UNIVERSITY OF ALBERTA

PERIODIC DIFFERENTIAL SYSTEMS
WITH APPLICATIONS TO ECOLOGICAL MODELLING

BY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled PERIODIC DIFFERENTIAL SYSTEMS WITH APPLICATIONS TO ECOLOGICAL MODELLING submitted by QIU-LIANG PENG in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in APPLIED MATHEMATICS.

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Abstract

This thesis deals with some models concerning various aspects of periodic systems of differential equations, including uniform persistence, and the existence and stability of 'interior' periodic solutions. Biological implications, significance and relevance of the results in each chapter are included. The mathematical techniques used include Floquet theory, persistence theory, dissipative theory, topological degree theory and the theory of monotone dynamical systems.

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CHAPTER 1

INTRODUCTION

Differential equations have played important roles in the history of theoretical population dynamics. and they will no doubt continue to serve as indispensable tools in future investigations. However, most of those discussion have been devoted to models governed by autonomous ordinary differential equations(ODEs). delay differential equations(DDEs) and reaction-diffusion equations(RDEs). Because of seasonal fluctuations and periodic availability of food. the question of a periodically varying environment has been attracting more and more attention(see the following chapters for references). Generally. a discussion of periodic systems is much more difficult than a discussion of autonomous systems. particularly for the study of stability of a periodic orbit. In this thesis. we are going to discuss periodic single-species models of dispersal in a patchy environment. a periodic chemostat with general uptake functions. and a periodic Gause-type predator-prey system with periodic time delays.

The subject of dispersal is a major area of mathematical ecology and the reader is refered to the excellent bibliography[Lev2]. There mainly exist two types of models involving populations moving through patchy environments: (i) models of populations dispersing among discrete patches involving ordinary differential equations, and (ii) models of populations diffusing in continuous patches involving parabolic partial differential equations. In a patchy environment. a species could disperse among different habitats at some cost to the population in the sense that the survival probability during a change of habitat may be less than one since there exist barrier strengths between different habitats. Generally, dispersal in a patchy environment is good for species survival. Once the population is too crowded in a patch. many individuals disperse to other patches. Once the environment in a certain patch degenerates. the population in that patch may seek temporary refuge in the other patches.

Competition modelling is one of the more challenging aspects of mathematical ecology. Competition is clearly important in nature. The simplest form of competition occurs when two or more populations compete for the same resource. for example, the same food supply or the same growth limiting nutrient. One can view the "competitors" as "predators" on the "nutrient". and this produces an entirely different type of behavior for the resulting dynamical systems.

The chemostat is a piece of laboratory apparatus used to culture microorganisms. The apparatus consists of three connected vessels. The first contains all of the nutrients needed for growth of a microorganism. all in excess except for one called the limiting nutrient. The nutrient is pumped into the second vessel. the culture vessel. The culture vessel is charged with a variety of microorganisms. so it contains a mixture of nutrient and organisms. Its output is collected in the third vessel which represents the "production" of the chemostat. The chemostat is of ecological interest because it is a laboratory model of a very simple lake. It also is one place where the mathematics is tractable. the parameters are measurable. and the experiments are reasonable.

Models of Gause-type predator-prey systems were introduced by Gause[Gau] and Gause, Smaragdova and Witt[GSW] to help analyze paramecium-didinium interactions. Since then, various forms of these models(both continuous and discrete) have been utilized by many experimental and field biologists in studying predator-prey interactions. Meanwhile, there have been many mathematicians attracted to the mathematical analysis of these models(see references contained in [Fr1]). However, most of the previous work done were concerned with the existence and local stability of equilibria or limit cycles in autonomous Gause-type predator-prey systems modeled by ODEs. More realistic models should include some of the past states of those systems and the environmental fluctuations. It is one of the purposes of this thesis to discuss the periodic Gause-type predator-prey system with periodic time delays.

A good understanding of a system largely depends on the availability of the detailed global analysis of the qualitative nature of the corresponding mathematical models. In a periodic ecological system, we are usually interested in the existence, uniqueness and stability(local or global) of non-negative periodic solutions. It is well-known that the existence, uniqueness and stability of periodic solutions of a periodic system of differential equations are equivalent to that of the fixed points of its associated Poincaré periodic mapping. It is also well-known that a periodic cooperative model or a periodic two-species competitive model generates a discrete monotone dynamical system. In chapter 4, we are going to prove some general results on global dynamics in discrete monotone dynamical systems. Floquet theory has played an important role in discussing the stability of a periodic solution. The Floquet theorem asserts that for linear periodic ordinary differential equations, there exists a linear invertible periodic transformation that will transform the equation to an autonomous one. For details on the Floquet theory, we refer to [Fa].

This thesis is organized as follows. In chapter 2, a single species which disperses among n patches with periodic or asymptotically periodic carrying capacities and barrier strengths is modeled by a system of time-dependent ordinary differential equations. Criteria for uniform persistence and the existence of globally stable periodic solutions are established. The case of time-dependent (inverse) barrier strengths is considered for the first time in the literature. In section 2.2, we first present a detailed description of our model, both biologically and mathematically. Then we discuss the uniform persistence and the existence of positive periodic solutions for the system. In section 2.4. we deal with the question of global asymptotic stability of the positive periodic solution in details. Section 2.5 contains a detailed discussion on the asymptotic periodic case. A brief discussion follows in the last section of this chapter.

In chapter 3. we consider a chemostat model of two microbial populations competing for a nutrient, where nutrient inputs and chemostat washouts are periodic. As well, general nutrient uptake functions which may also be time dependent and periodic are considered. Criteria are derived for there to exist a globally attracting positive periodic solution and a theorem on global monotonicity of attracting solutions between different systems is proved. In section 3.2. we describe the model and derive some preliminary results. In section 3.3. we consider the submodel consisting of nutrient and one microbial population. Here we obtain criteria for extinction of the microbes as well as criteria for the existence and global stability of a positive periodic solution. In section 3.4. we obtain criteria for the extinction of the second microbial population. as well as criteria for the existence of a positive periodic solution. In obtaining these latter results. we prove a comparison theorem concerning solutions of scalar periodic systems. which may be of independent interest. Furthermore. we address a conjecture on the local stability of a positive periodic solution. Based on the local stability, by topological degree theory we show that if on the boundary of $\mathbb{R}^3_+$ there exists no asymptotically stable solution, then the considered full chemostat system has a strictly positive periodic solution which is globally asymptotically stable. Usually, it is rather easier to discuss the local stability than to discuss the global stability. However. the difficulty here lies in the discussion of local stability and we state a conjecture for future research. In section 3.5, we discuss the structure of a global attractor of the full chemostat system. Finally, a brief discussion on the biological implications is contained in section 3.6.

In chapter 4, some results on the global dynamics in the theory of discrete monotone dynamical systems are obtained. Specifically, with weak monotonicity for a mapping and without the property that the Frechét derivative of the mapping at a fixed point is strongly positive, the existence and global attractivity of a strictly positive fixed point of the mapping are obtained. To the best of our knowledge, this is the first time this weak case has been dealt with.

As mentioned above, the systems considered in chapters 2 and 3 could generate discrete monotone dynamical systems. Generally, it is a little easier to discuss a periodic system generating a monotone periodic semiflow in terms of the theory of monotone dynamical systems(continuous or discrete) than to discuss a periodic system without any monotonicity. Furthermore, for a nonmonotone periodic system, specifically one which generates an infinite-dimensional dynamical system, a discussion of the dynamics is likely to be considerably more difficult.

In chapter 5, we consider a periodic Gause-type predator-prey system with periodic delays. It is difficult to describe completely the dynamics of the considered system since our model generates an infinite-dimensional nonmonotone semi-dynamical system($t \geq 0$). Hence we first discuss the long-term behavior described roughly by dissipativity and uniform persistence. Since the growth of the predator has no logistic self-limitation, this results in a nontrivial discussion of the dissipativity. Under some reasonable hypotheses, we prove that the considered system is point dissipative. Our result improves those in the related literature. Criteria are derived for the considered system to be uniformly persistent. In section 5.1, we present a detailed description of our model. Some related preliminary results on uniform persistence and global attractivity for dynamical systems(continuous or discrete) are introduced in section 5.2. A nontrivial dissipativity discussion follows in section 5.3. In section 5.4, we mainly show that the considered system is uniformly persistent. A brief discussion of periodic coexistence states and some remarks are also contained in section 5.4. Finally, we briefly explain our main result with biological implications.

The final chapter contains a concluding discussion and some remarks. Some interesting and challenging problems for future reseach are posed.

Some remarks on this thesis are necessary. We adopt the constructive method to prove the existence of positive periodic solutions for systems discussed in chapters 2 and 3 although we could do it by persistence theory, which may simplify our proofs. However, chapter 2 is based on [FrPe1] and chapter 3 is based on [PeFr1], which were done about two years ago. The most important reason why we keep the original versions is that the constructive method gives us more details and ideas. One can easily find that most results in chapters 2 and 3 could be proved by our general results proved in chapter 4.

Our main tools are persistence theory, dissipative theory, infinite-dimensional dynamical systems theory, monotone dynamical systems theory, topological degree theory and a standard but important comparison argument.

CHAPTER 2

DISPERSAL IN A PATCHY ENVIRONMENT *

2.1. Introduction

Models involving populations moving through patchy environments are mainly of two types: (i) models of populations dispersing among discrete patches involving ordinary differential equations, and (ii) models of populations diffusing in continuous patches involving parabolic partial differential equations. This chapter is concerned with the first of these, namely dispersal among discrete patches.

In the work done to date, the models were concerned with patches separated by a barrier with constant barrier strength [BeTa1], [Fr2], [Fr3], [FRW], [FrTa1], [FrTa2], [FrWa1], [Take1], [Take2], [Take3], [TOM]. In these papers, the systems were autonomous, i.e. the parameters of the models representing growth rates, carrying capacities, probabilities of survival while dispersing, etc., were all deemed to be constant. However, in the "real world", all these parameters may vary seasonally or even diurnally.

In this chapter we discuss a model of a single species dispersing among n patches, where all parameters may vary periodically in time. This would be the next step towards "reality". We then carry this even further by considering models where the parameters are asymptotic periodic. Our model is derived by modifying a submodel discussed in [FrTa1]] and [FrTa2]. Models involving interactions between several species are left to future work.

* This chapter is adopted from [FrPe1].

This chapter is organized as follows. In the next section we formulate our model. In section 3, we discuss the uniform persistence and the existence of periodic solutions for our model. Section 4 deals with the question of global stability of the periodic solution. In section 5, we consider the asymptotic periodic case. A brief discussion follows in the last section.

Throughout this chapter we assume that all functions are sufficiently smooth so that solutions to initial value problems exist, are unique and are continuable for all positive time.

2.2. The Patchy Model

We consider a time-dependent system in a patchy environment where a population is able to disperse among the n different habitats(see **Fig 2.1**) at some cost to the population in the sense that the probability of survival during a change of habitat may be less than one. We also suppose that both the barrier strengths and the survival probabilities vary either periodically in time with the same period as the species parameters and dispersing functions or are asymptotically periodic.

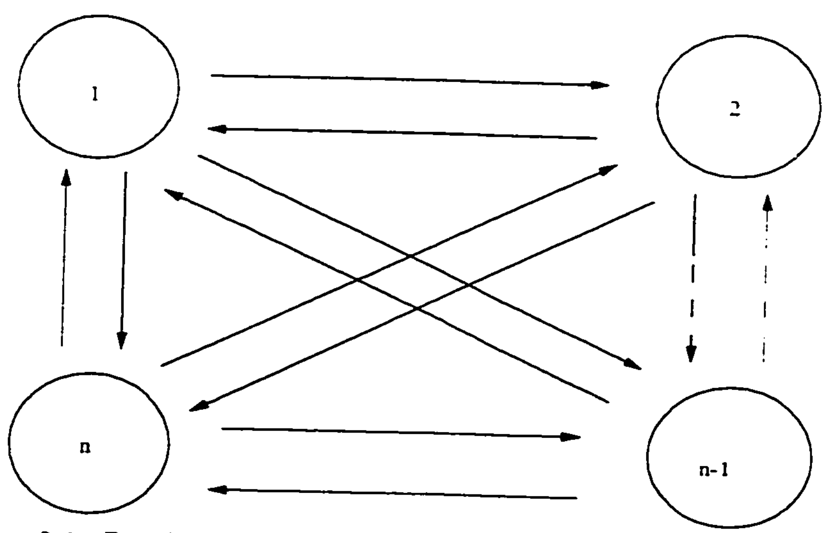

Figure 2.1: Patchy environment showing n interconnected patches

The model is described by the system of nonautonomous ordinary differential equations

$$\dot{x}_i = x_i g_i(t, x_i) - \varepsilon_i(t) h_i(t, x_i) + \sum_{j \in J_i} p_{ji}(t) \varepsilon_j(t) h_j(t, x_j)$$

$$x_i(0) \geq 0, \quad i = 1, \dots, n, \tag{2.1}$$

with $\sum_{j \in J_i}^{n} p_{ij} \leq 1$, where $\cdot = d/dt$, $J_i = \{1, \dots, i-1, i+1, \dots, n\}$, $g_i, h_i : \mathbb{R}^2 \to \mathbb{R}$ are continuously differentiable, positive, and either T-periodic or asymptotically T-periodic for some common period $T > 0$ in the variable t, and ε_i, $p_{ij} : \mathbb{R} \to \mathbb{R}$ are nonnegative and T-periodic or asymptotically T-periodic.

Here, $x_i(t)$ represents the same population in the ith patch, $i = 1, \dots, n$, at a given time $t \geq 0$; $g_i(t, x_i)$ is the intrinsic growth rate of the population in the i^{th} habitat at a given time $t \geq 0$; $\varepsilon_i(t)$, which is not necessarily small but is positive represents the inverse barrier strength at time t in going out of the i^{th} habitat; $h_i(t, x_i)$ is the rate of dispersal out of the i^{th} patch at time t and $p_{ji}(t)$ is the probability of successful transition from the j^{th} patch to the i^{th} patch, where i is different from j.

We make the following hypotheses, which are modified from the standard ones in modelling such phenomena [Fr1], [FrTa1].

(H_1) All solutions of the initial value problem (2.1) exist uniquely and are countinuable for all positive time.

(H_2) $g_i(t, 0) > 0$, $\frac{\partial g_i(t, x_i)}{\partial x_i} < 0$, $x_i g_i(t, x_i) \to -\infty$ as $x_i \to +\infty$, $i = 1, \dots, n$, for all time $t \geq 0$.

(H_3) $h_i(t, 0) = 0$, $\frac{\partial h_i(t, x_i)}{\partial x_i} > 0$, $i = 1, \dots, n$ at any time $t \geq 0$.

The inequalities in (H_3) above state that the rate of dispersal out of the i^{th} patch is density dependent and an increasing function of the population of the i^{th} patch for any fixed $t \geq 0$.

We note that the positive cone $\mathbb{R}_+^n$ in $\mathbb{R}^n$ is positively invariant.

2.3. Uniform Persistence and Periodic Solutions

In this section, we suppose that all functions contained in model (2.1) are T-periodic. Firstly, following [BFW], [BuWa], [FrMo], [FrWa1], [FrWa2] we recall briefly some terminology. Let $x(t)$ be the population density at time t. We say that $x(t)$, $x(0) > 0$, is persistent if $\liminf_{t \to \infty} x(t) > 0$. We say that $x(t)$ is uniformly persistent if there exists $\delta > 0$ such that $\liminf_{t \to \infty} x(t) \geq \delta$ independent of $x(0) > 0$. We say that a system exhibits (uniform) persistence if each component (uniformly) persists. Finally, we say that $x(t)$ exhibits extinction if $\limsup_{t \to \infty} x(t) = 0$ and a system exhibits extinction if at least one component becomes extinct.

Theorem 2.1. *Assume*

$$\int_0^T \left[g_i(t, 0) - \varepsilon_i(t) \frac{\partial h_i(t, 0)}{\partial x_i} \right] dt > 0, \quad i = 1, 2, \ldots, n. \tag{2.2}$$

holds. Then system (2.1) *exhibits uniformly persistence.*

Proof. Note that the positive cone $\mathbb{R}_+^n$ in $\mathbb{R}^n$ is positively invariant with respect to (2.1) and hence the term $\sum_{j \in J_i} p_{ji}(t)\varepsilon_j(t)h_j(t, x_j)$ is positive. Letting $u_i(t)$ $(i = 1, 2, \ldots, n)$ denote the solution of the following system

$$\dot{u}_i = u_i g_i(t, u_i) - \varepsilon_i(t) h_i(t, u_i)$$

$$u_i(0) = x_i(0)$$

then clearly, we have

$$x_i(t) \geq u_i(t) \quad \text{for all} \quad t \geq 0 \quad \text{and} \quad i = 1, 2, \ldots, n.$$

For the purpose of finding a persistent lower bound, we consider

$$\begin{aligned} \dot{y} &= y g(t, y) - \varepsilon(t) h(t, y) \\ y(0) &\geq 0. \end{aligned} \tag{2.3}$$

Here the functions $g(t,y)$, $\varepsilon(t)$ and $h(t,y)$ are a representative of $g_i(t,x_i)$, $\varepsilon_i(t)$ and $h_i(t,x_i)$ respectively. Obviously, $y=0$ is an equilibrium of (2.3) and $\mathbb{R}_+$ is also positively invariant. Now we will see that $y=0$ is unstable provided

$$\int_0^T \left[g(t,0) - \varepsilon(t)\,\frac{\partial h(t,0)}{\partial y}\right] dt > 0. \tag{2.4}$$

Indeed, the characteristic equation of (2.3) about the equilibrium $y=0$ is

$$\dot{y} = \left(g(t,0) - \varepsilon(t)\,\frac{\partial h(t,0)}{\partial y}\right) y. \tag{2.5}$$

We know that in (2.5), $y=0$ is unstable provided (2.4) holds. Hence under condition (2.4) we can conclude that there exists a constant $\delta > 0$, which could be sufficiently small but positive, such that $[\delta, +\infty)$ is positively invariant and globally attractive with respect to $\mathbb{R}_+$. Similarly, under condition (2.2), for each i there exists a $\delta_i > 0$ such that $[\delta_i, +\infty)$ has the same property. Let $\delta = \min_{1\le i\le n}\{\delta_i\}$. Then we have actually proved that

$$\Delta = \{(x_1,\ldots,x_n) \in \mathbb{R}_+^n \mid x_i \ge \delta,\ i=1,\ldots,n\}$$

is positively invariant and globally attractive with respect to $\mathbb{R}_+^n$. Thus, system (2.1) is uniformly persistent.

□

Theorem 2.2. *System* (2.1) *has at least one positive* T*-periodic solution under condition* (2.2).

Proof. From the fact that if $x = \sum_{i=1}^n x_i$, then

$$x' \le \sum_{i=1}^n x_i g_i(t,x_i)$$

and by (H_2) if $\|x\|$ is sufficiently large,

$$x' < 0,$$

it follows from the fact that $\mathbb{R}^n_+$ is positively invariant that there exists a constant $k > 0$ such that

$$x_i(t) \le k, \quad i = 1, \ldots, n, \quad \text{for} \quad t \quad \text{large enough.}$$

By condition (2.2) and the proof of theorem 2.1, it is obvious that the set

$$S = \{(x_1, \ldots, x_n) \in \mathbb{R}^n_+ | \ \delta \le x_i \le k, \ i = 1, \ldots, n\}$$

is not only positive invariant, but also globally attractive with respect to $\mathbb{R}^n_+$. We define $x(t, x_0)$ to be that solution of (2.1) such that $x_i(0, x_0) = x_{i0}$. If we further define $F : S \to \mathbb{R}^n$ by

$$F(r) = F(r_1, \ldots, r_n) = (r_1 - x_1(T, r), \ldots, r_n - x_n(T, r)).$$

then from degree theory, $\deg(F, \text{Int } S, 0) = 1$, where $\text{Int } S = \{(x_1, \ldots, x_n) \in \mathbb{R}^n_+ | \ \delta < x_i < k, \ i = 1, \ldots, n\}$. Actually, let $\bar{r} = (\bar{r}_1, \ldots, \bar{r}_n)$ be a definite point in $\text{Int } S$. For any $r = (r_1, \ldots, r_n) \in S$, since $\text{Int } S$ is convex, then for all $\lambda \in [0, 1]$, $(\bar{r}_1 + \lambda(x_1(T, r) - \bar{r}_1), \ldots, \bar{r}_n + \lambda(x_n(T, r) - \bar{r}_n)) = X(r, \lambda) \in \text{Int } S$, where $(x_1(t, r), \ldots, x_n(t, r))$ is the solution of system (2.1) with initial value r. We can define a homotopic mapping $H : S \times [0, 1] \to \mathbb{R}^n$ by $H(r, \lambda) = r - X(r, \lambda)$. Then $H(r, 1) = F(r)$ and $H(r, 0) = (r_1 - \bar{r}_1, \ldots, r_n - \bar{r}_n) = G(r)$. It is obvious that $\deg(G, \text{Int } S, 0) = 1$. By homotopy invariance of degree, it follows that

$$\deg(F, \text{Int } S, 0) = 1.$$

Hence, there exists at least one such $r^0 = (r^0_1, \ldots, r^0_n) \in \text{Int } S$ satisfying

$$F(r^0) = 0,$$

that is, system (2.1) has at least one positive T-periodic solution lying in S.

