are positive, then

$$\begin{aligned}&\alpha+\beta-m_2=m_1-m_2-\sqrt{m_2-m_1}=-\sqrt{m_2-m_1}(\sqrt{m_2-m_1}+1)<0,\\ &m_2-\beta=1+m_2-m_1+2\sqrt{m_2-m_1}.\end{aligned}$$

Note $m_2>m_1$, then $m_2-\beta>0$ and $\hat{b}\,(\alpha-2\beta+2m_2)+3>0$. This means that A¡0. By the normal form (4.3) and Theorem 3.1 in [21], we obtain the existence of supercritical Hopf bifurcation. What needs to be pointed out here is that another method for calculating the first Lyapunov coefficient is given in a recent article [3], and we can verify that the same calculation result can be obtained by this method.

Theorem 4.1. *Suppose* $1 < m_1 < m_2 < \frac{(m_1+1)^2}{4}$, $m = \frac{a\alpha}{1+\alpha\hat{b}}$, *then there exist* $\epsilon_0 > 0$ *and* $\lambda_0 > 0$ *such that for* $0 < \epsilon < \epsilon_0$, $|\lambda| < \lambda_0$, *the system (2.2a) has a unique positive equilibrium* E^* *in* $D = \{(x,y)|x > 1, 0 < x+y < \Lambda\}$, *which converges to the canard point* M *as* $(\epsilon, \lambda) \to (0,0)$. *Furthermore, there exists a curve* $\lambda_H(\sqrt{\epsilon})$ *such that* E^* *is stable when* $\lambda < \lambda_H(\sqrt{\epsilon})$. *And when* λ *passes through the curve* $\lambda_H(\sqrt{\epsilon})$, *the system undergoes a supercritical Hopf bifurcation, here,*

$$\begin{aligned}\lambda_H(\sqrt{\epsilon}) &= -\left(\frac{a_1+a_5}{2}\right)\epsilon + O\left(e^{3/2}\right)\\ &= \frac{\sqrt{\beta a}\left(\alpha+\alpha^2\hat{b}+\beta\right)(m_2-\alpha-\beta)}{2\sqrt{\alpha(m_2-m_1)}\left(\alpha\hat{b}\beta+\beta\right)}\epsilon + O\left(e^{3/2}\right).\end{aligned}$$

And by the theorem 3.5 of [21], we have the following

Theorem 4.2. *Suppose* $1 < m_1 < m_2 < \frac{(m_1+1)^2}{4}$, $m = \frac{a\alpha}{1+\alpha\hat{b}}$. *For system (2.2a), a* ϵ*-family of canard cycle without head* $\Gamma(\epsilon, s)$ *bifurcates from the limit periodic set* $\Gamma(s)$ *for* $s \in (0, y_M)$ *and some small* $\lambda = \lambda(s, \sqrt{\epsilon})$, $0 < \epsilon \ll 1$. *Moreover,* $\lambda(s, \sqrt{\epsilon})$ *satisfies*

$$|\lambda(s,\sqrt{\epsilon}) - \lambda_c(\sqrt{\epsilon})| \le e^{-1/\epsilon^K},$$

where $K > 0$ *is a constant and*

$$\begin{aligned}&\lambda_c(\sqrt{\epsilon})\\ &= -\left(\frac{a_1+a_5}{2}+\frac{A}{8}\right)\epsilon + O\left(\epsilon^{3/2}\right)\\ &= \frac{\sqrt{\beta a}(m_2-\alpha-\beta)}{2\sqrt{\alpha(m_2-m_1)}}\left(\frac{\alpha+\alpha^2\hat{b}+\beta}{\alpha\hat{b}\beta+\beta} + \frac{\alpha\left(\hat{b}(\alpha-2\beta+2m_2)+3\right)}{4\left(\alpha\hat{b}+1\right)^2(m_2-\beta)}\right)\epsilon + O\left(\epsilon^{3/2}\right).\end{aligned}$$

