Mathematical studies on resource competition and delayed feedback mechanism in biological systems

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Doctoral Thesis

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Preface

Resource competition is common in nature. The difference of resource exploitation among competitively interacting species often has a great impact on the population growth and determines the fate of species. The competitive exclusion principle (CEP) predicts that the number of species competing for the several available resources cannot exceed the number of available resources in steady state. Several basic mathematical models describing the resource competition for the limiting resources have been proposed and the consequences agree with the CEP. Of course, this prediction does not explain correctly what is observed in nature. This paradox has fascinated to propose driving factors which facilitate the coexistence of species in resource competition as opposed to the CEP. It is important not only to show or explain how competing species can coexist, but also to figure out the mathematical structure of resource competition systems. Notably, to figure out the mathematical structure of the resource competition system often relates to understand the mechanisms underlying species coexistence. Thus, mathematical studies on resource competition system are expected to bring knowledge and insight what is essential for the coexistence of species in resource competition.

Another main interest in this thesis is to study delayed feedback mechanisms in biological systems. The growth of individuals in terms of physiological traits such as the growth in terms of body size, the maturation of cells, or interactions with the other species often operates on the population growth as a delayed feedback. It has been revealed that oscillation or more complicated behaviors are typically observed in ecological communities, and they are supposed to be induced by delayed negative feedback mechanisms. Feedback systems are often the subject to study in the control theory. In biological systems, feedback mechanism often appears as a density dependent term in equations. The system is, in general, described by differential equations and may exhibit rich dynamics even though the algebraic structure of equations is very simple.

In biological systems, the interaction among individuals is diversified. This diversified interaction may fertilize phenomena observed at a population level. The relation between the interaction among individuals and the population level phenomena is often the subject to understand in ecology, epidemiology, cell biology or any fields treating "the dynamics in terms of the population number". Due to the fact that resource competition and delayed feedback mechanism essentially work and are observed at population level, the study on population dynamics governed by resource competition or delayed feedback mechanism may be expected to reveal a relation between the interaction at individual level and phenomena observed at population level.

Mathematical modeling enables us to describe explicitly how model ingredients relate to each other. The stability theory of dynamical systems helps us to understand what will occur as a result of resource competition, delayed feedback effect or whatever in a qualitative manner. The implementation of numerical simulations gives information in terms of the dynamical properties in quantitative and visible sense. Numerical computations enables us to obtain approximate solutions to nonlinear equations, and to evaluate quantities representing an important concept, such as the degree of competition among interacting species and so on.

In this thesis, we study mathematical properties of resource competition and delayed negative feedback mechanism on several population dynamics models. Methods developed in the stability theory of differential equations and dynamical systems, numerical simulations and numerical computations are collaborated to investigate the dynamics of interacting species on which resource competition or delayed feedback mechanism is operated.

In the first part of this thesis, the effect of delayed feedback mechanism on several biological systems is studied. In Chapter 1, we study the stability, bifurcation and chaotic behaviors in Lotka-Volterra predator-prey system with two delays. The stability of coexisting steady state (a positive equilibrium) can change depending on the value of time delays. This system exhibits rich dynamics; not only chaotic but also transient chaotic behaviors are observed. In Chapter 2, we study chemostat equations which describe a population dynamics of microorganisms or species living in an aquatic ecosystem. The nutrient recycling via bacterial decomposition acts as a delayed feedback mechanism. The coexistence of species as opposed to the CEP is observed.

In the second part of the thesis, resource competition models are studied. In Chapter 3, we study a Lotka-Volterra competition system. Competition functions are defined to measure the degree of the competition between competing two species. The competitively balanced set is also defined in which competition of two species are equilibriated. We study several properties of competitively balanced set and showed the global attractivity of the positive equilibrium. Another important result in this chapter is seen in a point that the stable manifold of the positive equilibrium is explicitly given for a special case. In Chapter 4, we study a periodic chemostat model in which three species are competing for one resource. The coexistent state of three species is investigated both analytically and numerically. It is revealed that the coexistence of three species is likely possible if the period is large.

In appendix A, theories and mathematical methods to analyze delay equations are summarized. In the first part, a geometric criteria for the roots of characteristic equation for delay equations with one delay is summarized.

Part I

Delayed feedback mechanism in population dynamics

Chapter 1

Lotka-Volterra predator-prey system with two delays

ABSTRACT

We consider the following Lotka-Volterra predator-prey system with two delays:

$$\begin{cases} x'(t) = x(t)\left[r_1 - ax(t-\tau_1) - by(t)\right] \\ y'(t) = y(t)\left[-r_2 + cx(t) - dy(t-\tau_2)\right]. \end{cases} \tag{E$_1$}$$

First, system (E_1) is formulated as a model for ecological species with delayed self toxic inhibiting effect, or for describing virus dynamics with the immune system. In the following, we show that a positive equilibrium of system (E_1) is globally attractive for small delays. Critical values of time delay through which system (E_1) undergoes a Hopf bifurcation are analytically determined. Some numerical simulations suggest the existence of subcritical Hopf bifurcation near the critical values of time delay. Further system (E_1) exhibits some chaotic behavior when τ_2 becomes large. On some particular set of parameters, chaotic transient dynamics is observed.

keywords: predator-prey, subcritical Hopf bifurcation, chaotic behavior, mathematical model, nonlinear dynamics.*

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*This chapter is mainly attributed to the paper [44] published in *Mathematical Biosciences and Engineering.*

1.1 Introduction

An extensive literature deals with various aspects of Lotka-Volterra delay systems. Many studies concern permanence, persistence and the stability of a positive equilibrium. Permanence and persistence for Lotka-Volterra delay systems are extensively studied, for example, by Burton and Hutson [7], Cao and Gard [10], Hale and Waltman [19], Saito [54], Wang and Ma [70]. In studying the stability of a positive equilibrium, one often classifies systems under consideration in two types. One type of systems contains undelayed (or instantaneous) intraspecific competitions which dominate over both delayed intraspecific and interspecific interactions. Another type of systems contains only delayed intraspecific competitions. For the former class, Lu and Wang [38] obtained a necessary and sufficient condition under which a positive equilibrium of a two-dimensional Lotka-Volterra system without any intraspecific time delay is globally asymptotically stable. Hofbauer and So [27] generalized the result in [38] to an arbitrary n-dimensional system. In both cases, it was shown that delays incorporated in the system are harmless under some appropriate condition, called a *weakly diagonally dominant condition* (see Hofbauer and Sigmund [26] for the definition of WDD). The other generalization of [38] was given by Saito [53], [55], in which a necessary and sufficient condition for a global asymptotic stability of positive equilibrium for a Lotka-Volterra system with intraspecific time delay is also given. It was pointed out by Kuang [31] that more realistic models should consist of delay differential systems without instantaneous intraspecific competitions, since instantaneous responses are rare or weak relative to delayed response in real-life interactions. Lotka-Volterra systems without instantaneous intraspecific competitions are often called "pure-delay-type" systems. Pure-delay-type systems have been extensively studied by He [20], [23], [24], Lu and Takeuchi [37], Ma and Takeuchi [39], Zhen and Ma [74], etc. Gopalsamy and He [15], He [25] and Kuang [31] improved existing results for the global attractivity of various Lotka-Volterra systems by assuming that an interaction matrix has the form of M-matrix. Recently 2/3-type criteria for the global attractivity of pure-delay-type systems were obtained by Tang et al. [66], [67], and similar types of criteria for the asymptotic stability of linear delay systems are given by So *et al.* [58], [59]. Each also assumes that an interaction matrix has the form of M-matrix.

On the other hand, it is known that time delays destabilize the system. Shibata and Saito [57] considered a pure-delay-type Lotka-Volterra competitive model with two delays and showed that complicated chaotic dynamics appear when time delays become large. Also, differential equations with two delays have been well studied by Li *et al.* [36] and Ruan and Wei ([52], [51], [71]), in which a Hopf bifurcation due to the effect of time delay is observed.

In this chapter, we consider the following Lotka-Volterra prey-predator system with distributed delays:

$$\begin{cases} x'(t) = x(t)\left[r_1 - a\displaystyle\int_{-\tau_1}^{0} x(t+s)\,d\mu_1(s) - by(t)\right], \\ y'(t) = y(t)\left[-r_2 + cx(t) - d\displaystyle\int_{-\tau_2}^{0} y(t+s)\,d\mu_2(s)\right] \end{cases} \tag{1.1}$$

with the initial condition

$$x(s) = \phi(s) > 0 \text{ and } y(s) = \psi(s) > 0 \text{ for } -\max_{i=1,2}\tau_i \leq s \leq 0. \tag{1.2}$$

Here, $x(t)$ and $y(t)$ denote the population densities of prey and predator, respectively; τ_i is nonnegative and the rest of parameters are positive. Further, we assume that $\mu_i : [-\tau_i, 0] \to \mathbf{R}$ is nondecreasing on $[-\tau_i, 0]$, continuous to the left on $(-\tau_i, 0)$ and satisfies $\int_{-\tau_i}^{0} d\mu_i(s) = 1$, $(i = 1, 2)$.

Throughout the remainder of this chapter we assume that

$$cr_1 - ar_2 > 0. \tag{1.3}$$

Then system (1.1) has a unique positive equilibrium (x^*, y^*):

$$x^* = \frac{dr_1 + br_2}{ad + bc}, \quad y^* = \frac{cr_1 - ar_2}{ad + bc}.$$

As a special case, system (1.1) contains the following predator-prey system with discrete delays:

$$\begin{cases} x'(t) = x(t)[r_1 - ax(t-\tau_1) - by(t)], \\ y'(t) = y(t)[-r_2 + cx(t) - dy(t-\tau_2)]. \end{cases} \tag{E$_1$}$$

In the case $\tau_2 = 0$, system (E$_1$) was considered by May [40] and Song and Wei [60]. Some existing results show that the positive equilibrium of (E$_1$) is globally attractive for sufficiently small delays (see [23] for example). On the other hand, in [60], the existence of a local Hopf bifurcation for the positive equilibrium and the global existence of periodic solutions for (E$_1$) are shown. It is expected that the dynamics of sytem (E$_1$) possesses various interesting properties.

In this chapter, we investigate the effect of time delays on the global dynamics of system (1.1) and (E$_1$). In the next section, we will show two biological phenomena which can be described by system (E$_1$). The global attractivity and local stability of (x^*, y^*) for system (1.1) are discussed in sections 1.3 and 1.4, respectively. In section 1.5, some numerical simulations are given for the global dynamics of system (E$_1$). One of the simulations demonstrates that chaotic behavior occurs. In section 1.6, we investigate an interesting dynamics called transient chaotic dyanmics which exhibits a chaotic behavior for a while, but it finally settles down a sustained oscillation.

1.2 Model formulations

In this section, we derive system (E_1) under some biologically feasible conditions. It will be revealed that system (E_1) describes a population growth of ecological species with delayed self toxic inhibitory effect. We will also show that system (E_1) can be interpreted as a model for virus dynamics against the immune system.

First, we derive a logistic equation from a resource-consumer model. The key assumption underlying the derivation is a high dilution rate, which in turn allows us to follow the quasi-steady state approach. It is well known that the resource-consumer model with high dilution rate is reduced to *Beverton-Holt equation* (see for example, [68]). Here we further reduce the Beverton-Holt equation to the logistic equation under some additional assumptions.

The resource-consumer model is given by

$$\begin{cases} F'(t) = D(1 - F(t)) - \gamma F(t)x(t), \\ x'(t) = \beta F(t)x(t) - \delta x(t), \end{cases} \tag{1.4}$$

where $F(t)$ and $x(t)$ denote the concentration of food (the only resource for the population) and the population, respectively. The food is supplied and removed at a constant rate D. γ is a consumption rate per unit food per unit time. β is a growth rate of the population per capita per unit time. δ is a death rate of the population. Assume that D is sufficiently large so that the dilution rate of the environment is very high. Put $\bar{\gamma} := \gamma/D$. It follows from the first equation of (1.4) that

$$\frac{1}{D}F'(t) = 1 - F(t) - \bar{\gamma}F(t)x(t).$$

By the quasi-steady state approach, we may suppose that $\frac{1}{D}F'(t) \simeq 0$. This yields

$$F(t) \simeq \frac{1}{1 + \bar{\gamma}x(t)}. \tag{1.5}$$

Substituting (1.5) into the second equation of (1.4) gives *Beverton-Holt equation*:

$$x'(t) = x(t)\left[\frac{\beta}{1 + \bar{\gamma}x(t)} - \delta\right]. \tag{1.6}$$

The reciprocal number of $\bar{\gamma}$ is often interpreted as a multiplication of the *searching time* and the *handling time*. Since D is sufficiently large, $\bar{\gamma} = \gamma/D$ might be sufficiently small. For sufficiently small y, we have the following approximation:

$$\frac{1}{1 + y} = 1 - y + \mathcal{O}(y), \quad y \ll 1.$$

Let us set r and K by

$$r = \beta - \delta \text{ and } K = \frac{1}{\bar{\gamma}}\left(1 - \frac{\delta}{\beta}\right).$$

Then (1.6) is approximately reduced to the logistic equation

$$x'(t) = rx(t)\left[1 - \frac{x(t)}{K}\right], \tag{1.7}$$

provided that $\bar{\gamma}x(t)$ is sufficiently small. Hereafter we further assume that $\delta < \beta$ but $\delta/\beta \simeq 1$ (we shall write $\delta/\beta \lessapprox 1$). Then $\bar{\gamma}K \ll 1$. Since all solutions of (1.7) with the initial value $x(0) \in (0, K)$ monotonically tend to K as $t \to \infty$, $\bar{\gamma}x(t) \ll 1$ for all t as long as $x(0) \in (0, K)$. Note that $r = \beta - \delta$ does not necessarily small even though $\delta/\beta \simeq 1$. Consequently, we obtain the logistic equation if the food dynamics is fast ($D \gg 1$) and the carrying capacity K is sufficiently large, or equivalently, $\delta/\beta \simeq 1$.

Next, we incorporate the effect of toxic substance which might be produced through the metabolic process of the population. The toxic substance may contaminate the environment so that the population growth is finally inhibited.

Let $p(t)$ denote the concentration of toxic substance at time t. It is often the case that the toxic feedback is delayed. $p(t)$ is given by

$$p(t) = \int_{-\infty}^{t} \mathcal{F}(t-s)x(s)ds,$$

where $\mathcal{F}(t-s)$ is called a *delay kernel* which measures the weight of toxicity on the population growth at time $t-s$. It is assumed that the inhibition of the population growth follows the mass action law. Then

$$\begin{aligned} x'(t) &= rx(t)\left[1 - \frac{x(t)}{K}\right] - ax(t)p(t) \\ &= rx(t)\left[1 - \frac{x(t)}{K} - \alpha\int_{-\infty}^{t} \mathcal{F}(t-s)x(s)ds\right]. \end{aligned} \tag{1.8}$$

Practically, the explicit form of delay kernel, such as Gamma-distribution is often exploited to study the effect of toxicant on the population growth. If the delay kernel is given by Gamma-distribution:

$$\mathcal{F}(t-s) = G_{n,\mu}(t-s) := \frac{\mu^n(t-s)^{n-1}e^{-\mu(t-s)}}{(n-1)!}, \quad t \geq s,$$

then (1.8) is reduced to the system of ordinary differential equations (see *the linear chain trick* [41]):

$$\begin{cases} x'(t) = rx(t)\left[1 - \dfrac{x(t)}{K} - \alpha x_n(t)\right], \\ x_i'(t) = \mu(x_{i-1}(t) - x_i(t)), \quad (i = 1, 2, \cdots, n), \end{cases} \tag{1.9}$$

where $x_0(t) = x(t)$ and

$$x_i(t) = \int_{-\infty}^{t} G_{i,\mu}(t-s)x(s)ds, \quad (i = 1, 2, \cdots, n).$$

It is quite natural that several metabolic processes are involved until the toxicant is finally produced. Note that the second equation of (1.9) can represent the transition of the toxic substance in several metabolic processes. Thus, if the toxic substance experiences n-metabolic processes, Gamma-distribution is an appropriate way for the toxic substance to describe the transition of several metabolic processes. If we further assume that the mean of the Gamma-distribution $G_{n,\mu}(t-s)$ is the same for all n, letting $\mu = n\tau$ yields

$$\int_{-\infty}^{t} \mathcal{F}(t-s)x(s)ds \to x(t-\tau) \tag{1.10}$$

as $n \to \infty$. Assuming that (1.10), $D \gg 1$ and $\delta/\beta \lessapprox 1$, we have

$$\begin{aligned} x'(t) &= rx(t)\left[1 - \frac{x(t)}{K} - \alpha \int_{-\infty}^{t} \mathcal{F}(t-s)x(s)ds\right] \\ &\simeq rx(t)\left[1 - \alpha x(t-\tau)\right] & (1.11) \\ &= x(t)[r - ax(t-\tau)]. & (1.12) \end{aligned}$$

Consequently, the well known Hutchinson equation (1.12) is derived from the fast food dynamics with the delayed toxic feedback to the environment. Assume that the self producing toxic substance inhibits the population growth of prey and predator species with time delay. This completes the formulation of system (E_1).

We conclude this section by showing how system (E_1) is interpreted as the model for virus dynamics with the immune system. The immune system protects the body from infection. The immune system creates and maintains a barrier that prevents bacteria and viruses from entering the body. If a pathogen gets into the body, the *innate immune response* equipped with specialized cells detects, and often eliminates, the invader before it is able to reproduce and cause potentially serious injury to the host. If a pathogen is able to successfully evade the innate immune cells, the immune system activates a second, *adaptive immune response* against the pathogen. It is through the adaptive immune response that the immune system gains the ability to recognize a pathogen. If a pathogen is recognized as "non-self" by the immune system, the reproduction of the pathogen is inhibited through innate or adaptive immune responses.

During the adaptive immune response, *Antigen presenting cells* (APCs) and *helper T-cells* are often involved. Helper T cells express *T-cell receptor (TCR)* that recognize a specific peptide antigen bound to *Class II MHC molecules.* APCs activate a naive helper T cell which mediates several adaptive immune responses. *B cells* are the major cell type involved in *humoral immunity.* Once a B cell encounters its specific antigen and receives additional signal from a helper T cell (predominately *Th2 type*), it can further differentiate into an effector cell (*plasma B cell*). Plasma B cells secrete antibodies that assist in the destruction of antigens. Consequently, the population growth of a pathogen is inhibited. This is called humoral immunity.

Another important immunity is known as *cell-mediated immunity. Cytotoxic T cells (CTLs)* are a sub-group of T cells which are capable of inducing the death of other cells. CTLs express TCRs that recognize, and have tight affinity for, a specific peptide antigen bound to *Class I MHC molecules.* Naive cytotoxic T cells are activated when their TCR strongly interacts with a peptide-bound MHC class I molecule. Once activated CTL undergoes a process called clonal expansion, it becomes an effector cell which is able to kill cells that are infected with viruses. Although CTL is activated by interacting with a peptide-bound MHC class I, CTL activation is tightly controlled and generally requires additional activation signals provided by helper T cells (*Th1 type* has predominantly contributed).

A third type of T lymphocyte, the *regulatory T cells (Treg)*, limits and suppresses the immune system. Similar to other T cells, regulatory T cells develop in the thymus. The latest research suggests that regulatory T cells are defined by expression of the forkhead family transcription factor FOXP3 (forkhead box p3). Expression of FOXP3 is required for regulatory T cell development and appears to control a genetic program specifying this cell fate. The large majority of FOXP3-presenting regulatory T cells are found within the class II MHC restricted CD4-expressing ($CD4^+$) helper T cell population and express high levels of the interleukin-2 receptor alpha chain (CD25). In addition to the FOXP3-expressing $CD4^+CD25^+$, there also appears to be a minor population of class I MHC restricted $CD8^+$ FOXP3-expressing regulatory T cells. Recent studies have also revealed that *The programmed death-1 (PD-1)* inhibitory pathway is also expected to regulate T cell activations which express ligands *PD-L1* and *PD-L2* for PD-1.

Note that the humoral immune response acts as a delayed negative feedback for the population growth of virus particles, while the cell-mediated immune response is affected by regulatory T cell activity as adelayed negative feedback. Let $v(t)$ and $x(t)$ denote the concentration of virus particles per unit volume and infected cells at time t, respectively. Assume that virus particles follow a logistic equation. If target cells for the virus is not limited, we can assume that the resource (in this case, the target cell for viruses) is regarded as being provided with a high dilution rate. The secretion of antibodies by plasma B cells inhibits the population growth of virus particles. We shall take into account for a time delay during which B cells differentiate into plasma B cells and get an ability to secrete antibodies specific to virus particles. Here the inhibition of the population growth of virus particles is given by the term $-v(t)v(t-\tau_1)$ as we adapted the similar manner above. Then the dynamics of virus particles is described by

$$v'(t) = v(t)\left[r - \alpha v(t-\tau_1)\right]. \tag{1.13}$$

Since virus particles are produced from infected cells, for the simplicity, we assume that $v(t) = kx(t)$. Then

$$x'(t) = x(t)\left[r_1 - ax(t-\tau_1)\right]. \tag{1.14}$$

CTLs can be regarded as a predatory species for infected cells. Let $y(t)$ denote the concentration of CTLs at time t. The CTLs is assumed to decrease at a constant rate $-r_2$. Assume that the attack of uninfected cells by CTLs follows mass action law and appears as $-bx(t)y(t)$ in (1.14). The clonal expansion of CTLs are assumed to be proportional with both infected cells and CTLs (so it follows mass action law). The delayed negative feedback by the activity of regulatory T cells inhibits the population growth of CTLs. Following the similar formulation for the dynamics of virus particles yields the dynamics of the CTL population:

$$y'(t) = y(t)\left[-r_2 + cx(t) - dy(t-\tau_2)\right]. \tag{1.15}$$

Here τ_2 represents a time delay during which regulatory T-cells, the activation of the PD-1-PD-L1 inhibitory pathway or any other effects may suppress the T-cell activation which in turn, bring the degradation of the number of activated CTLs. This yields system (E_1).

1.3 Global stability analysis

In this section, we discuss a global attractivity for the positive equilibrium of system (1.1). It is shown that the positive equilibrium is globally attractive for sufficiently small delays.

By using the transformation

$$\bar{x} = x - x^*,\ \bar{y} = y - y^*,\quad \bar{\phi} = \phi - x^*,\ \bar{\psi} = \psi - y^*,$$

system (1.1) is reduced to

$$\begin{cases} x'(t) = (x(t) + x^*)\left[-a\displaystyle\int_{-\tau_1}^{0} x(t+s)\,d\mu_1(s) - by(t)\right], \\ y'(t) = (y(t) + y^*)\left[cx(t) - d\displaystyle\int_{-\tau_2}^{0} y(t+s)\,d\mu_2(s)\right] \end{cases} \tag{1.16}$$

with the initial condition

$$x(s) = \phi(s) > -x^* \text{ and } y(s) = \psi(s) > -y^* \text{ for } -\max_{i=1,2} \tau_i \leq s \leq 0. \tag{1.17}$$

Here we used $x(t)$, $y(t)$, $\phi(t)$ and $\psi(t)$ again, instead of $\bar{x}(t)$, $\bar{y}(t)$, $\bar{\phi}(t)$ and $\bar{\psi}(t)$, respectively. Inequality (1.3) ensures that system (1.16) has the zero solution. For our main theorem, we exploit a basic result for the upper-boundedness of solutions of system (1.16). Note that we can apply a similar method developed in [20] and [70] to Lemma 1.1 so that we omit the proof.

Lemma 1.1. *Suppose that* (1.3) *holds. Let* $(x(t), y(t))$ *be an arbitrary solution of system* (1.16) *with* (1.17)*. Then there exists a positive value* T *such that for* $(t \geq T)$

$$x(t) + x^* \leq M_1 := \frac{r_1}{a} e^{r_1 \tau_1}, \quad y(t) + y^* \leq M_2 := \frac{-r_2 + cM_1}{d} e^{(-r_2 + cM_1)\tau_2}. \tag{1.18}$$

Let us define c_1 and c_2 by

$$c_1 = a^2 M_1 h_1 + \frac{b}{2}(aM_1 h_1 + dM_2 h_2) \ , \ c_2 = d^2 M_2 h_2 + \frac{c}{2}(aM_1 h_1 + dM_2 h_2).$$

where M_1 and M_2 are defined in (1.18). Also, h_is are defined by $h_i := \int_{-\tau_i}^{0} (-s) d\mu_i(s)$ $(i = 1, 2)$, respectively.

Theorem 1.1. *Assume that* (1.3) *holds. Then the zero solution of* (1.16) *is globally attractive if* $a > c_1$ *and* $d > c_2$.