□

Remark. The proof of theorem 2.2 does not imply that the T-periodic solution found is necessarily nontrivial. However, what is important in the periodic literature (i.e. in systems with periodic coefficients) is the existence of periodic solutions, whether trivial or not.

2.4. Global Stability

In this section we study the global stability of the positive periodic solution of the following system

$$\dot{x}_i = x_i g_i(t, x_i) - \varepsilon_i(t)x_i + \sum_{j\in J_i} p_{ji}(t)\varepsilon_j(t)x_j, \quad i = 1, 2, \ldots, n. \tag{2.6}$$

where $g_i(t, \cdot)$, $\varepsilon_i(t)$ and $p_{ji}(t)$ are T-periodic functions about the time variable t. Actually, if we assume the dispersal is proportional with the density of population, then system (2.1) becomes system (2.6) and (H_3) is still satisfied.

We suppose system (2.6) has at least one positive T-periodic solution and denote it by $x^*(t) = (x_1^*(t), \ldots, x_n^*(t))$ which lies in S. Consider the variational equation of system (2.6) about $x^*(t)$.

$$\dot{X} = \begin{pmatrix} g_1(t, x_1^*(t)) + x_1^*(t)\frac{\partial g_1(t, x_1^*(t))}{\partial x_1} - \varepsilon_1(t) & p_{21}(t)\varepsilon_2(t) & \cdots & p_{n1}(t)\varepsilon_n(t) \\ p_{12}(t)\varepsilon_1(t) & g_2(t, x_2^*(t)) + x_2^*(t)\frac{\partial g_2(t, x_2^*(t))}{\partial x_2} - \varepsilon_2(t) & \cdots & p_{n2}(t)\varepsilon_n(t) \\ \vdots & \vdots & & \vdots \\ p_{1n}(t)\varepsilon_1(t) & p_{2n}(t)\varepsilon_2(t) & \cdots & g_n(t, x_n^*(t)) + x_n^*(t)\frac{\partial g_n(t, x_n^*(t))}{\partial x_n} - \varepsilon_n(t) \end{pmatrix} X. \tag{2.7}$$

If we set $Q(t) = \operatorname{diag}(x_1^*(t), \ldots, x_n^*(t))$, then $Q(0) = Q(T)$. Apply the transformation $Y(t) = Q^{-1}(t)X(t)Q^{-1}(0)$. Then

$$\dot{Y}(t) = B(t)Y(t) \tag{2.8}$$

where

$$B(t)=\begin{pmatrix} x_1^*(t)\frac{\partial g_1(t,x_1^*(t))}{\partial x_1}-\sum\limits_{j\in J_1}p_{j1}(t)\varepsilon_j(t)\frac{x_j^*(t)}{x_1^*(t)} & p_{21}(t)\varepsilon_2(t)\frac{x_2^*(t)}{x_1^*(t)} & \cdots & p_{n1}(t)\varepsilon_n\frac{x_n^*(t)}{x_1^*(t)} \\ p_{12}(t)\varepsilon_1(t)\frac{x_1^*(t)}{x_2^*(t)} & x_2^*(t)\frac{\partial g_2(t,x_2^*(t))}{\partial x_2}-\sum\limits_{j\in J_1}p_{j2}(t)\varepsilon_j(t)\frac{x_j^*(t)}{x_2^*(t)} & \cdots & p_{n2}\varepsilon_n(t)\frac{x_n^*(t)}{x_2^*(t)} \\ \vdots & \vdots & \ddots & \vdots \\ p_{1n}(t)\varepsilon_1(t)\frac{x_1^*(t)}{x_n^*(t)} & p_{2n}(t)\varepsilon_2(t)\frac{x_2^*(t)}{x_n^*(t)} & \cdots & x_n^*(t)\frac{\partial g_n(t,x_n^*(t))}{\partial x_n}-\sum\limits_{j\in J_n}p_{jn}(t)\varepsilon_j(t)\frac{x_j^*(t)}{x_n^*(t)} \end{pmatrix}. \tag{2.9}$$

In order to obtain our results. we recall some concepts and known results concerning Floquet theory[Fa].

For an n-dimensional linear periodic differential system

$$\dot{x}=A(t)x \tag{2.10}$$

where $A(t)$ is a continuous, T-periodic $n\times n$ matrix. let $X(t)$ be a fundamental matrix of system (2.10) which satisfies $X(0)=I$. Then there exists a C^2 nonsingular T-periodic $n\times n$ matrix $W(t)$ and a constant $n\times n$ matrix R such that $X(t)=W(t)\exp(Rt)$. An eigenvalue of the matrix R is called a characteristic exponent or Floquet exponent of system (2.10).

Floquet theory implies that for each characteristic exponent μ there corresponds a solution $x(t)$ of system (2.10) with the form

$$x(t)=\beta(t)e^{\mu t}$$

where the vector function $\beta(t)$ is periodic in t with period T. i.e. $\beta(t+T)=\beta(t)$.

We denote an eigenvector of the matrix R corresponding to the eigenvalue μ by ν, i.e. $R\nu = \mu\nu$. Consider the solution $x(t)$ with initial value $x(0) = \nu$. Then

$$x(t) = X(t)\nu = W(t)\exp(Rt)\nu = W(t)e^{\mu t}\nu = W(t)\nu e^{\mu t} = \beta(t)e^{\mu t}$$

where $\beta(t) = W(t)\nu$ which is obviously T-periodic.

The following result is well-known.

Lemma 2.3. *System* (2.10) *is uniformly asymptotically stable if and only if all of its characteristic exponents have negative real parts, that is*

$$\operatorname{Re}\mu_i < 0$$

where μ_i *are the roots of* $\det(R - \mu I) = 0$.

□

Now let us continue discussing the stability of the positive T-periodic solution $x^*(t)$ of system (2.6).

Theorem 2.4. *Assume*

$$\int_0^t [\varepsilon_i(t) - g_i(t, 0)]dt < 0, \quad i = 1, 2, \ldots, n.$$

Then system (2.6) *has only one positive, T-periodic solution which is globally asymptotically stable with respect to the first octant* $\mathbb{R}_+^n$.

Proof. STEP 1. We prove system (2.8), namely, $\dot{Y}(t) = B(t)Y(t)$, where $B(t)$ has the form (2.9), is uniformly asymptotically stable.

Clearly, system (2.8) is a linear cooperative system since all off-diagonal elements in the coefficient matrix $B(t)$ are positive. Denote by $\Phi(t) = W(t)e^{Rt}$ the fundamental matrix solution of (2.8) satisfying $\Phi(0) = I(identity)$. Then

$\Phi(T) = e^{RT}$ and one can easily see that $\Phi(t) > 0$ for any $t > 0$. That is, the fundamental matrix is positive and irreducible. A standard argument(Peron-Frobenius theorem) shows that the largest Floquet multiplier λ of system (2.8) is an eigenvalue of $\Phi(T)$ with a positive eigenvector ν. Let μ be a characteristic exponent of system (2.8) corresponding to λ, and $y(t)$ be a nontrivial solution of system (2.8) of the form

$$y(t) = \beta(t)e^{\mu t}$$

where $\beta(t+T) = \beta(t)$ and the coordinates of β never vanish at the same time since $y(t)$ is nontrivial. Then $\mu \in \mathbb{R}$ and we can choose $\beta(t) \in \mathbb{R}^n$ for any $t \in [0, T]$. Indeed, any eigenvector of R corresponding to μ is also an eigenvector of $\Phi(T) = e^{RT}$ corresponding to $\lambda = e^{\mu T}$. Furthermore, since λ is an algebraically simple eigenvalue of $\Phi(T)$, the corresponding eigenspace is spanned by ν. Hence ν is also an eigenvector of R corresponding to μ. Choose $y(t) = \Phi(t)\nu$. Then $\beta(t) \in \mathbb{R}^n$. From

$$\dot{y} = \dot{\beta}e^{\mu t} + \mu\beta e^{\mu t} = B(t)y = B(t)\beta(t)e^{\mu t},$$

it follows that

$$\dot{\beta} = -\mu\beta + B(t)\beta. \tag{2.11}$$

Because $\beta(t)$ is T-periodic and continuously differentiable, there exist an integer k and a time $t_0 \in [0, T]$, such that

$$|\beta_k(t_0)| = \max_{1\le i\le n}\max_{t\in[0,T]} |\beta_i(t)|,$$

as a result of which we have

$$\dot{\beta}_k(t_0) = 0.$$

Substituting into (2.11) gives

$$-\mu\beta_k(t_0) + \sum_{j=1}^{n} b_{kj}(t_0)\beta_j(t_0) = 0 \tag{2.12}$$

where we denote $B(t) = \left(b_{ij}(t)\right)_{n\times n}$.

From (2.9), we know that

$$b_{kk}(t) = x_k^*(t)\,\frac{\partial g_k(t, x_k^*(t))}{\partial x_k} - \sum_{j\in J_k} p_{jk}(t)\varepsilon_j(t)\,\frac{x_j^*(t)}{x_k^*(t)},$$

$$b_{kj}(t) = p_{jk}(t)\varepsilon_j(t)\,\frac{x_j^*(t)}{x_k^*(t)}, \quad j \neq k. \tag{2.13}$$

Hence substituting (2.13) into (2.12) gives

$$-\mu\beta_k(t_0) + \left(x_k^*(t_0)\,\frac{\partial g_k(t_0, x_k^*(t_0))}{\partial x_k} - \sum_{j\in J_k} p_{jk}(t_0)\varepsilon_j(t_0)\,\frac{x_j^*(t_0)}{x_k^*(t_0)}\right)\beta_k(t_0)$$

$$+ \sum_{j\in J_k} p_{jk}(t_0)\varepsilon_j(t_0)\,\frac{x_j^*(t_0)}{x_k^*(t_0)}\,\beta_j(t_0) = 0.$$

Rewriting shows

$$\left(-\mu + x_k^*(t_0)\,\frac{\partial g_k(t_0, x_k^*(t_0))}{\partial x_k}\right)\beta_k(t_0) + \sum_{j\in J_k} p_{jk}(t_0)\varepsilon_j(t_0)\,\frac{x_j^*(t_0)}{x_k^*(t_0)}\left(\beta_j(t_0) - \beta_k(t_0)\right) = 0. \tag{2.14}$$

CASE 1. If $\beta_k(t_0) > 0$, then $\beta_j(t_0) \leq \beta_k(t_0)$ for any $j \neq k$.

Hence from (2.14), it follows that

$$-\mu + x_k^*(t_0)\,\frac{\partial g_k(t_0, x_k^*(t_0))}{\partial x_k} \geq 0,$$

that is,

$$\mu \leq x_k^*(t_0)\,\frac{\partial g_k(t_0, x_k^*(t_0))}{\partial x_k}.$$

CASE 2. If $\beta_k(t_0) < 0$, then $\beta_j(t_0) \geq \beta_k(t_0)$, for all $j \neq k$.

Similarly, we get

$$\mu \leq x_k^*(t_0)\,\frac{\partial g_k(t_0, x_k^*(t_0))}{\partial x_k}.$$

CASE 3. If $\beta_k(t_0) = 0$, then $\beta(t) \equiv 0$. This is a contradiction. Thus

$$\mu \leq x_k^*(t_0)\,\frac{\partial g_k(t_0, x_k^*(t_0))}{\partial x_k} < 0 \tag{2.15}$$

by (H_2) and hence from lemma 2.3, we know that system (2.8) is uniformly asymptotically stable.

STEP 2. Suppose $X(t)$ is a fundamental matrix of the variational equation (2.7) satisfying $X(0) = I$. We prove that there exist two constants $a, b > 0$ such that

$$|X(t)| \leq ae^{-bt}. \tag{2.16}$$

From step 1, we know there exist $a_1, b_1 > 0$ such that

$$|Y(t)| \leq a_1 e^{-b_1 t}.$$

The transformation $Y(t) = Q^{-1}(t)X(t)Q(0)$ gives

$$X(t) = Q(t)Y(t)Q^{-1}(0)$$

and hence

$$|X(t)| = |Q(t)Y(t)Q^{-1}(0)| \leq |Q(t)|\,|Q^{-1}(0)|\,|Y(t)|.$$

Here $Q(t) =$ diag $(x_1^*(t), \ldots, x_n^*(t))$ and the periodic solution $x^*(t)$ lies in S so $|Q(t)|\,|Q^{-1}(0)|$ is bounded and then (2.16) holds, that is, (2.7) is uniformly asymptotically stable.

STEP 3. From step 2, we see that every positive T-periodic solution of (2.6) is at least locally asymptotically stable. From step 1, we see that all the Floquet exponents of system (2.8) have negative real parts, which are independent of the specificity of a positive periodic solution $x^*(t)$. Indeed, from (2.15), we see that all Floquet exponents of sytem (2.8) are negative since the considered periodic solution $x^*(t) > 0$ and the hypothesis (H_2) implies $\frac{\partial f_i(t, x_i)}{\partial x_i} < 0$ in $[0, T] \times (0, +\infty)$. Moreover, under the transformation $Y(t) = Q^{-1}(t)X(t)Q(0)$, the linearized variational system (2.7) about $x^*(t)$ of system (2.6) is transformed into system (2.8) and since $Q(0) = Q(T)$. systems (2.7) and (2.8) have the same Floquet exponents. that is. all the Floquet exponents of system (2.7) are also negative. This implies that every fixed point of the corresponding Poincaré periodic map. if it exists, must be isolated and has index 1. where the index of a fixed point of the corresponding Poincaré periodic map is defined as usual by the Brouwer degree of the Poincaré periodic map at the fixed point [Ll]. Note that in either step 1 or step 2, we did not require any condition for the stability of $x^*(t)$ except for the positivity of $x^*(t)$. This is the key to show the global stability of a positive periodic solution and this is true only for certain systems. Recall that the compact set S is globally attractive with respect to $\mathbb{R}_+^n$. So if a positive periodic solution exists for system (2.6). it must be in S. It follows from a simple compactness argument that there are at most finitely many positive periodic solutions in S. Furthermore. from the proof of theorem 2.2, we know that $\deg(F, \text{Int } S, 0) = 1$. It follows immediately from the additivity of the fixed point index that the positive T-periodic solution of system (2.6) if it exists. must be unique since the sum of all indices is equal to $\deg(F, \text{Int } S, 0)$. Here $\frac{\partial h_i(tx_i)}{\partial x_i} \equiv 1$. So (2.2) becomes $\int_0^T [\varepsilon_i(t) - g_i(t, 0)]dt < 0$. under which the existence of a positive T-periodic solution holds. Hence system (2.6) does contain only one positive T-periodic solution.

STEP 4. Note that $S = \{(x_1, x_2, \ldots, x_n) \in \mathbb{R}_+^n \mid \delta \leq x_i \leq k, \; i = 1, 2, \ldots, n\}$ is globally attractive. So without loss of generality, we can limit our attention to these solutions initiating in S. Generally, let $A(t, x_0)$ $(t \geq 0)$ denote the semiflow of solutions of (2.6) initiating at some point $x_0 \in S$, i.e. $A(0, x_0) = x_0$. Then one can see that $A(t, x_0)$ is actually a monotone semiflow in the sense that $A(t, x_0) \geq A(t, y_0)$ if $x_0 \in S$, $y_0 \in S$ and $x_0 \geq y_0$. Here a vector $x_0 \geq y_0$ is in the componentwise sense. So for any $x_0 \in S$, if we denote

$\delta_0 = (\delta, \delta, \ldots, \delta) \in S$ and $k_0 = (k, k, \ldots, k) \in S$, then

$$A(t, \delta_0) \le A(t, x_0) \le A(t, k_0), \tag{2.17}$$

since $\delta \le x_i \le k$. Furthermore, one can verify that

$$\delta_0 = A(0, \delta_0) \le A(t, \delta_0) \le A(t+T, \delta_0) \le A(t+T, k_0) \le A(T, k_0) \le A(0, k_0) = k_0$$

for all $t \ge 0$. Now for all $t \in [0, T]$, the monotone sequences $\{A(t + nT, \delta_0)\}_{n=0}^{\infty}$ and $\{A(t+nT, k_0)\}_{n=0}^{\infty}$ are uniformly convergent to two positive T-periodic solutions. Based on the uniqueness of positive T-periodic solutions proved in step 3, the global attractivity of $x^*(t)$ follows from (2.17). In step 2, we also proved local stability, and therefore $x^*(t)$ is globally asymptotically stable.

□

2.5. The Asymptotic Periodic Case

In this section, we study the global properties of solutions of system (2.6), when all functions are asymptotically periodic.

Definition 2.1 [FRS]. Let $\varphi, \psi : [0, +\infty) \to \mathbb{R}$, φ is said to approach ψ asymptotically, in notation $\varphi \sim \psi$, if

$$\lim_{t \to \infty} |\varphi(t) - \psi(t)| = 0.$$

Definition 2.2. Let col $(\varphi_1, \ldots, \varphi_n)$, col $(\psi_1, \ldots, \psi_n) : [0, +\infty) \to \mathbb{R}^n$. Then

col $(\varphi_1, \ldots, \varphi_n)$ is said to approach col $(\psi_1, \ldots, \psi_n)$ asymptotically, in notation

col $(\varphi_1, \ldots, \varphi_n) \sim$ col$(\psi_1, \ldots, \psi_n)$, if $\varphi_i \sim \psi_i$ for all $i = 1, 2, \ldots, n$.

It is easy to verify that " $\sim$ " is an equivalence relationship. The main result of this section is the following theorem.

Theorem 2.5. *For all* $i, j = 1, \ldots, n$, *let* $\varepsilon_i(t), \widetilde{\varepsilon}_i(t), p_{ij}(t), \widetilde{p}_{ij}(t) : [0, +\infty) \to \mathbb{R}^+$ *be such that* $\varepsilon_i(t) \sim \widetilde{\varepsilon}_i(t)$, $p_{ij}(t) \sim \widetilde{p}_{ij}(t)$ *and let* $g_i(t, x_i), \widetilde{g}_i(t, x_i) : [0, +\infty) \times \mathbb{R}^+ \to \mathbb{R}^+$ *be such that* $g_i \sim \widetilde{g}_i$ *for each fixed second variable. Here* $\widetilde{\varepsilon}_i$, $\widetilde{p}_{ij}$ *and* $\widetilde{g}_i$ *are* T*-periodic in* t. *If, in addition, the inequalities*

$$\liminf_{t\to\infty} \int_t^{t+T} g_i(s, 0)ds - \limsup_{t\to\infty} \int_t^{t+T} \varepsilon_i(s)ds > 0, \quad i = 1, 2, \ldots, n \qquad (2.18)$$

hold, then for any positive solution $\operatorname{col}(x_1, \ldots, x_n)$ *of system* (2.6), *we have*

$$\operatorname{col}(x_1, \ldots, x_n) \sim \operatorname{col}(\widetilde{x}_1, \ldots, \widetilde{x}_n)$$

where $\operatorname{col}(\widetilde{x}_1, \ldots, \widetilde{x}_n)$ *is the globally asymptotically stable positive* T*-periodic solution of*

$$\dot{x}_i = x_i \widetilde{g}_i(t, x_i) - \widetilde{\varepsilon}_i(t) x_i + \sum_{j \in J_i} \widetilde{p}_{ji}(t) \widetilde{\varepsilon}_j(t) x_j, \quad i = 1, \ldots, n. \qquad (2.19)$$

We defer the proof to later in this section.

Corollary 2.6. *If* (2.18) *holds then system* (2.6) *is uniformly persistent.*

Firstly, we prove a general result concerning differential systems of the form

$$\dot{x}_i = f_i(x_1, \ldots, x_n; t) \qquad i = 1, 2, \ldots, n \qquad (2.20)$$

$$\dot{x}_i = \widetilde{f}_i(x_1, \ldots, x_n; \varepsilon, t), \qquad i = 1, 2, \ldots, n. \qquad (2.21)$$

Theorem 2.7. *Assume that both systems* (2.20) *and* (2.21) *are* T*-periodic systems. Suppose*

$$\lim_{\varepsilon\to 0} \widetilde{f}_i(x_1, \cdots, x_n; \varepsilon, t) = f_i(x_1, \cdots, x_n, t) \quad \text{for all} \quad i = 1, 2, \ldots, n$$

and there exist unique positive T*-periodic solutions* $\text{col}\,(u_1,\dots,u_n)$, $\text{col}\,(u_1^\varepsilon,\dots,u_n^\varepsilon)$ *of systems* (2.20) *and* (2.21) *respectively. Denote their trajectories by* Γ *and* Γ_ε *respectively. If in addition,* $\{\Gamma_\varepsilon \mid 0<\varepsilon<\varepsilon_0\}$ *is a bounded subset of* $\mathbb{R}^n$, *then for any* $\eta>0$, *no matter how small, there exists an* $\alpha>0$ *such that* $\Gamma_\varepsilon \subset O(\Gamma,\eta)$ *(the* η*-neighbourhood of* Γ *in* $\mathbb{R}^n$*) for all* $0<\varepsilon<\alpha$, *in notation*

$$\text{col}\,(u_1^\varepsilon,\dots,u_n^\varepsilon) \overset{\varepsilon}{\sim} \text{col}\,(u_1,\dots,u_n).$$

Proof. Because of the continuity of solutions of differential equations with respect to initial values and parameters, to prove $\text{col}\,(u_1^\varepsilon,\dots,u_n^\varepsilon) \overset{\varepsilon}{\sim} \text{col}\,(u_1,\dots,u_n)$, it suffices to show that for any $\eta>0$, there exists an $\alpha>0$ such that

$$d(\varepsilon)=\sum_{i=1}^{n}|u_i^\varepsilon(0)-u_i(0)|<\eta \tag{2.22}$$

for all $0<\varepsilon<\alpha$. Suppose (2.22) does not hold. Then

$$\limsup_{\varepsilon\to 0}\sum_{i=1}^{n}|u_i^\varepsilon(0)-u_i(0)| = \limsup_{\varepsilon\to 0} d(\varepsilon)=d>0.$$

Since $\{\Gamma_\varepsilon \mid 0<\varepsilon<\varepsilon_0\}$ is bounded in $\mathbb{R}^n$ and the Euclidean space $\mathbb{R}^n$ is complete, there exist a sequence $\{\varepsilon_j\}_1^\infty \subset (0,\varepsilon_0)$ such that

$$\lim_{\varepsilon_j\to 0} d(\varepsilon_j)=d>0$$

and $\lim_{\varepsilon_j\to 0}\text{col}\,(u_1^{\varepsilon_j}(0),\dots,u_n^{\varepsilon_j}(0)) = \text{col}\,(\overline{u}_1(0),\dots,\overline{u}_n(0))$.