Remark 4.2. In order to get a better interpretation for the biological meaning of our system, we use the original parameters of system (2.2a) to describe the bifurcation curve, that is

$$\begin{aligned}\lambda = \lambda_H(\sqrt{\epsilon}) \Leftrightarrow m &= \frac{\alpha a}{\alpha\hat{b}+1} + \frac{a^2\left(\alpha+\alpha^2\hat{b}+\beta\right)(\alpha+\beta-m_2)^2}{2(m_2-m_1)(m_2-\beta)\left(\alpha\hat{b}+1\right)^4}\epsilon + O\left(\epsilon^{3/2}\right),\\ \lambda = \lambda_c(\sqrt{\epsilon}) \Leftrightarrow m &= \frac{\alpha a}{\alpha\hat{b}+1} + \frac{\alpha a^2(\alpha+\beta-m_2)^2}{8\left(\alpha\hat{b}+1\right)^5(\alpha(m_2-m_1))(\beta-m_2)^2}\\ &\quad\times\left(2m_2\left(2(\alpha+\beta)+\alpha\hat{b}\left(4\alpha+2\alpha^2\hat{b}+3\beta\right)\right)\right)\\ &\quad-\beta\left(\alpha+\alpha\hat{b}\left(7\alpha+4\alpha^2\hat{b}+6\beta\right)+4\beta\right)\epsilon + O\left(\epsilon^{3/2}\right).\end{aligned}$$

5. Cyclicity of the slow-fast cycles

In the section, we will discuss the cyclicity of the slow-fast cycles by the slow divergence integral. Denote system (2.2c) as $X_{\epsilon,\lambda}$, where λ is the bifurcation parameter.

We know that $\lambda = 0$ is equal to $m = \frac{a\alpha}{1+\alpha\hat{b}}$, so there is a slow-fast cycle without head $\Gamma(s)$, $s \in (0, y_M), \alpha_s \in (x_1, x_M), \omega_s \in (x_M, x_2)$,

$$\Gamma(s) := \{(x, F(x))|x \in (\alpha_s, \omega_s)\} \bigcup \{(x, y_M - s)|x \in (\alpha_s, \omega_s)\}, s \in (0, y_M).$$

We first give the following lemma [5] to discuss the cyclicity $Cycl(X_{\epsilon,\lambda}, \Gamma(s_0), (0, \lambda_0)$ of the slow-fast cycles.

Lemma 5.1. *For the slow divergence integral*

$$I(s, \lambda_0) = \int_{\omega_s}^{\alpha_s} \frac{\partial f}{\partial x}(x, F(x), \lambda_0, 0) \frac{F'(x)}{g(x, F(x), \lambda_0, 0)} dx,$$

let $s_0 \in (0, y_M)$, then the following conclusions hold:
(1) if $I(s_0, \lambda_0) \neq 0$, then $Cycl(X_{\epsilon,\lambda}, \Gamma(s_0), (0, \lambda_0)) \leq 1$, and the limit cycle banached from $\Gamma(s_0)$ is hyperbolic, further more, the limit cycle is stable when $I(s_0, \lambda_0) < 0$, and unstable when $I(s_0, \lambda_0) > 0$.
(2) if $I(s_0, \lambda_0) = 0$ and $\frac{\partial I}{\partial s}(s_0, \lambda_0) \neq 0$, then $Cycl(X_{\epsilon,\lambda}, \Gamma(s_0), (0, \lambda_0)) \leq 2$;
(3) if $I(s_0, \lambda_0) = 0$ and (s_0, λ_0) is a zero point of $\frac{\partial I}{\partial s}$ with multiplicity m, then $Cycl(X_{\epsilon,\lambda}, \Gamma(s_0), (0, \lambda_0)) \leq 2 + m$.

Now, define $\sigma = \sigma(x)$, which is satisfied with $F(\sigma(x)) = F(x)$ for $x \in (x_M, x_2)$ and $\sigma(x) \in (x_1, x_M)$. Meanwhile, (x_M, y_M) is the unique extreme point of critical manifold S and it is a maximum point, it is obvious that $\sigma(x_M) = x_M$, $\sigma(\omega_s) = \alpha_s$. Moreover, by simply calculation, we can get $\sigma(x_2) = x_1$ and

$$\frac{d\sigma(x)}{dx} = \frac{F'(x)}{F'(\sigma(x))}, \qquad x \in (x_1, x_M). \tag{5.1}$$

Therefore, function $y = F(x), x \in (x_1, x_M)$ has a unique reversible single-valued continuous function $x = F^{-1}(x), y \in (0, y_M)$ according to the implicit function theorem. Define

$$h(x) = \frac{\frac{\partial f}{\partial x}(x, F(x), \lambda_0, 0)}{g(x, F(x), \lambda_0, 0)}, \tag{5.2}$$

then along the system(2.2a), we have

Lemma 5.2. *The slow divergence integral $I(s, \lambda_0)$ is equal to*

$$\int_{y_M}^{y_M - s} (h(\sigma) - h(x)) \,|_{\sigma(x) = x, x = F^{-1}(y)} \, dy.$$