Proof. Let us construct the following Liapunov functional:

$$V_1(x_t, y_t) = c\left\{x(t) - x^* \log\left[\frac{x(t) + x^*}{x^*}\right]\right\} + b\left\{y(t) - y^* \log\left[\frac{y(t) + y^*}{y^*}\right]\right\}. \tag{1.19}$$

Then the derivative of $V_1(x_t, y_t)$ through $(x(t), y(t))$ is given by

$$\begin{aligned} \dot{V}_1(x_t, y_t) =& cx(t)\left[-a\int_{-\tau_1}^{0} x(t+s)\, d\mu_1(s) - by(t)\right] \\ &+ by(t)\left[cx(t) - d\int_{-\tau_2}^{0} y(t+s)\, d\mu_2(s)\right]. \end{aligned} \tag{1.20}$$

We can calculate the first and the fourth terms in (1.20) as $\int_{-\tau_1}^{0} x(t+s)\, d\mu_1(s) = x(t) - \int_{-\tau_1}^{0}\int_{t+s}^{t} \dot{x}(u)\, du\, d\mu_1(s)$ and $\int_{-\tau_2}^{0} y(t+s)\, d\mu_2(s) = y(t) - \int_{-\tau_2}^{0}\int_{t+s}^{t} \dot{y}(u)\, du\, d\mu_2(s)$. Hence, we have

$$\begin{aligned} \dot{V}_1(x_t, y_t) =& -acx^2(t) + ac\int_{-\tau_1}^{0}\int_{t+s}^{t} x(t)\dot{x}(u)\, du\, d\mu_1(s) \\ &- bdy^2(t) + bd\int_{-\tau_2}^{0}\int_{t+s}^{t} y(t)\dot{y}(u)\, du\, d\mu_2(s). \end{aligned}$$

Let us denote I_1 and I_2 by

$$I_1 = ac\int_{-\tau_1}^{0}\int_{t+s}^{t} x(t)\dot{x}(u)\,du\,d\mu_1(s),\quad I_2 = bd\int_{-\tau_2}^{0}\int_{t+s}^{t} y(t)\dot{y}(u)\,du\,d\mu_2(s).$$

Taking the absolute value of I_1 gives

$$|I_1| \le ac\int_{-\tau_1}^{0}\int_{t+s}^{t}|x(t)|\,(x(u)+x^*)\left|-a\int_{-\tau_1}^{0}x(u+v)\,d\mu_1(v)-by(u)\right|du\,d\mu_1(s). \tag{1.21}$$

By Lemma 1.1, there exist $M_1 > 0$ and $T > 0$ such that $x(t)+x^* \le M_1$ for all $t \ge T$. Then for $t \ge T_1 := T + 2\max\{\tau_1, \tau_2\}$, we have

$$\begin{aligned}|I_1| \le & acM_1\int_{-\tau_1}^{0}\int_{t+s}^{t}|x(t)|\left\{a\left|\int_{-\tau_1}^{0}x(u+v)\,d\mu_1(v)\right|+b|y(u)|\right\}du\,d\mu_1(s)\\ \le & \frac{1}{2}acM_1\left[(a+b)h_1x^2(t)+\int_{-\tau_1}^{0}\int_{t+s}^{t}\left\{aR_1(u)+by^2(u)\right\}du\,d\mu_1(s)\right],\end{aligned}$$

where $R_1(u) = \left|\int_{-\tau_1}^{0}x(u+v)\,d\mu_1(v)\right|^2$. We used the relation $2\alpha\beta \le \alpha^2+\beta^2$ in evaluating the first inequality.

In the same way, we can estimate the absolute value of I_2 as follows:

$$|I_2| \le \frac{1}{2}bdM_2\left[(c+d)h_2y^2(t)+\int_{-\tau_2}^{0}\int_{t+s}^{t}\left\{dR_2(u)+cx^2(u)\right\}du\,d\mu_2(s)\right],$$

where $R_2(u) = \left|\int_{-\tau_2}^{0}y(u+v)\,d\mu_2(v)\right|^2$.

Additional Liapunov functionals V_2 and V_3 are defined by:

$$\begin{aligned}V_2(x_t, y_t) &= \frac{1}{2}acM_1\int_{-\tau_1}^{0}\int_{t+s}^{t}\left[ah_1x^2(\sigma)+\int_{\sigma}^{t}\{aR_1(u)+by^2(u)\}du\right]d\sigma\,d\mu_1(s),\\ V_3(x_t, y_t) &= \frac{1}{2}bdM_2\int_{-\tau_2}^{0}\int_{t+s}^{t}\left[dh_2y^2(\sigma)+\int_{\sigma}^{t}\{dR_2(u)+cx^2(u)\}du\right]d\sigma d\mu_2(s).\end{aligned}$$

Then the derivative of $V_2(x_t, y_t)$ through the solution $(x(t), y(t))$ is given by

$$\begin{aligned}\dot{V_2}(x_t, y_t) = \frac{1}{2}acM_1\Bigg[&ah_1x^2(t)+bh_1y^2(t)-\int_{-\tau_1}^{0}\int_{t+s}^{t}\left\{aR_1(u)+by^2(u)\right\}dud\mu_1(s)\\ &+ah_1\left\{R_1(t)-\int_{-\tau_1}^{0}x^2(t+s)d\mu_1(s)\right\}\Bigg].\end{aligned}$$

Note that $R_1(t)-\int_{-\tau_1}^{0}x^2(t+s)\,d\mu_1(s) = \left[\int_{-\tau_1}^{0}x(t+s)\,d\mu_1(s)\right]^2-\int_{-\tau_1}^{0}x^2(t+s)\,d\mu_1(s) \le 0$. Hence, we have

$$\dot{V_2}(x_t, y_t) \le \frac{1}{2}acM_1\left[ah_1x^2(t)+bh_1y^2(t)-\int_{-\tau_1}^{0}\int_{t+s}^{t}\{aR_1(u)+by^2(u)\}dud\mu_1(s)\right].$$

In the same way,

$$\dot{V}_3(x_t, y_t) \leq \frac{1}{2} bdM_2 \left[ch_2 x^2 + dh_2 y^2(t) - \int_{-\tau_2}^{0} \int_{t+s}^{t} \{dR_2(u) + cx^2(u)\} du d\mu_2(s) \right].$$

Consequently, an estimate of the derivative of $V := V_1 + V_2 + V_3$ is

$$\begin{aligned} \frac{d}{dt} V(x_t, y_t) \leq & - c \left[a - \frac{1}{2} a(2a + b) M_1 h_1 - \frac{1}{2} bdM_2 h_2 \right] x^2(t) \\ & - b \left[d - \frac{1}{2} d(2d + c) M_2 h_2 - \frac{1}{2} acM_1 h_1 \right] y^2(t) \\ = & -c(a - c_1) x^2(t) - b(d - c_2) y^2(t). \end{aligned}$$

If $a > c_1$ and $d > c_2$, the second method of Liapunov functional implies that the zero solution of (1.16) is globally attractive for $t \geq T_1$. This completes the proof. □

Finally let us compare Theorem 1.1 with the result obtained by X.-Z. He [23] on system (E_1). We have the following corollary from Theorem 1.1.

Corollary 1.1. *Assume that* (1.3) *holds. Then the positive equilibrium point of* (E_1) *is globally attractive if* $a > c_1$ *and* $d > c_2$, *where* c_1 *and* c_2 *are*

$$c_1 = a^2 M_1 \tau_1 + \frac{b}{2}(aM_1\tau_1 + dM_2\tau_2), \quad c_2 = d^2 M_2 \tau_2 + \frac{c}{2}(aM_1\tau_1 + dM_2\tau_2).$$

X.-Z. He [23] showed a sufficient condition for the positive equilibrium to be globally attractive as a corollary of his main theorem:

Corollary 1.2. *[23, Corollary 2]. Assume that* (1.3) *holds. Then the positive equilibrium point of* (E_1) *is globally attractive if* $a > d_1$ *and* $d > d_2$, *where* d_1 *and* d_2 *are*

$$d_1 = a^2 M_1 \tau_1 + \frac{by^*}{2x^*}(aM_1\tau_1 + dM_2\tau_2), \quad d_2 = d^2 M_2 \tau_2 + \frac{cx^*}{2y^*}(aM_1\tau_1 + dM_2\tau_2).$$

It is easy to see that $c_1 > d_1$ and $c_2 < d_2$ if $x^* > y^*$. While $c_1 < d_1$ and $c_2 > d_2$ if $x^* < y^*$. Conditions of global attractivity of system (E_1) are improved as $a > \min\{c_1, d_1\}$ and $d > \min\{c_2, d_2\}$ by combining Corollary 1.1 and 1.2.

1.4 Instability and Hopf bifurcation

The characteristic equation of the linearized system of (E_1) is given by

$$P(\lambda, \tau_1, \tau_2) = \lambda^2 + (pe^{-\lambda\tau_1} + qe^{-\lambda\tau_2})\lambda + pqe^{-\lambda(\tau_1+\tau_2)} + r = 0, \tag{1.22}$$

where $p = ax^*$, $q = dy^*$ and $r = bcx^*y^*$. Note that $\lambda = 0$ is not a solution of (1.22).

Substituting $\lambda = i\omega$ ($\omega > 0$) into (1.22) gives

$$q\omega \sin \omega\tau_2 + pq \cos \omega(\tau_1 + \tau_2) = \omega^2 - r - p\omega \sin \omega\tau_1, \tag{1.23}$$

$$q\omega \cos \omega\tau_2 - pq \sin \omega(\tau_1 + \tau_2) = -p\omega \cos \omega\tau_1. \tag{1.24}$$

Squaring and adding equations (1.23) and (1.24) gives

$$2p\omega(\omega^2 - r - q^2) \sin \omega\tau_1 = (\omega^2 - r)^2 + p^2\omega^2 - q^2\omega^2 - p^2q^2. \tag{1.25}$$

In the same manner, we have

$$2q\omega(\omega^2 - r - p^2) \sin \omega\tau_2 = (\omega^2 - r)^2 + q^2\omega^2 - p^2\omega^2 - p^2q^2. \tag{1.26}$$

Note that $p = q$ if $\omega^2 - r - q^2 = 0$. In fact, the right hand side of (1.25) is calculated as $(\omega^2 - r)^2 + p^2\omega^2 - q^2\omega^2 - p^2q^2 = (p^2 - q^2)r = 0$. In the same way, $p = q$ if $\omega^2 - r - p^2 = 0$. By taking contraposition, we obtain that $\omega^2 - r - p^2 \neq 0$ and $\omega^2 - r - q^2 \neq 0$ if $p \neq q$. Note that the characteristic equation (1.22) does not change its form by exchanging (p, τ_1) and (q, τ_2). Hence, throughout the remainder of this section, we can assume that $p < q$ without loss of generality. The particular case $p = q$ is out of consideration in this chapter. Then we have

$$\sin \omega\tau_1 = \frac{\omega^4 + (p^2 - q^2 - 2r)\omega^2 + r^2 - p^2q^2}{2p\omega(\omega^2 - r - q^2)}, \tag{1.27}$$

$$\sin \omega\tau_2 = \frac{\omega^4 + (q^2 - p^2 - 2r)\omega^2 + r^2 - p^2q^2}{2q\omega(\omega^2 - r - p^2)}. \tag{1.28}$$

Let us substitute (1.27) and (1.28) into (1.23). Direct calculation gives

$$\cos \omega(\tau_1 + \tau_2) = -\frac{p^2 + q^2}{2pq} + \frac{(p^2 - q^2)^2 r}{2pq(\omega^2 - r - p^2)(\omega^2 - r - q^2)}. \tag{1.29}$$

Let us define $f_1 : (0, r + q^2) \cup (r + q^2, \infty) \to \mathbb{R}$, $f_2 : (0, r + p^2) \cup (r + p^2, \infty) \to \mathbb{R}$ and $f_3 : [0, r + p^2) \cup (r + p^2, r + q^2) \cup (r + q^2, \infty) \to \mathbb{R}$ as

$$f_1(u) = \frac{u^2 + (p^2 - q^2 - 2r)u + r^2 - p^2q^2}{2p\sqrt{u}(u - r - q^2)}, \tag{1.30}$$

$$f_2(u) = \frac{u^2 + (q^2 - p^2 - 2r)u + r^2 - p^2q^2}{2q\sqrt{u}(u - r - p^2)}, \tag{1.31}$$

$$f_3(u) = -\frac{p^2 + q^2}{2pq} + \frac{(p^2 - q^2)^2 r}{2pq(u - r - p^2)(u - r - q^2)}. \tag{1.32}$$

Intervals I_1, I_2 and I_3 are defined by

$$\begin{aligned} I_1 &= \left\{u \in (0, r+q^2) \cup (r+q^2, \infty) : -1 \le f_1(u) \le 1\right\}, \\ I_2 &= \left\{u \in (0, r+p^2) \cup (r+p^2, \infty) : -1 \le f_2(u) \le 1\right\}, \\ I_3 &= \left\{u \in [0, r+p^2) \cup (r+q^2, \infty) : -1 \le f_3(u) \le 1\right\}. \end{aligned}$$

Note that it suffices to consider the interval I_3 without $(r+p^2, r+q^2)$, since for $u \in (r+p^2, r+q^2)$,

$$\begin{aligned} f_3(u) &= -\frac{p^2+q^2}{2pq} + \frac{(p^2-q^2)^2 r}{2pq(u-r-p^2)(u-r-q^2)} \\ &< -1 + \frac{(p^2-q^2)^2 r}{2pq(u-r-p^2)(u-r-q^2)} < -1. \end{aligned}$$

On $I := I_1 \cap I_2 \cap I_3$, inverse functions of $\sin \omega\tau_1$ and $\sin \omega\tau_2$ are well defined, and hence we obtain the following relations:

$$\begin{cases} \tau_1^k := \dfrac{\theta_1 + 2k\pi}{\omega}, \ \dfrac{\pi - \theta_1 + 2k\pi}{\omega}, & (k = 0, 1, 2, \cdots), \\ \tau_2^l := \dfrac{\theta_2 + 2l\pi}{\omega}, \ \dfrac{\pi - \theta_2 + 2l\pi}{\omega}, & (l = 0, 1, 2, \cdots). \end{cases} \tag{1.33}$$

Here, $\theta_1 = \sin^{-1} f_1(u)$ and $\theta_2 = \sin^{-1} f_2(u)$.

Proposition 1.1. (1.23) *and* (1.24) *are equivalent to* (1.27)–(1.29).

Proof. In the procedure of deriving (1.27)–(1.29) from (1.23) and (1.24), it is clear that (1.23) and (1.24) imply (1.27)–(1.29). Conversely, suppose that (1.27)–(1.29) hold. Then it is easy to see that (1.27)–(1.29) imply (1.23).

Let us check (1.24) by evaluating $(p\omega \cos \omega\tau_1 + q\omega \cos \omega\tau_2)^2 - \{pq \sin \omega(\tau_1 + \tau_2)\}^2$ as follows:

$$\begin{aligned} &(p\omega \cos \omega\tau_1 + q\omega \cos \omega\tau_2)^2 - \{pq \sin \omega(\tau_1 + \tau_2)\}^2 \\ =&p^2\omega^2(1 - \sin^2 \omega\tau_1) + q^2\omega^2(1 - \sin^2 \omega\tau_2) \\ &+ 2pq\omega^2\{\cos \omega(\tau_1+\tau_2) + \sin \omega\tau_1 \sin \omega\tau_2\} - p^2q^2\{1 - \cos^2 \omega(\tau_1+\tau_2)\} \\ =& - \omega^4 + (p^2+q^2)\omega^2 - p^2q^2 + \{pq \cos \omega(\tau_1+\tau_2) + \omega^2 + p\omega \sin \omega\tau_1 - q\omega \sin \omega\tau_2\} \times \\ &\{pq \cos \omega(\tau_1+\tau_2) + \omega^2 - p\omega \sin \omega\tau_1 + q\omega \sin \omega\tau_2\} \\ =& - \omega^4 + (p^2+q^2)\omega^2 - p^2q^2 + (2\omega^2 - r - 2q\omega \sin \omega\tau_2)(2\omega^2 - r - 2p\omega \sin \omega\tau_1). \end{aligned}$$

Here we used (1.23) in evaluating the last equality. By (1.27) and (1.28), $2p\omega \sin \omega\tau_1 = \omega^2 - r + p^2 + \frac{(p^2-q^2)r}{\omega^2-r-q^2}$ and $2q\omega \sin \omega\tau_2 = \omega^2 - r + q^2 + \frac{(q^2-p^2)r}{\omega^2-r-p^2}$. Direct calculation gives

$(p\omega\cos\omega\tau_1 + q\omega\cos\omega\tau_2)^2 - \{pq\sin\omega(\tau_1+\tau_2)\}^2 = 0$. Hence, either (1.24) or $p\omega\cos\omega\tau_1 + q\omega\cos\omega\tau_2 + pq\sin\omega(\tau_1+\tau_2) = 0$ holds. If $p\omega\cos\omega\tau_1 + q\omega\cos\omega\tau_2 + pq\sin\omega(\tau_1+\tau_2) = 0$, the same manner of deriving (1.25) and (1.26) gives $\sin\omega(\tau_1+2\tau_2) = \sin\omega\tau_1$ and $\sin\omega(2\tau_1+\tau_2) = \sin\omega\tau_2$. Consequently, $\sin\omega\tau_1 = \sin\omega\tau_2 = 0$. Then it follows from (1.27) and (1.28) that $p = q$. This is a contradiction and hence the proof is completed. □

Proposition 1.2. *Assume that* $r \neq pq$. *Then* I_1, I_2, I_3 *are not empty and* $I_1 = I_2 = I_3$. *Moereover, there exists a set of critical values* $(\omega, \tau_1^k, \tau_2^l)$ *such that* $(\omega, \tau_1^k, \tau_2^l)$ *satisfies* (1.27)–(1.29).

Proof. First, let us show I_3 is not an empty set. Direct calculation gives

$$f_3(0) + 1 = \frac{-(p-q)^2(r-pq)^2}{2pq(r+p^2)(r+q^2)} < 0.$$

Hence $f_3(0) < -1$. The derivative of $f_3(u)$ on $[0, r+p^2) \cup (r+q^2, \infty)$ is

$$-\frac{(p^2-q^2)^2 r\{(u-r-p^2)+(u-r-q^2)\}}{2pq(u-r-p^2)^2(u-r-q^2)^2}.$$

This implies that $f_3'(u)$ is positive on $[0, r+p^2)$ and negative on $(r+q^2, \infty)$. Hence, $f_3(u)$ is strictly monotonically increasing on $[0, r+p^2)$, and strictly monotonically decreasing on $(r+q^2, \infty)$. It is easy to see that $f_3(u) \to +\infty$ as $u \to r+p^2-0$ and $f_3(u) \to +\infty$ as $u \to r+q^2+0$. Moreover, $f_3(u) \to -\frac{p^2+q^2}{2pq} < -1$ as $u \to +\infty$. Therefore, $I_3 = [\bar{u}_{-L}, \bar{u}_{+L}] \cup [\bar{u}_{-R}, \bar{u}_{+R}]$, where $\bar{u}_{-L}$ and $\bar{u}_{+L}$ are roots of equations $f_3(u) = -1$ and $f_3(u) = 1$ on $[0, r+p^2)$, respectively, while $\bar{u}_{-R}$ and $\bar{u}_{+R}$ are respective roots of equations $f_3(u) = 1$ and $f_3(u) = -1$ on $(r+q^2, \infty)$ (see Fig. 1.3). It follows that

$$f_3(u) = 1 \Longleftrightarrow u^2 - (p^2+q^2+2r)u + (r+pq)^2 = 0, \tag{1.34}$$

$$f_3(u) = -1 \Longleftrightarrow u^2 - (p^2+q^2+2r)u + (r-pq)^2 = 0. \tag{1.35}$$

Hence, explicit values of $\bar{u}_{-L}$, $\bar{u}_{+L}$, $\bar{u}_{-R}$ and $\bar{u}_{+R}$ can be obtained by solving (1.34) and (1.35).

Second, let us show the following statement:

$$f_1(u) = -1 \text{ or } 1 \Longleftrightarrow f_2(u) = -1 \text{ or } 1 \Longleftrightarrow f_3(u) = -1 \text{ or } 1. \tag{1.36}$$

Suppose that $f_1(u) = 1$. By (1.27), $\sin\omega\tau_1 = f_1(u) = 1$. Hence, $\cos\omega\tau_1 = 0$. Then in (1.24), $q(\omega - p)\cos\omega\tau_2 = 0$. Assume that $\omega = p$. Then $r = 0$ in (1.23). This is a contradiction. Hence, $\cos\omega\tau_2 = 0$ and $f_2(u) = -1$ or 1. In the same manner, we can show that $f_1(u) = -1 \Longleftrightarrow$

$f_2(u) = -1$ or 1. Next, suppose that $f_3(u) = 1$. By (1.29), $\cos\omega(\tau_1+\tau_2) = f_3(u) = 1$. Hence, $\sin\omega(\tau_1+\tau_2) = 0$, or equivalently, $\sin\omega\tau_1\cos\omega\tau_2 + \cos\omega\tau_1\sin\omega\tau_2 = 0$. It follows from (1.24) that $p\cos\omega\tau_1 + q\cos\omega\tau_2 = 0$. Hence $\cos\omega\tau_2(p\sin\omega\tau_1 - q\sin\omega\tau_2) = 0$. If $p\sin\omega\tau_1 - q\sin\omega\tau_2 = 0$, it follows that

$$\begin{aligned}&(p\cos\omega\tau_1 + q\cos\omega\tau_2)^2 + (p\sin\omega\tau_1 - q\sin\omega\tau_2)^2\\ &= p^2 + q^2 + 2pq\cos\omega(\tau_1+\tau_2) = (p+q)^2 = 0.\end{aligned}$$

This is a contradiction, and hence $\cos\omega\tau_2 = \cos\omega\tau_1 = 0$. The other cases can be proved similarly.

Third, let us show I_1 and I_2 are not an empty set and $I_1 = I_2 = I_3$. Here, $g_1(u)$ denotes the numerator of $f_1(u)$. Then $g_1(0) = r^2 - p^2q^2$ and $g_1(r+q^2) = -(q^2-p^2)r$. If $r > pq$, $g_1(0) > 0$ and $g_1(r+q^2) < 0$, because $p < q$. Hence, for $u \in (0, r+q^2)$, we have $f_1(u) \to -\infty$ as $u \to 0+$, and $f_1(u) \to +\infty$ as $u \to r+q^2-0$. For $u \in (r+q^2, \infty)$, $f_1(u) \to -\infty$ as $u \to r+q^2+0$ and $f_1(u) \to +\infty$ as $u \to +\infty$. By (1.36), I_1 exists. Moreover, $f_1(\bar{u}_{-L}) = -1$, $f_1(\bar{u}_{+L}) = 1$, $f_1(\bar{u}_{-R}) = -1$ and $f_1(\bar{u}_{+R}) = 1$. Hence, $I_1 = I_3$ (see Fig. 1.1). Now, $g_2(u)$ denotes the numerator of $f_2(u)$. Then $g_2(0) = r^2 - p^2q^2$ and $g_2(r+p^2) = (q^2-p^2)r$. Since $r > pq$ and $p < q$, $g_2(0) > 0$ and $g_2(r+p^2) > 0$. Hence, for $u \in (0, r+p^2)$, we have $f_2(u) \to -\infty$ as $u \to 0+$, and $f_2(u) \to -\infty$ as $u \to r+p^2-0$. For $u \in (r+p^2, \infty)$, $f_2(u) \to +\infty$ as $u \to r+p^2+0$ and $f_2(u) \to +\infty$ as $u \to +\infty$. Since $f_2(u)$ is continuous on $(0, r+p^2) \cup (r+p^2, \infty)$, I_2 exists. Moreover, $f_2(\bar{u}_{-L}) = -1$, $f_2(\bar{u}_{+L}) = -1$, $f_2(\bar{u}_{-R}) = 1$, and $f_2(\bar{u}_{+R}) = 1$. Hence, $I_2 = I_3$ (see Fig. 1.2). If $r < pq$, the same approach can be used, and hence it is shown that I_1, I_2 are not empty and $I_1 = I_2 = I_3$.