Let $\text{col}\,(\overline{u}_1,\dots,\overline{u}_n)$ denote the solution of system (2.20) with the initial value $\text{col}\,(\overline{u}_1(0),\dots,\overline{u}_n(0))$. Continuous dependence of initial values and parameters for system (2.21) leads to

$$\lim_{\varepsilon_j\to 0}\text{col}\,(u_1^{\varepsilon_j}(t),\dots,u_n^{\varepsilon_j}(t)) = \text{col}\,(\overline{u}_1(t),\dots,\overline{u}_n(t))$$

for all $t\in[0,T]$. Then $\text{col}\,(\overline{u}_1(t),\dots,\overline{u}_n(t))$ is positive and T-periodic since col $(u_1^{\varepsilon_j}(t), \ldots, u_n^{\varepsilon_j}(t))$ is T-periodic and positive. Because of the uniqueness of positive T-periodic solutions of system (2.20), when we take col $(\overline{u}_1, \ldots, \overline{u}_n)$ as the unique T-periodic solution col $(u_1, \ldots, u_n)$ of system (2.20) as given in the hypotheses of this theorem, we have

$$0 = \sum_{i=1}^{n} |\overline{u}_i(0) - u_i(0)| = d > 0.$$

This contradiction shows that (2.22) holds. Thus

$$\text{col } (u_1^{\varepsilon}, \ldots, u_n^{\varepsilon}) \overset{\varepsilon}{\sim} \text{col } (u_1, \ldots, u_n).$$

Assume that $\varepsilon_i \sim \widetilde{\varepsilon}_i$, $p_{ij} \sim \widetilde{p}_{ij}$ and $g_i(t, \cdot) \sim \widetilde{g}_i(t, \cdot)$, $i, j = 1, 2, \ldots, n$, $i \neq j$. Then for any $\delta \in (0, \delta_0]$, there exists a $T_\delta > 0$ such that

$$\begin{aligned} &|\varepsilon_i(t) - \widetilde{\varepsilon}_i(t)| < \delta, \\ &|p_{ij}(t) - \widetilde{p}_{ij}| < \delta, \\ &|g_i(t, x_i) - \widetilde{g}_i(t, x_i)| < \delta \quad \text{when} \quad x = (x_1, \ldots, x_n) \in S \end{aligned} \tag{2.23}$$

for all $t \geq T_\delta$.

We construct the following two auxiliary systems:

$$\dot{x}_i = x_i(\widetilde{g}_i(t, x_i) - \delta) - (\widetilde{\varepsilon}_i(t) + \delta)x_i + \sum_{j \in J_i} (\widetilde{p}_{ji}(t) - \delta)(\widetilde{\varepsilon}_j(t) - \delta)x_j$$
$$i = 1, 2, \ldots, n \tag{2.24}$$

and

$$\dot{x}_i = x_i(\widetilde{g}_i(t, x_i) + \delta) - (\widetilde{\varepsilon}_i(t) - \delta)x_i + \sum_{j \in J_i} (\widetilde{p}_{ji}(t) + \delta)(\widetilde{\varepsilon}_j(t) + \delta)x_j$$
$$i = 1, 2, \ldots, n, \tag{2.25}$$

where we choose δ so small as to guarantee that

$$\widetilde{g}_i(t, x_i) - \delta > 0, \quad \widetilde{p}_{ji}(t) - \delta > 0, \quad \widetilde{\varepsilon}_i(t) - \delta > 0$$
$$i, j = 1, 2, \ldots, n, \quad i \neq j \quad \text{for all} \quad t \in [0, T], \quad 0 \leq x_i \leq k,$$

and

$$\int_0^T \left[(\widetilde{g}_i(t,0) - \delta) - (\widetilde{\varepsilon}_i(t) + \delta)\right] dt > 0 \tag{2.26}$$

under the assumption (2.18).

Theorem 2.8. *Assume inequalities* (2.26) *hold. Then there exist unique positive* T*-periodic solutions* $\mathrm{col}\,(u_1^{-\delta},\ldots,u_n^{-\delta})$, $\mathrm{col}\,(u_1^{\delta},\ldots,u_n^{\delta})$ *and* $\mathrm{col}\,(\widetilde{x}_1,\ldots,\widetilde{x}_n)$ *of systems* (2.24), (2.25) *and* (2.19) *respectively, which are globally asymptotically stable with respect to* $\mathbb{R}_+^n$.

Proof. The proof is analogous to the proofs of theorems 2.2 and 2.4, and we omit it.

□

Finally, in order to prove theorem 2.5, we give the following comparison relationship of solutions among systems (2.6), (2.24) and (2.25).

Lemma 2.9. *Suppose that* $\mathrm{col}\,(x_1^{-\delta},\ldots,x_n^{-\delta})$ *and* $\mathrm{col}\,(x_1^{\delta},\ldots,x_n^{\delta})$ *are solutions of systems* (2.24) *and* (2.25) *respectively, satisfying*

$$\mathrm{col}\,(x_1^{-\delta}(T_\delta),\ldots,x_n^{-\delta}(T_\delta)) = \mathrm{col}\,(x_1^{\delta}(T_\delta),\ldots,x_n^{\delta}(T_\delta)) \triangleq r^\delta \in \mathbb{R}_+^n.$$

Then

$$x_i^{-\delta}(t) < x_i(t) < x_i^{\delta}(t), \quad i = 1,\ldots,n \tag{2.27}$$

for all $t > T_\delta$, *where* $\mathrm{col}\,(x_1(t),\ldots,x_n(t))$ *is the solution of* (2.6) *with initial value* $\mathrm{col}\,(x_1(T_\delta),\ldots,x_n(T_\delta)) = V^\delta$.

Proof. Inequalities (2.23) lead to

$$\widetilde{\varepsilon}_i(t) - \delta < \varepsilon_i(t) < \widetilde{\varepsilon}_i(t) + \delta,$$

$$\widetilde{p}_{ij}(t) - \delta < p_{ij}(t) < \widetilde{p}_{ij}(t) + \delta,$$

$$\widetilde{g}_i(t, x_i) - \delta < g_i(t, x_i) < \widetilde{g}_i(t, x_i) + \delta$$

for all $t \geq T_\delta$, $i, j = 1, 2, \ldots, n$.

Then it follows that

$$\dot{x}_i(T_\delta) - \dot{x}_i^{-\delta}(T_\delta) > 0, \quad \dot{x}_i(T_\delta) - \dot{x}_i^{\delta}(T_\delta) < 0$$

and hence the inequalities (2.27), namely,

$$x_i^{-\delta}(t) < x_i(t) < x_i^{\delta}(t)$$

will hold for $t - T_\delta > 0$ and sufficiently small. If inequalities (2.27) do not hold for all $t > T_\delta$, there exist $T_1, T_2 > T_\delta$ such that

$$x_i^{-\delta}(t) < x_i(t) \quad \text{for all} \quad t \in (T_\delta, T_1), \quad i = 1, \ldots, n,$$

$$x_i(t) < x_i^{\delta}(t) \quad \text{for all} \quad t \in (T_\delta, T_2), \quad i = 1, \ldots, n,$$

and there exists at least one component, which we denote by i_0, such that

$$x_{i_0}^{-\delta}(T_1) = x_{i_0}(T_1), \quad x_i^{-\delta}(T_1) \leq x_i(T_1) \tag{2.28}$$

and

$$x_{i_0}(T_2) = x_{i_0}^{\delta}(T_2), \quad x_i(t_2) \leq x_i^{\delta}(T_2) \tag{2.29}$$

for all $i \neq i_0$. Suppose (2.28) holds. The fact that

$$x_{i_0}^{-\delta}(t) < x_{i_0}(t) \quad \text{for all} \quad t < T_1 \quad \text{and} \quad x_{i_0}^{-\delta}(T_1) = x_{i_0}(T_1)$$

gives that

$$\dot{x}_{i_0}^{-\delta}(T_1) - \dot{x}_{i_0}(T_1) \geq 0.$$

However, from (2.24) and (2.6), we have that

$$\dot{x}_{i_0}^{-\delta}(T_1) - \dot{x}_{i_0}(T_1) = x_{i_0}^{-\delta}(T_1)\big(\widetilde{g}_{i_0}(T_1, x_{i_0}^{-\delta}(T_1)) - \delta\big) - \big(\widetilde{\varepsilon}_{i_0}(T_1) + \delta\big)x_{i_0}^{-\delta}(T_1)$$

$$+ \sum_{j \in J_{i_0}} (\widetilde{p}_{ji_0}(T_1) - \delta)(\widetilde{\varepsilon}_j(T_1) - \delta) x_j^{-\delta}(T_1)$$

$$- x_{i_0}(T_1) g_{i_0}(T_1, x_{i_0}(T_1)) + \varepsilon_{i_0}(T_1) x_{i_0}(T_1)$$

$$- \sum_{j \in J_{i_0}} p_{ji_0}(T_1) \varepsilon_j(T_1) x_j(T_1)$$

$$< 0.$$

This contradiction shows that

$$x_i^{-\delta}(t) < x_i(t), \quad i = 1, 2, \dots, n$$

hold for all $t > T_\delta$.

Similary, (2.29) is also impossible. Thus we have proved (2.27) is true.

□

Now let us show the main result of this section.

Proof of theorem 2.5. Let $\text{col}\,(x_1, \dots, x_n)$ be a given positive solution of system (2.6). Since system (2.6) approaches system (2.19) asymptotically, given any $\delta > 0$, there exists a $T_\delta > 0$ such that (2.23) holds. From condition (2.18), we can pick up a sufficiently small $\delta > 0$ such that (2.26) holds. For the constructed systems (2.24) and (2.25) and from theorem 2.8, we know that there exist positive T-periodic solutions $\text{col}\,(u_1^{s\delta}, \dots, u_n^{s\delta})$, $s = -1$ or $+1$ and $\text{col}\,(\widetilde{x}_1, \dots, \widetilde{x}_n)$ of systems (2.24), (2.25) and (2.19) respectively, each of which is globally asymptotically stable with respect to $\mathbb{R}_+^N$.

From theorem 2.7, we have

$$\text{col}\,(u_1^{s\delta}, \dots, u_n^{s\delta}) \overset{\delta}{\sim} \text{col}\,(\widetilde{x}_1, \dots, \widetilde{x}_n) \tag{2.30}$$

where $s = \pm 1$. Take $\text{col}\,(x_1^{s\delta}, \dots, x_n^{s\delta})$, $s = -1$ or $+1$, as the solutions of systems (2.24) and (2.25) respectively, satisfying

$$\text{col}\,(x_1^{s\delta}(T_\delta), \dots, x_n^{s\delta}(T_\delta)) = \text{col}\,(x_1(T_\delta), \dots, x_n(T_\delta)).$$

Then from lemma 2.9, it follows that

$$x_i^{-\delta}(t) < x_i(t) < x_i^{\delta}(t), \quad i = 1, \ldots, n, \tag{2.31}$$

for all $t > T_\delta$.

Since col $(x_1^{s\delta}, \ldots, x_n^{s\delta}) \sim$ col $(u_1^{s\delta}, \ldots, u_n^{s\delta})$, (2.30) and (2.31) imply that col $(x_1, \ldots, x_n) \sim$ col $(\widetilde{x}_1, \ldots, \widetilde{x}_n)$ and the proof is completed.

□

2.6. Discussion

In this chapter we considered a model of a population dispersing among discrete patches in an environment whose carrying capacities, barrier strengths etc. fluctuate periodically or in an asymptotic periodic manner.

Our main focus was persistence, i.e. the survival in all patches of the population, and the existence of a periodic solution. We have shown that under very general conditions, the populations will settle down to a stable periodic fluctuation.

In theorem 2.1, condition (2.2) is natural, which says that in a period, once the average birth rate of the species is larger than the average rate of species going out in every patch, then the system is uniformly persistent, i.e. the species could survive forever in every patch. In theorem 2.2, it was shown that under the same condition for uniform persistence, the system has a positive periodic solution representing the survival of the population in every patch. In the case that the dispersal of species is proportional with the density of population, we proved in theorems 2.4-2.5 that under the corresponding uniform persistence condition, in such a case , the system exhibits certain stable structure in the sense that for any initial distribution, the long time behavior of the system could be described roughly by a positive periodic orbit. Biologically, for example, at different time, one could know in every habitat how many populations there are, and thereby choose the higher-density habitats to harvest.

Of course, in nature, most often, two or more populations will interact with each other in a given environment. Modeling several interacting populations can be very complicated, especially when periodicity and patchy environments are involved. For one thing, what may be a barrier to one of them may not be to the other [FrTa2]. This will be the next project in these models.

CHAPTER 3

A PERIODIC CHEMOSTAT *

3.1. Introduction

There has been a considerable interest over the past two decades in mathematical models of the chemostat and its extension (the gradostat). The basic theory and the initial chemostat models are reviewed in [Wa1]. Since the earliest models, attempts to generalize them so as to make them more realistic and/or more complex mathematically have followed several routes.

One such route is to consider models with general uptake functions [BaWo1], [BaWo2], [BuWo1], [BuWo2], [BuWo3], [SmWa], [Ta]. The original models utilized Michaelis-Menton uptakes. In the models mentioned above, except for [BuWo1], utilized general uptake functions which were monotonically increasing. In [BuWo1] even more general (piecewise monotonic) uptakes were considered.

Another route is to allow periodicities in the input or the washout (or both) [BSW], HaSo], [Sm1], [Sm7], [YaFr]. In this case the question of existence and stability of periodic solutions is of prime importance.

A third route is to incorporate time delays, both discrete and distributed, into the model [BBS], [BeTa2], [BeTa3], [FSW], [FrXu] Here one may also deduce the existence of periodic solutions as a function of the length of delay.

Of importance in the above models is the question of global stability of either equilibria or periodic solutions [BeTa2], [BeTa3], [Pe1]. This is usually the hardest

This chapter is mainly adopted from [PeFr1].

question to address.

In all the above considerations, it was assumed that the chemostat was "well stirred," i.e. diffusivity did not play a role. For the purpose of the present discussion, we continue to make this assumption.

In this chapter we consider a chemostat model of two microbial populations competing for a nutrient, with general, monotonically increasing (in nutrient density) uptake functions, and with periodicities in the nutrient input, washout, and uptakes. To the best of our knowledge, this is the first time that periodicities in the uptake of nutrient by the microbial populations is allowed.

In the next section we describe the model and derive some preliminary results. In section 3.3 we consider the submodel consisting of nutrient and one microbial population. Here we obtain criteria for extinction of the microbes as well as criteria for the existence and global stability of a positive periodic solution. In section 3.4, we obtain criteria for the extinction of the second microbial population, as well as criteria for the existence of a positive periodic solution. In obtaining these latter results, we prove a comparison theorem concerning solutions of scalar periodic systems, which may be of independent interest. Furthermore, we address a conjecture on the local stability of a positive periodic solution. Based on the local stability, by topological degree theory we show that if on the boundary of $\mathbb{R}^3_+$ there exists no asymptotically stable solution, then the considered full chemostat system has a strictly positive periodic solution which is globally asymptotically stable. Usually, it is rather easier to discuss the local stability than to discuss the global stability. However, the difficulty here lies in the discussion of local stability and we state a conjecture for future research. In section 3.5, we discuss the structure of a global attractor of the full chemostat system. Finally, a brief discussion on the biological implications is contained in section 3.6.

Throughout this chapter, we assume that all functions are sufficiently smooth so that solutions to initial value problems exist uniquely and are continuable for all positive time.

3.2. The Model

The chemostat is a piece of laboratory apparatus used to culture microorganisms. The apparatus consists of three connected vessels. The first contains all of the nutrients needed for growth of a microorganism, all in excess except for one called the limiting nutrient. The nutrient is pumped into the second vessel, the culture vessel. The culture vessel is charged with a variety of microorganisms, so it contains a mixture of nutrient and organisms. Its output is collected in the third vessel which represents the "production" of the chemostat(see **Fig 3.1**).

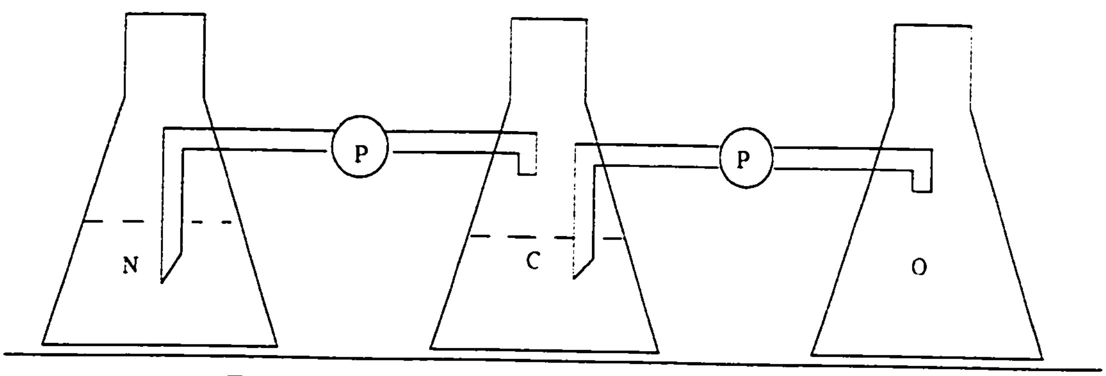

Figure 3.1: A schematic of a simple chemostat

The chemostat model to be analyzed in this chapter is of the form

$$\begin{aligned}
\dot{S}(t) &= D(t)(S^0 + be(t) - S(t)) - x(t)p(t,S(t)) - y(t)q(t,S(t)) \\
\dot{x}(t) &= x(t)(p(t,S(t)) - D(t)) \\
\dot{y}(t) &= y(t)(q(t,S(t)) - D(t))
\end{aligned} \tag{3.1}$$

$$S(0) = S_0 \geq 0, \quad x(0) = x_0 \geq 0, \quad y(0) = y_0 \geq 0.$$

where S^0, $b > 0$ and $D(t)$, $p(t,\cdot)$, $q(t,\cdot)$ are continuous, positive ω-periodic functions of t, and $e(t)$ is a continuous periodic function of period ω.

In these equations, at given time t, S represents the nutrient concentration. x and y denote the concentrations of the competing microorganism populations, p and q are the uptake functions representing the rate of nutrient conversion to biomass, that is, the per capita growth rate as functions of both time and nutrient. $S^0 + be(t)$ denotes the periodically varying nutrient concentration in the feed bottle. $D(t)$ is the input rate from the feed bottle containing the nutrient substrate as well as the washout rate of substrate and microorganisms.

We make the following reasonable assumptions concerning the parameters and functions involved in (3.1):

$$0 \leq b < S^0; \quad |e(t)| \leq 1 \tag{3.2}$$

and $p, q : R_+ \times R \to R$ are continuously differentiable in t, S satisfying

$$p(t, 0) = 0, \quad q(t, 0) = 0,$$

$$\frac{\partial p(t, S)}{\partial S} > 0, \quad \frac{\partial q(t, S)}{\partial S} > 0. \tag{3.3}$$

In the remainder of this section we obtain some preliminary results. First we note that every solution is nonnegative and bounded (as it should be for any reasonable model of a chemostat). We then show the invariance of system (3.1) in the region of interest.

Lemma 3.1. R^3_+ *is invariant for system* (3.1).

Proof. $\dot{S}|_{S=0} = D(t)(S^0 + be(t)) > 0$,

$$x(t) = x_0 \exp\Big(\int_0^t (p(\xi, S(\xi)) - D(\xi))\, d\xi$$

$$y(t) = y_0 \exp\Big(\int_0^t (q(\xi, S(\xi)) - D(\xi))\, d\xi.$$

Hence R^3_+ is invariant. □

We now consider the submodel describing the behaviour of nutrient in the absence of microbes

$$\dot{S}(t) = D(t)(S^0 + be(t) - S(t)), \quad S(0) = S_0 \geq 0. \tag{3.4}$$

Theorem 3.2. *There exists a unique positive periodic solution* $S_0^*(t)$ *of* (3.4) *which is globally asymptotically stable. Moreover*

$$S^0 - b \leq S^*(t) \leq S^0 + b \tag{3.5}$$

for all $t \geq 0$.