Proof.

$$\begin{aligned} I(s, \lambda_0) = &\int_{x_M}^{\alpha_s} \frac{\partial f}{\partial z}(z, F(z), \lambda_0, 0) \frac{F'(z)}{g(z, F(z), \lambda_0, 0)} dz \\ &- \int_{x_M}^{\omega_s} \frac{\partial f}{\partial x}(x, F(x), \lambda_0, 0) \frac{F'(x)}{g(x, F(x), \lambda_0, 0)} dx. \end{aligned}$$

For the first integral, make a change of variable $z = \sigma(x)$, then

$$\begin{aligned} I(s, \lambda_0) = \int_{x_M}^{\alpha_s} &\frac{\partial f}{\partial z}(\sigma, F(\sigma), \lambda_0, 0) \frac{F'(\sigma)}{g(\sigma, F(\sigma), \lambda_0, 0)} \frac{d\sigma(x)}{dx} \\ &- \frac{\partial f}{\partial x}(x, F(x), \lambda_0, 0) \frac{F'(x)}{g(x, F(x), \lambda_0, 0)} dx. \end{aligned}$$

According to (5.1), we get

$$I(s,\lambda_0)=\int_{x_M}^{\alpha_s}\left(\frac{\frac{\partial f}{\partial x}(\sigma,F(\sigma),\lambda_0,0)}{g(\sigma,F(\sigma,\lambda_0,0))}-\frac{\frac{\partial f}{\partial x}(x,F(x),\lambda_0,0)}{g(x,F(x),\lambda_0,0))}\right)F'(x)dx.$$

By use of $y=F(x), x\in(x_m,\alpha_s)$ and (5.2), the conclusion holds. □

Next, we discuss the sign of function $h(\sigma)-h(x)$. First, define

$$\begin{aligned}h(x)&=\frac{(1-x)(1+\hat{b}x)(1+\alpha\hat{b})((1-x)^2+m_1-m_2)}{x(x-\alpha)\tilde{a}(m_1-m_2)(m+2+-1+x-m_1)x)},\\ \sigma(x)&=\frac{1}{2}\left(1-y+m_1-\sqrt{(1-y+m_1)^2+4(y-m_2)}\right),\end{aligned}$$

here $y\le y_M$ and

$$x=\frac{1}{2}\left(1-y+m_1+\sqrt{(1-y+m_1)^2+4(y-m_2)}\right).$$

By direct calculation, it is easy to get

$$\sigma(x)+x=1-y+m_1, \sigma(x)x=m_2-y.$$

So

$$\begin{aligned}h(\sigma(x))-h(x)&=\frac{1+\alpha\hat{b}}{a(m_1-m_2)}\left(\frac{(x-1)(1+\hat{b}x)((x-1)^2+m_1-m_2)}{x(x-\alpha)(x(-1+x-m_1)+m_2)}\right.\\ &\quad\left.-\frac{(\sigma-1)(1+\sigma\hat{b})((\sigma-1)^2+m_1-m_2)}{\sigma(\sigma-\alpha)(\sigma(\sigma-1-m_1)+m_2)}\right)\\ &=-\frac{(1+\alpha\hat{b})y(m_2-y)\sqrt{(1-y+m_1)^2+4(y-m_2)}}{a(m_2-m_1)\sigma(\sigma-\alpha)x(x-\alpha)}\times\frac{G(y)}{h_1(x)h_1(\sigma)},\end{aligned}\tag{5.3}$$

here

$$\begin{aligned}&h_1(x)=x(x-1-m_1)+m_2=x^2-(m_1+1)x+m_2,\\ &G(y)=g_1(\hat{b})y^2+g_2(\hat{b})y+g_3,\end{aligned}\tag{5.4}$$

where,

$$\begin{aligned}g_1(\hat{b})&=(-1+\alpha)\hat{b},\\ g_2(\hat{b})&=1-\alpha-m_1+m_2-\hat{b}(1-\alpha+(1+\alpha)m_1+(-3+\alpha)m_2),\\ g_3(\hat{b})&=1-\alpha+m_1^2+(-3+2\alpha+\hat{b}-\alpha\hat{b})m_2-2\hat{b}m_2^2\\ &\quad+m_1(2-\alpha+(-1+\hat{b}+\alpha\hat{b})m_2).\end{aligned}$$

It is easy to find x_1 and x_2 are exactly the intersection points of $y=h_1(x)$ and the x-axis. And $h_1(x),h_1(\sigma)<0$ because of $x\in(x_M,x_2)$, $\sigma(x)\in(x_1,x_M)$, $y<m_2$. Thus, the sign of $h(\sigma)-h(x)$ is determined by $G(y)$ and we only need to discuss the function $G(y)$.