By substituting (1.33) into (1.29), we obtain the following equations with respect to u :

$$\begin{cases}\cos\left[\sin^{-1} f_1(u) + \sin^{-1} f_2(u)\right] = f_3(u),\\ \cos\left[\sin^{-1} f_1(u) - \sin^{-1} f_2(u)\right] = -f_3(u).\end{cases} \tag{1.37}$$

Note that $f_3(u)$ is a monotone function on I and $f_3(I) = [-1, 1]$. Hence, the intermediate theorem implies that there exists at least one root of (1.37) on I. This completes the proof. □

Hereafter, let us suppose that there exists at least one positive root ω of (1.23) and (1.24). Let τ_2 be arbitrary fixed. Derivatives of $P(\lambda, \tau_1, \tau_2)$ with respect to λ and τ_1 at $\lambda = i\omega$, $\tau_1 = \tau_1^k$ and $\tau_2 = \tau_2^l$ are

$$\begin{aligned}\frac{\partial P(i\omega, \tau_1^k, \tau_2^l)}{\partial\lambda} =& 2\lambda + pe^{-\lambda\tau_1} + qe^{-\lambda\tau_2} - (p\tau_1 e^{-\lambda\tau_1} + q\tau_2 e^{-\lambda\tau_2})\lambda\\ &- pq(\tau_1+\tau_2)e^{-\lambda(\tau_1+\tau_2)}\Big|_{\substack{\lambda=i\omega\\ \tau_1=\tau_1^k, \tau_2=\tau_2^l}}\end{aligned}$$

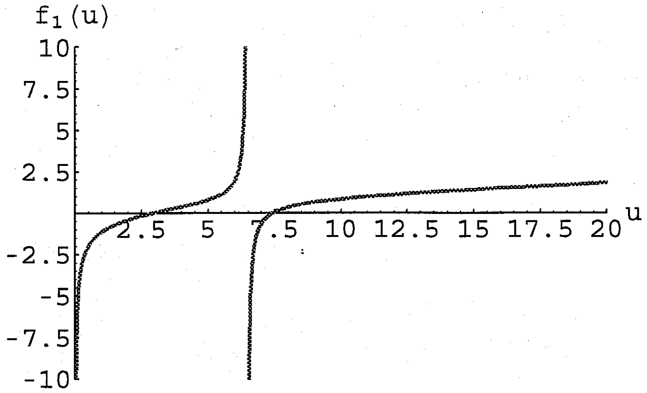

Figure 1.1: $f_1(u)$

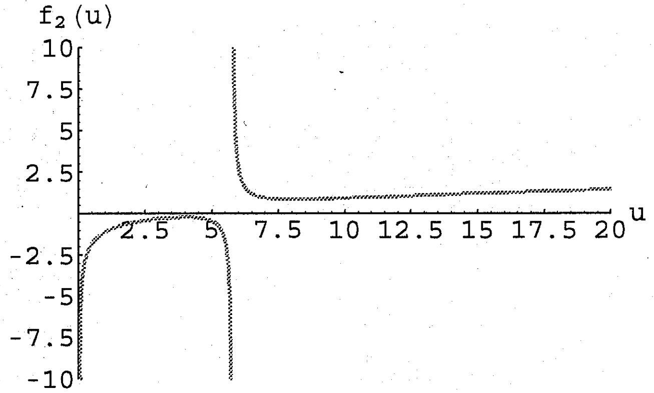

Figure 1.2: $f_2(u)$

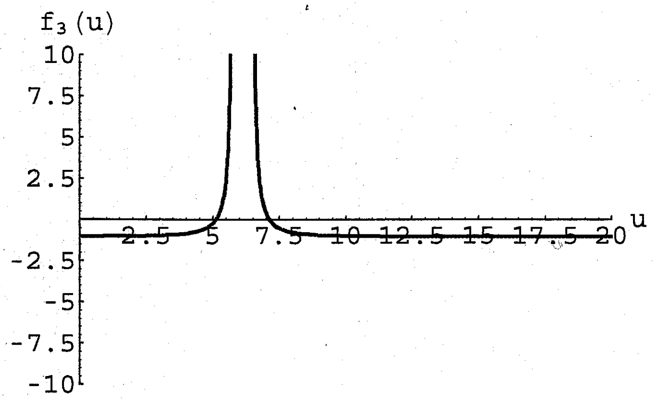

Figure 1.3: $f_3(u)$

$$\frac{\partial P(i\omega,\tau_1^k,\tau_2^l)}{\partial \tau_1} = -\, pe^{-\lambda\tau_1}(\lambda + qe^{-\lambda\tau_2})\lambda\Big|_{\substack{\lambda=i\omega\\ \tau_1=\tau_1^k,\tau_2=\tau_2^l}},$$

respectively. If $\lambda + pe^{-\lambda\tau_1} = 0$, then it follows from (1.22) that $r = 0$, since (1.22) is written as $(\lambda+pe^{-\lambda\tau_1})(\lambda+qe^{-\lambda\tau_2})+r = 0$. Consequently, $\lambda+pe^{-\lambda\tau_1} \neq 0$. In the same way, $\lambda+qe^{-\lambda\tau_2} \neq 0$. Hence, the implicit function theorem gives

$$\begin{aligned}\frac{\partial\tau_1}{\partial\lambda} &= -\frac{\tau_1+\tau_2}{\lambda} + \frac{\lambda^2 - r - pqe^{-\lambda(\tau_1+\tau_2)} + \tau_2(pe^{-\lambda\tau_1} - qe^{-\lambda\tau_2})\lambda^2}{pe^{-\lambda\tau_1}(\lambda + qe^{-\lambda\tau_2})\lambda^2}\\ &:= -\frac{\tau_1+\tau_2}{\lambda} + \frac{F_1(\lambda,\tau_1,\tau_2)}{G_1(\lambda,\tau_1,\tau_2)}.\end{aligned}$$

Define δ_1 as

$$\begin{aligned}\delta_1 := (\omega^2 - r)\{\omega^2 + r + pq\cos\omega(\tau_1^k + \tau_2^l)\} - q\omega\{(\omega^2 + r)\sin\omega\tau_2^l - pq\sin\omega\tau_1^k\}\\ + \omega^2\tau_2^l\left[pq\omega\sin\omega(\tau_1^k - \tau_2^l) + (\omega^2 - r)(p\cos\omega\tau_1^k - q\cos\omega\tau_2^l)\right].\end{aligned}$$

Let us show

$$\operatorname{sgnRe}\left[-\frac{\frac{\partial P(\lambda,\tau_1,\tau_2)}{\partial\lambda}}{\frac{\partial P(\lambda,\tau_1,\tau_2)}{\partial\tau_1}}\Bigg|_{\substack{\lambda=i\omega\\ \tau_1=\tau_1^k,\tau_2=\tau_2^l}}\right] = \operatorname{sgn}\delta_1. \tag{1.38}$$

In fact, $\operatorname{sgnRe}\left[\frac{\partial\tau_1}{\partial\lambda}\Big|_{\substack{\lambda=i\omega\\ \tau_1=\tau_1^k,\tau_2=\tau_2^l}}\right] = \operatorname{sgn}\left[F_{1R}G_{1R} + F_{1I}G_{1I}\right]$, where $F_{1R} = \mathrm{Re}[F_1(i\omega,\tau_1^k,\tau_2^l)]$, $F_{1I} = \mathrm{Im}[F_1(i\omega,\tau_1^k,\tau_2^l)]$, $G_{1R} = \mathrm{Re}[G_1(i\omega,\tau_1^k,\tau_2^l)]$ and $G_{1I} = \mathrm{Im}[G_1(i\omega,\tau_1^k,\tau_2^l)]$. By (1.23), we have

$$\begin{aligned}G_{1R} &= -\omega^2(\omega^2 - r - q\omega\sin\omega\tau_2^l),\\ G_{1I} &= q\omega^3\cos\omega\tau_2^l.\end{aligned}$$

Direct calculation gives

$$\begin{aligned}&(F_{1R}G_{1R} + F_{1I}G_{1I})/\omega^2 =\\ &(\omega^2 - r - q\omega\sin\omega\tau_2^l)\left\{\omega^2 + r + pq\cos\omega(\tau_1^k + \tau_2^l) + \tau_2^l\omega^2(p\cos\omega\tau_1^k - q\cos\omega\tau_2^l)\right\}\\ &- q\omega\cos\omega\tau_2^l\left\{-pq\sin\omega(\tau_1^k + \tau_2^l) + \tau_2^l\omega^2(-p\sin\omega\tau_1^k + q\sin\omega\tau_2^l)\right\} = \delta_1.\end{aligned}$$

Hence, (1.38) holds. By (1.38), $\partial P(i\omega,\tau_1^k,\tau_2^l)/\partial\lambda \neq 0$ if and only if $\delta_1 \neq 0$. If $\delta_1 \neq 0$, again using the implicit function theorem gives

$$\operatorname{sgnRe}\left[\frac{\partial\lambda}{\partial\tau_1}\Big|_{\substack{\lambda=i\omega\\ \tau_1=\tau_1^k,\tau_2=\tau_2^l}}\right] = \operatorname{sgnRe}\left[\left(-\frac{\frac{\partial P(\lambda,\tau_1^k,\tau_2^l)}{\partial\lambda}}{\frac{\partial P(\lambda,\tau_1^k,\tau_2^l)}{\partial\tau_1}}\right)^{-1}\right] = \operatorname{sgn}\delta_1.$$

Define δ_2 as

$$\delta_2 := (\omega^2 - r)\{\omega^2 + r + pq\cos\omega(\tau_1^k + \tau_2^l)\} - p\omega\{(\omega^2 + r)\sin\omega\tau_1^k - pq\sin\omega\tau_2^l\} \\ + \omega^2\tau_1^k\left[pq\omega\sin\omega(\tau_2^l - \tau_1^k) + (\omega^2 - r)(q\cos\omega\tau_2^l - p\cos\omega\tau_1^k)\right].$$

In the same way, we can show that $\mathrm{sgnRe}\left[\left.\frac{\partial\lambda}{\partial\tau_2}\right|_{\substack{\lambda=i\omega \\ \tau_1=\tau_1^k,\tau_2=\tau_2^l}}\right] = \mathrm{sgn}\delta_2$. Hence, we obtain the following result:

Theorem 1.2. *Assume that* ω^* *is a positive real root of* (1.23) *and* (1.24). *Then a pair of simple conjugate pure imaginary roots* $\lambda_+ = i\omega^*$ *and* $\lambda_- = -i\omega^*$ *of* (1.22) *exists at* $\tau_1 = \tau_1^k$ *and* $\tau_2 = \tau_2^l$, *which crosses the imaginary axis as* τ_1 (τ_2) *increases for fixed* τ_2 (τ_1) *from left to right if* $\delta_1 > 0$ ($\delta_2 > 0$) *and right to left if* $\delta_1 < 0$ ($\delta_2 < 0$).

Finally let us show the existence of Hopf bifurcation. By Proposition 1.2, there exists at least one set of critical values $(\omega, \tau_1^k, \tau_2^l)$ which satisfies (1.27)–(1.29) if $r \neq pq$. Since a number of ω which satisfies (1.27)–(1.29) is finite, there exists a set of minimum values (τ_1^*, τ_2^*). Since all roots of the characteristic equation (1.22) have negative real parts when $\tau_1 = \tau_2 = 0$, The Hopf bifurcation theorem [18, p. 332, Theorem 1.1.] is applicable to system (E_1).

Corollary 1.3. *Assume that* $ax^* \neq dy^*$ *and* $ad - bc \neq 0$. *Let* ω^* *be a positive real root of* (1.23) *and* (1.24). *If either* $\delta_1 > 0$ *or* $\delta_2 > 0$, *a family of periodic solutions of* (E_1) *bifurcates from the positive equilibrium for* τ_1 *near* τ_1^* *or* τ_2 *near* τ_2^*. *Furthermore, the period of periodic solution is approximately* $2\pi/\omega^*$.

1.5 Chaotic behavior

In this section, let us apply the results obtained in section 1.4 and give some numerical simulation results. Hereafter, parameters are fixed at the following values:

$$r_1 = 2.4,\ r_2 = 2.1,\ a = 1.4,\ b = 2.2,\ c = 5.5,\ d = 3.3. \tag{P}$$

Then $p = 1.05$, $q = 2.025$ and $r = 5.56875$. Note that if $\tau_2 = 0$, Corollary 1.4-(i) holds. Hence the positive equilibrium is locally asymptotically stable for all $\tau_1 \geq 0$ with $\tau_2 = 0$. Since $r \neq pq$, Proposition 1.2 implies that I_1, I_2, I_3 are not empty and $I = I_1 = I_2 = I_3$. The interval I becomes $[0.760643, 5.42423] \cup [10.9164, 15.58]$. By (1.33) and (1.37), $(\omega^*, \tau_1^*, \tau_2^*)$ is approximately calculated as $\omega^* = 3.63978$, $\tau_1^* = 0.706884$ and $\tau_2^* = 0.365617$.

In the remainder of this section, some numerical simulation results of (E_1) are given. The positive equilibrium is numerically calculated as $(x^*, y^*) = (0.75, 0.6136)$. First, let us fix τ_1 and τ_2 as $\tau_1 = 0.7$ and $\tau_2 = 0.35$. Hence all roots of (1.22) have negative real parts. Figures 1.4 and 1.5 illustrate the time series and the projection into xy plane of the trajectory of the solution of (E_1) with initial functions $\phi = 0.75$ and $\psi = 0.1$, respectively. It is observed that the solution tends to the positive equilibrium (see Figs. 1.4 and 1.5). Next, let us show figures on which only the initial function ψ is changed from 0.1 to 0.05. Then it is observed in Figures 1.6 and 1.7 that the solution evolves to some periodic solution; δ_1 and δ_2 are numerically calculated as $\delta_1(\tau_2^*) = -0.673553 < 0$ and $\delta_2(\tau_1^*) = 20.2818 > 0$. Corollary 1.3 implies that a family of periodic solution bifurcates from the positive equilibrium for τ_2 near τ_2^*. Figures 1.8 and 1.9 illustrate the trajectory of the solution with (P), $\tau_1 = 0.71$ and $\tau_2 = 0.37$. The initial functions are taken near the equilibrium point, $(\phi, \psi) = (0.75, 0.6)$. Then it is observed that the solution evolves to some periodic solution (see Figs. 1.8 and 1.9). In Figures 1.4–1.9, it seems that an unstable closed curve appears around the positive equilibrium. Further, the solution starting at the inside of the closed curve tends to the positive equilibrium (Figs. 1.4 and 1.5), while the solution starting at the outside of the curve evolves to some robust periodic solution (Figures 1.6 and 1.7). Since the positive equilibirum is locally asymptotically stable and system (E_1) undergoes a Hopf bifurcation by Corollary 1.3, the exsitence of a subcritical Hopf bifurcation is suggested from these figures. Finally, let us change the values of τ_2 from 0.37 to 1.73. Then, a complicated dynamics is observed in Figure 1.10. The trajectory of the solution of (E_1) with $\phi = 0.75$ and $\psi = 0.6$ is attracted in a shark-head shaped region. In other words, shark-head chaos occurs on system (E_1) as the time delay in an intraspecific competition of predator becomes large. We observe that shark-head chaos is formed by repeating the following three steps:

Step 1. The low density of the predator makes the density of the prey increase.

Step 2. The growth of the predator follows the growth of the prey with delay.

Step 3. The exhaustion of the prey results in the decrease of the predator.

Chaotic behavior occurs markably in Step 2 : it seems that the trajectory forms the upper lip of the *shark* with the high growth of predator y, while the trajectory forms the lower lip of the *shark* with the relatively low growth of predator y. The predator repeats such high and low growth alternatively. The solution never moves on the same path and finally the shark-head region is filled densely.

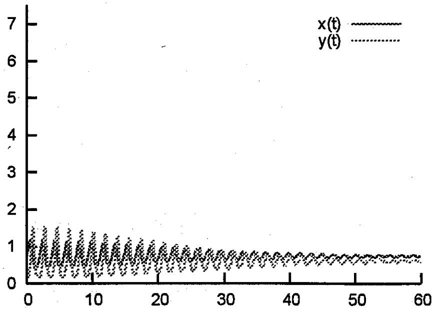

Figure 1.4: $\tau_1 = 0.7$, $\tau_2 = 0.35$

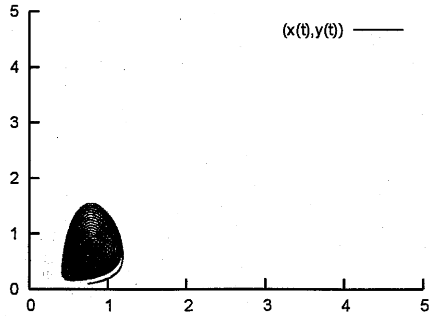

Figure 1.5: $\phi = 0.75$, $\psi = 0.1$

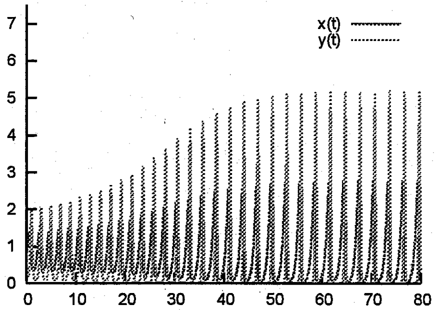

Figure 1.6: $\tau_1 = 0.7$, $\tau_2 = 0.35$

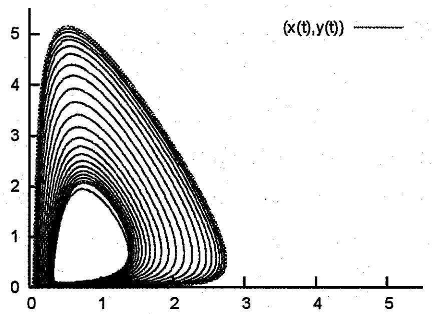

Figure 1.7: $\phi = 0.75$, $\psi = 0.05$

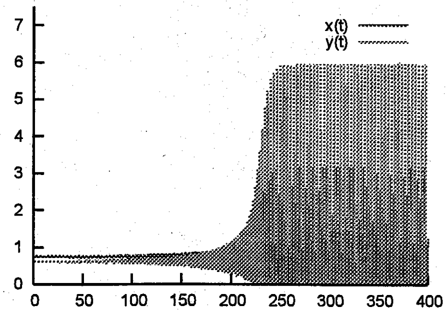

Figure 1.8: $\tau_1 = 0.71$, $\tau_2 = 0.37$

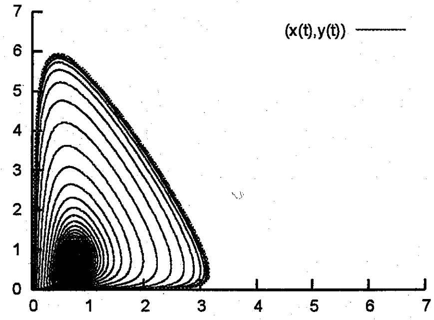

Figure 1.9: $\phi = 0.75$, $\psi = 0.6$

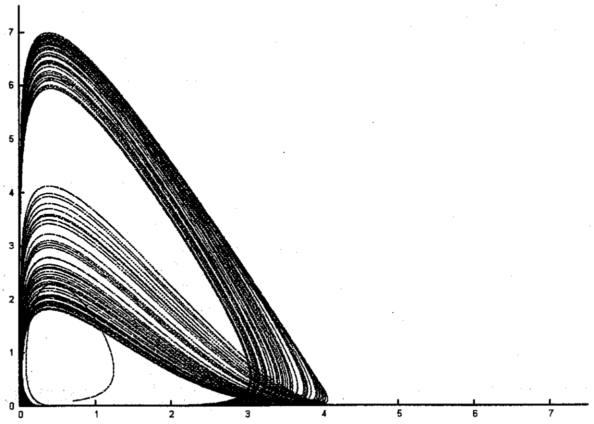

Figure 1.10: $\tau_1 = 0.71$, $\tau_2 = 1.73$, $\phi = 0.75$, $\psi = 0.6$: shark-head chaos

1.6 Chaotic transient

System (E_1) also exhibits an interesting behavior called *transient chaos.* The transient behavior of the dynamics is chaotic, but asymptotically the solution of system (E_1) converges to some regular dynamics for some particular set of parameters. It is possible to reduce parameters by scaling time and variables. Introducing new time variable $s = \tau_2 t$ and variables $u(t) = a\tau_2 x(t)$ and $v(t) = d\tau_2 y(t)$, system (E_1) is reduced to the following system of equations:

$$\begin{cases} x'(t) = x(t)\left[r_1 - ax(t-\tau_1) - y(t)\right] \\ y'(t) = y(t)\left[-r_2 + cx(t) - y(t-1)\right], \end{cases} \tag{1.39}$$

where we exploit old variables and parameters instead of s, $u(t)$ and $v(t)$. We put $r_1 = 4.6800$, $r_2 = 2.1450$, $b = 0.2791$, $c = 1.6176$ and $\tau_1 = 0.3590$. Figures 1.11 shows the time series of the solution of (1.39) with initial functions $\phi(s) = 0.7$ for the first variable x and $\psi(s) = 0.1$ for the second variable y. It is observed that the behavior of the solution is chaotically, but finally it settles to sustained periodic solution. Figures (1.12) give phase portrait of $(x(t), y(t))$.

1.7 Discussion

In section 1.2, system (E_1) was derived as a model for two species as predator and prey, both of whose population growth are inhibited by their self produced toxic substrates, respectively.

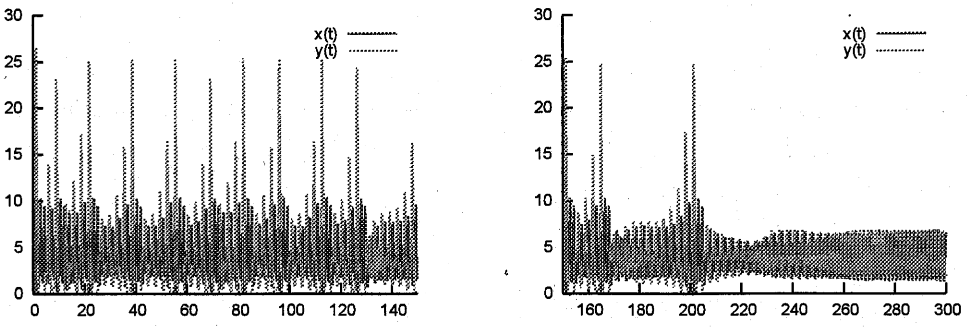

Figure 1.11: $r_1 = 4.6800$, $r_2 = 2.1450$, $b = 0.2791$, $c = 1.6176$, $\tau_1 = 0.3590$

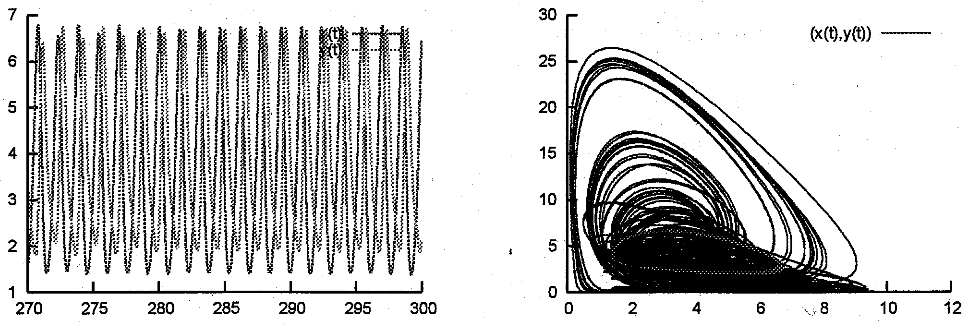

Figure 1.12: $r_1 = 4.6800$, $r_2 = 2.1450$, $b = 0.2791$, $c = 1.6176$, $\tau_1 = 0.3590$

Another interpretation for system (E_1) is a model which describes the virus dynamics with the immune system. In section 1.3, we obtained Theorem 1.1 for global attractivity of the positive equilibrium of (1.1). The theorem for global attractivity of system (E_1) is improved by combining with the result obtained by He [23]. It was also shown that Liapunov functionals used in the proof of global attractivity are also applicable to prove the uniform stability for the zero solution of linearized system. In section 1.4, critical values of time delay through which system (E_1) undergoes a Hopf bifurcation were analytically determined. Furthermore, for the existence of local Hopf bifurcation, the result by Song and Wei [60] is obtained as a special case. If $\tau_2 = 0$, the same result obtained by Song and Wei [60] is obtained.