Proof. Clearly $[S^0 - b, S^0 + b]$ is an invariant closed interval of system (3.4). It is easy to find the general solution of equation (3.4) as follows:

$$\begin{aligned} S(t) = S_0 \exp\Big(-\int_0^t D(u)du\Big) + \exp\Big(-\int_0^t D(u)du\Big) \\ \times \int_0^t \big[\exp\big(\int_0^u D(v)dv\big)\big] D(u)(S^0 + be(u))\,du. \end{aligned} \tag{3.6}$$

Clearly. $S(t)$ is an ω-periodic solution of (3.4) if

$$\int_0^\omega D(u)du \neq 0. \tag{3.7}$$

and $S(t)$ is globally asymptotically exponentially stable if

$$\int_0^\omega D(u)du > 0. \tag{3.8}$$

In our case, $D(t)$ is a positive ω-periodic function. Therefore $S_0^*(t)$ is globally asymptotically exponentially stable and satisfies (3.5).

□

From now on, we always denote by $S_0^*(t)$ the solution of (3.4) as given in the above theorem.

Finally we show that for the full system (3.1), $S_0^*(t)$ is an attractor for $S(t) + x(t) + y(t)$.

Theorem 3.3. *Define*

$$I(t) = S(t) + x(t) + y(t). \tag{3.9}$$

Then if $S_0, x_0, y_0 \geq 0$, *for system* (3.1), $I(t)$ *tends exponentially to* $S_0^*(t)$.

Proof. Computing $\dot{I}(t)$, we obtain

$$\dot{I}(t) = -D(t)I + D(t)(S^0 + b\epsilon(t)). \tag{3.10}$$

Since (3.10) is another version of (3.4), the theorem follows from theorem 3.2, i.e. we always have

$$\lim_{t\to\infty} |S(t) + x(t) + y(t) - S_0^*(t)| = 0. \tag{3.11}$$

□

3.3. The Single Microbe Subcase

In this section we consider the subcase of a single microbe living on the nutrient. The system then reduces to

$$\begin{aligned} \dot{S}(t) &= D(t)(S^0 + b\epsilon(t) - S(t)) - x(t)p(t, S(t)) \\ \dot{x}(t) &= x(t)(p(t, S(t)) - D(t)), \end{aligned} \tag{3.12}$$

where the assumptions on the parameters and functions are similar to those given in section 2. We introduce the notation $\langle f \rangle$ to mean the mean value of any continuous ω-periodic function f, i.e.

$$\langle f \rangle = \frac{1}{\omega} \int_0^\omega f(t)dt. \tag{3.13}$$

Obviously, $(S_0^*(t), 0)$ is an ω-periodic solution of system (3.12). Our first concern is the stability of $(S_0^*(t), 0)$. The following theorem gives a criterion for stability which is equivalent to the extinction of microorganism $x(t)$ due to a lack of nutrient.

Theorem 3.4. *For system* (3.12), *the solution* $(S_0^*(t), 0)$ *is asymptotically stable if*

$$\langle p(t, S_0^*(t)) - D(t)\rangle < 0$$

and unstable if

$$\langle p(t, S_0^*(t)) - D(t)\rangle > 0.$$

Proof. Consider the variational equation about the ω-periodic solution $(S_0^*(t), 0)$ of (3.12),

$$\dot{X} = \begin{pmatrix} -D(t) & -p(t, S_0^*(t)) \\ 0 & p(t, S_0^*(t)) - D(t) \end{pmatrix} X. \tag{3.14}$$

Then the characteristic multipliers, ρ_1, ρ_2, of (3.14) can be computed as follows:

$$\rho_1 = \exp\left(-\int_0^{\omega} D(t)dt\right), \quad \rho_2 = \exp\left(\int_0^{\omega} (p(t, S_0^*(t)) - D(t))dt\right).$$

Hence $(S_0^*(t), 0)$ is asymptotically stable when $\langle p(t, S_0^*(t)) - D(t)\rangle < 0$ and unstable when $\langle p(t, S_0^*(t)) - D(t)\rangle > 0$, since $|\rho_1| < 1$.

□

We now show the existence and stability of a positive ω-periodic solution of system (3.12) under the condition $\langle p(t, S_0^*(t)) - D(t)\rangle > 0$ (survival of the microbe).

Theorem 3.5. *There exists a unique positive* ω*-periodic solution of system* (3.12) *which is globally asymptotically stable provided* $\langle p(t, S_0^*(t)) - D(t)\rangle > 0$.

In order to prove theorem 3.5, we first need to prove some lemmas.

Lemma 3.6. *Any solution* $(S(t), x(t))$ *of* (3.12) *with* $S(0) > 0$, $x(0) > 0$ *has the property that* $x(t) + S(t)$ *exponentially approaches* $S_0^*(t)$.

Proof. This is a special case of theorem 3.3 when $y(t) \equiv 0$.

□

Now consider the equation

$$\dot{x}(t) = x(t)\big(p(t, S_0^*(t) - x(t)) - D(t)\big). \tag{3.15}$$

Obviously the interval $[0, S^0 + b]$ is invariant with respect to (3.15). From the hypothesis

$$\langle p(t, S_0^*(t)) - D(t)\rangle = \frac{1}{\omega}\int_0^\omega (p(t, S_0^*(t)) - D(t))dt > 0,$$

we can choose a constant $\delta > 0$ satisfying $\delta < S^0 - b$ and

$$\langle p(t, S_0^*(t) - \delta) - D(t)\rangle > 0.$$

Let $D_0 = \max_{0\le t\le\omega} D(t)$. The next result gives the lower boundary of solutions of (3.15).

Lemma 3.7. *If* $x(t)$ *is a solution of* (3.15) *satisfying* $x(0) \ge \delta$, *then*

$$x(t) \ge \delta e^{-D_0\omega} \quad \textit{for all} \quad t \ge 0.$$

Proof. Assume there exists some $T > 0$ such that

$$x(T) < \delta e^{-D_0\omega}.$$

Let $T_0 = \sup\{t | x(t) = \delta, \ 0 \le t < T\}$. Then $x(T_0) = \delta$, $x(t) < \delta$ for any $t \in (T_0, T]$ and $T - T_0 < \omega$. If $T - T_0 \ge \omega$, i.e. $T \ge T_0 + \omega$, then $x(t) < \delta$ for all $t \in (T_0, T_0 + \omega] \subset (T_0, T]$. Hence

$$\begin{aligned}
\delta > x(T_0 + \omega) &= x(T_0)\ \exp\Big(\int_{T_0}^{T_0+\omega} (p(t, S_0^*(t) - x(t)) - D(t))dt\Big) \\
&\ge x(T_0)\ \exp\Big(\int_{T_0}^{T_0+\omega} (p(t, S_0^*(t) - \delta) - D(t))dt\Big) \\
&= x(T_0)\ \exp\Big(\int_0^\omega (p(t, S_0^*(t) - \delta) - D(t))dt\Big) \\
&\ge x(T_0) = \delta,
\end{aligned}$$

a contraction. So $T - T_0 < \omega$, in which case

$$\delta e^{-D_0\omega} > x(T) = x(T_0)\ \exp\Big(\int_{T_0}^{T} (p(t, S_0^*(t) - x(t)) - D(t))dt\Big)$$

$$\geq x(T_0)\ \exp\Big(\int_{T_0}^{T} (p(t, S_0^*(t) - \delta) - D(t))dt\Big)$$

$$\geq x(T_0)\ \exp\int_{T_0}^{T} -D_0 dt$$

$$= \delta\ \exp(-D_0(T - T_0))$$

$$> \delta e^{-D_0\omega}.$$

This is also a contradiction, implying $x(t) \geq \delta e^{-D_0\omega}$ for all $t \geq 0$.

□

From the above we know the solution $x(t, x_0)$ of (3.15) has the following property:

$$x(t, [\delta, S^0 + b]) \subset [\delta e^{-D_0\omega}, S^0 + b] \quad \text{for all} \quad t \geq 0.$$

The next result implies the existence of a positive ω-periodic solution of (3.15).

Lemma 3.8. *Under the assumption*

$$\langle p(t, S_0^*(t)) - D(t) \rangle > 0. \tag{3.16}$$

equation (3.15) *has at least one positive* ω*-periodic solution* $x_0^*(t)$.

Proof. Consider a solution $x(t)$ of (3.15) satisfying $x(0) \in [\delta, S^0 + b]$. Then $x(t) \in [\delta e^{-D_0\omega}, S^0 + b]$, that is $\delta e^{-D_0\omega} \leq x(t) \leq S^0 + b$ for all $t \geq 0$.

CASE 1. If $x(0) = x(\omega)$, then $x(t+\omega) = x(t)$, that is, $x(t)$ is an ω-periodic solution of (3.15).

CASE 2. If $x(0) < x(\omega)$, define $x_n(t) = x(t + n\omega)$, where n is any integer. Then $x_n(t)$ is also a solution of (3.15) with $x_n(0) = x(n\omega)$. By uniqueness of solutions of initial value problems, the inequality

$$x(0) < x(\omega) = x_1(0) \quad \text{gives} \quad x(t) < x_1(t) = x(t+\omega) \quad \text{for all} \quad t \geq 0.$$

Similarly, by induction

$$0 < \delta e^{-D_0\omega} \leq x(t) < x_1(t) < x_2(t) < \cdots < x_n(t) < x_{n+1}(t) < \cdots \leq S^0 + b.$$

Hence there exists $x_0^*(t)$ such that $\lim_{n\to\infty} x_n(t) = x_0^*(t)$. Obviously $x_0^*(t)$ must be in $[\delta e^{-D_0\omega}, S^0 + b]$. Furthermore

$$x_0^*(t+\omega) = \lim_{n\to\infty} x_n(t+\omega) = \lim_{n\to\infty} x_{n+1}(t) = x_0^*(t),$$

i.e. $x_0^*(t)$ is an ω-periodic function.

On the other hand, since the monotone increasing sequence $\{x_n(t)\}$ is uniformly bounded and equicontinuous in $[0, \omega]$, it follows that $x_n(t)$ converges uniformly to $x_0^*(t)$ in $[0, \omega]$. Thus $x_0^*(t)$ is an ω-periodic solution of (3.15) and lies in the interval $[\delta e^{-D_0\omega}, S^0 + b]$.

CASE 3. If $x(0) > x(\omega)$, a similar discussion as in Case 2 will also result in an ω-periodic solution of (3.15). Consequently, condition (3.16) guarantees the existence of a positive ω-periodic solution of (3.15) and the lemma is proved.

□

The next lemma addresses the question of global stability.

Lemma 3.9. *If* (3.16) *holds, the positive ω-periodic solution $x_0^*(t)$ described in the above lemma is globally asymptotically stable.*

Proof. Given any solution $x(t)$ of (3.15) with $x(0) > 0$, define a Liapunov function by $V(t) = |\ln x(t) - \ln x_0^*(t)|$. Then

$$\begin{aligned} D^+V &= -|p(t, S_0^*(t) - x(t)) - p(t, S_0^*(t) - x_0^*(t))| \\ &= -\frac{\partial p(t,\varphi)}{\partial S} |x - x_0^*| \end{aligned}$$

where φ is between $S_0^* - x$ and $S_0^* - x_0^*$.

Let $C = \min\limits_{\substack{0 \le S \le S^0 + b \\ 0 \le t \le \omega}} \frac{\partial p(t,S)}{\partial S} > 0$. Then $D^+V \le -C|x - x_0^*|$. Similarly, we have $\lim\limits_{t \to \infty} |x(t) - x_0^*(t)| = 0$.

Consider the linearized equation about $x_0^*(t)$ as a solution of (3.15):

$$\dot{z} = \left(p(t, S_0^*(t) - x_0^*(t)) - D(t) - x_0^*(t) \cdot \frac{\partial p(t, S_0^*(t) - x_0^*(t))}{\partial S}\right) z.$$

Let $W = \frac{z}{x_0^*}$. Then $\dot{W} = -x_0^* \cdot \frac{\partial p(t, S_0^*(t) - x_0^*(t))}{\partial S} W$. So $x_0^*(t)$ is asymptotically stable, and hence globally asymptotically stable.

□

Corollary 3.10. *Under condition* (3.16), *equation* (3.15) *has a unique positive* ω*-periodic solution which is globally asymptotically stable.*

NOTE: for T big enough, the following hold

$$x(t) < S_0^*(t) \quad \text{for all} \quad t \ge T \quad \text{and} \tag{3.17}$$

$$x_0^*(t) < S_0^*(t) \quad \text{for all} \quad t \ge 0. \tag{3.18}$$

Proof. Firstly we prove (3.18). Let $x_0^*(t_0) = \max\limits_{0 \le t \le \omega} x_0^*(t)$. Then $\dot{x}_0^*(t_0) = 0$. Hence $p(t_0, S_0^*(t_0) - x_0^*(t_0)) = D(t_0) > 0$, and so $S_0^*(t_0) > x_0^*(t_0)$. We claim that $S_0^*(t) > x_0^*(t)$ for all $t \ge t_0$. For otherwise choosing $t_1 = \sup\{t^* | S_0^*(t) > x_0^*(t)$ for all $t \ge t_0$ and $t < t^*\}$, it follows that $S_0^*(t_1) = x_0^*(t_1)$ and $S_0^*(t) > x_0^*(t)$ for all $t \in [t_0, t_1)$. So $\dot{S}_0^*(t_1) - \dot{x}_0^*(t_1) \le 0$. However

$$\begin{aligned} \dot{S}_0^*(t_1) - \dot{x}_0^*(t_1) &= D(t_1)(S^0 + be(t_1) - S_0^*(t_1)) - x_0^*(t_1)(p(t_1, S_0^*(t_1) - x_0^*(t_1)) - D(t_1)) \\ &= D(t_1)(S^0 + be(t_1)) > 0, \end{aligned}$$

a contradiction. Moreover because both of $S_0^*(t)$ and $x_0^*(t)$ are ω-periodic, it must be that $S_0^*(t) > x_0^*(t)$ for all $t \ge 0$ and (3.18) holds.

Now we prove (3.17). Assume that $x(t) \geq S_0^*(t)$ for all $t \geq 0$. Then

$$\dot{x}(t) = x(t)(p(t, S_0^* - x(t)) - D(t)) \leq -D(t)x(t) \leq -D_{\min}x(t).$$

As a result, $\lim_{t\to\infty} x(t) = 0$ holds. On the other hand $S_0^*(t) \geq S^0 - b > 0$ for all $t \geq 0$. This is a contradiction. Therefore, there exists T sufficiently large such that $x(T) < S_0^*(T)$. Then similarly, we can claim (3.17) holds for all $t \geq T$.

□

For the sake of emphasis, we rewrite (3.18) as the following lemma.

Lemma 3.11. *Under condition* (3.16), $S_0^*(t) > x_0^*(t)$ *for all* $t \geq 0$.

Proof of theorem 3.5. We shall prove that $(S_0^*(t) - x_0^*(t), x_0^*(t))$ is the unique positive ω-periodic solution of (3.12) which is globally asymptotically stable under the condition (3.16). Denote $I^*(t) = S_0^*(t) - x_0^*(t) > 0$. Then

$$\begin{aligned}\dot{I}^* = \dot{S}_0^* - \dot{x}_0^* &= D(t)(S^0 + be(t) - S_0^*) - x_0^*(p(t, S_0^* - x_0^*) - D(t)) \\ &= D(t)(S^0 + be(t) - I^*) - x_0^* p(t, I^*);\end{aligned}$$

$$\dot{x}_0^* = x_0^*(p(t, S_0^* - x_0^*) - D(t)) = x_0^*(p(t, I^*) - D(t)).$$

Consequently, $(I^*(t), x_0^*(t))$ is a solution of (3.12).

From lemmas 3.6, 3.9 and 3.11, we know that $(I^*(t), x_0^*(t))$ is the unique positive ω-periodic solution of (3.12) which is globally asymptotically stable and the theorem is proved.

□

3.4. The Full Model

Suppose (I_1^*, x_0^*) and (I_2^*, y_0^*) are positive ω-periodic solutions of system (3.12) and the system

$$\begin{aligned} \dot{S}(t) &= D(t)\big(S^0 + b\epsilon(t) - S(t)\big) - y(t)q(t, S(t)) \\ \dot{y}(t) &= y(t)\big(q(t, S(t)) - D(t)\big). \end{aligned} \tag{3.19}$$

respectively. Then $(I_1^*, x_0^*, 0)$ and $(I_2^*, 0, y_0^*)$ are nonnegative ω-periodic solutions of system (3.1). First we discuss the stability of $(I_1^*, x_0^*, 0)$. The appropriate variational system is

$$\dot{X} = \begin{pmatrix} -D(t) - x_0^* \frac{\partial p(t, I_1^*)}{\partial S} & -p(t, I_1^*) & -q(t, I_1^*) \\ x_0^* \frac{\partial p(t, I_1^*)}{\partial S} & p(t, I_1^*) - D(t) & 0 \\ 0 & 0 & q(t, I_1^*) - D(t) \end{pmatrix} X.$$

Theorem 3.12. *If (I_1^*, x_0^*) is a positive asymptotically stable ω-periodic solution of system (3.12), then $(I_1^*, x_0^*, 0)$ is asymptotically stable provided*

$$\langle q(t, S_0^*(t) - x_0^*(t)) - D(t) \rangle < 0$$

and is unstable if

$$\langle q(t, S_0^*(t) - x_0^*(t)) - D(t) \rangle > 0. \tag{3.20}$$

□

For $(I_2^*, 0, y_0^*)$, there exists a similar conclusion, given as follows.

Theorem 3.13. *If (I_2^*, y_0^*) is a positive asymptotically stable ω-periodic solution of system (3.19), then $(I_2^*, 0, y_0^*)$ is asymptotically stable if*

$$\langle p(t, S_0^*(t) - y_0^*(t)) - D(t) \rangle < 0$$

and is unstale provided

$$\langle p(t, S_0^*(t) - y_0^*(t)) - D(t) \rangle > 0. \tag{3.21}$$

$\square$

What we are really interested in is the existence and stability of a strictly positive ω-periodic solution of system (3.1). Thus in the following theorem we assume inequalities (3.20) and (3.21) hold.

Theorem 3.14. *Assume inequalities* (3.20) *and* (3.21) *are valid. Then, there exists at least one strictly positive ω-periodic solution of system* (3.1).

To prove theorem 3.14, we first require the following lemma.

Theorem 3.15. (Monotonicity of attracting solutions). *Consider*

$$\text{(a)} \quad \dot{u} = f(t, u) \qquad \text{and} \qquad \text{(b)} \quad \dot{v} = g(t, v).$$

Let $f(t, u)$, $g(t, v) : R \times R \to R$ be sufficiently smooth so that solutions to initial value problems exist uniquely and are continuable for $t \geq 0$. Suppose $u^*(t)$ and $v^*(t)$ are attracting ω-periodic solutions of (a) *and* (b) *respectively, i.e. any solution $u(t)$ of* (a) *and $v(t)$ of* (b) *satisfy*

$$\lim_{t \to \infty} |u(t) - u^*(t)| = 0 \quad \text{and} \quad \lim_{t \to \infty} |v(t) - v^*(t)| = 0.$$

Then if $f(t, \cdot) > g(t, \cdot)$, it follows that $u^*(t) > v^*(t)$ for all t.

Proof. CASE 1. If there exists t_0 such that $u^*(t_0) > v^*(t_0)$, then $u^*(t) > v^*(t)$ for all $t \geq t_0$. For otherwise let $t_1 = \sup\{t^* | u^*(t) > v^*(t)$ for all $t \geq t_0$ and $t < t^*\}$ Then $u^*(t_1) = v^*(t_1)$ and $u^*(t) > v^*(t)$ for all $t \in [t_0, t_1)$. So $\dot{u}^*(t_1) - \dot{v}^*(t_1) \leq 0$. However $\dot{u}^*(t_1) - \dot{v}^*(t_1) = f(t_1, u^*(t_1)) - g(t_1, v^*(t_1)) > 0$. This is a contradiction. Further, because u^* and v^* are ω-periodic, then $u^*(t) > v^*(t)$ for all t.

CASE 2. If there exists t_0 such that $u^*(t_0) = v^*(t_0)$, then by hypothesis there must be $t_1 > t_0$ and near to t_0 such that $u^*(t_1) > v^*(t_1)$. By Case 1, this is a contradiction.

Case 3. Let $u^*(t) < v^*(t)$ for all t. Suppose $v^*(t_0) = \max_{0 \le t \le \omega} v^*(t)$ and let $u(t)$ be the solution of (a) satisfying $u(t_0) = v^*(t_0)$. Then similarly to the previous case, $u(t) > v^*(t)$ for all $t > t_0$. Denote $d = \text{dist}\,(u^*, v^*) = \inf_{0 \le t \le \omega} |u^*(t) - v^*(t)| > 0$.

From the assumption $v^*(t) > u^*(t)$, we have $u(t) - u^*(t) > v^*(t) - u^*(t) \ge d > 0$. This is a contradiction because $u^*(t)$ is the attracting solution of (a) and the lemma is proved.