It is easy to prove $g_3{}'(\hat{b}) = m_2\sqrt{m_2-m_1}(m_1-1-2\sqrt{m_2-m_1}) > 0$, so $g_3(\hat{b})$ is increasing for $\hat{b}$, then when $m_2 < m_1+1$,

$$\begin{aligned} g_3(\hat{b}) &> g_3(0) \\ &= m_1^2 - \sqrt{m_2-m_1} - m_1(-1+m_2+\sqrt{m_2-m_1}) + m_2(-1+2\sqrt{m_2-m_1}) \\ &= (m_1-1-2\sqrt{m_2-m_1})\sqrt{m_2-m_1}(1-\sqrt{m_2-m_1}) \\ &> 0. \end{aligned}$$

For $g_2(\hat{b})$, we have

$$\begin{aligned} g_2'(\hat{b}) &= \sqrt{m_2-m_1}(1-m_2-m_1+2\sqrt{m_2-m_1}) \\ &= -\sqrt{m_2-m_1}((\sqrt{m_2-m_1}-1)^2+2(m_1-1)) \\ &< 0, \end{aligned}$$

that is $g_2(\hat{b})$ is decreasing for $\hat{b}$, thus

$$g_2(\hat{b}) < g_2(0) = \sqrt{m_2-m_1}(\sqrt{m_2-m_1}-1) < 0.$$

Let $G'(y) = 2g_1y + g_2 = 0$, then the stationary point is $y = -\frac{g_2}{2g_1}$, that is $G(y)$ is monotone decreasing for $y < -\frac{g_2}{2g_1}$ and increasing for $y > -\frac{g_2}{2g_1}$. By direct calculation, when $m_2 < m_1 - 1$, we get $-\frac{g_2}{2g_1} > y_M$ because of

$$-g_2 - 2g_1y_M = \sqrt{m_2-m_1}(1-\sqrt{m_2-m_1}) + \hat{b}(\sqrt{m_2-m_1}+1)^2 > 0.$$

Therefore, $G(y) > G(y_M) = 0$ for all $0 < y < y_M$.

Now, we discuss the sign of $I(s,\lambda_0)$. For $x \in (x_M, x_2)$, $\sigma(x) \in (x_1, x_M)$. Since $y < m_2$, $h_1(x) < 0$, $h_1(\sigma) < 0$, so we can get $I(s,\lambda_0) < 0$ for $x \in (x_M, x_2)$ directly. By Fenichels invariant manifold theory [10–13] and slow divergence integral theory [7], the following result is hold:

Theorem 5.1. *For system (2.2a), if $1 < m_1 < m_2 < \frac{(m_1+1)^2}{4}$, all of canard cycles without head $\Gamma(s,\sqrt{\epsilon})$ can bifurcate from $\Gamma(s)$, and $Cycl(X_{\epsilon,\lambda}, \Gamma(s), (0,\lambda_0)) \leq 1$. Moreover, all the canard cycles are stable.*

6. Discussion

The study of dynamics of food chain models is very difficult because of high dimensions and complicated dynamic phenomena.

The paper [18] points out the existence of limit cycles in such models. However, the cyclicity of limit cycles has not been resolved yet. In this paper, we establish a chemostat model with constant yield. Unlike the classic predator-prey models and chemostat models without harvesting, our model has no positive invariant set, which leads to difficulty for analysis. However, we study the existence of canard cycle without head in section 4 by the theory of geometric singular perturbation, and prove the cyclicity of canard cycle bifurcated from slow-fast limit periodic set is 1 in section 5. These results reflect the complexity of our system.

As well known, the chemostat model can simulate the dynamics evolution process of population numbers in predicting the population in lakes, making it easier for management agencies to assess the sustainability of fishery resources. In our model, introduced predator populations are seen as an invader, and they contaminate the preparation unit. However, the natural conditions of the chemostat are not very suitable for the growth of these invaders, so we assume that the conversion rate of invaders to food bait is extremely small. Our results show that invaders can survive and produce a slow-fast oscillation with the microbial population even if in a very hostile environment. This oscillation can have very serious consequences. For example, the size of the population becomes so small that it cannot maintain a minimum viable population. This puts microbial populations at risk of extinction, though the pollution mentioned above occurs on a small scale . Hence, our results may be useful for applications in biological practice.

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