Corollary 1.4. *[60, Theorem 2.1.] Assume that $\tau_2 = 0$. Let*

($H1$) *either $r > pq$ and $q^2 - p^2 - 2r > 0$ or $(q^2 - p^2 - 2r)^2 - 4(r^2 - p^2q^2) < 0$,*

($H2$) *either $r < pq$ or $q^2 - p^2 - 2r < 0$ and $(q^2 - p^2 - 2r)^2 - 4(r^2 - p^2q^2) = 0$,*

($H3$) *$r > pq$, $q^2 - p^2 - 2r < 0$ and $(q^2 - p^2 - 2r)^2 - 4(r^2 - p^2q^2) > 0$.*

1. *If ($H1$) holds, then the positive equilibrium of (E_1) is (locally) asymptotically stable for all $\tau_1 \geq 0$.*
2. *If ($H2$) holds, then the positive equilibrium of (E_1) is (locally) asymptotically stable for $\tau_1 \in [0, \tau_{10}^+)$ and unstable for $\tau_1 > \tau_{10}^+$. System (E_1) undergoes a Hopf bifurcation at the positive equilibrium for $\tau_1 = \tau_{10}^+$.*
3. *If ($H3$) holds, a finite number of stability switches occurs. Finally system (E_1) becomes unstable.*

Here $\omega = \omega_\pm$ are real roots of the polynomial equation

$$\omega^4 + (q^2 - p^2 - 2r)\omega^2 + r^2 - p^2q^2 = 0 \tag{1.40}$$

satisfying $\omega_- < \omega_+$; $\tau_{10}^\pm$ is defined by $\frac{1}{\omega_\pm}\cos^{-1}\left[\frac{-qr}{p(\omega_\pm + q^2)}\right]$.

Proof. Note that (1.40) is derived from (1.28). If (H1) holds, (1.40) has no real roots. Since all roots of the characteristic equation (1.22) have negative real parts when $\tau_1 = \tau_2 = 0$, (i) holds. It follows that (1.40) has at least one positive root if and only if either (H2) or (H3) holds. Then, δ_1 is calculated as follows:

$$\delta_1 = (\omega^2 - r)(2\omega^2 - p\omega \sin \omega\tau_1) + pq^2\omega \sin \omega\tau_1$$

$$= \omega^4 - (r^2 - p^2q^2). \tag{1.41}$$

Here we used (1.23) with $\tau_2 = 0$ and (1.27). If (H2) holds, then it immediately follows from (1.41) that $\delta_1 > 0$. If (H3) holds, then $\omega_-^2 < -(q^2 - p^2 - 2r)/2 < \omega_+^2$. Moreover, $\delta_1 > 0$ for $\omega = \omega_+^2$ and $\delta_1 < 0$ for $\omega = \omega_-^2$. The remainder of the proof proceeds as the same manner used by Cooke and van den Driessche [11]. This completes the proof. □

We show another corrollary in which we assume that $\tau_2 = 2\tau_1$ and $r < pq$. We do not write the subscript of τ_1 for the convenience.

Corollary 1.5. *Assume that $\tau_2 = 2\tau_1 = 2\tau$ and $r < pq$. Then a pair of simple conjugate pure imaginary roots $\lambda_+ = i\omega^*$ and $\lambda_- = -i\omega^*$ of (1.22) exists at some $\tau = \tau^k$, which crosses the imaginary axis as τ increases from left to right if $\delta > 0$ and right to left if $\delta < 0$.*

Proof. In this case, (1.27), (1.28) and (1.29) are equivalent to

$$\begin{cases} \sin\omega\tau = f_1(u), \\ \sin 2\omega\tau = f_2(u), \\ \cos 3\omega\tau = f_3(u). \end{cases} \tag{1.42}$$

Note that

$$\begin{aligned} f_2(u) &= \sin 2\omega\tau = 2\sin\omega\tau\cos\omega\tau \\ &= 2f_1(u)\cos\omega\tau, \\ f_3(u) &= \cos 3\omega\tau \\ &= \cos 2\omega\tau\cos\omega\tau - 2\cos\omega\tau\sin^2\omega\tau \\ &= (1 - 4f_1^2(u))\cos\omega\tau. \end{aligned}$$

We claim that $f_1(u) = \sin\omega\tau \neq 0$. In fact, if $f_1(u) = \sin\omega\tau = 0$, it follows from (1.42) that (i) $f_2(u) = 0$ and $f_3(u) = 1$ or (ii) $f_2(u) = 0$ and $f_3(u) = -1$. Both cases contradict to (1.36). Thus we obtain

$$f_2(u)(1 - 4f_1^2(u)) - 2f_1(u)f_3(u) = 0.$$

Define $g_1(u)$, $g_2(u)$ and $g_3(u)$ as

$$\begin{aligned} g_1(u) &= u^2 + (p^2 - q^2 - 2r)u + r^2 - p^2q^2, \\ g_2(u) &= u^2 + (q^2 - p^2 - 2r)u + r^2 - p^2q^2, \\ g_3(u) &= -(p^2 + q^2)(u - r - p^2)(u - r - q^2) + (p^2 - q^2)^2 r. \end{aligned}$$

Immediately, we have

$$\begin{aligned}&2p^2qu\sqrt{u}(u-r-p^2)(u-r-q^2)^2\{f_2(u)(1-4f_1^2(u))-2f_1(u)f_3(u)\}\\&=g_2(u)[p^2u(u-r-q^2)^2-g_1^2(u)]-ug_1(u)g_3(u).\end{aligned}$$

Hence (1.42) is equivalent to the following polynomial equation $h(u)=0$, where

$$\begin{aligned}h(u)&:=g_2(u)[p^2u(u-r-q^2)^2-g_1^2(u)]-ug_1(u)g_3(u)\\&=-u^6+c_1u^5+c_2u^4+c_3u^3+c_2u^4+c_5u+c_6.\end{aligned}$$

We do not show explict values of $c_1,\cdots,c_5$. Since $r<pq$, $g_1(0)=g_2(0)=r^2-p^2q^2$ and hence

$$c_6=h(0)=-g_2(0)g_1^2(0)=-(r^2-p^2q^2)^3>0.$$

Hence the intermediate theorem implies that there exists at least one positive root of the polynomial equation $h(u)=0$ on $[0,\infty)$. Substituting a positive root of the polynomial equation $h(\omega^2)=0$ into (1.42), the critical value of time delay τ^k can be obtained. Thus we can calculate $\delta(\tau^k)$. If $\delta(\tau^k)>0$, a pair of simple conjugate pure imaginary roots crosses the imaginary axes from left to right. This completes the proof. □

In section 1.5, some numerical simulations were carried out and it was suggested that subcritical Hopf bifurcation occurs on system (E_1). Moreover chaotic behavior was observed when the time delay in an intraspecific competition of predator τ_2 becomes large. The chaotic behavior was not discussed in He [23]. We believe this is the first time such chaotic behavior has been observed. Compared to results of May [40] and Song and Wei [60], our model brings new aspects of the effect of time delay, since $\tau_2=0$ in their model. Other values of τ_2 may generate other type of chaotic behavior, which is an interesting problem. We also observed a chaotic transient dynamics on some particular set of parameters, but the investigation for such kind of dynamics is not sufficient. Further analyses and considerations for the global dynamics of (E_1) are left for future works.

Chapter 2

Resource competition and delayed nutrient recycling

ABSTRACT

Competition on a model with nutrient recycling is considered. The model is based on a chemostat-type equation which is used to study population dynamics of microorganisms. The model consists of four organisms competing for a limiting nutrient. Nutrient is supplied both from the in-flow of medium and a recycling with delay, the latter is generated from dead organisms by bacterial decomposition. This chapter shows that the model undergoes a Hopf bifurcation through a critical value of time delay when the in-flow is small. The coexistence of four organisms competing for one limiting nutrient is indicated by numerical simulation results.
keywords: Chemostat; Competition in two habitats; Nutrient diffusion; Competitive exclusion; Bacterial decomposition with delay; Periodic coexistence*

2.1 Introduction

Chemostat equations have been used to study population dynamics of microorganisms in experimental apparatuses or aquatic ecosystems such as lakes. An important difference between "chemostat" situation and "lake" situation appears in the fact that lakes generally have residence time of nutrient and sediments measured in years (Powell and Richerson [47]). This implies that

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*This chapter is mainly attributed to the paper [45] published in *Mathematical Biosciences*.

in the model of natural systems, a smaller wash-out rate constant and the regeneration of nutrient due to bacterial decomposition of the dead biomass must be considered (Svirezhev and Logofet [64]). Moreover a delay due to bacterial decomposition is always present and increases as temperature decreases in natural systems (Whittaker [72]). Chemostat-type equations with delayed nutrient recycling have extensively studied by many authors. Beretta *et al.* [2] proposed an open system with a single species feeding on a limiting nutrient. Global asymptotic stability of the positive equilibrium is studied by Beretta & Takeuchi ([3], [4]) and He & Ruan [21]. Freedman & Yuantong [13] extended the model in [2] and obtained persistence and extinction criteria for the competing populations. Ruan & He [22] generalized the model of [13] to arbitrary n-competing organisms and showed a global asymptotic stability of the positive equilibrium.

It is important to consider models incorporating predator-prey response if a true lake community is to be modeled. Butler *et al.* [8] considered a chemostat model with three trophic levels where two predators compete for one prey. Predator-prey response also appears in zooplankton-phytoplankton-nutrient models, which are extensively studied by Ruan ([49], [50]) and the other authors. The spatial distribution of nutrient is also thought as an important factor which makes difference between "chemostat" situation and "lake" situation. In an environment with a small dilution, dead organisms usually settle and accumulate on the bottom of "lake". This makes bacterial decomposition take place on the bottom of the environment and the recycled nutrient appears from there. Moreover nutrient is not stirred instantaneously. The mixing of nutrient is mainly achieved through diffusion.

To incorporate the spatial distribution of nutrient, let us consider

$$\begin{cases} S'(t) =(S^0 - S(t))D - \sum_{i=1}^{2} b_i U_i(S(t))x_i(t) + d(R(t) - S(t)), \\ R'(t) =\gamma \sum_{i=1}^{2} \{x_i(t-\tau) + y_i(t-\tau)\} - \nu R(t) - \sum_{i=1}^{2} c_i V_i(R(t))y_i(t) + d(S(t) - R(t)), \\ x_i'(t) =x_i(t)\left(b_i U_i(S(t)) - \mu\right), \\ y_i'(t) =y_i(t)\left(c_i V_i(R(t)) - \mu\right), \quad (i=1,2) \end{cases} \tag{E$_2$}$$

with the initial function

$$\begin{cases} S(0) > 0, R(0) > 0, x_i(s) = \phi_i(s) > 0 \text{ for } (-\tau \leq s \leq 0), \\ y_i(s) = \psi_i(s) > 0 \text{ for } (-\tau \leq s \leq 0), (i=1,2). \end{cases} \tag{I}$$

Here S denotes the concentration of dissolved nutrient in the environment, while R denotes the concentration of dissolved nutrient which is settled on the bottom of the environment. Each x_i and y_i $(i=1,2)$ are measures for populations of some organisms. We suppose that y_is belong to a group of so-called *benthos*; organisms of which habitats are the bottoms of lakes, rivers, and creeks. As we see in (E_2), x_is compete only for the limiting resource S, while y_is compete only for the limiting resource R. It is assumed that x_i (or y_i) never feeds the nutrient R (or S). By this assumption, system (E_2) models a lake community with two segregated habitats in terms of nutrient. S^0 is the constant input concentration of dissolved nutrient, and D is the dilution rate. d is the diffusion rate due to the mixing (stirring) effect of the environment. ν is the rate of self-purification of the environment. Self-purification is typically brought by aquatic plants which exploit nutrients accumulated on the bottom of the environment. Each x_i has the maximum specific growth rate b_i, while each y_i has the maximum specific growth rate c_i. Note that respective maximum uptake rate of x_i and y_i correspond to the maximum specific growth rate. All organisms are assumed to have the same removal rate μ. Removal rate means the addition of the death and the dilution rate. γ is the recycle rate of dead organisms which satisfies $0 \leq \gamma < \mu$. τ is the constant decomposition duration. All parameters except for γ and τ are positive, γ and τ are nonnegative.

The diffusion between S and R is described by $d(R(t) - S(t))$ for S and $d(S(t) - R(t))$ for R. Functions U_i and V_i $(i = 1, 2)$ describe the nutrient uptake of organisms x_i and y_i, respectively. Assume that

1. $U_i(\xi)$ is continuously differentiable, bounded.
2. $U_i(0) = 0$, $U_i'(\xi) > 0$ for $\xi > 0$, $U_i(\xi) \to 1$ as $\xi \to \infty$.

A typical example of U_i is the Michaelis-Menten function of the form:

$$U_i(\xi) = \frac{\xi}{A_i + \xi}, (i = 1, 2),$$

where $A_i > 0$ is called a half-saturation constant or Michaelis-Menten constant. The hypotheses for V_i are given in the same manner.

Finally the process of nutrient recycling is formulated as follows: $Q(t)$ denotes the concentration of accumulated dead organisms. The input to $Q(t)$ is assumed to be proportional with the amount of living organisms at time t, $\delta \sum_{i=1}^{2} \{x_i(t) + y_i(t)\}$. Here δ denotes the death rate of organisms. Let $P_1(t)$ be the probability that organisms become dead organisms at time 0 and still remain as the form of dead organisms (or are not decomposed yet) at time t. Then

$$Q(t) = \int_0^t P_1(t - s)\delta \left[\sum_{i=1}^{2} \{x_i(s) + y_i(s)\} \right] ds.$$

A measure for the population of bacteria is assumed to be constant B_0. If the decomposition follows the simple mass action law, then the total amount of recycled nutrient $N(t)$ from the dead organisms is

$$N(t) = \beta \int_0^t P_2(t-s) B_0 Q(s)\, ds.$$

Here $P_2(t)$ is the probability that dead organisms at time 0 are still stored in bacteria (or do not still become recycled nutrient yet) at time t. β is the conversion rate at which dead organisms become nutrient.

For more simplification, we continue to add some assumptions. Assume that $P_1(t) = \delta(t)$ where $\delta(t)$ is the Dirac's delta function. Then

$$Q(t) = \delta \sum_{i=1}^{2} \{x_i(t) + y_i(t)\}. \tag{2.1}$$

If the decomposition period is assumed to have a constant duration, that is, $P_2(t) = 1$ for $0 \le t \le \tau$ and $P_2(t) = 0$ for $t > \tau$, then

$$N(t) = \beta \int_{t-\tau}^{t} B_0 \delta \sum_{i=1}^{2} \{x_i(s) + y_i(s)\}\, ds. \tag{2.2}$$

Differentiating (2.2) with respect to t gives

$$N'(t) = \beta B_0 \delta \sum_{i=1}^{2} \{x_i(t) + y_i(t)\} - \beta B_0 \delta \sum_{i=1}^{2} \{x_i(t-\tau) + y_i(t-\tau)\}.$$

Finally $\beta B_0 \delta \sum_{i=1}^{2} \{x_i(t-\tau) + y_i(t-\tau)\}$ enters the bottom nutrient at time t. By setting $\beta B_0 \delta = \gamma$, we have (E_2).

Note that (2.1) considers a situation where there is no accumulation of dead organisms, whereas this is opposite to [47]. It would be more realistic to consider accumulated dead organisms. If the bacterial decomposition is assumed to be carried out at the constant rate d_B, then $P_1(t) = e^{-d_B t}$ and hence

$$Q(t) = \int_0^t e^{-d_B(t-s)} \delta \left[\sum_{i=1}^{2} \{x_i(s) + y_i(s)\} \right] ds. \tag{2.3}$$

Differentiating (2.3) with respect to t gives

$$Q'(t) = -d_B Q(t) + \delta \sum_{i=1}^{2} \{x_i(t) + y_i(t)\}. \tag{2.4}$$

A model with (2.4) rather than (2.1) is studied in Section 2.4 by numerical simulations. It will be shown that the qualitative outcome of the model with (2.4) is the same as the outcome of system (E_2) (model with (2.1)).

In Section 2.2, the existence of nonnegative equilibria of system (E$_2$) is derived. In Section 2.3, the stability of nonnegative equilibria is studied in which it is shown that all equilibria become unstable as time delay increases and system (E$_2$) undergoes a Hopf bifurcation under some suitable assumptions. In Section 2.4, it is shown by means of numerical simulations that the coexistence of all organisms is possible in the form of periodic oscillation if all equilibria are unstable. Finally we discuss our results in Section 2.5.

2.2 Classification of equilibria

Equilibria of system (E$_2$) are nonnegative roots of the following system of equations:

$$\begin{aligned}
&(S^0 - S)D - \sum_{i=1}^{2} b_i U_i(S) x_i + d(R - S) = 0,\\
&\gamma \sum_{i=1}^{2} (x_i + y_i) - \nu R - \sum_{i=1}^{2} c_i V_i(R) y_i + d(S - R) = 0,\\
&(b_i U_i(S) - \mu) x_i = 0,\\
&(c_j V_j(R) - \mu) y_j = 0 \quad (i, j = 1, 2).
\end{aligned}$$

Let us set

$$S_w = \frac{(d+\nu)S^0 D}{Dd + d\nu + D\nu}, \quad R_w = \frac{dS^0 D}{Dd + d\nu + D\nu}$$

and $E_w = (S_w, R_w, 0, 0, 0, 0)$. E_w denotes the *washout equilibrium* which always exists. If $b_i > \mu$ and $c_i > \mu$, there exist positive numbers S_i^* and R_j^* such that

$$S_i^* = U_i^{-1}\left(\frac{\mu}{b_i}\right), \; R_j^* = V_j^{-1}\left(\frac{\mu}{c_j}\right), \quad (i, j = 1, 2).$$

Throughout the reminder of this chapter, assume that

$$S_1^* \neq S_2^* \quad \text{and} \quad R_1^* \neq R_2^*. \tag{2.5}$$

The case $S_1^* = S_2^*$ or $R_1^* = R_2^*$ represents a degenerate case, which is less expected in nature so that we exclude it.

By (2.5), all equilibria of system (E$_2$) are E_w and

$$\begin{aligned}
&E_{x_1} = (S_1^*, \bar{R}_1, \bar{x}_1, 0, 0, 0), \quad E_{x_2} = (S_2^*, \bar{R}_2, 0, \bar{x}_2, 0, 0),\\
&E_{y_1} = (\bar{S}_1, R_1^*, 0, 0, \bar{y}_1, 0), \quad E_{y_2} = (\bar{S}_2, R_2^*, 0, 0, 0, \bar{y}_2),\\
&E_{11} = (S_1^*, R_1^*, x_{11}^*, 0, y_{11}^*, 0), \quad E_{12} = (S_1^*, R_2^*, x_{12}^*, 0, 0, y_{12}^*),\\
&E_{21} = (S_2^*, R_1^*, 0, x_{21}^*, y_{21}^*, 0), \quad E_{22} = (S_2^*, R_2^*, 0, x_{22}^*, 0, y_{22}^*),
\end{aligned}$$

where

$$\bar{S}_i = \frac{S^0 D + dR_i^*}{d+D},\ \bar{x}_i = \frac{(d+\nu)S^0 D - (Dd + d\nu + D\nu)S_i^*}{d(\mu-\gamma)+\mu\nu},$$
$$\bar{R}_j = \frac{\gamma S^0 D + (d(\mu-\gamma)-\gamma D)\, S_j^*}{d(\mu-\gamma)+\mu\nu},\ \bar{y}_j = \frac{dS^0 D - (Dd + d\nu + D\nu)R_j^*}{(d+D)(\mu-\gamma)},$$
$$x_{ij}^* = \frac{(S^0 - S_i^*)D + d(R_j^* - S_i^*)}{\mu} \text{ and } y_{ij}^* = \frac{\gamma(S^0 - S_i^*)D + d(\mu-\gamma)(S_i^* - R_j^*) - \mu\nu R_j^*}{\mu(\mu-\gamma)}.$$

Each equilibrium of system (E_2) must be nonnegative, that is, $E_\cdot \in \mathbf{R}^6_+$ where

$$\mathbf{R}^6_+ \equiv \left\{\mathbf{z} = (z_1, z_2, z_3, z_4, z_5, z_6) \in \mathbf{R}^6 \middle|\, z_i \geq 0\, (i = 1, 2, \cdots, 6)\right\}.$$

Proposition 2.1. *Suppose that* $b_i > \mu$, $c_j > \mu$ *and* (2.5).

1. $E_{x_i} \in \mathbf{R}^6_+$ *iff* $S_w \geq S_i^*$. *Moreover* $\bar{x}_i > 0$ *iff* $S_w > S_i^*$.
2. $E_{y_j} \in \mathbf{R}^6_+$ *iff* $R_w \geq R_j^*$. *Moreover* $\bar{y}_j > 0$ *iff* $R_w > R_j^*$.
3. $E_{ij} \in \mathbf{R}^6_+$ *iff* $\bar{S}_j \geq S_i^*$ *and* $\bar{R}_i \geq R_j^*$. *Moreover* $x_{ij}^* > 0$ *and* $y_{ij}^* > 0$ *iff* $\bar{S}_j > S_i^*$ *and* $\bar{R}_i > R_j^*$.

Proof. Obviously $S_i^* > 0$. Since $\mu > \gamma$, $\bar{x}_i \geq 0$ if and only if $(d+\nu)S^0 D - (Dd + d\nu + D\nu)S_i^* \geq 0$. Then $S_i^* \leq (d+\nu)S^0 D/(Dd + d\nu + D\nu) = S_w$. Moreover we see that $\bar{R}_i \geq 0$ if $S^0 \geq S_i^*$ since $S^0 \geq S_w \geq S_i^*$. Hence the assertion (1) holds true. The proof of assertions (2) and (3) are similar. This completes the proof. □

Proposition 2.2. $S_w > \bar{S}_j$ *if* $R_w > R_j^*$. *On the other hand, there exists* $\bar{\gamma}$ *satisfying* $0 < \bar{\gamma} < \mu$ *such that* $R_w = \bar{R}_i$ *for* $\gamma = \bar{\gamma}$ *if* $S_w > S_i^*$. *Moreover* $R_w > \bar{R}_i$ *if* $\gamma < \bar{\gamma}$ *and* $R_w < \bar{R}_i$ *if* $\gamma > \bar{\gamma}$.

Proof. Direct calculation gives $S_w - \bar{S}_j = d(R_w - R_j^*)/(d+D) > 0$. Hence the first assertion holds true. Let us calculate the derivative of $\bar{R}_i$ with respect to γ. Since $S_w > S_i^*$,

$$\frac{\partial \bar{R}_i(\gamma)}{\partial \gamma} = \frac{\mu\left\{(d+\nu)S^0 D - (Dd + d\nu + D\nu)S_i^*\right\}}{(d(\mu-\gamma)+\mu\nu)^2} > 0.$$

This implies that $\bar{R}_i$ is monotone increasing with respect to γ. Hence $\bar{R}_i(0) \leq \bar{R}_i(\gamma) < \bar{R}_i(\mu)$. For $0 \leq \gamma < \mu$, we have

$$R_w - \bar{R}_i(0) = \frac{d\left\{(d+\nu)S^0 D - (Dd + d\nu + D\nu)S_i^*\right\}}{(d+\nu)(Dd + d\nu + D\nu)} > 0,$$
$$R_w - \bar{R}_i(\mu) = -\frac{D\left\{(d+\nu)S^0 D - (Dd + d\nu + D\nu)S_i^*\right\}}{\nu(Dd + d\nu + D\nu)} < 0.$$

By the intermediate theorem, there exists $\bar{\gamma} > 0$ such that $R_w = \bar{R}_i(\bar{\gamma})$. This completes the proof. □

By summarizing Proposition 2.1 and 2.2, we have the following theorem:

Theorem 2.1. *If* $S_i^* < \bar{S}_j$ *and* $R_j^* < \min\{\bar{R}_i, R_w\}$, *then* $E_{x_i} \in \mathbf{R}_+^6$, $E_{y_j} \in \mathbf{R}_+^6$ *and* $E_{ij} \in \mathbf{R}_+^6$ *where* $\bar{x}_i > 0$, $\bar{y}_j > 0$, $x_{ij}^* > 0$ *and* $y_{ij}^* > 0$ $(i,j = 1,2)$.

2.3 Local stability of boundary equilibria

Let us consider the local stability of system (E_2) around nonnegative equilibria. We expect that $E_{x_i} \in \mathbf{R}_+^6$, $E_{y_j} \in \mathbf{R}_+^6$ and $E_{ij} \in \mathbf{R}_+^6$. Suppose that

$$S_i^* < \bar{S}_j \text{ and } R_j^* < \min\{\bar{R}_i, R_w\}, \quad (i,j = 1,2). \tag{2.6}$$

Then by Theorem 2.1, $E_{x_i} \in \mathbf{R}_+^6$, $E_{y_j} \in \mathbf{R}_+^6$ and $E_{ij} \in \mathbf{R}_+^6$ where $\bar{x}_i > 0$, $\bar{y}_j > 0$, $x_{ij}^* > 0$ and $y_{ij}^* > 0$. By (2.5), we can assume that $S_1^* < S_2^*$ and $R_1^* < R_2^*$ without loss of generality.