□

Next we construct monotone sequences which are convergent to the solution we need. Our attention will mostly focus on the related model:

$$\begin{aligned} \dot{x}(t) &= x(t)\big(p(t, S_0^*(t) - x(t) - y(t)) - D(t)\big) \\ \dot{y}(t) &= y(t)\big(q(t, S_0^*(t) - x(t) - y(t)) - D(t)\big). \end{aligned} \tag{3.22}$$

Lemma 3.16. *System* (3.22) *has at least one positive* ω*-periodic solution provided inequalities* (3.20) *and* (3.21) *hold.*

Proof. Step 1. Condition (3.21) guarantees that $\dot{x} = x(p(t, S_0^* - x - y_0^*) - D(t))$ has a unique positive ω-periodic solution $x_\infty^*(t)$ which is globally attracting. Condition (3.20) gives that $\dot{y} = y(q(t, S_0^* - x_0^* - y) - D(t))$ has a unique positive ω-periodic solution $y_\infty^*(t)$ which is globally attracting.

By theorem 3.15 we know that $y_\infty^*(t) < y_0^*(t)$ and $x_\infty^*(t) < x_0^*(t)$ for all $t \ge 0$.

Step 2. Consider $\dot{x} = x(p(t, S_0^* - y_\infty^* - x) - D(t))$. Since $\langle p(t, S_0^* - y_\infty^*) - D(t)\rangle > \langle p(t, S_0^* - y_0^*) - D(t)\rangle > 0$, then there exists a unique positive ω-periodic solution

$x_1^*(t)$ which is globally attracting. By theorem 3.15

$$x_\infty^*(t) < x_1^*(t) < x_0^*(t) \quad \text{for all} \quad t \geq 0.$$

STEP 3. Consider $\dot{y} = y(q(t, S_0^* - x_1^* - y) - D(t))$. From $\langle q(t, S_0^* - x_1^*) - D(t)\rangle > \langle q(t, S_0^* - x_0^*) - D(t)\rangle > 0$, there exists a unique positive ω-periodic solution $y_1^*(t)$ which is globally attracting and similarly

$$y_\infty^*(t) < y_1^*(t) < y_0^*(t) \quad \text{for all} \quad t \geq 0.$$

STEP 4. Consider $\dot{x} = x(p(t, S_0^* - y_1^* - x) - D(t))$. Similarly, there exist a unique positive globally attracting ω-periodic solution $x_2^*(t)$ satisfying

$$x_\infty^*(t) < x_2^*(t) < x_1^*(t) < x_0^*(t) \quad \text{for all} \quad t \geq 0.$$

STEP 5. Consider $\dot{y} = y(q(t, S_0^* - x_2^* - y) - D(t))$, and obtain a similar solution $y_2^*(t)$ satisfying $y_\infty^*(t) < y_1^*(t) < y_2^*(t) < y_0^*(t)$ for all $t \geq 0$.

STEP 6. According to the proofs in steps 1 to 5 above, we may construct similar related equations giving two monotone sequences $\{x_n^*(t)\}$ and $\{y_n^*(t)\}$ which are positive ω-periodic functions satisfying

$$0 < x_\infty^*(t) < \cdots < x_{n+1}^*(t) < x_n^*(t) < \cdots < x_2^*(t) < x_1^*(t) < x_0^*(t) \leq S^0 + b$$

and

$$0 < y_\infty^*(t) < y_1^*(t) < y_2^*(t) < \cdots < y_n^*(t) < y_{n+1}^*(t) < \cdots < y_0^*(t) \leq S^0 + b.$$

for all $t \geq 0$.

STEP 7. From the previous steps, there exist functions $u^*(t)$ and $v^*(t)$ defined on $[0, \infty)$ such that

$$\lim_{n\to\infty} x_n^*(t) = u^*(t) \quad \text{and} \quad \lim_{n\to\infty} y_n^*(t) = v^*(t) \quad \text{for all} \quad t \geq 0. \tag{3.23}$$

Furthermore, $u^*(t)$ and $v^*(t)$ are ω-periodic functions because

$$u^*(t+\omega) = \lim_{n\to\infty} x_n^*(t+\omega) = \lim_{n\to\infty} x_n^*(t) = u^*(t),$$
$$v^*(t+\omega) = \lim_{n\to\infty} y_n^*(t+\omega) = \lim_{n\to\infty} y_n^*(t) = v^*(t).$$

By the ω-periodicity in t and the boundedness of the right-hand sides of all the equations constructed above, it follows that the derivatives of the members of the sequences $\{x_n^*(t)\}$ and $\{y_n^*(t)\}$ are bounded in $[0,\infty)$, that is $\{x_n^*(t)\}$ and $\{y_n^*(t)\}$ are uniformly bounded and equicontinuous. Then by virtue of Arzela-Ascoli's lemma [CoLe], for any compact subinterval of $[0,\infty)$, there exist subsequences of $\{x_n^*(t)\}$ and $\{y_n^*(t)\}$ which converge uniformly to $u^*(t)$ and $v^*(t)$ respectively on this subinterval. Thus $u^*(t)$ and $v^*(t)$ are continuous. By the monotonicity of these sequences we see that the convergences given by (3.23) are uniform on any compact subinterval of $[0,\infty)$. Hence by Dini's theorem [Kel], $u^*(t)$ and $v^*(t)$ are continuously differentiable and

$$\begin{aligned} \dot{u}^* &= u^*\big(p(t, S_0^* - u^* - v^*) - D(t)\big) \\ \dot{v}^* &= v^*\big(q(t, S_0^* - u^* - v^*) - D(t)\big), \end{aligned} \tag{3.24}$$

that is to say (u^*, v^*) is a solution of system (3.22). Obviously, (u^*, v^*) is positive and ω-periodic and we have really constructed a positive ω-periodic solution $(u^*(t), v^*(t))$ of system (3.22) and the lemma is proved.

□

Similar to lemma 3.11, we have:

Lemma 3.17. $S_0^*(t) - u^*(t) - v^*(t) > 0$ *for all* $t \geq 0$. □

We are now ready to prove the first main result of this section.

Proof of theorem 3.14. Under assumptions (3.20) and (3.21), we show that $(S_0^* - u^* - v^*, u^*, v^*)$ is a positive ω-periodic solution of system (3.1).

Define $I^*(t) = S_0^*(t) - u^*(t) - v^*(t)$. Then $I^*(t) > 0$ and

$$\dot{I}^* = D(t)(S^0 + be(t) - S_0^*(t)) - u^*(p(t, S_0^* - u^* - v^*) - D(t))$$
$$- v^*(q(t, S_0^* - u^* - v^*) - D(t))$$
$$= D(t)(S^0 + be(t) - I^*) - u^*p(t, I^*) - v^*q(t, I^*).$$

Rewriting (3.24) gives

$$\dot{u}^* = u^*(p(t, I^*) - D(t)) \quad \text{and} \quad \dot{v}^* = v^*(p(t, I^*) - D(t)).$$

Thus (I^*, u^*, v^*) is exactly a positive ω-periodic solution of system (3.1), proving the theorem.

□

To discuss the stability of (I^*, u^*, v^*), we require the analysis of the stability of (u^*, v^*) as a solution of system (3.22). The variational system about the positive ω-periodic solution (u^*, v^*) of (3.22) is:

$$\dot{X} = \begin{pmatrix} p(t, I^*) - D(t) - u^* \frac{\partial p(t, I^*)}{\partial S} & -u^* \frac{\partial p(t, I^*)}{\partial S} \\ -v^* \frac{\partial q(t, I^*)}{\partial S} & q(t, I^*) - D(t) - v^* \frac{\partial q(t, I^*)}{\partial S} \end{pmatrix} X.$$

Let $p(t) \triangleq \begin{pmatrix} u^*(t) & 0 \\ 0 & -v^*(t) \end{pmatrix}$. The change of variable $Y = p^{-1}X$ gives

$$\dot{Y} = \begin{pmatrix} -u^* \frac{\partial p(t, I^*)}{\partial S} & v^* \frac{\partial p(t, I^*)}{\partial S} \\ u^* \frac{\partial q(t, I^*)}{\partial S} & -v^* \frac{\partial q(t, I^*)}{\partial S} \end{pmatrix} Y \triangleq A(t)Y. \tag{3.25}$$

We know that the local stability of (u^*, v^*) is the same as the stability of $(0, 0)$ in (3.25). Clearly, for any fixed t, one of the eigenvalues of $A(t)$ is 0 and another one is negative. However in a linear periodic system, the eigenvalues of the coefficient matrix cannot supply the same information as in an autonomous linear system on the stability of the trivial solution. Here the matrix $A(t)$ is very special and we have reason to address the following conjecture.

Conjecture 3.18. *Assume inequalities* (3.20) *and* (3.21) *hold. Further assume that* $\frac{\frac{\partial p(t,S)}{\partial S}}{\frac{\partial q(t,S)}{\partial S}}$ *is not a constant. Then system (3.25) is asymptotically stable, i.e. system* (3.1) *has a positive* ω*-periodic solution which is asymptotically stable.*

If conjecture 3.18 is true, then we are able to show the asymptotic stability of the ω-periodic solution (I^*, u^*, v^*) to be global under (3.20) and (3.21). To do this, we first set up the fixed point index machinery. In the remainder of this section, we assume that conjecture 3.18 is true and the Floquet characteristic multipliers of (3.25) have moduli less than 1 under (3.20) and (3.21).

Let (E, P) be an ordered Banach space with positive normal cone P. Following [Dan1], for $y \in P$, define

$$\mathcal{P}_y = \{x \in E : y + tx \in P \quad \text{for some } t > 0\}$$

and

$$\mathcal{S}_y = \{x \in \bar{\mathcal{P}}_y : -x \in \bar{\mathcal{P}}_y\}.$$

Let a be a fixed point of some compact operator $T : P \to P$, and denote by $\mathcal{L}$ the Frechét derivative of T at a. We say that $\mathcal{L}$ has property α at a if there exists $t \in (0, 1)$ and $y \in \bar{\mathcal{P}}_a \setminus \mathcal{S}_a$ such that $y - t\mathcal{L}y \in \mathcal{S}_a$. We state a general result of Dancer([Dan1], [Dan4]) on fixed point index with respect to the positive cone P (see also [DL1], [DL2], [Li1], [Li2]).

Proposition 3.19.

(i) If $I - \mathcal{L}$ *is invertible on* E, *and* $\mathcal{L}$ *has property* α *on* $\bar{\mathcal{P}}_a$, *then* $index_P(T, a) = 0$;

(ii) If $I - \mathcal{L}$ *is invertible on* E, *and* $\mathcal{L}$ *does not have property* α *on* $\bar{\mathcal{P}}_a$, *then* $index_P(T, a) = (-1)^\sigma$, *where* σ *is the sum of the algebraic multiplicities of the eigenvalues of* $\mathcal{L}$ *whose moduli are greater than 1;*

(iii) If $I - \mathcal{L}$ *is not invertible on* E *but* $Ker(I - \mathcal{L}) \bigcap \bar{P}_a = \varnothing$, *then* $index_P(T, a) = 0$.

□

Suppose E_1 and E_2 are ordered Banach spaces with positive cones C_1 and C_2, respectively. Let $E = E_1 \oplus E_2$ and $C = C_1 \oplus C_2$. Then clearly E is an ordered Banach space with positive cone C. Let Ω be an open set in C containing O and $A_i : \bar{\Omega} \to C_i$ be completely continuous operators, $i = 1, 2$. Denote by (u, v) a general element in C with $u \in C_1$ and $v \in C_2$. Let $A : \bar{\Omega} \to C$ be defined by

$$A(u, v) = (A_1(u, v), A_2(u, v)).$$

Also we define

$$C_2(\varepsilon) = \{v \in C_2 : \|v\|_{E_2} < \varepsilon\}.$$

The following general result of Dancer and Du ([DaDu], theorem 2.1) on degree calculation is crucial for our applications.

Proposition 3.20. *Suppose* $U \subset C_1 \cap \Omega$ *is relatively open and bounded, and*

$$A_1(u, 0) \neq u \qquad \text{for} \quad u \in \partial U$$

$$A_2(u, 0) \equiv 0 \qquad \text{for} \quad u \in \bar{U}.$$

Suppose $A_2 : \Omega \to C_2$ *extends to a continuously differentiable mapping of a neighbourhood of* Ω *into* E_2, $C_2 - C_2$ *is dense in* E_2 *and* $T = \{u \in U : u = A_1(u, 0)\}$. *Then the following are true:*

(i) $deg_C(I - A, U \times C_2(\varepsilon), 0) = 0$ *for* $\varepsilon > 0$ *small if for any* $u \in T$, *the spectral radius* $r(A_2'(u, 0)|_{C_2}) > 1$ *and* 1 *is not an eigenvalue of* $A_2'(u, 0)|_{C_2}$ *corresponding to a positive eigenvector;*

(ii) $deg_C(I - A, U \times C_2(\varepsilon), 0) = deg_{C_1}(I - A_1|_{C_1}, U, 0)$ *for* $\varepsilon > 0$ *small, if for any* $u \in T$, $r(A_2'(u,0)|_{C_2}) < 1$.

□

In our system (3.1), theorem 3.3 implies that (I^*, u^*, v^*) is globally stable with respect to (3.1) provided that (u^*, v^*) is globally stable with respect to (3.22). In the following, we are going to show that (u^*, v^*) is a globally stable solution of system (3.22) under the condition that inequalities (3.20) and (3.21) hold.

Denote by $S = (S_1, S_2)$ the ω-periodic Poincaré mapping generated by system (3.22). It is well-known that S is a compact operator and every ω-periodic solution of system (3.22) corresponds to a fixed point of S. Clearly, $(0,0)$, $(x_0^*, 0)$ and $(0, y_0^*)$ are all of the ω-periodic solutions of system (3.22) on the boundary of $\mathbb{R}_+^2$. We denote by a^* the fixed points of S in $int(\mathbb{R}_+^2)$. For the simplicity of notation, we further denote the fixed points of S on the boundary $\mathbb{R}_+^2$ by O, x^* and y^* respectively. The indices of all fixed points ([Ll],[Ro]) of S in the cone $\mathbb{R}_+^2$ are calculated in the following theorem.

Theorem 3.21. *Assume inequalities (3.20) and (3.21) hold. Then the following are true:*

(i) $index(S) = 1$, *where* $index(S) = deg(I - S, O)$ *which means the Brouwer degree in the cone* $\mathbb{R}_+^2$;

(ii) $index(S, O) = 0$;

(iii) $index(S, x^*) = index(S, y^*) = 0$;

(iv) $index(S, a^*) = 1$.

Proof.

(i) Clearly, system (3.22) is point dissipative and S is compact. It follows from [Hale2] or [HaWa] that there exists a connected global attractor $\mathcal{A}$ of S in $\mathbb{R}^2_+$. Hence all fixed points of S in $\mathbb{R}^2_+$ must be contained in $\mathcal{A}$. Without loss of generality, we suppose $\mathcal{A} \subset [0, K^*] \times [0, K^*]$ for certain constant $K^* > 0$. Recall that system (3.22) is of the form

$$\dot{x}(t) = x(t)\big(p(t, S_0^*(t) - x(t) - y(t)) - D(t)\big)$$

$$\dot{y}(t) = y(t)\big(q(t, S_0^*(t) - x(t) - y(t)) - D(t)\big).$$

Furthermore functions p and q satisfy (3.3), that is

$$p(t, 0) = 0, \quad q(t, 0) = 0,$$

$$\frac{\partial p(t, S)}{\partial S} > 0, \quad \frac{\partial q(t, S)}{\partial S} > 0.$$

As a result, we can choose constant K^* large enough to guarantee that $[0, K^*] \times [0, K^*]$ is not only globally attractive but also positively invariant. Clearly, for any constant $\hat{K}^* > K^*$, $[0, \hat{K}^*) \times [0, \hat{K}^*)$ is positively invariant. Let $\Omega = [0, K^* + 1) \times [0, K^* + 1) \subset \mathbb{R}^2_+$. Clearly Ω is open in $\mathbb{R}^2_+$ with relative boundary $\partial\Omega = \{(x, y) \in \mathbb{R}^2_+ : \ |(x, y)|_{sup} = K^* + 1\}$. By the excision property of topological degree, it follows that

$$deg(I - S, O) = deg(I - S, \Omega, O).$$

Define a homotopy

$$H(t) = I - tS : \Omega \to \mathbb{R}^2.$$

Claim:. *$H(t)$ is Ω -admissible for all $t \in [0, 1]$, i.e. $O \notin (I - tS)(\partial\Omega)$.*

It suffices to show that for any $(x, y) \in \partial\Omega$, $(I - tS)(x, y) \neq (0, 0)$. Clearly, when $t = 0$, then $I - tS = I$ and $(0, 0) \notin \partial\Omega$. When $t = 1$, then $I - tS = I - S$, and since we have supposed that all fixed points of S in $\mathbb{R}^2_+$ are contained in $\mathcal{A} \subset [0, K^*] \times [0, K^*]$, hence $(0, 0) \notin (I - S)(\partial\Omega)$. Similarly, for any $t \in (0, 1)$, $(0, 0) \notin (I - tS)(\partial\Omega)$ since

Ω is positively invariant. This completes the proof of our claim. Thus by homotopy invariance, we have

$$\begin{aligned} deg(I - S, \Omega, O) &= deg(H(1), \Omega, O) \\ &= deg(H(0), \Omega, O) \\ &= deg(I, \Omega, O) \\ &= 1, \end{aligned}$$

where the last identity is because of the normalization property of topological degree. Hence $deg(I - S, O) = 1$ and $index(S) = 1$.

(ii) Let us prove $index(S, O) = 0$. By definition, we know that

$$\mathcal{P}_O = \{(x, y) \in \mathbb{R}^2 : O + t(x, y) \in \mathbb{R}^2_+ \quad \text{for some } t > 0\} = \mathbb{R}^2_+,$$

and

$$\begin{aligned} \mathcal{S}_O &= \{(x, y) \in \bar{\mathcal{P}}_O : -(x, y) \in \bar{\mathcal{P}}_O\} \\ &= \{(x, y) \in \mathbb{R}^2_+ : -(x, y) \in \mathbb{R}^2_+\} \\ &= \{O\}. \end{aligned}$$

The variational system about (0, 0) of (3.22) is:

$$\dot{X} = \begin{pmatrix} p(t, S_0^*) - D(t) & 0 \\ 0 & q(t, S_0^*) - D(t) \end{pmatrix} X.$$

By a standard argument, one can easily verify that

$$DS(O)(x, y) = \left(x \exp\left(\int_0^\omega [p(t, S_0^*) - D(t)]dt\right), y \exp\left(\int_0^\omega [q(t, S_0^*) - D(t)]dt\right)\right), \tag{3.26}$$

where $DS(O)$ is the Frechét derivative of S at O. Furthermore, it follows from inequalities (3.20) and (3.21) that

$$\begin{aligned} r_1 &\triangleq \exp\left(\int_0^\omega [p(t, S_0^*) - D(t)]dt\right) > 1, \\ r_2 &\triangleq \exp\left(\int_0^\omega [q(t, S_0^*) - D(t)]dt\right) > 1. \end{aligned} \tag{3.27}$$

Now one can easily see that $DS(O)$ has property α. Indeed, by the definition, it suffices to choose certain $(x, y) \in \mathbb{R}^2_+ \setminus \{O\}$ such that for some $t_0 \in (0, 1)$, $t_0 DS(O)(x, y) = (x, y)$, i.e. $(t_0 r_1 x, t_0 r_2 y) = (x, y)$. Clearly, we can choose any $(x, 0)$ with $x > 0$ and $t_0 = \frac{1}{r_1} \in (0, 1)$ since $r_1 > 1$. Furthermore, clearly $I - DS(O)$ is invertible and $(0, 0)$ is an isolated fixed point of S. Therefore it follows from proposition 3.19(i) that $index(S, O) = 0$.

(iii) We are going to apply proposition 3.20 to show that

$$index(S, x^*) = index(S, y^*) = 0.$$

It suffices to show $index(S, x^*) = 0$. Similarly, one can show $index(S, y^*) = 0$. Replace A_1, A_2 in proposition 3.20 by S_1, S_2 respectively. One can easily verify that all conditions required in proposition 3.20 are satisfied here. Clearly, we have

$$T = \{u \in \mathbb{R}_+ : u = S_1(u, 0)\} = \{0, x_0^*\}.$$

Furthermore, it follows from (3.26) and (3.27) that $r_2 > 1$ is the only eigenvalue of $DS_2(0, 0)$. The variational system about $(x_0^*, 0)$ of (3.22) is:

$$\dot{X} = \begin{pmatrix} p(t, S_0^* - x_0^*) - D(t) - x_0^* \frac{\partial p(t, S_0^* - x_0^*)}{\partial S} & -x_0^* \frac{\partial p(t, S_0^* - x_0^*)}{\partial S} \\ 0 & q(t, S_0^* - x_0^*) - D(t) \end{pmatrix} X. \tag{3.28}$$

Clearly, $r_3 \triangleq \exp(\int_0^\omega [q(t, S_0^* - x_0^*) - D(t)]dt)$ is the only eigenvalue of $DS_2(x_0^*, 0)$ and $r_3 > 1$ because of (3.20). Therefore it follows from proposition 3.20(i) that $index(S, x^*) = 0$. Analogously, it follows from (3.21) that $index(S, y^*) = 0$.

(iv) For any fixed points $a^* \in int(\mathbb{R}^2_+)$ of S, from the previous assumption, it follows that $\rho(DS(a^*)) < 1$ under (3.20) and (3.21). Note that both

(3.20) and (3.21) are independent of a^* itself. According to [Dan4. lemma 2(c)]. $DS(a^*)$ does not have property α. Again by proposition 3.19(ii). one can easily see that $index(S. a^*) = 1$.