The characteristic equation for the linearized system of (E_2) around E_w is

$$\begin{aligned}(\lambda + \mu - b_1 U_1(S_w))(\lambda + \mu - b_2 U_2(S_w))(\lambda + \mu - c_1 V_1(R_w))\\ \times (\lambda + \mu - c_2 V_2(R_w))(\lambda^2 + (2d + D + \nu)\lambda + Dd + d\nu + D\nu) = 0.\end{aligned} \tag{2.7}$$

Proposition 2.3. E_w *is unstable if* (2.6) *holds.*

Proof. By (2.6), $R_w > R_2^* > R_1^*$. Since V_1 is monotone increasing, $-\mu + c_1 V_1(R_w) > -\mu + c_1 V_1(R_1^*) = 0$. Note that $-\mu + c_1 V_1(R_w)$ is a root of (2.7). This implies that E_w is unstable since there exists at least one root of (2.7) whose real part is positive (see Elsgol *et.al.* [12]). This completes the proof. □

The characteristic equation for E_{x_i} and E_{y_j} is

$$(\lambda + \mu - b_{k_i} U_{k_i}(S_i^*))(\lambda + \mu - c_1 V_1(\bar{R}_i))(\lambda + \mu - c_2 V_2(\bar{R}_i))(P_{x_i}(\lambda) + Q_{x_i}(\lambda)e^{-\lambda\tau}) = 0, \tag{2.8}$$

$$(\lambda + \mu - b_1 U_1(\bar{S}_j))(\lambda + \mu - b_2 U_2(\bar{S}_j))(\lambda + \mu - c_{k_j} V_{k_j}(R_j^*))(P_{y_j}(\lambda) + Q_{y_j}(\lambda)e^{-\lambda\tau}) = 0 \tag{2.9}$$

where $k_i = 2$ if $i = 1$ and $k_i = 1$ if $i = 2$. Here we omit to give explicit forms of $P_{x_i}(\lambda)$, $Q_{x_i}(\lambda)$, $P_{y_j}(\lambda)$ and $Q_{y_j}(\lambda)$ because E_{x_i} and E_{y_j} are unstable if (2.6) holds.

Proposition 2.4. E_{x_i} *and* E_{y_j} *are unstable if* (2.6) *holds.*

Proof. By (2.6), $\bar{R}_i > R_2^* > R_1^*$. Then $-\mu + c_1V_1(\bar{R}_i) > -\mu + c_1V_1(R_1^*) = 0$. Note that $-\mu + c_1V_1(\bar{R}_i)$ is a root of (2.8). Hence E_{x_i} is unstable. In the same manner, we can show that E_{y_j} is unstable. ☐

Finally, let us consider the local stability of E_{ij}. The characteristic equation for E_{ij} is

$$(\lambda + \mu - b_{k_i}U_{k_i}(S_i^*))(\lambda + \mu - c_{k_j}V_{k_j}(R_j^*))(P_{ij}(\lambda) + Q_{ij}(\lambda)e^{-\lambda\tau}) = 0. \tag{2.10}$$

$P_{ij}(\lambda)$ and $Q_{ij}(\lambda)$ are given as follows:

$$\begin{aligned} P_{ij}(\lambda) =& \lambda^4 + (2d + D + \nu + \sigma_i + \rho_j)\lambda^3 \\ &+ \{dD + d\nu + D\nu + (d + \mu + \nu)\sigma_i + (d + D + \mu)\rho_j + \sigma_i\rho_j\}\lambda^2 \\ &+ \mu\{(d + \nu + \rho_j)\sigma_i + (d + D + \sigma_i)\rho_j\}\lambda + \mu^2\sigma_i\rho_j, \\ Q_{ij}(\lambda) =& -\rho_j\gamma\lambda^2 - \gamma\{d\sigma_i + (d + D + \sigma_i)\rho_j\}\lambda - \mu\gamma\sigma_i\rho_j, \end{aligned} \tag{2.11}$$

where $\sigma_i = b_iU_i'(S_i^*)x_{ij}^*$ and $\rho_j = c_jV_j'(R_j^*)y_{ij}^*$. It suffices to consider the local stability only for E_{11} since (2.10) and (2.11) preserves its symmetricity by replacing the subscripts i and j. Hereafter we omit to write subscripts of σ_i and ρ_j for the notational convenience.

Proposition 2.5. *E_{12}, E_{21} and E_{22} are unstable if* (2.6) *holds.*

Proof. Since $S_1^* < S_2^*$ and U_1 is monotone increasing, $-\mu + b_1U_1(S_2^*) > -\mu + b_1U_1(S_1^*) = \mu - \mu = 0$. Moreover since $-\mu + b_1U_1(S_2^*)$ is a root of (2.10), E_{2j} is unstable ($j = 1, 2$). In the same way, we can show that E_{12} is unstable. This completes the proof. ☐

By proposition 2.3, 2.4 and 2.5, all equilibria except for E_{11} is unstable whether time delay is incorporated or not. Note that these properties hold under the assumptions $S_1^* < S_2^*$ and $R_1^* < R_2^*$. For E_{11}, two eigenvalues given by the first two factors in (2.10), $-\mu + b_2U_2(S_1^*)$ and $-\mu + c_2V_2(R_1^*)$ are negative. Hence the stability of E_{11} depends on the solution given by the last factor in (2.10). Now we look for the possibility that E_{11} becomes unstable as time delay increases. Hereafter let us denote $P_{11}(\lambda) = P(\lambda)$ and $Q_{11}(\lambda) = Q(\lambda)$ (see (2.11)). Consider

$$P(\lambda) + Q(\lambda)e^{-\lambda\tau} = 0. \tag{2.12}$$

Let us apply the geometric stability switch criteria (see Appendix A) for (2.12). Clearly (B1)–(B3) hold for (2.12). (B4) is also true since $P(0) + Q(0) = \mu(\mu - \gamma)\sigma\rho > 0$. Define $F(u) \equiv |P(i\omega)|^2 - |Q(i\omega)|^2$ where $u = \omega^2$. Direct calculation gives

$$F(u) = u^4 + a_3u^3 + a_2u^2 + a_1u + \mu^2(\mu^2 - \gamma^2)\sigma^2\rho^2, \tag{2.13}$$

where

$$\begin{aligned} a_1 =& 2\gamma^2\mu\rho^2\sigma - 2\mu^3\rho\sigma(\rho+\sigma) - \gamma^2(d\sigma + \rho(d+D+\sigma))^2 + \mu^2((d+\nu)^2\sigma^2 \\ &+ 2\rho\sigma(d^2 + (d+\nu)\sigma) + \rho^2((d+D+\sigma)^2 + \sigma^2)), \\ a_2 =& 2\rho(d+D+\sigma)(D\nu + d(D+\nu) + (d+\nu)\sigma) + (D\nu + d(D+\nu) + (d+\nu)\sigma)^2 \\ &+ \rho^2((d+D+\sigma)^2 - \gamma^2) + \mu^2(\rho^2 + 4\rho\sigma + \sigma^2) \\ &- 2\mu(\sigma(d+\nu+\rho)^2 + \rho(d+D+\sigma)^2 + d^2(\sigma+\rho)), \\ a_3 =& (d+\nu+\rho)^2 + (d+D+\sigma)^2 + 2d^2 - 2\mu(\rho+\sigma). \end{aligned}$$

Since $F(u) = 0$ is a quaternary equation, $F(u) = 0$ has exactly four zeroes and hence (B5) holds. Note that (2.13) has exactly two or four positive roots whenever they exist because $F(0) > 0$ and $F(u) \to \infty$ as $u \to \infty$.

It seems hard to find positive roots of (2.13). Here we shall decompose (2.13) into simpler forms. $F(u)$ can be divided into three polynomials as $F(u) = G_1(u)G_2(u) + duH(u)$, where

$$\begin{aligned} G_1(u) =& u^2 + \{(D+\sigma)^2 - 2\mu\sigma\}u + \mu^2\sigma^2, \\ G_2(u) =& u^2 + \left\{(\nu+\rho)^2 - 2\mu\rho\right\} u + (\mu^2 - \gamma^2)\rho^2, \\ H(u) =& 2(2d + D + \nu + \sigma + \rho)u^2 + [-4\left\{(d+\nu)\sigma + (d+D+2\sigma)\rho\right\}\mu \\ &+ d(D+\nu+\sigma+\rho)^2 + 2(D+\sigma)(\nu+\rho)(D+\nu+\sigma+\rho)]\, u \\ &+ [(\mu^2-\gamma^2)\left\{d(\sigma+\rho)^2 + 2\rho\left(\sigma^2 + \rho(D+\sigma)\right)\right\} + 2\mu^2\nu\sigma^2 - 2D\sigma\rho\gamma^2]. \end{aligned}$$

Obviously $F(u) = 0$ if and only if $G_1(u)G_2(u) = -duH(u)$. Hence we can obtain the existence of positive roots of (2.13) by finding intersections of the graphs $G_1(u)G_2(u)$ and $-duH(u)$.

Let us derive a sufficient condition which ensures the existence of positive roots of $F(u) = 0$ under some suitable assumptions. First suppose that

$$\frac{\mu}{b_i} = 1 - \kappa_1 \text{ and } \frac{\mu}{c_j} = 1 - \kappa_2, \tag{2.14}$$

where κ_1 and κ_2 are positive constants. Let us fix κ_1 and κ_2. By adjusting b_i and c_j, S_i^* and R_j^* are kept constants if the value of μ changes. Moreover suppose that

$$\varepsilon := 1 - \frac{\gamma}{\mu};\quad d = \varepsilon\bar{d}\,,\ D = \varepsilon\bar{D} \text{ and } \nu = \varepsilon\bar{\nu}.$$

According to the definition of σ_i and ρ_j,

$$\begin{aligned} \sigma_i &= \frac{U_i'(U_i^{-1}(1-\kappa_1))}{1-\kappa_1}\left[(S^0 - S_i^*)\bar{D} + \bar{d}(R_j^* - S_i^*)\right]\varepsilon \propto \varepsilon, \\ \rho_j &= \frac{V_j'(V_j^{-1}(1-\kappa_2))}{1-\kappa_2}\left[(1-\varepsilon)(S^0 - S_i^*)\bar{D} - \bar{\nu}R_j^* - \bar{d}(R_j^* - S_i^*)\varepsilon\right]. \end{aligned}$$

Hence we can see that σ_i is proportional to ε, while ρ_j is not. By collecting these observations, we suppose that

$$\varepsilon := 1 - \frac{\gamma}{\mu}; \quad d = \varepsilon \bar{d}\ ,\ D = \varepsilon \bar{D}\ ,\ \nu = \varepsilon \bar{\nu} \text{ and } \sigma = \varepsilon \bar{\sigma}. \tag{L}$$

In (L), all of d, D, ν, σ are the same order in terms of ε. If $\varepsilon \ll 1$, (L) represents the chemostat model with small in-flow, small self-purification, small diffusion and high recycle rate of bacterial decomposition. These assumptions would be reasonable to consider the dynamics such as in lakes.

Since $G_1(u) = (u - \mu\sigma)^2 + (D + \sigma)^2 u$, $G_1(u) = 0$ cannot have a positive root. $G_2(u) = 0$ has two positive roots if and only if

$$(\nu + \rho)^2 - 2\mu\rho < 0 \text{ and } \mathcal{D}(G_2)(\mu) = [(\nu + \rho)^2 - 2\mu\rho]^2 - 4(\mu^2 - \gamma^2)\rho^2 > 0. \tag{2.15}$$

It is easy to see that $\mathcal{D}(G_2)(\mu) = 4\rho^2(1-\varepsilon)^2\mu^2 - 4\rho(\nu+\rho)^2\mu + (\nu+\rho)^4 > 0$ for sufficiently large μ. Hence (2.15) holds true for sufficiently large μ and small ε.

Let us rewrite $H(u)$ as $H(u) = \alpha_0 u^2 + \alpha_1 u + \alpha_2$. $H(u) = 0$ has two positive real roots if and only if

$$\alpha_1 < 0 \text{ and } \mathcal{D}(H) = \alpha_1^2 - 4\alpha_0\alpha_2 > 0. \tag{2.16}$$

$\alpha_1 < 0$ if and only if

$$\mu > \frac{d(D + \nu + \sigma + \rho)^2 + 2(D + \sigma)(\nu + \rho)(D + \nu + \sigma + \rho)}{4\{(d + \nu)\sigma + (d + D + 2\sigma)\rho\}}.$$

To check the signature of $\mathcal{D}(H)$, let us arrange the coefficient α_k according to the order of ε. Then each α_0, α_1 and α_2 is represented by $\alpha_0 = \zeta_{00} + \zeta_{01}\varepsilon$, $\alpha_1 = \zeta_{11}\varepsilon + \zeta_{12}\varepsilon^2 + \zeta_{13}\varepsilon^3$ and $\alpha_2 = \zeta_{22}\varepsilon^2 + \zeta_{23}\varepsilon^3 + \zeta_{24}\varepsilon^4$. Here $\zeta_{k\ell}$ denotes the coefficient of ε^ℓ in α_k. Note that $\zeta_{00} = 2\rho$, $\zeta_{11} = -4(\bar{d}+\bar{D}+2\bar{\sigma})\rho\mu + 2(\bar{D}+\bar{\sigma})\rho^2$ and $\zeta_{22} = (\bar{d}+2(\bar{D}+\bar{\sigma}))\rho^2\mu^2 - 2\bar{D}\bar{\sigma}\rho\mu^2$. Direct calculation gives $\mathcal{D}(H) = \alpha_1^2 - 4\alpha_0\alpha_2 = (\zeta_{11}^2 - 4\zeta_{00}\zeta_{22})\varepsilon^2 + \mathcal{O}(\varepsilon^2)$. Moreover

$$\begin{aligned}\zeta_{11}^2 - 4\zeta_{00}\zeta_{22} =& 8\left\{2(\bar{d} + \bar{D} + 2\bar{\sigma})^2 - ((\bar{d} + 2(\bar{D} + \bar{\sigma}))\rho + 2\bar{D}\bar{\sigma}\right\}\rho^2\mu^2 \\ &- 16(\bar{D} + \bar{\sigma})(\bar{d} + \bar{D} + 2\bar{\sigma})\rho^3\mu + 4(\bar{D} + \bar{\sigma})^2\rho^4.\end{aligned}$$

Hence it is easy to see that $\mathcal{D}(H) > 0$ for sufficiently large μ and small ε if $2(\bar{d} + \bar{D} + 2\bar{\sigma})^2 - (\bar{d} + 2(\bar{D} + \bar{\sigma}))\rho + 2\bar{D}\bar{\sigma} > 0$, or equivalently,

$$\varepsilon\rho < \frac{2(d + D + 2\sigma)^2 + 2D\sigma}{d + 2(D + \sigma)}. \tag{2.17}$$

(2.17) holds true for sufficiently small ε. Consequently (2.16) holds true for sufficiently large μ and small ε. Let u_h^- and u_h^+ denote positive roots of the quadratic equation $H(u) = 0$ satisfying

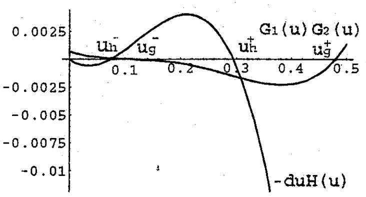

Figure 2.1: Graphs of $G_1(u)G_2(u)$ and $-duH(u)$

$u_h^- < u_h^+$. Then the graphs $G_1(u)G_2(u)$ and $H(u)$ have at least two intersections on $[0, \infty)$ if a positive root of the quadratic equation $G_2(u) = 0$ satisfies $u_g^\pm \in (u_h^-, u_h^+)$ (see, Fig. 2.1).

Lemma 2.1. *Assume that* (L) *and sufficiently large* μ *and small* ε *to ensure that* (2.15) *and* (2.16) *hold. Then* E_{11} *becomes eventually unstable as* τ *increases if* $u_h^- < u_g^-$ *or* $u_g^+ < u_h^+$.

In the end of this section, let us check whether system (E_2) undergoes a Hopf bifurcation. It is necessary to check the following three hypotheses (see [18, pp. 332, Theorem 1.1.]):

(H1) For $\tau \in [0, \tau^*)$, all eigenvalues of characteristic equation (2.12) have negative real parts.

(H2) For τ near τ^*, there exists a pair of simple and complex conjugate eigenvalues $\lambda(\tau)$ and $\bar{\lambda}(\tau)$ of (2.12) such that $\mathrm{Re}\,(\lambda(\tau)) = 0$, $\mathrm{Im}\,(\lambda(\tau)) > 0$ and $\mathrm{Re}\,(\partial\lambda(\tau)/\partial\tau) > 0$ at $\tau = \tau^*$.

(H3) All the other eigenvalues of (2.12) at $\tau = \tau^*$ have negative real parts.

(H2) holds if the assumptions of Lemma 2.1 are satisfied. To confirm (H1) and (H3), consider the case $\tau = 0$. Then (2.12) becomes a fourth order polynomial equation of the form:

$$\begin{aligned}
&\lambda^4 + (2d + D + \nu + \sigma + \rho)\lambda^3 \\
&+ [dD + d\nu + D\nu + (d + \mu + \nu)\sigma + (d + D + \sigma)\rho + (\mu - \gamma)\rho]\lambda^2 \\
&+ [(\nu + \rho)\mu\sigma + (\mu - \gamma)\{d\sigma + (d + D + \sigma)\rho\}]\lambda + \mu(\mu - \gamma)\sigma\rho = 0.
\end{aligned} \tag{2.18}$$

Let us rewrite (2.18) as $\lambda^4 + \beta_1\lambda^3 + \beta_2\lambda^2 + \beta_3\lambda + \beta_4 = 0$. By the well known Routh-Hurwitz criterion, all roots of (2.18) have negative real parts if and only if $\mathcal{R} = \beta_1\beta_2\beta_3 - \beta_3^2 - \beta_1^2\beta_4 > 0$. Let us arrange the coefficient β_k according to the order of ε. Then $\beta_1 = \eta_{10} + \eta_{11}\varepsilon$, $\beta_2 = \eta_{21}\varepsilon + \eta_{22}\varepsilon^2$, $\beta_3 = \eta_{31}\varepsilon + \eta_{32}\varepsilon^2 + \eta_{33}\varepsilon^3$ and $\beta_4 = \eta_{42}\varepsilon^2$. Here $\eta_{k\ell}$ denotes the coefficient of ε^ℓ in β_k. In particular $\eta_{10} = \rho$, $\eta_{21} = \mu\bar{\sigma} + (\bar{d} + \bar{D} + \bar{\sigma})\rho + \mu\rho$, $\eta_{31} = \mu\bar{\sigma}\rho$ and $\eta_{42} = \mu^2\bar{\sigma}\rho$. Direct calculation gives $\mathcal{R} = (\eta_{10}\eta_{21}\eta_{31} - \eta_{31}^2 - \eta_{10}^2\eta_{42})\varepsilon^2 + \mathcal{O}(\varepsilon^2)$. Moreover we have $\eta_{10}\eta_{21}\eta_{31} - \eta_{31}^2 - \eta_{10}^2\eta_{42} = \mu\bar{\sigma}\rho^3(\bar{d} + \bar{D} + \bar{\sigma}) > 0$. Hence $\mathcal{R} > 0$ if $\varepsilon \ll 1$.

Lemma 2.2. *Assume that* (L) *holds for sufficiently small* ε. *Then* E_{11} *is locally asymptotically stable for sufficiently small* τ.

Corollary 2.1. *If the assumptions of Lemma 2.1 and 2.2 are satisfied, a family of periodic solutions bifurcates from* E_{11} *for* τ *near* $\tau^* > 0$. *After system* (E_2) *undergoes a Hopf bifurcation, species* x_1 *and* y_1 *survive in the form of periodic oscillation on* x_1y_1*-plane.*

Finally let us show an example of Corollary 2.1. Suppose that the nutrient uptake functions $U_i(\xi)$ and $V_j(\xi)$ are Michaelis-Menten type, that is,

$$U_i(S) = \frac{S}{B_i + S}, \quad V_j(R) = \frac{R}{C_j + R}.$$

Parameters are given by

$$\begin{cases} S^0 = 3, D = 0.1, \nu = 0.05, d = 0.5, b_1 = 1.155, B_1 = 0.05, c_1 = 1.15, \\ C_1 = 0.048, b_2 = 2.8, B_2 = 0.6, c_2 = 3, C_2 = 0.72, \mu = 1 \text{ and } \gamma = 0.8. \end{cases} \tag{P}$$

Then $S_1^* = 0.322581 < S_2^* = 0.333333$, $R_1^* = 0.32 < R_2^* = 0.36$, $\sigma = 0.110848$, $\rho = 0.404453$. We can confirm that (2.13) and (2.16) hold. Approximately, we have $u_h^- = 0.0730887 < u_g^- = 0.122793$. Since the assumptions of Lemma 2.1 are satisfied, E_{11} becomes unstable as τ increases. Moreover $\mathcal{R} = 0.0838494 > 0$. Hence a family of periodic solution bifurcates from E_{11} as τ increases. Note that by Remark A.1, the explicit value of τ which may cause a Hopf bifurcation is numerically calculated as $\tau^* = 8.45155$.

2.4 Numerical simulations

In this section, let us show some numerical simulation results. In Section 2.3, it was shown that a family of periodic solutions bifurcates from E_{11} for τ near τ^* for the set of parameter (P). Note that $\tau^* \approx 8.45155$. Figs 2.2 and 2.3 illustrate the trajectories of the solution of (E_2) for (P) and $\tau = 10$. The initial functions are given by $(0.7, 0.4, 0.3 - 0.05\cos 3t, 0.5 - 0.2\cos 4t, 0.3 - 0.1\cos 2t, 0.4 - 0.2\sin t)$. It is observed that all organisms survive periodically. These figures suggest that periodic coexistence of organisms occurs.

Finally, let us study the model with (2.4) rather than (2.1) by numerical simulations. As we can see in (E_2), accumulation of dead organisms is ignored. This seems unrealistic since it is

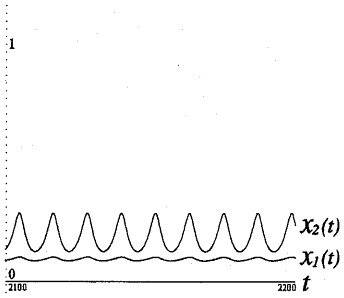

Figure 2.2: $x_1(t)$ and $x_2(t)$ of (E$_2$)

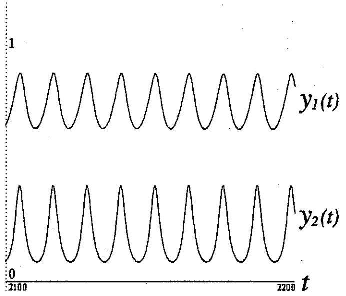

Figure 2.3: $y_1(t)$ and $y_2(t)$ of (E$_2$)

opposite to [47]. Let us consider

$$\begin{cases} S'(t) =(S^0 - S(t))D - \sum_{i=1}^{2} b_i U_i(S(t))x_i(t) + d(R(t) - S(t)), \\ R'(t) =\beta B_0 Q(t-\tau) - \nu R(t) - \sum_{i=1}^{2} c_i V_i(R(t))y_i(t) + d(S(t) - R(t)), \\ Q'(t) = - d_B Q(t) + \delta \sum_{i=1}^{2} \{x_i(t) + y_i(t)\}, \\ x_i'(t) =x_i(t)\left(b_i U_i(S(t)) - \mu\right), \\ y_i'(t) =y_i(t)\left(c_i V_i(R(t)) - \mu\right). \quad (i = 1,2) \end{cases} \tag{2.19}$$

Let us set the same parameters and initial functions for Figs 2.2 and 2.3. Moreover let us set $d_B = 2.2$, $\beta B_0 = 2.1$, $\delta = 0.8$ and $Q(\theta) = 0.3 - 0.1 \sin\theta$ ($\theta \in [-\tau, 0]$). Figs 2.4 and 2.5 show the trajectories of the solution of (2.19) and $\tau = 25$. It is observed that all organisms survive periodically. By comparing Figs 2.2 and 2.3 to Figs 2.4 and 2.5, we can see that the

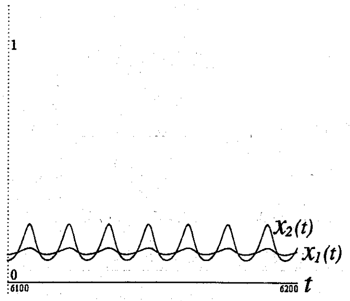

Figure 2.4: $x_1(t)$ and $x_2(t)$ of (2.19)

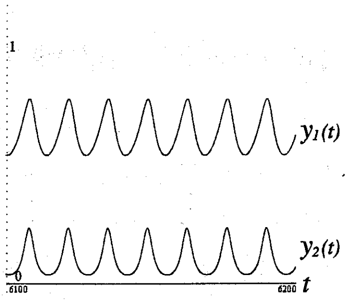

Figure 2.5: $y_1(t)$ and $y_2(t)$ of (2.19)

qualitative outcome is the same: periodic coexistence occurs. These simulation results suggest that instability comes from the delay due to bacterial decomposition rather than accumulation of dead organisms.

2.5 Discussion

In Section 2.1, we modeled chemostat-type equations for lake community by introducing spatial distribution and recycle of nutrient. The spatial distribution of nutrient is expressed by two distinct nutrients: dissolved nutrient in the lake S and accumulated nutrient on the bottom of the lake R. Delayed nutrient recycling is derived by describing the process of bacterial decomposition. In real lake community, the segregation of nutrient uptake between aquatic organisms (in system (E_2), x_i) and benthos (in system (E_2), y_j) is not always expected. Cross nutrient uptake of aquatic organisms and benthoses would be an interesting problem. In Section 2.3, it was shown that all equilibria become unstable and system (E_2) undergoes a Hopf bifurcation as time delay increases through a critical value of time delay. By mathematical analysis, we obtained that Hopf bifurcation occurs on the system with small dilution rate D, small self-purification rate ν, small diffusion rate d and high recycle rate γ. In particular, small dilution rate would well describe "lake" situation. In Section 2.4, it is observed that all organisms coexist in the form of periodic oscillation if all equilibria are unstable. Known results dealing with competition in chemostat-type equations with delayed nutrient recycling show that direct (or intra/inter-specific) competition terms among competing species realize coexistence (see, Freedman & Yuantong [13] and Ruan & He [22]). This type of coexistence cannot be expected on system (E_2) where direct competition terms never appear. Only exploitative competition appears in system (E_2). If there is no diffusion, or $d = 0$, system (E_2) is closed with three variables $S(t)$, $x_1(t)$ and $x_2(t)$. Subsystem $(S(t), x_1(t), x_2(t))$ forms a standard chemostat model and competitive exclusion principle hold true (see Armstrong and McGehee [1], Smith and Waltman [62]). Our study suggests that the diffusion of nutrient and the delay due to bacterial decomposition create the coexistence of species. For system (E_2), periodic coexistence is a key of further analysis. The periodic coexistence of competing organisms is extensively observed in chemostat equations both for nonautonomous system (see Butler *et al.*, Hsu [28], Smith [61]) and for autonomous system (see Butler *et al.* [8], Li and Smith [34], [35]). Further study leaves for future consideration.

Part II

Competition in population dynamics

Chapter 3

Relative competition

3.1 Introduction

In this chapter, let us consider the simplest expression of competing two species, which is called a Lotka-Volterra competition system:*

$$
\begin{cases} x_1'(t) = x_1(t)[r_1 - ax_1(t) - bx_2(t)], \\ x_2'(t) = x_2(t)[r_2 - cx_1(t) - dx_2(t)]. \end{cases} \tag{3.1}
$$

Here $x_i(t)$ denotes the i-th population densities of competing two species $(i = 1, 2)$. All parameters are assumed to be positive. Let E_0, E_1 and E_2 denote equilibria of system (3.1) which always exist:

$$
E_0 = (0, 0), \quad E_1 = \left(\frac{r_1}{a}, 0\right), \quad E_2 = \left(0, \frac{r_2}{d}\right).
$$

Suppose that

$$
\frac{b}{d} < \frac{r_1}{r_2} < \frac{a}{c}. \tag{3.2}
$$

Then system (3.1) has a unique positive equilibrium which is a stable node:

$$
E^* := (x_1^*, x_2^*) = \left(\frac{dr_1 - br_2}{ad - bc}, \frac{ar_2 - cr_1}{ad - bc}\right).
$$

It is well known that the positive equilibrium of system (3.1) is globally asymptotically stable if (3.2) holds. Various approaches are known to show the global attractivity result of the positive equilibrium: The second method of Liapunov can give a global stability result when a suitable

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*This chapter is mainly attributed to the paper [42] published in *Sūrikaisekikenkyūsho Kōkyūroku*.

Liapunov function is found (see for example, [26] and [65]). On planar systems, Poincaré-Bendixon Theorem is a powerful tool to figure out the behavior of system dynamics. Monotone theory is also a powerful and conceptual tool if one considers competitive (cooperative) system (see [63] and references therein).

Here we take a different approach to show the global attractivity result for the positive equilibrium of system (3.1): By introducing a function with respect to the ratio between densities of two species $P_{ij} = x_i/x_j$, we will show the global attractivity of the positive equilibrium if (3.2) holds. Moreover we will give the explicit form of separatrix if system (3.1) is bistable. In the next section, basic properties for the function P_{ij} are shown. In Section 3.3, we show that the positive equilibrium is globally attractive if it exists. On the other hand, if we consider a *bistable case*, applying the same proof which will be developed in Section 3.3 shows the explicit form of the separatrix curve for $r_1 = r_2$. In Section 3.4, the graph of the trajectory of the solution of (3.1) are shown. Finally we discuss our results in Section 3.5.

3.2 Preliminaries

Consider the following general autonomous planar system:

$$\begin{cases} x_1' = x_1 f_1(x_1, x_2), \\ x_2' = x_2 f_2(x_1, x_2), \end{cases} \tag{G}$$

with the initial condition

$$x_1(0) > 0 \text{ and } x_2(0) > 0, \tag{3.3}$$

where f_1 and f_2 are continuously differentiable. The function π is said to be a continuous dynamical system if π is continuous and has the following properties:

1. $\pi(x, 0) = x$;
2. $\pi(x, t + s) = \pi(\pi(x, t), s)$.

Then (G) generates a continuous dynamical system by defining $\pi(x,t) = x(t)$, where $x(t) = (x_1(t), x_2(t))$ is a solution of (G) satisfying (3.3). Given a point x, the set $\{\pi(x,t) | t \geq 0\}$ is called the *positive trajectory*. A set S is said to be *positively invariant* if all trajectories that begin in S remain in S for all positive time. Let $\{t_n\}_{n=1}^{\infty}$ be a sequence of real numbers which tends to infinity as n tends to infinity. If $P_n = \pi(x, t_n)$ converges to a point P, then P is said to be an omega limit point of x. The set of all such omega limit points is called the *omega limit set* of x, denoted as $\omega(x)$. An equilibrium point of (G) (if exists) is said to be *repeller* if it cannot be in the omega limit set of any trajectory other than itself. The dynamical system is said to be *dissipative* if all positive trajectories eventually lie in a bounded set. If the system is dissipative, the omega limit set is a non-empty, compact, connected, invariant set (see also a standard textbook of dynamical systems, e.g. Bhatia and Szegő [5]).

Let $P_{ij} : [0,\infty) \times (0,\infty) \to [0,\infty)$ be a continuously differentiable function ($i, j = 1, 2, i \neq j$). P_{ij} is defined by

$$P_{ij}(x_i, x_j) = x_i/x_j. \tag{3.4}$$

By the definition, it follows that

P-(i): $P_{ij} \cdot P_{ji} = 1$,

P-(ii): $P_{ij} = 0$ iff $x_i = 0$.

The derivative of P_{ij} along the solution of (G) is denoted by $\dot{P}_{ij}(x(t))$. Direct calculation gives

$$\frac{\dot{P}_{ij}(x(t))}{P_{ij}(x(t))} = f_i(x(t)) - f_j(x(t)).$$

Note that this property is stated as the *quotient rule* on replicator dynamics (Excersise 7.1.1 in [26]). Hereafter we simply write $\dot{P}_{ij}(x(t))$ as $\dot{P}_{ij}(t)$ for the convenience.

Competitively Advantage Set, or simply *Advantage Set* $\mathcal{A}_1$ and $\mathcal{A}_2$ are defined by

$$\mathcal{A}_1 := \left\{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) > f_2(x_1, x_2)\right\},$$
$$\mathcal{A}_2 := \left\{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) < f_2(x_1, x_2)\right\}.$$

Competitively Balance Set, or simply *Balance Set* $\mathcal{B}$ is defined by

$$\mathcal{B} := \left\{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) = f_2(x_1, x_2)\right\}.$$

Note that for any $x(t) \in \mathcal{B}$, $\dot{P}_{ij}(t) = 0$. Moreover $\dot{P}_{ij}(t) > 0$ if $x(t) \in \mathcal{A}_i$, while $\dot{P}_{ij}(t) < 0$ if $x(t) \in \mathcal{A}_j$.

Strongly Advantage Set $\mathcal{S} = \mathcal{S}_1 \oplus \mathcal{S}_2$ is defined by

$$\mathcal{S}_1 := \{(x_1, x_2) \in \mathcal{A}_1 | f_1(x_1, x_2) > 0 \text{ and } f_2(x_1, x_2) < 0\},$$
$$\mathcal{S}_2 := \{(x_1, x_2) \in \mathcal{A}_2 | f_1(x_1, x_2) < 0 \text{ and } f_2(x_1, x_2) > 0\}.$$

The null clines of $f_1(x_1, x_2)$ and $f_2(x_1, x_2)$ are denoted by $\mathcal{N}_1$ and $\mathcal{N}_2$, respectively. That is,

$$\mathcal{N}_1 = \{(x_1, x_2) \in \mathbb{R}^2_+ | f_1(x_1, x_2) = 0\},$$
$$\mathcal{N}_2 = \{(x_1, x_2) \in \mathbb{R}^2_+ | f_2(x_1, x_2) = 0\}.$$

Let $x_1^\dagger$ and $x_2^\dagger$ denote roots of $f_1(x_1, 0) = f_2(x_1, 0)$ and $f_1(0, x_2) = f_2(0, x_2)$ (if they exist), respectively. In general, $\mathcal{B}$ is a curve on $\mathbb{R}_+^2$ which is formed by connecting two points $(x_1^\dagger, 0) \in \mathcal{B}$ and $(0, x_2^\dagger) \in \mathcal{B}$. Note that $\mathcal{B}$ is a line for system (3.1). $\mathrm{int}\mathbb{R}_+^2$ denotes the interior of $\mathbb{R}_+^2$. $\mathrm{int}\mathbb{R}_+^2$ is divided by $\mathcal{B}$, that is, $\mathrm{int}\mathbb{R}_+^2 = \mathcal{A}_1 \oplus \mathcal{B} \oplus \mathcal{A}_2$. (see Figs 3.1 and 3.2 in Section 3.4). Finally the *solution ratio line* $\mathcal{L}_t$ is defined by

$$\mathcal{L}_t := \left\{(x_1, x_2) \in \mathbb{R}_+^2 | x_i = P_{ij}(t) x_j\right\}. \tag{3.5}$$

Then $x(t) \in \mathcal{L}_t$.

3.3 Global attractivity

Let us set $f_1(x_1, x_2) = r_1 - a x_1 - b x_2$ and $f_2(x_1, x_2) = r_2 - c x_1 - d x_2$. First we state some basic properties of system (3.1) without the proof. Throughout the reminder of this section, we assume that (3.2) holds.

Proposition 3.1. *System* (3.1) *is dissipative. E_0 is a repeller. Moreover E_1 and E_2 are also repellers if* (3.2) *holds.*

Proposition 3.2. *Assume that* (3.2) *holds. Then $E^* \in \mathcal{B}$. $E_0 \in \mathcal{B}$ if and only if $r_1 = r_2$. $E_1 \notin \mathcal{B}$ and $E_2 \notin \mathcal{B}$.*

Proof. The first and the second assertions are clear. By (3.2), $ad - bc > 0$. Then $a \neq c$ or $b \neq d$. Suppose that $a \neq c$. Then $x_1^\dagger = (r_1 - r_2)/(a - c)$ exists. Since (3.2) holds, direct calculation shows that $x_1^\dagger - \frac{r_1}{a} = (c r_1 - a r_2)/a(a - c) \neq 0$. Consequently $E_1 \notin \mathcal{B}$ if $a \neq c$. In the same way, we can show that $E_2 \notin \mathcal{B}$ if $b \neq d$. This completes the proof. □

Let E denote a set of equilibria of system (3.1)

$$E = \{E_0, E_1, E_2, E^*\}.$$

Proposition 3.3. *Assume that $r_1 = r_2$ and* (3.2) *holds. Then $\mathcal{B}$ is positively invariant.*

Proof. We claim that $x_2 f_2(x_1, x_2) \neq 0$ for any $x = (x_1, x_2) \in \mathcal{B} \setminus E$. In fact, $x_2 f_2(x_1, x_2) = 0$ if and only if $x_2 = 0$ or $f_2(x_1, x_2) = 0$. Note that $x_2 = 0$ iff $x \in E_0$ on $\mathcal{B}$. Moreover $\mathcal{B} \cap \mathcal{N}_2 = E^*$. Hence the implicit function theorem implies that for any $x \in \mathcal{B} \setminus E$,

$$\frac{\partial x_1}{\partial x_2} = -\frac{x_1 f_1(x_1, x_2)}{x_2 f_2(x_1, x_2)} = -\frac{x_1}{x_2}.$$

It follows from (3.2) that $a > c$ and $d > b$ if $r_1 = r_2$. Hence $x \in \mathcal{B} \setminus E$ satisfies $x_1/x_2 = \frac{d-b}{a-c} = x_1^*/x_2^*$. Consequently we obtain that $x_1(t) = x_1^*/x_2^* x_2(t)$ for any $x(t) \in \mathcal{B}$. That is, $\mathcal{L}_t \equiv \mathcal{B}$. This completes the proof. □

Proposition 3.4. *Assume that* $r_1 \neq r_2$ *and* (3.2) *holds. Then* $\mathcal{B} \setminus E$ *is not positively invariant.*

Proof. Assume that there exists $T \geq 0$ such that $x(t) \in \mathcal{B} \setminus E$ for any $t > T$. Hereafter let us fix t arbitrary for $t > T$. Then $\dot{P}_{12}(t) = 0$. Hence $P_{12}(t)$, or equivalently, $x_1(t)x_2^{-1}(t)$ is a positive constant, which is denoted by C. Moreover $\mathcal{L}_t$ is fixed, which is denoted by $\mathcal{L}$. Then $x(t) \in \mathcal{B} \cap \mathcal{L}$. It is clear that $\mathcal{B} \cap \mathcal{L} \neq \emptyset$. Since both of $\mathcal{B}$ and $\mathcal{L}$ are lines on $\mathbb{R}_+^2$, either (i) $\mathcal{B} = \mathcal{L}$ or (ii) $\mathcal{B} \cap \mathcal{L}$ is a point set. Note that $\mathcal{B} = \mathcal{L}$ if and only if $r_1 = r_2$ and $C = \frac{d-b}{a-c} = x_1^*/x_2^*$. Since we assume $r_1 \neq r_2$, only the case (ii) is possible. Then $x(t)$ must be an equilibrium point. More specifically, Proposition 3.2 implies that $x(t) \equiv E^*$. This is a contradiction since $x(t) \in \mathcal{B} \setminus E$. This completes the proof. □

Proposition 3.5. *Assume that* (3.2) *holds. Then* $P_{ij}(t) \not\to 0$ *if* $t \to \infty$.

Proof. Assume that $P_{ij}(t) \to 0$ as $t \to \infty$. Then there exists a monotone increasing sequence $\{t_n\}_{n=1}^{\infty}$ such that $\dot{P}_{ij}(t_n) \to 0$ as $n \to \infty$. Note that for any $x(t) \in \mathcal{B}$, $\dot{P}_{ij}(t) = 0$. Hence for any initial point $x^0 \in \mathrm{int}\mathbb{R}_+^2$, $\omega(x^0) \subset \mathcal{B} \cup E$. Since system (3.1) is dissipative, $\omega(x^0)$ is positively invariant. Note that by Proposition 3.1, E_0, E_1 and E_2 are repellers. Moreover Propositions 3.3 and 3.4 imply that $\omega(x^0) \subset \mathcal{B} \setminus E_0$ if $r_1 = r_2$ and $\omega(x^0) \in E^*$ if $r_1 \neq r_2$. This is a contradiction and hence completes the proof. □

In the same way as the proof of Proposition 3.5, we can show the following:

Proposition 3.6. *Assume that* (3.2) *holds. If there exists a positive constant* P_{ij}^* *such that* $P_{ij}(t) \to P_{ij}^*$ *as* $t \to \infty$, *then* $x(t) \to E^*$ *as* $t \to \infty$.

Proposition 3.7. *Assume that* (3.2) *holds. If* $x(t)$ *eventually remains either in* $\mathcal{A}_1$ *or* $\mathcal{A}_2$, *then* $x(t) \to E^*$ *as* $t \to \infty$.

Proof. Note that if $x(T) \in \mathcal{A}_1$ for some $T \geq 0$, $\dot{P}_{12}(t) > 0$ as long as $x(t) \in \mathcal{A}_1$ for $t \geq T$. Similarly if $x(T) \in \mathcal{A}_2$ for some $T \geq 0$, $\dot{P}_{12}(t) < 0$ as long as $x(t) \in \mathcal{A}_2$ for $t \geq T$. Hereafter we only consider the case where $x(t) \in \mathcal{A}_1$ for $t \geq T$. Then we claim that there exists a positive constant P_{12}^* such that $P_{12}(t) \to P_{12}^*$ as $t \to \infty$. Assume that $P_{12}(t) \to \infty$ as $t \to \infty$. Since system (3.1) is dissipative, $x_2(t) \to 0$ as $t \to \infty$. Then by P-(ii), $P_{21}(t) \to 0$ as $t \to \infty$. However this contradicts to Proposition 3.5. Therefore Proposition 3.6 implies that $x(t) \to E^*$ as $t \to \infty$. This completes the proof. □

Proposition 3.8. *Assume that* (3.2) *holds.* $\mathcal{S} \cup \mathcal{N}_1 \cup \mathcal{N}_2$ *is positively invariant.*

Proof. It is sufficient to notice for the solutions on the boundary of $\mathcal{S}$. Note that the boundary of S consists of null clines $\mathcal{N}_1$ and $\mathcal{N}_2$. If there exists $T \geq 0$ such that $x(T) \in \mathcal{A}_1 \cap \mathcal{N}_1$, then $\dot{x}_1(T) = 0$ and $\dot{x}_2(T) < 0$. By the continuity of the solution, there exists $\varepsilon > 0$ such that $x(t) \in \mathcal{S}_1$ for $T < t \leq T + \varepsilon$. The same procedure proves the assertion (see Figure 3.2). □

Theorem 3.1. *Assume that* (3.2) *holds. Then all solutions tend to the positive equilibrium as t tends to infinity.*

Proof. First let us consider the case $r_1 \neq r_2$. If there exists $T \geq 0$ such that $x(T) \in \mathcal{S} \cup \mathcal{N}_1 \cup \mathcal{N}_2$, Proposition 3.7 together with 3.1 implies that $x(t) \to E^*$ as $t \to \infty$ and hence the assertion is true. Otherwise, all solutions remain in $\mathrm{int}\mathbb{R}^2_+ \setminus \mathcal{S}$ for any positive t. We claim that such solutions also eventually remain either in $\mathcal{A}_1$ or $\mathcal{A}_2$. The following two cases are possible: (i) There is no solution which crosses $\mathcal{B}$ or (ii) There is a solution which crosses $\mathcal{B}$. The claim is true for the case (i) by Proposition 3.7. So let us consider the case (ii). If there exists $T_0 \geq 0$ such that $x(T_0) \in \mathcal{B}$, Proposition 3.4 implies that there exists $T_1 > T_0$ such that $x(T_1) \notin \mathcal{B}$. More specifically, if $\dot{x}_1(T_0) > 0$, then $x(T_1) \in \mathcal{A}_2$. Conversely if $\dot{x}_1(T_0) < 0$, then $x(T_1) \in \mathcal{A}_1$. In both cases, we can see that $x(t) \in \mathcal{A}_1$ or $x(t) \in \mathcal{A}_2$ for any $t \geq T_1$. Hence the claim holds true by Proposition 3.7.

Next suppose that $r_1 = r_2$. Since $\mathcal{B}$ is positively invariant, it is sufficient to consider either (iii) $x(t) \notin \mathcal{B}$ for all $t \geq 0$ or (iv) $x(t) \in \mathcal{B}$ for all $t \geq 0$. In the case (iii), $x(t) \in \mathcal{A}_1$ or $x(t) \in \mathcal{A}_2$ for all $t \geq 0$. Hence Proposition 3.7 implies that $x(t) \to E^*$ as $t \to \infty$ and the assertion holds true. This completes the proof. □

We can obtain further interesting property for the solution of (3.1) starting on the balance set $\mathcal{B}$ if $r_1 = r_2$.

Remark 3.1.

Note that $f_1(x_1, x_2) = f_2(x_1, x_2) = f(x_1, x_2)$ on $\mathcal{B}$. Let $x = x_1 + x_2$. Then

$$\begin{aligned} x' &= x_1' + x_2' \\ &= x_1 f_1(x_1, x_2) + x_2 f_2(x_1, x_2) \\ &= x f(x_1, x_2). \end{aligned}$$

Observe that x is expressed by x_1 and x_2 explicitly if and only if the following system of equations has a unique root:

$$\begin{cases} x_1 + x_2 = x, \\ a x_1 + b x_2 = c x_1 + d x_2 \end{cases}.$$

Since $a - c \neq b - d$, direct calculation gives

$$x_1 = \frac{(d-b)x}{a-c-(b-d)} \text{ and } x_2 = \frac{(a-c)x}{a-c-(b-d)}.$$

Then $x(t)$ is a solution of following differential equation

$$x' = rx\left(1 - \frac{x}{K}\right), \quad x \in \mathcal{B} \tag{3.6}$$

where $r = r_1$ and $K = \frac{a-c+(d-b)}{ad-bc}r = x_1^* + x_2^*$. Then (3.6) becomes the Logistic equation and hence $x(t) \to x_1^* + x_2^*$ as $t \to \infty$ on $\mathcal{B}$.

In the end of this section, we suppose that

$$\frac{a}{c} < \frac{r_1}{r_2} < \frac{b}{d}. \tag{3.7}$$

Then system (3.1) has a unique positive equilibrium which is a saddle:

$$E^* := (x_1^*, x_2^*) = \left(\frac{dr_1 - br_2}{ad-bc}, \frac{ar_2 - cr_1}{ad-bc}\right).$$

System (3.1) is called *bistable* if (3.7) holds. The theory of dynamical systems implies that there is a separatrix by which the extinction of species is determined depending on the initial value. For system (3.1) with (3.7), the separatrix corresponds to a set of (global) stable manifold of the positive equilibrium. Applying the previous proof, we obtain the following result;

Corollary 3.1. *Assume that $r_1 = r_2$ and (3.2) hold. Then $\mathcal{B}$ corrsponds to the separatrix.*

Finally we consider the variant of system (3.1) which is no longer a competitive system. The system is given by

$$\begin{cases} x_1'(t) = x_1(t)[r_1 - ax_1(t) - bx_2(t)], \\ x_2'(t) = x_2(t)[r_2 - cx_1(t) - dx_2(t) + g(x_1(t))], \end{cases} \tag{3.8}$$

where

$$g(x_1) = -\varepsilon x_1(x_1 - \gamma).$$

System (3.8) corresponds to system (3.1) if $\varepsilon = 0$. System (3.8) can be interpreted as a model for microbial competition in which species 1 products "byproduct" during the metabolic process. We assume that byproduct is an another resource for species 2, but the excessive amount of byproduct may inhibit the population growth of species 2. It is often the case that the excessive amount of resource can inhibit the population growth of microorganisms (see Chapter 4 of the book for chemostats, [62]). Thus, for species 2, byproduct is benetifical if the amount is not too much, but harmful if the amount is too much. The parameter γ is a threshold value by which byproduct owes to activate or inhibit the population growth of species 2. In fact, $g(\gamma) = 0$, $g(x_1) > 0$ for $0 < x_1 < \gamma$ and $g(x_1) < 0$ for $x_1 > \gamma$.

Note that

$$\frac{\partial f_2(x_1, x_2)}{\partial x_1} = (\varepsilon\gamma - c) - 2\varepsilon x_1. \tag{3.9}$$

If $\varepsilon\gamma - c > 0$, then (3.9) is positive if $0 \leq x_1 < \frac{1}{2\varepsilon}(\varepsilon\gamma - c)$. Thus we see that system (3.8) is not a competitive system although $\frac{\partial f_1(x_1,x_2)}{\partial x_2} < 0$ for all $x_2 > 0$.