□

Theorem 3.22. *Assume inequalities (3.20) and (3.21) are valid. Then. there exists a strictly positive ω-periodic solution of system (3.1) which is globally asymptotically stable.*

Proof. Since system (3.22) generates a discrete monotone dynamical system $\{S^m\}_{m=0}^{\infty}$. we need only to prove the uniqueness of a strictly positive ω-periodic solution of system (3.22). It follows from a simple compactness argument that there are at most finitely many fixed points of S in $int(\mathbb{R}^2_+)$. Let them be $\{x_i^* : 1 \leq i \leq l\}$ where $l \in \mathbb{Z}$. From theorem 3.21. we have $index(S. x_i^*) = 1$. $index(S. O) = 0$, $index(S. x^*) = 0$. $index(S. y^*) = 0$ and $index(S) = 1$. Hence by the additivity of the fixed point index. it follows that

$$1 = index(S) = index(S. O) + index(S. x^*) + index(S. y^*) + \Sigma_{i=1}^{l} index(S. x_i^*) = l.$$

This implies the uniqueness. The global asymptotical stability follows from theorem 4.10 in chapter 4. completing the proof.

□

Remark. Theorem 3.22 implies that if on the boundary of $\mathbb{R}^3_+$ there exists no asymptotically stable solution, then system (3.1) has a strictly positive ω-periodic solution which is globally asymptotically stable. Therefore. if one can prove that under (3.20) and (3.21) the two Floquet multipliers of (3.25) have moduli less than 1, then the structure of the global attractor of system (3.1) is very simple, just a positive ω-periodic solution.

3.5. Global Attractor

Since at present we are unable to prove conjecture 3.18, in this section we are going to discuss the structure of a global attractor of system (3.1) in terms of some general results in competitive systems due to Hsu, Smith and Waltman([HSW]).

Clearly, system (3.1) is a point dissipative ordinary differential system. It follows from Hale's dissipative theory([Hale2]) that there is a connected global attractor in system (3.1). Furthermore, theorem 3.3 implies that $S(t)+x(t)+y(t)$ tends exponentially to $S_0^*(t)$. Therefore to discuss the structure of a global attractor of system (3.1) is equivalent to discussing the structure of a global attractor of system (3.22). Obviously system (3.22) is an ω-periodic competitive system between two species. Hence system (3.22) generates a strictly order-preserving ω-periodic semiflow with respect to the competitive order $<_K$, where for any $(x_i, y_i) \in \mathbb{R}_+^2$ we define $(x_1, y_1) \ll_K (x_2, y_2)$ if $x_1 < x_2$ and $y_1 > y_2$, $(x_1, y_1) \leq_K (x_2, y_2)$ if $x_1 \leq x_2$ and $y_1 \geq y_2$, $(x_1, y_1) <_K (x_2, y_2)$ if $(x_1, y_1) \leq_K (x_2, y_2)$ and $(x_1, y_1) \neq (x_2, y_2)$. Denote by $T : \mathbb{R}_+^2 \to \mathbb{R}_+^2$ the standard Poincaré ω-periodic mapping generated by system (3.22). It is easy to verify that $(H_1)-(H_4)$ in [HSW](page 4084) hold by (3.3) and since system (3.22) is of Kolmogrov type. Recall that in lemma 3.16, we have proved that under (3.20) and (3.21), system (3.22) has at least one strictly positive ω-periodic solution. That is, T has at least one strictly positive fixed point corresponding to (u^*, v^*). Denote $E_0 = (0, 0)$, $E_1 = (x_0^*(0), 0)$, $E_2 = (0, y_0^*(0))$, $E = (u^*(0), v^*(0))$. Then E_0, E_1, E_2 and E are fixed points of T in $\mathbb{R}_+^2$. Furthermore it follows from theorem 3.15 that $E_2 <_K E <_K E_1$. Inequalities (3.20) and (3.21) imply that E_0, E_1 and E_2 are all isolated and unstable. It is well-known that for any $(x, y) \in \mathbb{R}_+^2$ and $n \in \mathbb{Z}^+$ we have

$$T^n(0, y) \leq_K T^n(x, y) \leq_K T^n(x, 0).$$

From lemma 3.9, we know that

$$\lim_{n\to\infty} T^n(x,0) = E_1 \quad \text{for all } x > 0.$$

and

$$\lim_{n\to\infty} T^n(0,y) = E_2 \quad \text{for all } y > 0.$$

Hence the order interval $[E_2, E_1]_K = \{(x,y) : 0 \le x \le x_0^*(0), \quad 0 \le y \le y_0^*(0)\}$ is a global attractor of mapping T. Moreover, it follows from proposition 2 in [HSW](page 4086) that there exist two positive fixed points E_* and E_{**} such that

$$T^n(x) \to E_* \quad \text{for all } x = (x_1, x_2) \quad \text{satisfying } E_* \le_K x <_K E_1 \quad \text{and } x_2 \ne 0.$$

and

$$T^n(y) \to E_{**} \quad \text{for all } y = (y_1, y_2) \quad \text{satisfying } E_2 <_K y \le_K E_{**} \quad \text{and } y_1 \ne 0.$$

Note that from proposition 2 in [HSW], we only know that E_* and E_{**} are positive. Actually, from lemma 3.9, we further know that except for E_0, E_1, E_2 there does not exist any other semitrivial fixed point on the boundary of $\mathbb{R}^2_+$. Therefore E_* and E_{**} are strictly positive.

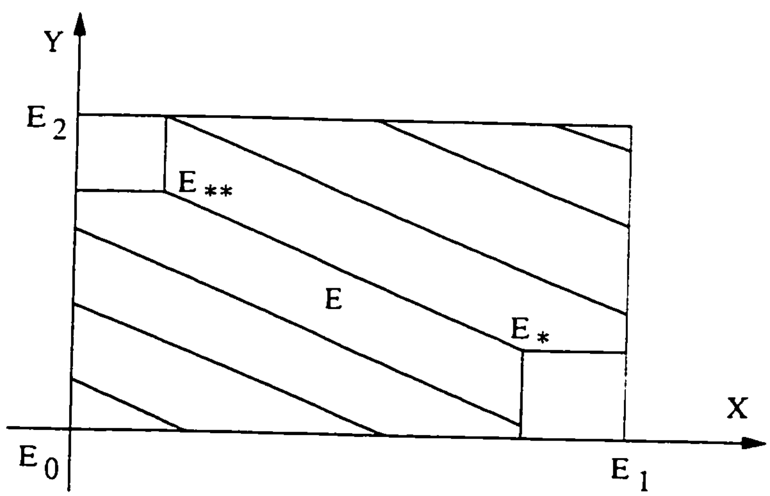

Figure 3.2: Structure of a global attractor of T

The structure of a global attractor of (3.22) is shown as the shadowed part in **Fig 3.2** described by the corresponding Poincaré periodic mapping. Clearly, if conjecture 3.18 is true. then $E_* = E_{**} = E$. that is the global attractor of T in $int(\mathbb{R}^2_+)$ is just one point E and $(S_0^*(t) - u^*(t) - v^*(t), u^*(t), v^*(t))$ is globally attractive with respect to system (3.1) in $int(\mathbb{R}^3_+)$.

3.6. Discussion

The chemostat is a piece of laboratory apparatus used to culture microorganisms. In this chapter. we discussed the competition for microbial organisms competing in a mixed-growth laboratory culture with a periodically varying capacity environment. The competition takes place in a well-stirred chemostat with general monotonically increasing(in nutrient density) uptake functions. and with periodicities in the nutrient input. washout. and uptakes. In a chemostat. temperature and nutrient input are controlled by the experimenter. If temperature is adjusted periodically and nutriend is input periodically with a common period. then system (3.1) well models such an experiment mechanism. The key feature of model (3.1) is the periodicity to simulate the periodically varying(seasons or day/night cycles) culture environment. We derived criteria for the coexistence or non-coexistence of the competing species. Mathematically. we roughly know the structure of the global attractor of system (3.1).

CHAPTER 4

DISCRETE MONOTONE DYNAMICAL SYSTEMS *

4.1. Introduction

As remarked by Hal Smith([Sm8]). there is a long history of applications of monotone methods and comparison arguments in differential equations. Usually. to study a periodic system is equivalent to studying the corresponding Poincaré periodic mapping. Hence the theory of discrete monotone dynamical systems. which is contributed to by Dancer and Hess([DaHe]). is important in the study of periodic monotone systems. Generally. the theory of discrete monotone dynamical systems is more difficult than that of continuous monotone dynamical systems since the monotonicity does not restrict the dynamics of mappings as severely as it does continuous flows. In the related literature. except for the order compactness. it is usually required to show the strong monotonicity of the mapping or the strong positivity of the Frechét derivative of the mapping at some fixed points. It is well-known that in parabolic systems. a maximum principle plays a key role. As a result, strong monotonicity is usually satisfied in systems generated by reaction-diffusion differential equations. However, in a large class of biological models described by delayed functional differential equations, there are no such strong monotonicity and strong positivity properties. Hence it is necessary to discuss

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* This chapter is adopted from [PeFr3]. The application part of [PeFr3] is not included here.

the dynamics of a weakly monotone semi-flow. In this chapter, we develop some results in discrete monotone dynamical systems with weak monotonicity.

In section 4.2, we list some preliminary results which are often basic tools in discussing discrete monotone dynamical systems.

In section 4.3, theorem 4.4 is an extension of some ideas of Hirsch([Hir1]), Dancer and Hess([DaHe]), which says that the uniqueness of fixed points of the mapping implies the global attractivity of the fixed point. We then prove some results on the global dynamics when the Frechét derivative of the mapping is strongly positive(theorems 4.6 and 4.8). Finally, we set up two important results on the existence and global dynamics with weak monotonicity(theorems 4.9 and 4.10). Theorem 4.9 tells us when a positive fixed point still exists without strong monotonicity and strong positivity. Theorem 4.10 deals with the case when the positive fixed point is globally attractive. These two results are very important in discussing a system with delay. All these conditions given in theorems 4.9 and 4.10 are often satisfied in applications.

4.2. Preliminary Results

In the present section, we make some related preparation for the following discussion on the global properties in monotone(order-preserving) discrete dynamical systems. The fundamental work in discrete monotone dynamical systems is due to Dancer and Hess([DaHe]). For a general theory of continuous-time monotone dynamical systems, we refer to the AMS monograph [Sm8] and references therein.

Let (E, P) be an ordered Banach space with positive normal cone P (i.e. a closed convex cone with vertex at O such that $P \bigcap (-P) = \{O\}$) whose interior, denoted as $int(P)$, is nonempty. For $x, y \in E$, we write

$$x \geq y \quad \text{if } x - y \in P;$$

$$x > y \quad \text{if } x - y \in P \setminus \{O\};$$

$$x \gg y \quad \text{if } x - y \in int(P).$$

Let V be an open subset of E. A continuous mapping $S : V \to V$ is said to be monotone(order-preserving) if $S(x) \geq S(y)$ whenever $x, y \in V$ with $x \geq y$, strictly monotone if $x > y$ implies $S(x) > S(y)$, and strongly monotone if $S(x) \gg S(y)$ whenever $x, y \in V$ with $x > y$.

A linear operator $K \in \mathcal{L}(E)$ is called strongly positive if $K(P \setminus \{O\}) \subset int(P)$. For a given compact and strongly positive operator $K \in \mathcal{L}(E)$, we denote $\rho(K)$ as its spectral radius. The following well-known Krein-Rutman theorems are often powerful in discussing the uniqueness and stability of fixed points of a Frechét differentiable mapping.

Proposition 4.1(Klein-Rutman). *Let* (E, P) *be an ordered Banach space with* $int(P) \neq \varnothing$, *and let* $K \in \mathcal{L}(E)$ *be compact and strongly positive. Then* $\rho(K)$ *is the unique eigenvalue of K having a positive engenfunction* x, *that is,* $x \gg O$, *and* $\rho(K)$ *is an algebraically simple eigenvalue. Moreover* $|\lambda| < \rho(K)$ *for all* $\lambda \in \sigma(K)$ *with* $\lambda \neq \rho(K)$.

Proposition 4.2(Klein-Rutman). *Let* (E, P) *be an ordered Banach space with a totally ordered cone, i.e,* $E = Cl(P - P)$. *Let* $K \in \mathcal{L}(E)$ *be compact and positive, and assume* $\rho(K) > 0$. *Then* $\rho(K)$ *is an eigenvalue of* K *with eigenfunction* $x > O$.

Often $\rho(K)$ is also called the principal eigenvalue of K and x is called the corresponding principal eigenfunction. We consider now the inhomogeneous equation

$$\lambda u - Ku = h > O \quad \text{in E}. \tag{4.1}$$

Proposition 4.3. *Suppose that K satisfies all the assumptions of proposition 4.1. Then:*

(i) equation (4.1) has a unique solution u *if* $\lambda > \rho(K)$, *and* $u \gg O$:

(ii) equation (4.1) has no positiove solution if $\lambda \leq \rho(K)$;

(iii) for $\lambda = \rho(K)$, *there exists no solution of (4.1) at all.*

For the proofs of the above results, we refer to ([De], [Kra], [KrRu], [Ze]).

Finally, we state two fundamental principles of set theory(see, for example,[Fol]), which play important roles in the study of discrete monotone dynamical systems(e.g, [DaHe]).

The Hausdorff Maximal Principle. *Every partially ordered set has a maximal totally ordered subset.*

Zorn's Lemma. *If X is a partially ordered set and every totally ordered subset of X has an upper bound, then X has a maximal element.*

4.3. Global Dynamics

Based on previously published works, it seems that some improvements in the theory of the global stability in discrete monotone dynamical systems are needed, utilizing certain conditions that are usually satisfied in applications.

Theorem 4.4. *Let P be an ordered cone with nonempty interior. Assume that*

(i) P has the property that for any two elements $x, y \in P$, $\{x, \ y\}$ *have a least upper bound element in P;*

(ii) $S : P \to P$ *is a continuous and monotone mapping;*

(iii) $S(O) = O$ *and O is the unique fixed point of* S *in P;*

(iv) There exists a compact subset K *in P such that* K *attracts each point of P under* S.

Then $x = O$ *is globally attractive with respect to P, i.e.* $\omega(x) = \{O\}$, *for all* $x \in P$.

Before we proceed with the lengthy proof, we make the following remarks.

Remark 4.1. Comparing with some related works(for examples, [DaHe] and [Zh2]), here we do not require either that S is a strongly order-preserving mapping or that P is a normal cone.

Remark 4.2. Condition (i) is natural and motivated by the following fact: For any $\phi_1, \phi_2 \in C^+ \triangleq C^+([-\tau, 0], \mathbb{R}^n)$, define $\psi \in C^+$ by $\psi(\theta) = \max\{\phi_1(\theta), \phi_2(\theta)\}$. Then ψ is the least upper bound element of ϕ_1, ϕ_2 in C^+. Recall the proof in Massera's theorem([Mas]), where the hypothesis of the uniqueness of initial value problems(IVPs) is not necessary since we can consider the least upper bound solution instead.

Remark 4.3. In condition (iv), it is not necessary for $\mathcal{K}$ to be a global attractor. What is necessary here is the compactness of $\mathcal{K}$ as an attractive region of P. This hypothesis corresponds to the assumptions that $S(V)$ is relatively compact[DaHe] and that S is order-compact[Zh2]. In applications, the existence of such a $\mathcal{K}$ is trivial from Hale's dissipative theory([Hale2]), since the dissipativity in a considered FDE or RDFDE is often satisfied.

Proof of theorem 4.4. We divide the complicated proof into several steps. It is an extension of some ideas of Hirsch [Hir1], Dancer and Hess [DaHe]. From condition (iv), to show that $x = O$ is globally attractive with respect to P, it is equivalent to show that $\omega(x) = \{O\}$ for any $x \in \mathcal{K}$.

Step 1. First, for any $x \in \mathcal{K}$, $\omega(x)$ is nonempty and compact. Recall that a point $p \in P$ is wandering if there exist a neighborhood U of p and $n_0 \in \mathbb{Z}^+$ such that $U \bigcap S^n U = \emptyset$ for all $(n > n_0)$. A point $p \in P$ is nonwandering if it is not wandering, i.e. for any neighborhood U of p and $k \in \mathbb{Z}^+$ there exists an integer $n_k > k$ such that $U \bigcap S^{n_k} U \neq \emptyset$. Then the nonwandering set contains all limit points $\omega(x)$ for any $x \in P$ (see [Hir1]). Denote $\mathcal{B} = Cl \bigcup_{x \in P} \omega(x)$. Clearly, $O \in \mathcal{B}$ and $\mathcal{B}$ is a subset of the nonwandering set. Indeed, for any point $b \in \mathcal{B}$, there is a sequence $b_n \in \omega(x_n)$ such that $b_n \to b$ as $n \to \infty$. Then for any neighborhood U of b, there exists certain integer N such that for any $n > N$, U is also a neighborhood of b_n, which is nonwandering. Hence it follows from the definition that $\mathcal{B}$ is a subset of the nonwandering set. Furthermore $\mathcal{B} \subset \mathcal{K}$. $\mathcal{B}$ is closed and thereby compact. Next we claim that $\mathcal{B}$ is inductively ordered, that is, each totally ordered subset $T \subset \mathcal{B}$ has an upper bound in $\mathcal{B}$. Indeed, using a positive linear functional $f \in E^*$, we may represent T as $T = \{x_\alpha : \alpha \in \mathcal{A}_T \subset \mathbb{R}\}$, where $\alpha_1 < \alpha_2$ implies $x_{\alpha_1} < x_{\alpha_2}$ (set $\alpha = < f, x >$)(see [DaHe]). By the Hausdorff Maximal Principle, we can suppose that $\{x_{\alpha_n}\}$ is the maximal totally ordered subset containing T in $\mathcal{B}$. Let $\alpha_n \nearrow \sup \mathcal{A}_T = \sup\{\alpha_n\} \leq +\infty$, as $n \to \infty$. Then $\{x_{\alpha_n}\} \subset \mathcal{B}$ is a nondecreasing precompact sequence since $\mathcal{B}$ is compact. Thus, there exists an $x_0 \in \mathcal{B}$ such that $x_{\alpha_n} \nearrow x_0$ as $n \to \infty$. Clearly x_0 is an upper bound of T in $\mathcal{B}$. By Zorn's Lemma, $\mathcal{B}$ has a maximal element $p \in \mathcal{B}$. If $p = O$, then we have nothing to prove. In the following, we suppose $p > O$.

Step 2. Fix $y \in P$ such that $y \gg p$, the existence of which is guaranteed by the assumption that P is an ordered cone with nonempty interior. Indeed, for any $p_1 \in int(P)$, by definition $p_1 + p \gg p$. Since $p \in \mathcal{B}$, then p is a nonwandering point and there exist $x_j \to p$ as $j \to \infty$ in P and an integer sequence $n_j \to \infty$ such that $S^{n_j}(x_j) \to p$ as $j \to \infty$ (see [Hir1]). By the choice of $y \gg p$, there exists a j_0 such that for any $j \geq j_0$, $x_j \leq y$. Since $\{S^{n_j}(y)\}_j$ is precompact, there exists a subsequence $\{n_{j_k}\} \subset \{n_j\}$ such that

$S^{n_{j_k}}(y) \to q$ as $k \to \infty$. By the monotonicity of S. it follows that $q \geq p$. Obviously $q \in \mathcal{B}$. Recall that p is a maximal element in $\mathcal{B}$. Hence $q = p$. i.e. $S^{n_{j_k}}(y) \to p$ as $k \to \infty$. Again from the choice of $y \gg p$. there must be an integer. say $m > 0$ such that $S^m(y) \ll y$.

Step 3. Denote $T = S^m$. Then $T(y) \ll y$. Clearly from the properties of S. T is also a continuous and monotone mapping. Now we get a strictly supersolution y of T. That is. the sequence $\{T^n(y)\}$ is nonincreasing and precompact. Thus there exists a unique element $y_0 \in \omega(y) \subset \mathcal{B}$ such that $T^n(y) \searrow y_0$ as $n \to \infty$ and $T(y_0) = y_0$. That is. $S^m(y_0) = y_0$ and $\omega(y) = \{y_0, S(y_0), \ldots, S^{m-1}(y_0)\}$ which is an m-cycle. We have already shown that $p = q \in \omega(y)$. so we can represent $\omega(y)$ as $\omega(y) = \{p, S(p), \ldots, S^{m-1}(p)\}$.

Step 4. We finally claim that $m = 1$. i.e. p is a fixed point of S. Assume. by contradiction. that $m > 1$. From condition (i). we can choose the least upper bound element of $\omega(y)$. denoted by u. i.e. $u = \inf\{x \in P : x \geq S^j(p), j = 0, 1, \ldots, m-1\}$. Note that $u \in P$ and u may not be in $\mathcal{B}$. Then $S(u) \geq \omega(y)$ since S is monotone and $\omega(y)$ is invariant. Therefore $S(u) \geq u$ by the choice of u. It follows from an analogous proof to step 3 for T. that $\omega(u) = \{v\}$ and $v \geq u \geq p$. Hence $v \geq p$. Clearly $v \in \mathcal{B}$. Since p is a maximal element in $\mathcal{B}$. then $v = p$. Therefore p is a fixed point of S in P.

Step 5. It follows from condition (iii) that $p = O$. That is. any maximal element in $\mathcal{B}$ is O itself. Hence $\mathcal{B} = \{O\}$. Therefore $\omega(x) = \{O\}$ for any $x \in P$ since $\omega(x)$ is nonempty. That is. $x = O$ is globally attractive with respect to P. Hence if we know further that $x = O$ is also locally stable. then $x = O$ is globally asymptotically stable with respect to P.

□

In the following. we first answer when $x = O$ is the unique fixed point of

S in P and when $x = O$ is locally stable.

Definition 4.1([DaHe]). *A fixed point* $u \in P$ *is stable with respect to P provided for each* $\varepsilon > 0$, *there exists* $\delta > 0$ *such that* $S^n(x) \in N(u, \varepsilon) \bigcap P$ *for all* $x \in N(u, \delta) \bigcap P$ *and all* $n \in \mathbb{N}$.

Remark 4.4. The stability in the sense of Dancer and Hess(Definition 4.1) is equivalent to Lyapunov stability.

Theorem 4.5. *Assume that*

(i) $S : P \to P$ *is a continuous and monotone mapping;*

(ii) $S(O) = O$, $DS(O)$ *is compact and strongly positive with* $\rho(DS(O)) \leq 1$, *where* $DS(O)$ *is the Frechét derivative of* S *at* O;

(iii) $DS(O)x > x$ *for any* $x \in P \setminus \{O\}$ *with* $S(x) = x$.

Then $x = O$ *is the unique fixed point of S in P.*

Proof. According to the Krein-Rutman theorem, assumption (ii) makes sense. Suppose that there exists an $x \in P \setminus \{O\}$ such that $S(x) = x$. Then $-x < O$ and by assumption (iii), it follows that

$$(-x) - DS(O)(-x) = DS(O)x - x > O.$$

Checking proposition 2.3, it is easily seen that $\rho(DS(O)) > 1$, which contradicts assumption (ii). Therefore $x = O$ is the unique fixed point of S in P.

□

As an immediate result of theorems 4.4 and 4.5, we have:

Theorem 4.6. *Assume that*

(i) P is a normal order cone and has the property that any two elements $x, y \in P$ *have a least upper bound element in P;*

(ii) $S : P \to P$ *is a continuous and monotone mapping, and there exists a compact subset* K *of P such that* K *attracts each point in P under* S;

(iii) $S(O) = O$. $DS(O)$ *is compact and strongly positive with* $\rho(DS(O)) \leq 1$;

(iv) $DS(O)x > x$ *for all* $x \in P \setminus \{O\}$ *with* $S(x) = x$.

Then $x = O$ *is globally attractive with respect to P. Moreover, if* $\rho(DS(O)) < 1$ *then* $x = O$ *is globally asymptotically stable with respect to P.*

Proof. It follows directly from theorems 4.4 and 4.5 that $x = O$ is globally attractive with respect to P. Suppose $\rho(DS(O)) < 1$. Let $\epsilon \gg O$ with $\|\epsilon\|_E = 1$ be the corresponding principal eigenfunction of $DS(O)$. Then $DS(O)\epsilon = \rho(DS(O))\epsilon$. Since $\rho(DS(O)) < 1$ and for each sufficiently small $\delta > 0$,

$$\begin{aligned} S(\delta\epsilon) &= S(O) + DS(O)\delta\epsilon + o(\delta) \\ &= \delta DS(O)\epsilon + o(\delta) \\ &= \delta\rho(DS(O))\epsilon + o(\delta), \end{aligned}$$

there exists a $\delta_0 > 0$ such that for any $\delta \in [0, \delta_0]$, $S(\delta\epsilon) \leq \delta\epsilon$. Therefore $\{S^n(\delta\epsilon)\}$ is a nonincreasing sequence in P and $\lim_{n\to\infty} S^n(\delta\epsilon) = O$. For any given $\varepsilon > 0$, choose $\Delta = \min\{\varepsilon, \delta_0\}$. Then for any $x \in \mathcal{N}(O, \Delta) \bigcap P$ and all $n \in \mathbb{N}$, there exists certain $\delta \in (0, \Delta]$ such that $O \leq x \leq \delta\epsilon$ and

$$O \leq S^n(x) \leq S^n(\delta\epsilon) \leq \delta\epsilon \leq \Delta\epsilon \leq \varepsilon\epsilon.$$

Hence $S^n(x) \in \mathcal{N}(O, \varepsilon) \bigcap P$, that is, $x = O$ is stable with respect to P, where the normality of cone P is required. Thus $x = O$ is globally asymptotically stable with respect to P.

□

Remark 4.5. A similar result([Zh2], theorem 2.2) was proved under stronger conditions. For the purpose of comparing, we cite it here. Let either $V = [O, b]_E$ with $b \gg O$ or $V = P$, $S : V \to V$ be a continuous and strongly order-preserving mapping(i.e. $x, y \in V$, $x > y$ implies $S(x) \gg S(y)$) and order-compact(i.e. $S([u, v]_E$ is relatively compact for all $u, v \in V$ with $u < v$). Assume that

(1) $S(O) = O$, $DS(O)$ is compact and strongly positive, and $\rho(DS(O)) \leq 1$;

(2) $S(u) < DS(O)u$ for any $u \in V$ with $u \gg O$. Then $u = O$ is globally asymptotically stable with respect to V.

Recall that a continuous mapping $S : X \to X$ is said to be asymptotically smooth if for any nonempty closed and bounded set $\mathcal{B} \subset X$ for which $S(\mathcal{B}) \subset \mathcal{B}$, there is a compact set $\mathcal{K} \subset \mathcal{B}$ such that $\mathcal{K}$ atracts $\mathcal{B}$, i.e, for any $\varepsilon > 0$ there exists an $n_0 = n_0(\varepsilon, \mathcal{K}, \mathcal{B})$ such that $S^n(\mathcal{B})$ is contained in the ε -neighborhood of $\mathcal{K}$ for all $n \geq n_0$. Clearly for an asymptotically smooth mapping, any bounded positive orbit $\gamma^+(x)$ is precompact. For more details and examples of interesting asymptotically smooth mappings, we refer to the AMS monograph [Hale2].

The following result is theorem 2.1 and remark 2.1 in[ZhJi], which is very similar to a result due to Hal Smith([Sm3], theorem 2.1).

Proposition 4.1. *Let P be a normal cone with nonempty interior. Assume that*

(1) $S : V = a + P \to V$ *is a continuous and monotone mapping and any bounded positive orbit in V is precompact(i.e. for any* $x \in V$ *for which* $\gamma^+(x)$ *is bounded, then* $Cl\gamma^+(x)$ *is compact in V);*

(2) $S(a) = a$, $DS(a)$ *is compact and strongly positive, and* $\rho(DS(a)) > 1$.

Then either

(i) for any $u > a$, $\lim_{n\to\infty} \|S^n(u)\|_E = \infty$

or alternatively

(ii) there exists $u^* = S(u^*) \gg a$ *such that for any* $a < u \ll u^*$, $\lim_{n\to\infty} S^n(u) = u^*$.

Moreover, if S is also asymptotically smooth, then in the alternative (ii), there exists a monotone entire orbit $\{u_n\}$ *connecting a and* u^*, *i.e.* $u_{n+1} = S(u_n)$, $u_{n+1} \geq u_n$, $n \in \mathbb{Z}$, $\lim_{n\to-\infty} u_n = a$ *and* $\lim_{n\to+\infty} u_n = u^*$.

Remark 4.6. In the alternative (ii), $u^* \gg a$ since $DS(a)$ is strongly positive and in a small neighborhood of a, S almost operates as a strongly monotone mapping. The Dancer-Hess connecting orbit theorem implies the existence of such a monotone entire orbit, but not an entire orbit of strictly subsolutions, connecting a and u^* (see, [DaHe], proposition 1 and remark 1.1).

An inductive result of proposition 4.1 is the following

Corollary 4.7. *Let* P *be a normal cone with nonempty interior. Assume that*

(1) $S : P \to P$ *is a continuous and monotone mapping and every bounded positive orbit in P is precompact;*

(2) $S(O) = O$, $DS(O)$ *is compact and strongly positive, and* $\rho(DS(O)) > 1$.

Then we have

(i) S is uniformly persistent.

(ii) The following statements are equivalent.

$(ii)_a$ *There exists at least one strictly positive fixed point of S in* $int(P)$.

$(ii)_b$ *There exists a bounded nonzero orbit in* P.

□

From the general persistence theory, we know that condition $\rho(DS(O)) > 1$ is almost sufficient to guarantee that S is uniformly persistent. Comparing corollary 4.7 with proposition 5.4 in chapter 5, it is not too hard to note some advantages of monotone systems. Clearly, in a monotone system generated by an asymptotically smooth mapping S, uniform persistence and point dissipativity together imply the existence of a coexistence state of S. One of our ultimate purposes is to derive certain conditions under which the discrete semiflow $\{S^n\}$ has a unique strictly positive coexistence state which is globally asymptotically stable with respect to the positive cone P. We first state the following result, from which one can see another advantage of monotone semiflows on the global stability.

Theorem 4.8. *Let P be a normal order cone with nonempty interior. Assume that*

(i) P has the property that any two elements $x, y \in P$ have a least upper bound element in P;

(ii) $S : P \to P$ is a continuous and monotone mapping;

(iii) $S(O) = O$. $DS(O)$ is compact and strongly positive, and $\rho(DS(O)) > 1$;

(iv) there exists a compact subset $\mathcal{K}$ in P such that $\mathcal{K}$ attracts each point of P under S.

Then there exists a fixed point $a \in int(P)$, i.e. $S(a) = a$, such that for any $O < x \le a$, $\lim_{n\to\infty} S^n(x) = a$, and for any $x > O$, $\liminf_{n\to\infty} S^n(x) \ge a$, i.e. S is uniformly persistent.

Furthermore, if in addition

(v) $x = a$ is the unique fixed point of S in $int(P)$,

then $x = a$ is globally attractive with respect to $P\backslash\{O\}$, i.e. $\lim_{n\to\infty} S^n(x) = a$ for all $x > O$.

Proof. Condition (iv) implies that any bounded positive orbit in P is precompact and the discrete monotone semiflow generated by S is point dissipative. According to proposition 4.1, there exists a fixed point $a \gg O$, i.e. $a \in int(P)$ and $S(a) = a$ such that for any $O < x \le a$, $\lim_{n\to\infty} S^n(x) = a$.

Claim 1:. *For any $x > O$, $\omega(x) \ge a$.*

Firstly, condition (iv) implies that $\omega(x) \ne \varnothing$. For any small $\varepsilon > 0$ such that

$\varepsilon x \leq x$, we have

$$S(x) \geq S(\varepsilon x) = S(O) + DS(O) \,.\, \varepsilon x + o(\varepsilon) = \varepsilon DS(O)x + o(\varepsilon).$$

Since $DS(O)$ is strongly positive and $x > O$, $DS(O)x \gg O$ and hence there exists $\varepsilon_0 > 0$ such that for all $\varepsilon \in (0, \varepsilon_0]$, $\varepsilon DS(O)x + o(\varepsilon) \gg O$. Let $\epsilon \gg O$ be the corresponding principal eigenfunction of $DS(O)$ with $\|\epsilon\|_E = 1$, i.e. $DS(O)\epsilon = \rho(DS(O))\epsilon$, whose existence comes from the Klein-Rutman theorem. Then there exist $t_1 > 0$ and $t_2 > 0$ such that $t_1\epsilon \leq S(x)$ and $t_2\epsilon \leq a$ since $S(x) \gg O$ and $a \gg O$. Choose $t_0 = \min\{t_1, t_2\}$. Then $t_0 > 0$ and $O < t_0\epsilon \leq S(x)$, $O < t_0\epsilon \leq a$. By the monotonicity of S, we have

$$S^n(t_0\epsilon) \leq S^n(S(x)) = S^{n+1}(x).$$

Therfore it follows from $\lim_{n\to\infty} S^n(t_0\epsilon) = a$ that $\omega(x) \geq a$. That is for any $x > O$, $\liminf_{n\to\infty} S^n(x) \geq a$ and S is uniformly persistent.

Claim 2:. *Under additional condition (v),* $\omega(x) = \{a\}$ *for any* $x > O$.

Let $P_0 = \{x \in P : x \geq a\}$. Define $T : P_0 \to P_0$ by $T(x) = S(x)$. Then T is a continuous and monotone mapping, which generates a discrete monotone semiflow $\{T^n\}$ defined on P_0. Clearly from conditions (iv) and (v), $\mathcal{K} \bigcap P_0 \neq \varnothing$ since at least $a \in \mathcal{K} \bigcap P_0$. Furthermore $\mathcal{K} \bigcap P_0$ is compact and attracts all points in P_0. A completely analogous manner to the proof of theorem 3.1 shows that for any $x \in P_0$, $\lim_{n\to\infty} T^n(x) = a$. That is for any $x \geq a$, $\lim_{n\to\infty} S^n(x) = a$. Thus for any $x \in P$ for which either $O < x \leq a$ or $x \geq a$ holds, we have $\lim_{n\to\infty} S^n(x) = a$. Now pick an $x \in P \setminus \{O\}$ and suppose that there is no partial order relationship between x and a. From condition (i), there exists a $u \in P$ such that u is the least upper bound element of x and a in P. Then $x < u$ and $a < u$. Clearly $S^n(x) \leq$

$S^n(u) \to a$ as $n \to \infty$. Hence it also follows that $\omega(x) \leq a$. Together with Claim 1, we have $\omega(x) = \{a\}$ since $\omega(x) \neq \varnothing$. That is $\lim_{n\to\infty} S^n(x) = a$ for all $x \in P \setminus \{O\}$.

□

Remark 4.7. There is a similar result on a continuous monotone semiflow $U(t)$ due to Hirsch([Hir2], theorems 3.2-3.3). We cite it here from ([MaSm], theorem 4.1). Suppose $\mathcal{A}$ is a compact attractor for the semiflow U. Then $\mathcal{A}$ contains an equilibrium and if $\mathcal{A}$ contains exactly one equilibrium, p, then every orbit attracted to $\mathcal{A}$ converges to p.

In applications, it is very easy to verify conditions (i)-(iv) listed in theorem 4.8. However, it is not so easy to check condition (v). For the uniqueness of coexistence states, in published works, some popular conditions on the mapping S are the properties such as concavity(i.e. $DS(v) - DS(u) > O$ if $u \gg v \gg O$), strong concavity(for any $u \gg O$, $\alpha \in (0,1)$, there exists $\eta = \eta(u, \alpha) > 0$ such that $S(\alpha u) \geq (1+\eta)\alpha S(u)$), sublinearity or subhomogeneity(for any $u \in P$, $\alpha \in [0,1]$, $S(\alpha u) \geq \alpha S(u)$), strict sublinearity or strictly subhomogeneity(for any $u \in P$, $\alpha \in (0,1)$, $S(\alpha u) > \alpha S(u)$), and strongly subhomogeneity(for any $u \in P$, $\alpha \in (0,1)$, $S(\alpha u) \gg \alpha S(u)$). For details, we refer to [FrZh], [Hes], [Hir4], [Kra], [KrNu], [Mar], [Sm2], [Taka1], [Taka2], [Zh2] and some references therein. Those assumptions could upon occassion work in showing the uniqueness of coexistence states in autonomous FDE or RDFDE systems since there the coexistence states are same as the equilibra or coexistence states in a corresponding system without delays. However, in non-autonomous systems, the situation becomes much more complicated. We are going to deal with the uniqueness of coexistence states in terms of the topological degree theory.

In applications, there is another exception, that is, $DS(O)$ in theorem 4.8

may not be strongly positive, but only positive. Then the above arguments will not work well. We are going to give an example from which one will see that this case often happens. Consider the following scalar monotone system

$$\dot{x}(t) = x(t)g(t, x(t), x(t - \tau(t)))$$
$$x_0 \in C^+ = C([-\tau^*, 0], \mathbb{R}^+). \tag{4.2}$$

where $g(t, x, y)$ is ω-periodic in t and continuously differentiable in each variable. For system (4.2) to generate a monotone ω-periodic semi-dynamical system, a sufficient condition on g is often given by the following quasimonotone condition.

(QM). $\partial g(t, x, y)/\partial y \geq 0$ *in* $[0, \omega] \times C^+ \times C^+$.

If g is not continuously differentiable, we refer to a corresponding quasi-monotone condition explicitly described by the order in C ([Sm8], page 78). Clearly, the ω-periodic semiflow generated by (4.2) is monotone but not strongly monotone. Moreover, $x = O$ is a trivial ω-periodic solution. Denote $S(\phi)(\theta) = x(\omega + \theta, \phi)$ for all $\theta \in [-\tau^*, 0]$, $\phi \in C^+$, where $x(t, \phi)$ is the solution of (4.2) with $x(\theta, \phi) = \phi(\theta)$ in $[-\tau^*, 0]$. Then $S : C^+ \to C^+$ is a continuous and monotone mapping with $S(O) = O$. Consider the linearized variational equation of system (4.2) at $x = O$

$$\dot{z}(t) = z(t)g(t, 0, 0)$$
$$z_0 = \phi \in C.$$

Clearly $z(t) = \phi(0)\exp\left(\int_0^t g(s, 0, 0)ds\right)$.

By a standard argument, it follows that the Frechét derivative of S at O,

$DS(O) : C \to C$ is given by

$$
\begin{aligned}
DS(O)\phi(\theta) &= \phi(0)\exp\left(\int_0^{\omega+\theta} g(t,0,0)dt\right) \\
&= \exp\left(\int_0^{\omega} g(t,0,0)dt\right)\phi(0)\exp\left(\int_\omega^{\omega+\theta} g(t,0,0)dt\right) \\
&= \exp\left(\int_0^{\omega} g(t,0,0)dt\right)\phi(0)\exp\left(\int_0^{\theta} g(t,0,0)dt\right).
\end{aligned}
$$

It is well-known that $DS(O)$ is compact and positive but it is not strongly positive. For instance, when the initial ϕ satisfies $\phi(\theta) > 0$ in $[-\tau^*, 0)$ and $\phi(0) = 0$, then in the usual pointwise ordering $\phi > 0$ implies $DS(O)\phi = O$. Furthermore, $DS(O)$ has $\gamma \triangleq \exp\left(\int_0^\omega g(t,0,0)dt\right)$ as an eigenvalue with an eigenfunction $\exp\left(\int_0^\cdot g(t,0,0)dt\right)$ in $int(C^+)$. Hence if we suppose that system (4.2) is point dissipative, then it follows from the following theorem 4.9 that there exists a strictly positive ω-periodic solution, denoted by x^*, for system (4.2) provided

$$\int_0^\omega g(t,0,0)dt > 0. \tag{3.2}$$

Now let us analyze under what conditions in this weak case, there still exists a strictly positive fixed point of S which is also globally attractive. As demonstrated in the above example, the following theorems will play important roles in applications.

Theorem 4.9. *Let P be a normal cone with nonempty interior. Assume that*

(i) $S : P \to P$ is a continuous and monotone mapping;

(ii) $S(O) = O$, $DS(O)$ is compact and positive. Moreover, there exists at least one eigenvalue, denoted by γ of $DS(O)$ such that $\gamma > 1$, which has a corresponding eigenfunction in $int(P)$;

(iii) there exists a compact subset $\mathcal{K} \subset P$ such that $\mathcal{K}$ attracts each point of P under S.

Then there exists a fixed point $a \in int(P)$, *i.e,* $S(a) = a$ *with* $a \gg 0$.

Proof. Let $e \in int(P)$ with $\|e\|_E = 1$ such that $DS(O)e = \gamma e$. For small $\varepsilon > 0$,

$$S(\varepsilon e) = S(O) + \varepsilon DS(O)e + o(\varepsilon) = \gamma\varepsilon e + o(\varepsilon).$$

Since $\gamma > 1$, $e \in int(P)$, there exists certain $\varepsilon_0 > 0$ such that for any $\varepsilon \in (0, \varepsilon_0]$, $(\gamma - 1)\varepsilon e + o(\varepsilon) \in int(P)$, and hence

$$S(\varepsilon e) - \varepsilon e = (\gamma - 1)\varepsilon e + o(\varepsilon) \gg O, \quad i.e. \quad S(\varepsilon e) \gg \varepsilon e \gg O.$$

So we get a nondecreasing sequence $\gamma^+ = \{S^n(\varepsilon e)\}_{n=0}^{\infty}$ which is precompact in P from assumption (iii). Therefore there exists an $a \in P$ such that

$$S^n(\varepsilon e) \nearrow a, \quad \text{as } n \to \infty.$$

Clearly, $S(a) = a$ and $a \in int(P)$ since $a \geq S^n(\varepsilon e) \gg \varepsilon e \gg O$ for all $n \geq 1$.

□

Remark 4.8. Here we do not require that S is compact, but we need the corresponding eigenfunction of γ to be strictly positive. From another Krein-Rutman theorem(proposition 4.2), we can only draw the conclusion that $\rho(DS(O)) > 0$ is an eigenvalue of $DS(O)$ with an eigenfunction $x > O$, not $x \gg O$.