Note thathe equilibrium points E_0, E_1 and E_2 for system (3.1) are also equilibrium points for system (3.8). More precisely, $E_0 = (0, 0)$, $E_1 = (\frac{r_1}{a}, 0)$ and $E_2 = (0, \frac{r_2}{d})$ are equilibrium points not only for (3.1) but also for (3.8). The positive equilibrium E^* of system (3.1) is different from that of (3.8). If ε is sufficiently small, then it is possible to show that the positive equilibrium E^* of system (3.8) uniquely exists and locally stable if $ad - bc > 0$. In this case, we have to take the value of γ sufficiently large to ensure that $\varepsilon\gamma - c > 0$.

Note that the method developed in this chapter can be exploited to show the global attractivity for the positive equilibrium of system (3.8). Since the competitively balance set $\mathcal{B}$ is not a line but a curve, we do not necessarily devide the proof into two case whether $r_1 = r_2$ or not. Thus, we only have to show that Propositions 3.1, 3.2, 3.4, 3.5, 3.6, 3.7 and 3.8 hold for system (3.8). In the same way, we can show that the positive equilibrium of system (3.8) is globally attractive if $ad - bc > 0$.

Corollary 3.2. *Assume that $\varepsilon \ll 1$, $\varepsilon\gamma > c$ and (3.7) holds. Then a positive equilibrium of (3.8) uniquely exists and it is globally asymptotically stable.*

3.4 Trajectories

In this section, let us show some projections onto x_1x_2-phase plane of trajectories for different sets of parameters. Due to the symmetry of system (3.1), we can assume that $r_1 \geq r_2$. Figs 3.1 and 3.2 illustrate the null-clines and the balance line, each of which corresponds to dashed lines and the thick line. Figs 3.3–3.4 illustrate the trajectories of the solution of (3.1). On these figures, the balance line is drawn by thin line, while the trajectory is drawn by thick line. On Fig.3.3, the parameters satisfy that $r_1 > r_2$, $\frac{d-b}{a-c} < 0$ and (3.2) holds. The initial point x^0 is taken on $\mathcal{B}$. The trajectory is immediately away from $\mathcal{B}$ and eventually lies in $\mathcal{S}_1$. On Fig.3.4, the parameters satisfy that $r_1 > r_2$, $\frac{d-b}{a-c} > 0$ and (3.2) holds. The initial point is also taken on $\mathcal{B}$. The trajectory is also away from $\mathcal{B}$ and finally converges to the positive equilibrium. On Fig.3.5, the parameters satisfy that $r_1 = r_2$. The initial point is taken on $\mathcal{B}$. Note that by Proposition 3.3, $\mathcal{B}$ is positively invariant. The solution converges to the positive equilibrium along the line $x_2 = x_2^*/x_1^* x_1$. Finally Fig. 3.6 illustrates the trajectory for $r_1 = r_2$. The initial point is taken on $\mathcal{A}_2$. The solution eventually lies on $\mathcal{S}_2$ and converges to the positive equilibrium.

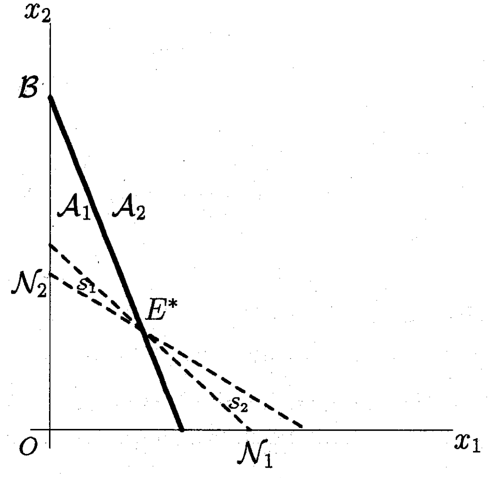

Figure 3.1: $r_1 > r_2$, $\frac{d-b}{a-c} < 0$ $(a \neq c)$

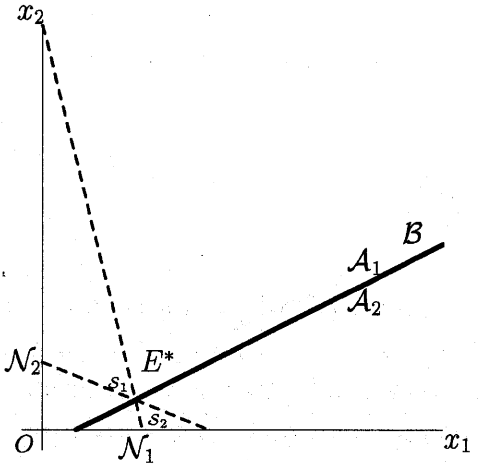

Figure 3.2: $r_1 > r_2$, $\frac{d-b}{a-c} > 0$ $(a \neq c)$

3.5 Conclusions

We proved the global attractivity of solutions of system (3.1) by introducing the function in terms of the ratio between x_1 and x_2. It was shown that the balance set $\mathcal{B}$ separates the positive cone. One of separated regions $\mathcal{A}_1$ gives a competitive advantage for x_1, while another region $\mathcal{A}_2$ gives a competitive advantage for x_2. For almost sets of parameters under the situation where the positive equilibrium exists, the balance line $\mathcal{B}$ except for the positive equilibrium is not positively invariant. On the region $\mathcal{A}_1 \cap \{(x_1, x_2) \in \mathbb{R}_+^2 | f_1(x_1, x_2) < 0, f_2(x_1, x_2) < 0\}$, it can happen that the ratio x_1/x_2 increases although x_1 decreases (see Figs 3.3 and 3.4). This situation is likely to occur when x_1 has the low density while x_2 has the high density.The density dependence effect highly decreases the density of x_2 even if x_1 is decreasing. If $r_1 = r_2$ and $x^0 \in \mathcal{B}$, as we have shown in Proposition 3.3 and Theorem 3.1, the solution converges to the positive equilibrium along the line. Moreover the total density $x_1 + x_2$ follows the logistic equation (see also Fig.3.5). This implies that two species are regarded as the same species on $\mathcal{B}$ if $r_1 = r_2$. Geritz *et. al* considered the dynamics of a population of residents that is being invaded

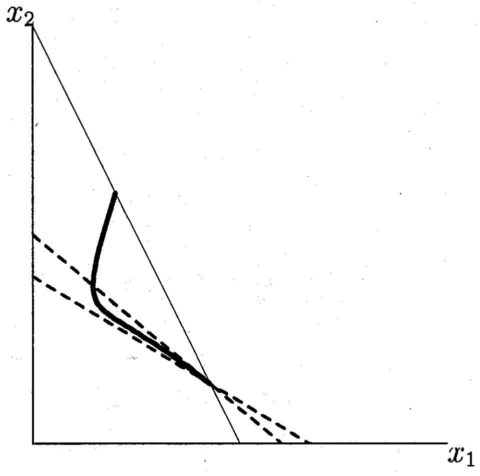

Figure 3.3: $r_1 > r_2$, $\frac{d-b}{a-c} < 0$, $x^0 \in \mathcal{B}$.

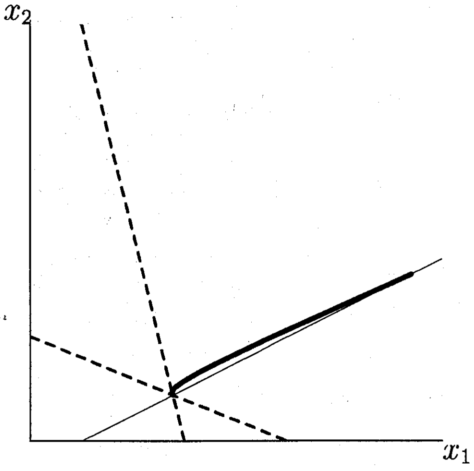

Figure 3.4: $r_1 > r_2$, $\frac{d-b}{a-c} > 0$, $x^0 \in \mathcal{B}$.

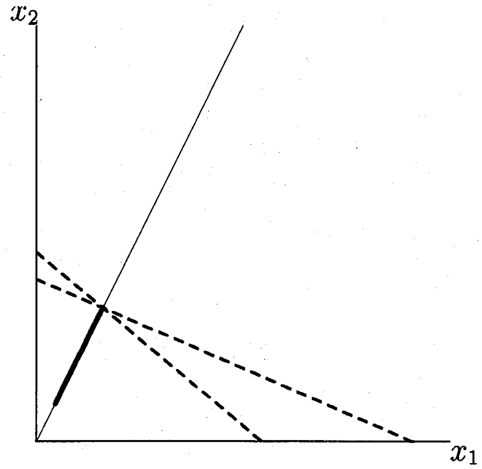

Figure 3.5: $r_1 = r_2$, $x^0 \in \mathcal{B}$.

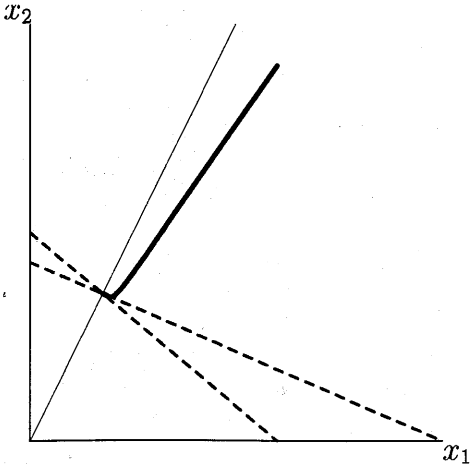

Figure 3.6: $r_1 = r_2$, $x^0 \in \mathcal{A}_2$.

by an initially rare mutant [14]. They showed in [14] that under relatively mild conditions *the sum of the mutant and resident population sizes* stays arbitrarily close the initial attractor of the monomorphic resident population whenever the mutant has a strategy sufficiently similar to that of the resident (This is called a Tube Theorem). This result implies that the orbit will stay in *a narrow tube* in the resident-mutant population state space. Schreiber [56] considered a model for apparent competition where two prey share one predator. In [56], it was shown that a model without the positive equilibrium is almost surely permanence. The similar idea of Tube Theorem is exploited in the proof. It would be interesting to study the relationship between the tube set and the balance set. Since system (3.1) satisfying (3.2) is dissipative and permanent, there must exist an accumulation set of the ratio function P_{ij} on some compact subset of the positive cone. In this chapter, it was shown that the accumulation set corresponds to the positive equilibrium point. If the accumulation set consists of two points, then the solution will be periodic. It is expected that chaotic behaviors will appear in such a way that the ratio function has infinitely multiple accumulation points. In this chapter, we only considered the case where the stable positive equilibrium exists. It is well known that there is a separatrix curve if system (3.1) is bistable. Simple consideration shows that the balance set $\mathcal{B}$ corresponds to the separatrix curve if $r_1 = r_2$ and system (3.1) is bistable. It is interesting to give explicit form of the separatrix curve for $r_1 \neq r_2$. This leaves for our future consideration. On the systems where more than three species are interacting with, the chaotic behavior can occur. The method exploited in this chapter should be also exploited to higher dimensional systems. This also leaves for our future consideration.

Chapter 4

Three species competition

ABSTRACT

A competition model of three species for one resource in a chemostat with a periodic washout rate is considered. Coexistence is indicated in [33] by numerical bifurcation analysis and in [73] by mathematical analysis. By introducing average competition functions, we obtain a necessary condition for the coexistence of a positive periodic solution and show that the condition restricts possible parameter value set to be relatively small. Further we show that the coexistence is enhanced when the period of the washout rate becomes large.

Key word: Chemostat equations, periodic washout rate, coexistence, Michaelis-Menten functional response, Conservation principle, Average competition function. *

4.1 Introduction

Chemostat equations have been used to study population dynamics of microorganisms in experimental apparatuses or aquatic ecosystems such as lakes. The Competitive Exclusion Principle states that among several species competing for common resources, the number of coexistent species does not exceed the number of available resources (see Grover [16] for example). The mathematical results on the standard chemostat equations of competition for a single limiting

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*This chapter is mainly attributed to the paper [43] published in *Difference equations and discrete dynamical systems.*

resource show that only the species with the lowest break even concentration survives (see Armstrong and McGehee [1], Smith and Waltman [62, Chapter 1, Chapter 2]). On the other hand, the competitive exclusion principle is not valid for chemostat equations if a fluctuating environment is under consideration. In fact, many studies have revealed that the coexistence of two species competing for one resource is possible if a nutrient input varies periodically (see Hsu [28] and Smith [61], for example). Butler *et al.* [9] showed that the coexistence of two species is also possible in the case where the washout rate varies periodically. In [9], coexistence is expected if the washout rate varies in such a way that each competitor has its own competitive advantage depending on the concentration of the resource (see also Lenas & Pavlou [32] and Pilyugin & Waltman [48]).

It is a fundamental interest and problem on chemostat equations whether fluctuating environments can support the coexistence of more than three species under only one resource. Lenas and Pavlou [33] showed by numerical bifurcation analysis that the coexistence of three species is possible. Wolkowicz and Zhou [73] gave sufficient conditions for the uniform persistence of competing arbitrary N-species on a periodic chemostat. In [73], for the three species competition case, they considered the following system of equations:

$$\begin{aligned} \frac{dS(t)}{dt} &= (S^0(t) - S(t))D_0(t) - \sum_{i=1}^{3} P_i(t, S(t))x_i(t), \\ \frac{dx_i(t)}{dt} &= x_i(t)(P_i(t, S(t)) - D_0(t)), \quad (i = 1, 2, 3). \end{aligned} \tag{4.1}$$

Here $S(t)$ denotes the concentration of the limiting nutrient, $x_i(t)$ $(i = 1, 2, 3)$ denotes the measure of i-th species at time t. $P_i(t, S)$ $(i = 1, 2, 3)$ represents the specific per capita nutrient uptake function of i-th species, $S^0(t)$ and $D_0(t)$ are the input nutrient concentration and the washout rate, respectively. $S^0(t)$ and $D_0(t)$ are continuous, ω-periodic and positive functions, and each $P_i(t, S)$ satisfies

1. $P_i(t, S)$ is locally Lipschitz in S,
2. $P_i(t, 0) = 0$ for $t \geq 0$ and for any $t \geq 0$, $P_i(t, S)$ is strictly increasing for $S \in \mathbf{R}_+$.

They showed the existence condition for a positive ω-periodic solution
$(S(t), x_1(t), x_2(t), x_3(t))$ of (4.1) with $S(0) \geq 0$ and $x_i(0) > 0$ $(i = 1, 2, 3)$. The detail is as follows:

Let $V_0^*(t)$ be the unique, globally attracting, positive ω-periodic solution of

$$\frac{dV}{dt} = (S^0(t) - V(t))D_0(t).$$

For each $1 \leq i \leq 3$, there is a corresponding single-species periodic equation

$$\frac{dx_i}{dt} = x_i(P_i(t, V_0^*(t) - x_i) - D_0(t)). \tag{E_i^*}$$

There is also, for each $1 \leq i \leq 3$, a corresponding two-species periodic competition system

$$\frac{dx_j}{dt} = x_j \left(P_j(t, V_0^*(t) - \sum_{k=1, k \neq i}^{3} x_k) - D_0(t) \right), \quad 1 \leq j \leq 3, j \neq i. \tag{$\bar{\mathrm{E}}_i$}$$

Theorem 4.1. *[73, Theorem 4.2.] Assume that*

1. $\mu_i \equiv \int_0^\omega (P_i(t, V_0^*(t)) - D_0(t))dt > 0,\ 1 \leq i \leq 3;$
2. $\mu_{ji} \equiv \int_0^\omega (P_i(t, V_0^*(t) - x_j^*(t)) - D_0(t))dt > 0,\ 1 \leq i, j \leq 3,\ i \neq j,\ j \neq 2,$ *and* $\mu_{21} \equiv \int_0^\omega (P_1(t, V_0^*(t) - x_2^*(t)) - D_0(t))dt > 0;$
3. $\bar{\mu}^i \equiv \int_0^\omega \left(P_i(t, V_0^*(t) - \sum_{j=1, j \neq i}^3 \bar{x}_j^i(t)) - D_0(t) \right) dt > 0,\ 2 \leq i \leq 3,$

where $x_i^*(t)$ *is the unique positive* ω*-periodic solution of* (E_i^*) $(1 \leq i \leq 3)$ *and* $(\bar{x}_1^2(t), \bar{x}_3^2(t))$ *and* $(\bar{x}_1^3(t), \bar{x}_2^3(t))$ *are the unique positive,* ω*-periodic solution of* $(\bar{\mathrm{E}}_2)$ *and* $(\bar{\mathrm{E}}_3)$*. Then system* (4.1) *admits a positive* ω*-periodic solution* $(S(t), x_1(t), x_2(t), x_3(t))$ *with* $S(0) \geq 0$ *and* $x_i(0) > 0$ $(i = 1, 2, 3)$.

An interesting example of Theorem 4.1 is given in [73], which is also adopted to show the coexistence of three species in [33]: Let $S^0(t) = 11$ and $D_0(t) = u_0 + a \cos 2\pi/\omega t$ where $u_0 = 0.4675$, $a = 0.3$ and $\omega = 31.4$. Nutrient uptake functions are Michaelis-Menten type functional responses $P_i(t, S(t)) = m_i S(t)/(a_i + S(t))$, where $m_1 = 1$, $a_1 = 1$, $m_2 = 0.7$, $a_2 = 0.3$, $m_3 = 0.64$ and $a_3 = 0.2$. Each integral in Theorem 4.1 is evaluated numerically as $\mu_1 = 14.1111$, $\mu_2 = 6.7205$, $\mu_3 = 5.0603$, $\mu_{12} = 0.6780$, $\mu_{13} = 1.87861$, $\mu_{21} = 0.7909$, $\mu_{31} = 0.2990$, $\mu_{32} = 0.8122$, $\bar{\mu}^2 = 0.0012$ and $\bar{\mu}^3 = 0.009$. This example suggests that competition mediates coexistence in the following sense: If x_1 is absent and x_2 & x_3 compete, then x_2 drives x_3 to extinction. However, this extinction of x_3 is avoided simply by introducing x_1. Once x_1 is introduced, all three species persist in sustained oscillation (see [73, pp. 486–487]).

The purpose of our study is to investigate how three species can coexist in a periodic chemostat. There are still unknown aspects on periodic chemostat models. First, as in [33], the region of parameters which ensures the coexistence of three species actually exists, but it is narrow. An adequate interpretation why the coexistence region is narrow should be proposed. Second, it is unknown and therefore should be figured out what factors realize the coexistence of three species.

In this chapter, let us consider periodic chemostat equations of the form

$$\begin{cases} S' = (S^0 - S)D(t) - \sum_{j=1}^{3} f_j(S)x_j, \\ x_i' = x_i\left(f_i(S) - D(t)\right), \quad (i = 1, 2, 3). \end{cases} \tag{E}$$

Here S^0 is a positive constant and $D : [0, \infty) \to [0, \infty)$ is a positive, ω-periodic function. We assume that $D(t)$ is not constant, since the coexistence of three competitors is impossible under constant environment. The mean value of the periodic function $D(t)$ is denoted by $\langle D \rangle$:

$$\langle D \rangle = \frac{1}{\omega}\int_0^{\omega} D(s)\, ds.$$

We assume the following for the functional response f_i of i-th species.

F-(i) $f_i : \mathbf{R}_+ \to \mathbf{R}_+$ is continuously differentiable,

F-(ii) $f_i(0) = 0,\ f_i'(S) > 0$.

A typical example of f_i is Michaelis-Menten functional response of the form :

$$f_i(S) = \frac{m_i S}{a_i + S}, \quad (i = 1, 2, 3). \tag{4.2}$$

Here a_i and m_i $(i = 1, 2, 3)$ are positive constants.

In the next section, system (E) is reduced to the limiting system. In Section 4.3, an average competition function is introduced which is exploited to measure the degree of competition and to give sufficient conditions for the competitive exclusion and a necessary condition for the periodic coexistence. Section 4.4 gives some numerical simulation results which demonstrate how the coexistence of three species is realized as the period of the washout rate increases. Section 4.5 gives conclusions of our study.

4.2 Reduction to the limiting system

By measuring all variables in unit of S^0 and time in unit of $\langle D \rangle^{-1}$, that is,

$$\frac{S}{S^0} \mapsto S\ ,\ \frac{x_i}{S^0} \mapsto x_i \text{ and } \langle D \rangle t \mapsto t,$$

system (E) takes the form:

$$\begin{cases} S' = (1 - S)D(t) - \sum_{j=1}^{3} f_j(S)x_j, \\ x_i' = x_i\left(f_i(S) - D(t)\right), \quad (i = 1, 2, 3). \end{cases} \tag{4.3}$$

Here we relabeled $f_i(S)$ and $D(t)$ in the equations (4.3), each of which is actually $\langle D\rangle^{-1}f_i(S^0S)$ and $\langle D\rangle^{-1}D(t/\langle D\rangle)$ in (E), respectively. Note that this scaling affects both the period and the mean value of D. The former becomes $\langle D\rangle\omega$, which we relabel ω and the latter becomes the unity: $\langle D\rangle = 1$.

Set $\Sigma = S + \sum_{j=1}^{3} x_j - 1$. Adding the equations (4.3) gives the periodic linear system

$$\Sigma'(t) = -D(t)\Sigma(t). \tag{4.4}$$

Then (4.3) corresponds to

$$\begin{cases} \Sigma' = -D(t)\Sigma, \\ x_i' = x_i\left(f_i\left(\Sigma - \sum_{j=1}^{3} x_j + 1\right) - D(t)\right), \quad (i = 1,2,3). \end{cases} \tag{4.5}$$

Since $\langle D\rangle = 1$, solving (4.4) gives

$$\Sigma(t) = \Sigma(0)\exp\left[-\int_0^t (D(s) - 1)ds\right]e^{-t}.$$

Hence we have

$$\lim_{t\to\infty} \Sigma(t) = 0.$$

Hereafter let us consider the system (4.5) restricted to the invariant hyperplane $\Sigma = 0$, to which all solutions are attracted at an exponential rate. Therefore setting $\Sigma = 0$, or equivalently, $S = 1 - \sum_{j=1}^{3} x_j$ yields the limiting system:

$$x_i' = x_i\left(f_i\left(1 - \sum_{j=1}^{3} x_j\right) - D(t)\right), \quad i = 1,2,3. \tag{L}$$

Biologically relevant initial data for (L) belong to

$$\Omega = \left\{(x_1, x_2, x_3)^T \in \mathbf{R}_+^3 : \sum_{j=1}^{3} x_j \leq 1\right\},$$

where

$$\mathbf{R}_+^3 = \left\{(x_1, x_2, x_3)^T \in \mathbf{R}^3 : x_i \geq 0, (i = 1,2,3)\right\}.$$

It is shown that Ω is positively invariant for (L). Convergence theorem obtained by Thieme [68] motivates us to consider the limiting system. Throughout the remainder of this chapter, we consider system (L).

4.3 Average competition

In this section, let us introduce an average competition function. The definition of this function is motivated by Hutson [29].

Let $P_{kl} : [0, \infty) \times (0, \infty) \to [0, \infty)$ be continuously differentiable function $(k, l = 1, 2, 3, k \neq l)$. Average competition functions P_{kl} are defined by

$$P_{kl}(x_k, x_l) = x_k x_l^{-1}. \tag{4.6}$$

By the definition, it follows that

P-(i): $P_{kl} \cdot P_{lk} = 1$,

P-(ii): $P_{kl} = 0$ iff $x_k = 0$.

The derivative of P_{kl} along the solution of (L) is denoted by $\dot{P}_{kl}(x_k(t), x_l(t))$. Direct calculation gives

$$\frac{\dot{P}_{kl}(x_k(t), x_l(t))}{P_{kl}(x_k(t), x_l(t))} = f_k\left(1 - \sum_{j=1}^{3} x_j\right) - f_l\left(1 - \sum_{j=1}^{3} x_j\right). \tag{4.7}$$

Proposition 4.1. *Let $(\bar{x}_1(t), \bar{x}_2(t), \bar{x}_3(t))$ be a positive ω-periodic solution of* (L). *Then*

$$\left\langle \frac{\dot{P}_{12}(\bar{x}_1, \bar{x}_2)}{P_{12}(\bar{x}_1, \bar{x}_2)} \right\rangle = \left\langle \frac{\dot{P}_{13}(\bar{x}_1, \bar{x}_3)}{P_{13}(\bar{x}_1, \bar{x}_3)} \right\rangle = \left\langle \frac{\dot{P}_{23}(\bar{x}_2, \bar{x}_3)}{P_{23}(\bar{x}_2, \bar{x}_3)} \right\rangle = 0. \tag{BC}$$

Proof. Since $\bar{x}_1(t)$ is a positive ω-periodic solution of (L),

$$\bar{x}_1(0) = \bar{x}_1(\omega) = \bar{x}_1(0) \exp\left[\int_0^{\omega} (f_1(1 - \bar{x}_1(s) - \bar{x}_2(s) - \bar{x}_3(s)) - D(s))\, ds\right].$$

Since $\langle D \rangle = 1$, $\langle f_1(1 - \bar{x}_1 - \bar{x}_2 - \bar{x}_3) \rangle = 1$. In the same way, $\langle f_2(1 - \bar{x}_1 - \bar{x}_2 - \bar{x}_3) \rangle = 1$ and $\langle f_3(1 - \bar{x}_1 - \bar{x}_2 - \bar{x}_3) \rangle = 1$ Hence (BC) holds. This completes the proof. ☐

Suppose that there exist positive constants S^*_{kl} $(k, l = 1, 2, 3,\ k < l)$ such that $f_k(S^*_{kl}) = f_l(S^*_{kl})$. Without loss of generality, we can assume that $S^*_{12} < S^*_{13} < S^*_{23}$. Further we assume $f_3(S) < f_2(S) < f_1(S)$ for $S \in [0, S^*_{12})$, $f_3(S) < f_1(S) < f_2(S)$ for $S \in (S^*_{12}, S^*_{13})$, $f_1(S) < f_3(S) < f_2(S)$ for $S \in (S^*_{13}, S^*_{23})$ and $f_1(S) < f_2(S) < f_3(S)$ for $S \in (S^*_{23}, \infty)$ (see, for example, Fig.4.2).

Let us denote the nutrient $S(t)$ by

$$S(t) := 1 - \sum_{j=1}^{3} x_j(t). \tag{4.8}$$

In particular, $\bar{S}(t)$ denotes the periodic nutrient when the solution of (L) is periodic. In addition, let us set $g_{kl}(S) \equiv f_k(S) - f_l(S)$. The graph of g_{kl} is illustrated on Fig. 4.1 in the case where f_i takes the form of Michaelis-Menten functional response. Note that g_{kl} corresponds to the right hand side of (4.7). Further, $g_{kl}(S) > 0$ for $S < S^*_{kl}$ and $g_{kl}(S) < 0$ for $S > S^*_{kl}$.

Remark 4.1. (BC) *represents that average competition among all species is balanced if the solution of* (L) *is periodic.* $\langle \dot{P}_{kl}(\bar{x}_k, \bar{x}_l)/P_{kl}(\bar{x}_k, \bar{x}_l)\rangle$ *represents the integral of* $g_{kl}(\bar{S})$ *on the range of the periodic nutrient (gray region on Fig. 4.1). Hence minima* S^- *and maxima* S^+ *of the periodic nutrient are determined in order that the integral equals to zero (that is,* $\langle g_{kl}(\bar{S})\rangle = 0$*).*

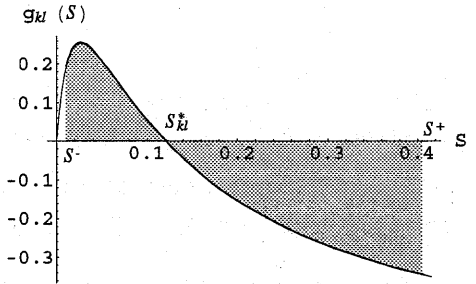


Figure 4.1: The graph of $g_{kl}(\bar{S})$, $(k < l)$

Note that since the integrand of $\langle \dot{P}_{kl}(\bar{x}_k, \bar{x}_l)/P_{kl}(\bar{x}_k, \bar{x}_l)\rangle$ is a composition function of $g_{kl}(S)$ and $S(t)$, it is possible that

$$\frac{1}{\omega}\int_{S^-}^{S^+} g_{kl}(r)dr > 0 \quad \text{but} \quad \frac{1}{\omega}\int_0^{\omega} g_{kl}(\bar{S}(t))dt = 0. \tag{4.9}$$

Proposition 4.2. (*competitive exclusion*) *Let* $(x_1(t), x_2(t), x_3(t))$ *be a positive solution of* (L).

C-(i) *If there exists* $T_1 > 0$ *such that* $S(t) < S^*_{12}$ *for all* $t \geq T_1$*, then* $x_2(t) \to 0$ *and* $x_3(t) \to 0$ *at some exponential rate as* $t \to \infty$.

C-(ii) *If there exists* $T_2 > 0$ *such that* $S^*_{12} < S(t) < S^*_{23}$ *for all* $t \geq T_2$*, then* $x_1(t) \to 0$ *and* $x_3(t) \to 0$ *at some exponential rate as* $t \to \infty$.

C-(iii) *If there exists* $T_3 > 0$ *such that* $S^*_{23} < S(t)$ *for all* $t \geq T_3$*, then* $x_1(t) \to 0$ *and* $x_2(t) \to 0$ *at some exponential rate as* $t \to \infty$.

Proof. It is sufficient to show case (i). The other cases are proved in the same manner. The derivative of P_{21} along the solution of (L) with a positive initial value $x(0) \in \Omega$ is

$$\frac{\dot{P}_{21}(x_2(t), x_1(t))}{P_{21}(x_2(t), x_1(t))} = f_2(S(t)) - f_1(S(t)) = g_{21}(S(t)).$$

Hereafter simply we write $P_{kl}(x_k(t), x_l(t))$ as $P_{kl}(t)$. Since we assume $S(t) < S_{12}^*$ for all $t \geq T_1$, $f_2(S(t)) < f_1(S(t))$ and hence $\dot{P}_{21}(t)/P_{21}(t) < 0$ for all $t \geq T_1$. Recall that $P_{21}(t) \geq 0$. Then there exists $P_{21}^* \geq 0$ such that $P_{21}(t) \to P_{21}^*$ as $t \to \infty$. In the same way, there exists $P_{31}^* \geq 0$ such that $P_{31}(t) \to P_{31}^*$ as $t \to \infty$. To complete the proof, it is sufficient to show that $P_{21}^* = P_{31}^* = 0$ since $P_{kl} = 0$ iff $x_k = 0$ by P-(ii). We claim that $S(t) \to S_{12}^*$ as $t \to \infty$ when $P_{21}^* > 0$. In fact, if not, there exist monotone increasing sequences $\{t_n\}_{n=1}^{\infty} > T_1$ and a sufficiently small positive constant δ such that $g_{21}(S(t_n)) < g_{21}(S_{12}^* - \delta) < 0$ for $n \in \mathbb{N}$. Then immediately we have $\dot{P}_{21}(t_n)/P_{21}(t_n) = g_{21}(S(t_n)) < g_{21}(S_{12}^* - \delta)$ for each $n \in \mathbb{N}$. Since $g_{21}(S_{12}^* - \delta)$ is a strictly negative constant, $P_{21}(t_n) \to 0$ as $n \to \infty$. This implies that $P_{21} \to P_{21}^* = 0$ as $t \to \infty$, but which is a contradiction. Hence $S(t) \to S_{12}^*$ as $t \to \infty$ when $P_{21}^* > 0$. Now we suppose $P_{21}^* > 0$ or $P_{31}^* > 0$. Since $x_1(t)$ is bounded, $x_2(t) \to P_{21}^* x_1(t)$ and $x_3(t) \to P_{31}^* x_1(t)$ as $t \to \infty$. Then $x_1(t) \to x_1^* \equiv (1 - S_{12}^*)/(1 + P_{21}^* + P_{31}^*) > 0$ as $t \to \infty$. This implies that $(x_1^*, P_{21}^* x_1^*, P_{31}^* x_1^*)$ is an equilibrium point of (L). Then the solution with a nonnegative initial value $(x_1^*, P_{21}^* x_1^*, P_{31}^* x_1^*)$ must satisfy

$$x_1^* = x_1^* \exp\left[\int_0^t (f_1(S_{12}^*) - D(s))ds\right]$$

for any positive t, or equivalently, $f_1(S_{12}^*) \equiv D(t)$. This is a contradiction since $D(t)$ is not constant. Hence $P_{21}^* = P_{31}^* = 0$. This completes the proof. □

Note on Proposition 4.2

Assume that $S(t) < S_{23}^*$ for all sufficiently large t. Here we do not necessarily assume that $S_{12}^* < S(t)$. By the assumption, we can show that there exists $P_{32}^* \geq 0$ such that $P_{32}(t) \to P_{32}^*$ as $t \to \infty$. Moreover we can show that $S(t) \to S_{23}^*$ and $x_3(t) \to P_{32}^* x_2(t)$ as $t \to \infty$ when $P_{32}^* > 0$. Although $x_3(t) \to 0$ as $t \to \infty$ both in C-(i) and C-(ii), in this situation, there might be a *positive* solution $(x_1(t), x_2(t), x_3(t))$ of (L) such that $x_1(t) + x_2(t) + x_3(t) \to 1 - S_{23}^*$ and $x_3(t) \to P_{32}^* x_2(t)$ as $t \to \infty$. It is clear that species x_3 never enjoys competitive advantage as long as $S(t) < S_{23}^*$. However species x_3 still has the possibility to persist. The problem would be more difficult to figure out whether x_3 persists or not in this situation. It leaves for our future consideration.

4.4 Numerical simulations

Let us show some numerical simulation results which are carried out by using *Mathematica*. Assume that nutrient uptake functions of competing three species take the form of Michaelis-

Menten functional response (4.2). The washout rate $D(t)$ is given by

$$D(t) = 1 + d\cos(2\pi t/\omega), \tag{4.10}$$

where d is a positive constant satisfying $0 < d < 1$. Throughout the remainder of this section, parameters and initial values are fixed at the following respective values:

$$\begin{cases} a_1 = 0.018181 \ , \ a_2 = 0.272727 \ , \ a_3 = 0.090909, \\ m_1 = 1.36898 \ , \ m_2 = 1.49733 \ , \ m_3 = 2.13904 \ , \ d = 0.64171, \\ x_1(0) = 0.5 \ , \ x_2(0) = 0.2 \ , \ x_3(0) = 0.3. \end{cases} \tag{P}$$

Note that these values are taken almost equal to the parameters adopted in [33, p.122] and [73, pp. 486–487]. The graph of respective functional response of competing three species with (P) is illustrated on Fig. 4.2. Note that every species can take competitive advantage since the washout rate varies between the range in which every competitor has the chance to be superior to the other competitors in terms of nutrient uptake (note that $d = 0.64171$). The intersection points S^*_{12}, S^*_{13} and S^*_{23} are numerically calculated as $S^*_{12} = 0.078788$, $S^*_{13} = 0.111111$ and $S^*_{23} = 0.121212$.

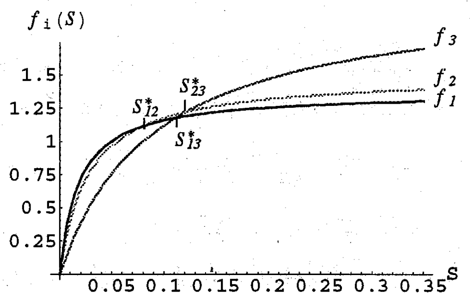


Figure 4.2: Functional responses of three species for (P)

Let us show some figures which illustrate trajectories of the solution of (L) with (P) for different values of period ω. Figs 4.3–4.8 illustrate the time series and the projections into $x_1 - x_2 - x_3$ phase space of trajectories for ω = 4, 6, 8, 12.5, 20 and 50, respectively. Let us denote the end time of numerical simulation by t_{max}. Here $t_{max} = 6000$. The time series of trajectories are shown for $2900 \leq t \leq 3000 < t_{max}$. In the case $\omega = 4$, only x_2 can survive (see Fig. 4.3). We can confirm that $x_1(t_{max}) \sim 1.6 \times 10^{-21}$ and $x_3(t_{max}) \sim 3.7 \times 10^{-6}$. In the case $\omega = 6$, that is, on Fig. 4.4, it is observed that x_2 and x_3 survive, while x_1 goes extinct

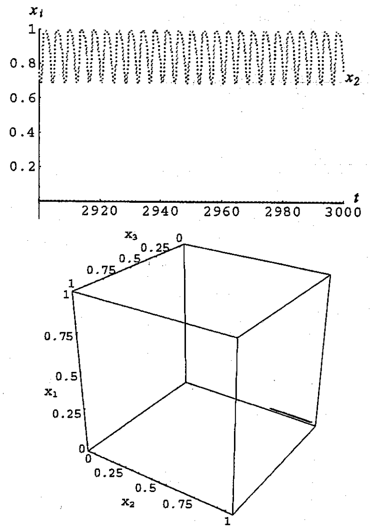


Figure 4.3: $\omega = 4$.

Only x_2 survives.

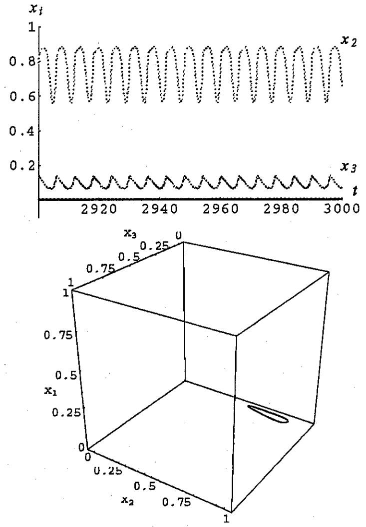


Figure 4.4: $\omega = 6$.

x_2 and x_3 coexist.

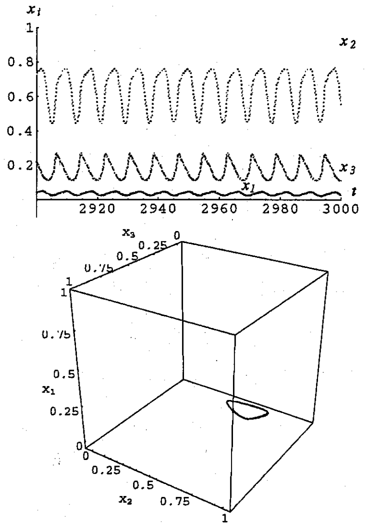


Figure 4.5: $\omega = 8$.

Three species coexist.

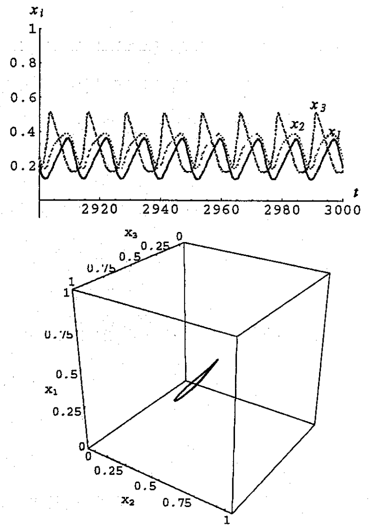


Figure 4.6: $\omega = 12.5$.

Three species coexist.

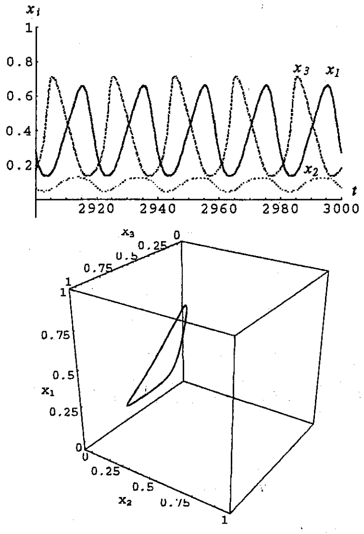


Figure 4.7: $\omega = 20$.

Amplitude grows large.

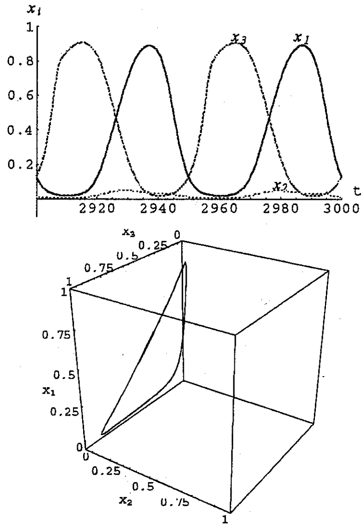


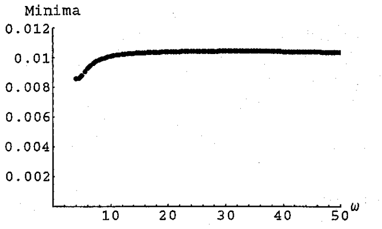
Figure 4.8: $\omega = 50$.

Three species still coexist.

($x_1(t_{max}) \sim 5.8 \times 10^{-6}$). In the case $\omega = 8$, three species coexist (see Fig. 4.5). On Figs 4.6–4.8, three species still coexist.

The mechanism of coexistence is intuitively interpreted as follows: Assume that $f_3(1) > D_{max} = 1 + d$. First consider the situation that the nutrient $S(t)$ satisfies $S_{23}^* < S(t_1)$ and $f_3(S(t_1)) < D(t_1)$ at some t_1. Then all of x_1, x_2 and x_3 decrease at their respective exponential rates as long as t satisfies the relation $f_3(S_{23}^*) < f_3(S(t)) < D(t)$. If this relation holds true for all $t > t_1$, $S(t) \to 1$ as $t \to \infty$, but which contradicts with the assumption $f_3(1) > D_{max}$. Hence within a finite time $t_2 > t_1$, we have $f_3(S_{23}^*) < D(t_2) < f_3(S(t_2))$. Then according to the proof of Proposition 4.2 – (iii), $x_1(t_2)$ and $x_2(t_2)$ still decreases at their respective exponential rates, while $x_3(t_2)$ increases at some exponential rate. Note that $S(t)$ decreases as $x_3(t)$ increases. If the increase of $x_3(t)$ leads the inequality $S_{12}^* < S(t_3) < S_{23}^*$ for some $t_3 > t_2$, Proposition 4.2 – (ii) implies that $x_1(t_3)$ and $x_3(t_3)$ decreases, while $x_2(t_3)$ increases. Further if there exists $t_4 > t_3$ such that $S(t_4) < S_{12}^*$, then $x_2(t_4)$ and $x_3(t_4)$ decreases, while $x_1(t_4)$ increases. Consequently, if $S(t)$ moves in such a way that all species can grow in each dominant interval, the coexistence of three species is possible.

We can see on Figs 4.3–4.8, the amplitude of the nutrient (4.8) becomes large as ω increases. In fact, minima of $\bar{S}(t)$ for different values of ω are approximately equal to 0.01 (see Fig. 4.9), while maxima of $\bar{S}(t)$ increases as ω increases (see Fig. 4.10). Hence S_{12}^*, S_{13}^* and S_{23}^* belong to the range of $\bar{S}(t)$ and the assumptions of Proposition 4.2 don't hold.



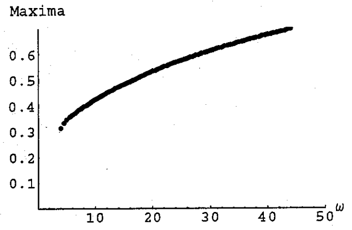


Figure 4.9: ω vs minima of $\bar{S}(t)$

Figure 4.10: ω vs maxima of $\bar{S}(t)$

Finally let us propose an intuitive interpretation why maxima of $\bar{S}(t)$ increase as ω increases. Since the presence of species inhibits the increase of the nutrient, the timing when $\bar{S}(t)$ attains its maxima (minima) almost corresponds to that of $D(t)$. Note that when $D(t)$ changes slowly, that is, when ω is large, every species can enjoy competitive advantage for a long term. In particular, the long term dominance of x_3 makes the nutrient decrease intensively since x_3 consumes the nutrient with a high rate. Then x_1 takes competitive advantage before $D(t)$ attains its minima and begins to grow as $D(t)$ decreases. Since x_1 dominates the other competitors, x_2 and x_3 cannot grow rather decrease by Proposition 4.2. Soon $D(t)$ becomes large and then x_1 decreases. As all of nutrient, x_2 and x_3 are still low density, the nutrient can increase intensively. The slow change of $D(t)$ also promotes the increase of the nutrient (see Fig. 4.11).

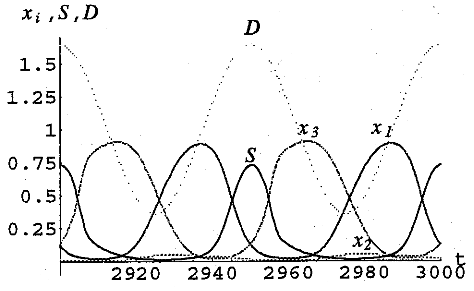


Figure 4.11: The time series of x_1, x_2, x_3, $S(t)$ and $D(t)$ for (P) with $\omega = 50$.

Let us summarize numerical simulation results:

Remark 4.2. *Three species coexistence occurs as ω increases if $\bar{S}(t)$ has small minima and large maxima. Maxima of $\bar{S}(t)$ are likely to become large as ω increases. This suggests that a long term period of periodic washout rate promotes the coexistence of three species competing for a single resource.*

4.5 Discussion

In this chapter, we considered chemostat equations with a periodic washout rate in which three species compete for one limiting nutrient. We introduced an average competition function P_{kl} by which it was shown that positive ω-periodic solutions of system (L) must satisfy the condition (BC). As we remarked in Remark 4.1, (BC) highly restricts the range of amplitude of $\bar{S}(t)$ since $\langle \dot{P}_{kl}/P_{kl} \rangle = 0\,(1 \leq k, l \leq 3,\, k < l)$. Hence (BC) would restrict the parameter sets of the equations to be narrow to ensure three species coexistence. In Section 4.4, it was demonstrated that the number of survivors increases as the period of the washout rate becomes large. In other words, a long term period enhances the coexistence of three species. Since the result obtained in this chapter is just analyzed by mathematics partially, further mathematical analysis is necessary. This leaves for our future consideration.

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Appendix A

Appendices

A.1 Characteristic equation

Consider the equation

$$P(\lambda) + Q(\lambda)e^{-\lambda\tau} = 0. \tag{A.1}$$

For the analysis of the characteristic equation (A.1), we will refer "*Geometric stability switch criteria*" obtained by Cooke and van den Driessche [11]. The correction of [11] is proposed by Boese [6]. The result is as follows:

Theorem A.1. *[11], [6] Suppose that*

(B1) (A.1) *has no common imaginary root,*

(B2) $\overline{P(-i\omega)} = P(i\omega)$, $\overline{Q(-i\omega)} = Q(i\omega)$ *for* $\omega \in \mathbf{R}$,

(B3) $\limsup_{|\lambda|\to\infty, \mathrm{Re}\lambda\geq 0} |Q(\lambda)/P(\lambda)| < 1$,

(B4) $P(0) + Q(0) \neq 0$,

(B5) $F(\omega) = |P(i\omega)|^2 - |Q(i\omega)|^2$ *for* $\omega \in \mathbf{R}$ *has at most a finite number of zeroes.*

Then the following statements hold true:

(C1) If $F(\omega) = 0$ *has no positive roots, then no stability switch may occur.*

(C2) If $F(\omega) = 0$ *has at least one positive root and each of them is simple, then there exists* $\tau^* > 0$ *such that the equation* (A.1) *is unstable for all* $\tau > \tau^*$. *As* τ *varies from* 0 *to* τ^*, *at most a finite number of stability switches may occur.*

Remark A.1. *For* $\theta \in (0, 2\pi)$, $\cos\theta = \frac{\varphi}{|Q(i\omega)|^2}$ *and* $\sin\theta = -\frac{\vartheta}{|Q(i\omega)|^2}$ *where* $\varphi = P_R Q_R + P_I Q_I$ *and* $\vartheta = P_R Q_I - P_I Q_R$. P_R *(or* Q_R*) denotes the real part of* $P(i\omega)$ *(or* $Q(i\omega)$*), while* P_I *(or* Q_I*) denotes the imaginary part of* $P(i\omega)$ *(or* $Q(i\omega)$*). Then following statements are true:*

- $\theta = \arctan(-\vartheta/\varphi)$ *if* $\sin\theta > 0$ *and* $\cos\theta > 0$,
- $\theta = \pi/2$ *if* $\sin\theta = 1$,
- $\theta = \pi + \arctan(-\vartheta/\varphi)$ *if* $\cos\theta < 0$,
- $\theta = 3\pi/2$ *if* $\sin\theta = -1$,
- $\theta = 2\pi + \arctan(-\vartheta/\varphi)$ *if* $\sin\theta < 0$ *and* $\cos\theta > 0$.

Let $\bar{\omega}$ *be a positive root of* $F(\omega) = 0$. *Then stability switch may occur for* $\tau = \tau_n$ *where*

$$\tau_n = \frac{\theta + 2n\pi}{\bar{\omega}}, \quad n = 0, 1, 2, \cdots.$$