Theorem 4.10. *Let P be a normal order cone with nonempty interior. Assume that*

(i) P has the property that any two elements $x, y \in P$ *have a least upper bound element and a greatest lower bound element in P;*

(ii) $S : P \to P$ *is a continuous and monotone mapping;*

(iii) $S(O) = O$, $DS(O)$ *is compact and positive. Moreover, there exists at least one eigenvalue, denoted by* γ *of* $DS(O)$ *such that* $\gamma > 1$ *and has a corresponding eigenfunction in* $int(P)$;

(iv) *there exists a compact subset* $\mathcal{K}$ *in* P *such that* $\mathcal{K}$ *attracts each point of* P *under* S;

(v) $x = a$ *is the unique fixed point of* S *in* $int(P)$, *where* $x = a$ *is a fixed point of* S *as showed in theorem 4.9.*

Then $x = a$ *is globally attractive with respect to* $int(P)$. *i.e.* $\lim_{n\to\infty} S^n(x) = a$ *for all* $x \gg O$.

Proof. The proof is standard and analogous to those of theorems 4.4 and 4.9. We omit the details.

□

CHAPTER 5

A PREDATOR-PREY SYSTEM WITH PERIODIC DELAYS *

5.1. Introduction

A basic problem in population dynamics is to derive criteria for the long-term coexistence of interacting species. The main object of this chapter is to study the problem of coexistence for two interacting species, one predator and one prey, modeled by the following periodic Gause-type predator-prey system involving discrete but periodic delays

$$\begin{aligned} \dot{x}(t) &= x(t)g(t, x(t), x(t-\tau(t))) - y(t)p(t, x(t)) \\ \dot{y}(t) &= y(t)(-r(t) + c(t)p(t, x(t-\sigma(t)))) \qquad (5.1) \\ x(s) &= \phi(s) \geq 0, \quad \text{for all } s \in [-\tau_0, 0] \quad \text{and } y(0) \geq 0 \end{aligned}$$

where $\cdot = d/dt$, $\tau_0 = \max_{t\in[0,\omega]}\{\tau(t), \sigma(t)\}$ and where $x(t)$, $y(t)$ represent the population densities of prey and predator at time t, respectively. $g(t, x(t), x(t-\tau(t)))$ is the specific growth function of the prey in the absence of predators. $p(t, x(t))$ is the predator response function, which satisfies $p(t, 0) \equiv 0$ and $\partial p(t, x)/\partial x \geq 0$, which are natural assumptions since if there are no prey, the predator can not get energy, and the more prey there are, the more energy for the predators. $c(t)$ is the energy conversion efficiency function which could be interpreted to represent energy transfer from prey to predators since

* This chapter is adopted from [PeFr2].

there must be some energy loss during the conversion. The transfer process is not uniform but changes with the varying environment. The delays $\tau(t)$ and $\sigma(t)$ both reflect certain time lags in the energy transfer, and also vary with the season and the environment. $r(t)$, a nonnegative function satisfying $\int_0^\omega r(t)dt > 0$, represents the death rate of the predator, and implies that the predator will die out in the absence of prey. Here we suppose that all functions $g(t,\dots)$, $p(t,.)$, $r(t)$, $c(t)$, $\tau(t)$ and $\sigma(t)$ are periodic in t with constant period ω. This could be due for example to a periodically varying environment. We further assume that all functions are smooth enough such that solutions to initial value problems exist uniquely and are continuable for all positive time. We are going to show the dissipativity, uniform persistence and the existence of strictly positive periodic solutions of the retarded functional differential equation system (5.1) which has the feature of periodicity of time delays due to gestation and other birth considerations in a periodically varying environment.

This research is motivated by the laboratory work of the group led by Halbach [BWH], [Ha1], [Ha2], [Ha3], [HSWK], [WBH] on rotifers and a mathematical analysis by Freedman and Wu [FrWu] which is the first paper with periodic delay considered in the literature. Laboratory work showed that in laboratory populations, periodic phenomena due to time delays in gestation occured, and that the length of delay was a function of the controlled temperature. These periodic variations in population numbers also occured when the temperature itself was varied periodically(thereby inducing periodic delays) on a daily basis. This leads to a natural conjecture that there should exist periodic solutions in such delay models with periodic delays. In [FrWu], such a conjecture was proved for single-species delay models with periodic delay. It was shown that if the self-inhibition rate is sufficiently large compared to the reproduction rate, then the model equation has a globally asymptotically stable positive periodic solution.

However, their models are of Lotka-Voterra type and some of the technical steps in their method of proofs require the Lotka-Volterra format. The main tools applied there are Horn's fixed point theorem([Horn]) and Lyapunov-Razumikhim stability arguments([Hale1], [Ku1]). More specifically, the models discussed in [FrWu] belong to intra-species cooperative type and generate monotone semiflows. Hence the theory of monotone dynamical systems could be applied. Following the work of [FrWu], another discussion on Lotka-Volterra models with periodic delays was given by Wang, Chen and Lu([WCL]) in which some easier verifiable conditions were obtained for there to be a globally asymptotically stable periodic solution. Similarly, their analysis still depended on the Lotka-Volterra format.

It is difficult to describe completely the dynamics of system (5.1) since our model generates an infinite-dimensional non-monotone semi-dynamical system($t \geq 0$). Hence we first discuss the long-term behavior described roughly by dissipativity and uniform persistence. The advantage in doing this is that it provides criteria for long-term coexistence but does not require a complete knowledge of the dynamics of the system. There have been extensive studies on uniform persistence(see the review paper [HuSc] or the survey paper [Wa2] and references therein). Most of those discussions have been devoted to those systems modeled by autonomous differential equations(ODEs, FDEs and reaction-diffusion equations). Because of seasonal fluctuations and periodic availability of food, the question of a periodically varying environment has been attracting more and more attention [BrHe], [BuFr], [FrPe1], [Go], [Hes], [Sm1], [Sm4], [Sm5], [Sm7], [YaFr], [Zh1], [ZhHu]. Generally, a discussion of periodic systems is much more difficult than a discussion of autonomous systems, particularly for the study of stability of a periodic orbit. It is easier to discuss a periodic system generating a monotone periodic semiflow in terms of the theory of monotone dynamical systems(continuous or discrete) due to Müller, Kamke, Hirsch, Matano, Smith, Thieme and Dancer. Hess (see [DaHe], [Sm8] and references therein) than to discuss a periodic system without any monotonicity. However for a nonmonotone periodic system. specifically one which generates an infinite-dimensional dynamical system. a discussion of the dynamics is likely to be considerably more difficult. Our analysis is based on persistence theory. dissipativity theory, infinite-dimensional system theory and a standard but important comparison argument.

The organization of this chapter is as follows. Some related preliminary results on uniform persistence, global attractivity and periodic coexistence states for dynamical systems(continuous or discrete) are introduced in section 5.2. A nontrivial dissipativity discussion follows in section 5.3. In section 5.4. we mainly show that system (5.1) is uniformly persistent. A brief discussion of periodic coexistence states and some remarks are also contained in section 5.4. Finally, we briefly explain our main result with biological implications.

5.2. Definitions and Preliminary Results

In this section we establish our terminologies and give some background material on uniform persistence as well as the existence of a global attractor and coexistence states for either continuous periodic or discrete semi-dynamical systems.

Let (X, d) be a complete metric space with metric d and suppose that $T(t) : X \to X, t \geq 0$, is a C^0-semigroup on X, that is. $T(0) = I, T(t+s) = T(t)T(s)$ for all $t, s \geq 0$, and $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$. The positive orbit γ^+ through $x \in X$ is defined by $\gamma^+ = \bigcup_{t \geq 0}\{T(t)x\}$. Given a subset B of X, the positive orbit $\gamma^+(B)$ is given by

$$\gamma^+(B) = \bigcup_{x \in B} \gamma^+(x).$$

The ω-limit set of $x \in X$ is defined as

$$\omega(x) = \bigcap_{s \geq 0} Cl \bigcup_{t \geq s} \{T(t)x\}.$$

This is equivalent to saying that $y \in \omega(x)$ if and only if there is a sequence $t_n \to \infty$ as $n \to \infty$ such that $T(t_n)x \to y$ as $n \to \infty$. Similarly, we define the ω-limit set of $B \subset X$ as

$$\omega(B) = \bigcap_{s \geq 0} Cl \bigcup_{t \geq s} T(t)B$$

where $T(t)B = \bigcup_{x \in B}\{T(t)x\}$. This is equivalent to saying that $y \in \omega(B)$ if and only if there exist sequences $t_n \to \infty$ and $\{x_n\} \subset B$ such that $T(t_n)x_n \to y$ as $n \to \infty$. Note that the set $\bigcup_{x \in B} \omega(x)$ is generally smaller than the set $\omega(B)$.

A set $B \subset X$ is said to be invariant if $T(t)B = B$ for all $t \geq 0$. This implies, in particular, that there is a negative orbit passing through each point of an invariant set. This observation sometimes plays an important role. A nonempty invariant subset $M \subset X$ is called an isolated invariant set if it is the maximal invariant set of a neighborhood of itself. The stable (or attracting) set of a compact invariant set A, denoted by $W^s(A)$, is defined as

$$W^s(A) = \{x \in X : \omega(x) \neq \varnothing \quad \text{and} \quad \omega(x) \subset A\}.$$

From this definition, we see that if A consists of a single point x^* and for every $x \in X$, $\gamma^+(x)$ is precompact, then

$$W^s(\{x^*\}) = \{x \in X : \omega(x) = \{x^*\}\} = \{x \in X : \lim_{t \to \infty} T(t)x = x^*\}.$$

This simple observation will play a role in proving uniform persistence.

A set $\mathcal{A}$ is said to be a global attractor if it is compact, invariant and for any bounded set $B \subset X$, $\delta(T(t)B, \mathcal{A}) \to 0$ as $t \to \infty$, where $\delta(B, A)$ is the unsymmetric distance from the set B to the set A :

$$\delta(B, A) = \sup_{y \in B} \inf_{x \in A} d(y, x).$$

Specifically, this implies that $\omega(B)$ is nonempty and belongs to A. A global attractor is always a maximal compact invariant set.

The semigroup $T(t)$ is said to be asymptotivally smooth if for any bounded subset $B \subset X$, for which $T(t)B \subset B$ for all $t \geq 0$, there exists a compact set $K \subset B$ such that $\delta(T(t)B, K) \to 0$ as $t \to \infty$. Hence $\omega(B) \subset K$. The semigroup $T(t)$ is said to be point dissipative (compact dissipative) if there is a bounded set $B \subset X$ that attracts each point of X (each compact set of X), that is, there is a bounded nonempty set $B \subset X$ such that, for any point $x \in X$ (for any compact set $K \subset X$), there is a $t_0 = t_0(x, B)$ ($t_0 = t_0(K, B)$) such that $T(t)x \in B$ ($T(t)K \subset B$) for all $t \geq t_0$. In the classical theory of differential equations, "point dissipative" is often referred to as "ultimately bounded".

Suppose that $S : X \to X$ is a continuous mapping. The set $\{S^n\}_{n=0}^{\infty}$ is said to be a discrete semi-dynamical system generated by S if $S^0 = I$, $S^{m+n} = S^m S^n$ for all integers $m, n \geq 0$. For each point $x \in X$, the positive orbit $\gamma^+(x)$ through x is defined as $\gamma^+(x) = \bigcup_{n \geq 0} S^n(x)$. The ω-limit set $\omega(x)$ is defined as

$$\omega(x) = \bigcap_{n \geq 0} Cl \bigcup_{k \geq n} S^k(x).$$

For any set $B \subset X$, define the positive orbit $\gamma^+(B)$ and the ω-limit set $\omega(B)$ of B as

$$\gamma^+(B) = \bigcup_{x \in B} \gamma^+(x),$$

$$\omega(B) = \bigcap_{n \geq 0} Cl \bigcup_{k \geq n} S^k(B)$$

where $S(B) = \bigcup_{x \in B} S(x)$. Clearly, $y \in \omega(x)$ if and only if there is a sequence of integers $n_j \to \infty$ such that $S^{n_j}(x) \to y$ as $j \to \infty$ while $y \in \omega(B)$ if and only if there is a sequence $\{x_j\} \subset B$ and a sequence of integers $n_j \to \infty$ such that $S^{n_j}(x_j) \to \infty$ as $j \to \infty$. Similarly, the set $\bigcup_{x \in B} \omega(x)$ is generally much smaller than the set $\omega(B)$.

A set $B \subset X$ is said to be invariant under S if $S(B) = B$. A set $\mathcal{A}$ is said to be a global attractor if it is compact, invariant and for any bounded set $B \subset X$, $\delta(S^n(B), \mathcal{A}) \to 0$ as $n \to \infty$.

A continuous mapping $S : X \to X$ is asymptotically smooth if for any nonempty closed bounded set $B \subset X$ for which $S(B) \subset B$, there is a compact set $K \subset B$ such that K attracts B. A continuous mapping S on a complete metric space X is said to be point dissipative (compact dissipative) on X if there is a bounded set $B \subset X$ such that B attracts each point in X (each compact set of X) under S.

A continuous mapping $S : X \to X$ is α-condensing if S is bounded, i.e. takes bounded sets into bounded sets, and $\alpha(S(A)) < \alpha(A)$ for any bounded set $A \subset X$ with $\alpha(A) > 0$. Here $\alpha(A)$ is the Kuratowski measure of noncompactness of A, defined by

$$\alpha(A) = \inf\{\varepsilon : A \text{ has a finite cover of diameter} < \varepsilon\}.$$

A continuous mapping $S : X \to X$ is an α-contraction of order k, $0 \leq k < 1$, if $\alpha(S(A)) \leq k\alpha(A)$ for all bounded sets $A \subset X$ for which $S(A)$ is bounded.

The above definitions are taken from [Hale2]. In what follows, for some unexplained terminologies, we still refer to [Hale2].

Now suppose that $T(t) : X \to X$, $t \geq 0$, is an ω-periodic semiflow on X with constant period $\omega > 0$, that is, $T(0) = I, T(t + \omega) = T(t)T(\omega)$

for all $t \geq 0$ and $T(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$. A point x^* corresponds to an ω-periodic orbit if $T(t+\omega)x^* = T(t)x^*$ for all $t \geq 0$. For an ω-periodic semiflow, the point x^* is exactly a fixed point of its associated Poincaré mapping $T(\omega)$.

We further assume that the metric space X is the closure of an open set X^0, that is, $X = X^0 \bigcup \partial X^0$, where ∂X^0 is the boundary of X^0, and X^0 is positively invariant, i.e, $T(t)X^0 \subset X^0$ for all $t \geq 0$. We say that a set U in X^0 is strongly bounded in X^0 if it is bounded in X and there is an $\eta \geq 0$ such that

$$d(x, \partial X^0) \geq \eta \quad \text{for all } x \in U.$$

For the purpose of emphasis, we note the following two definitions.

Definition 5.1. *A periodic semiflow* $T(t)$, $t \geq 0$ *(or discrete semiflow* $\{S^n\}_{n=0}^{\infty}$ *) is said to be uniformly persistent with respect to* $(X^0, \partial X^0)$ *if there is an* $\eta > 0$ *such that for any* $x \in X^0$, $\liminf_{t\to\infty} d(T(t)x, \partial X^0) \geq \eta$ *(or* $\liminf_{n\to\infty} d(S^n x, \partial X^0) \geq \eta$ *).*

Difinition 5.2. *A point* x^* *is said to be a coexistence state of the discrete semiflow* $\{S^n\}_{n=0}^{\infty}$ *if* x^* *is a fixed point of* S *in* X^0, *i.e.* $x^* \in X^0$ *and* $S(x^*) = x^*$. *A coexistence state of a periodic semiflow* $T(t)$, $t \geq 0$ *refers to a periodic orbit in* X^0.

The following are some basic facts that will be applied to discuss uniform persistence and coexistence states.

Proposition 5.1([Hale2], theorem 2.4.7). *If* $S : X \to X$ *is completely continuous and point dissipative, then there is a connected global attractor* $\mathcal{A}$.

Proposition 5.2([FrSo] and [HoSo]). *Let* $S : X \to X$ *be a continuous mapping with* $S(X^0) \subset X^0$. *Assume that* *(i)* $S : X \to X$ *has a global attractor* $\mathcal{A}$;

(ii) let $\mathcal{A}_\partial$ *be the maximal compact invariant set of* S *in* ∂X^0. $\tilde{A}_\partial = \bigcup_{x \in \mathcal{A}_\partial} \omega(x)$ *has an isolated and acyclic covering* $\bigcup_{i=1}^k M_i$ *in* ∂X^0, *that is,* $\tilde{A}_\partial \subset \bigcup_{i=1}^k M_i$, *where* $M_1, M_2, \ldots, M_k$ *are pairwise disjoint, compact and isolated invariant sets of* S *in* ∂X^0 *such that each* M_i *is also an isolated invariant set in* X, *and no subset of the* M_i *'s forms a cycle for* $S_\partial = S|\mathcal{A}_\partial$ *in* $\mathcal{A}_\partial$.

Then S *is uniformly persistent if and only if for each* M_i, $i = 1, 2, \ldots, k$,

$$W^s(M_i) \bigcap X^0 = \varnothing.$$

Proposition 5.3([Zh1]). *Let* $T(t)$ *be an* ω*-periodic semiflow in* X *with* $T(t)X^0 \subset X^0$, $t \geq 0$. *Assume that* $S = T(\omega)$ *satisfies the following conditions:*

(i) S *is point dissipative;*

(ii) S *is compact; or alternatively,* S *is asymptotically smooth and* $\gamma^+(U)$ *is strongly bounded in* X^0 *if* U *is strongly bounded in* X^0.

Then the uniform persistence of S *with respect to* $(X^0, \partial X^0)$ *implies the uniform persistence of* $T(t)$ *with respect to* $(X^0, \partial X^0)$.

Proposition 5.4([Zh1]). *Let* $S : X \to X$ *be a continuous map with* $S(X^0) \subset X^0$. *Assume that:*

(i) $S : X \to X$ *is point dissipative;*

(ii) S *is compact; or alternatively,* S *is* α*-condensing and* $\gamma^+(U)$ *is strongly bounded in* X^0 *if* U *is strongly bounded in* X^0;

(iii) S *is uniformly persistent with respect to* $(X^0, \partial X^0)$.

Then there exists a global attractor $\mathcal{A}_0$ *for* S *in* X^0 *relative to strongly bounded sets in* X^0 *and* S *has a coexistence state* $x_0 \in \mathcal{A}_0$.

5.3. Dissipativity

In this section, we discuss the dissipativity of the following system:

$$\dot{x}(t) = x(t)g(t, x(t), x(t-\tau(t))) - y(t)p(t, x(t)) \triangleq F(t, x(t), x(t-\tau(t)), y(t)) \qquad (5.2)_a$$

$$\dot{y}(t) = y(t)(-r(t) + c(t)p(t, x(t-\sigma(t))) \triangleq y(t)G(t, x(t-\sigma(t)), y(t)). \qquad (5.2)_b$$

Denote $\tau_0 = \max_{0\le t\le\omega}\{\tau(t), \sigma(t)\}$. Let $X = C([-\tau_0, 0], R)\times R$. For any $(\phi, y) \in X$, define $\|(\phi, y)\| = \max_{-\tau_0\le\theta\le 0}|\phi(\theta)| + |y|$. Then $(X, \|\cdot\|)$ is a Banach space. Let $X^+ = \{(\phi, y) \in X : \phi(\theta) \ge 0$ for all $\theta \in [-\tau_0, 0]$ and $y \ge 0\}$ with a metric d deduced from the above norm $\|\cdot\|$. Then (X^+, d) is a complete metric space. Denote

$$X^0 = \{(\phi, y) \in X^+ : \phi(0) \ne 0 \quad \text{and } y \ne 0\}$$

and

$$\partial X^0 = \{(\phi, y) \in X^+ : \quad \text{either } \phi(0) = 0 \quad \text{or } y = 0\}.$$

It is easy to verify that X^0 and ∂X^0 are relatively open and closed subsets of X^+, respectively, with $X^+ = X^0 \bigcup \partial X^0$ and $X^0 \bigcap \partial X^0 = \varnothing$. For any pair of initial values $(\phi, y_0) \in X^+$, let $(x(t, \phi, y_0), y(t, \phi, y_0))$ be the solution of (5.2) with $x(\theta, \phi, y_0) = \phi(\theta)$ for all $\theta \in [-\tau_0, 0]$ and $y(0, \phi, y_0) = y_0$. Clearly $(x(t, \phi, y_0), y(t, \phi, y_0)) \in X^+$. Define $T(t)(\phi, y_0) \in X^+$, $t \ge 0$, by $T(t)(\phi(\theta), y_0) = (x(t+\theta, \phi, y_0), y(t, \phi, y_0))$, $-\tau_0 \le \theta \le 0$. Then $T(t)$, $t \ge 0$ is a continuous ω-periodic semiflow satisfying $T(t)X^0 \subset X^0$ and $T(t)\partial X^0 \subset \partial X^0$ for all $t \ge 0$. It is well-known that $T(t)$ is completely continuous for all $t \ge \tau_0$. We say that $T(t)$ is strongly point dissipative in X^0 if there is a strongly bounded set $B \subset X^0$ such that for any $(\phi, y_0) \in X^0$, there is a $t_0 = t_0(\phi, y_0, B)$ such that $T(t)(\phi, y_0) \in B$ for all $t \ge t_0$.

In applications, we usually need to suppose that the considered system is point dissipative, i.e. all solutions are ultimately bounded. For system (5.2), point dissipativity is not trivial and in fact is rather complicated. We will impose the following assumption on (5.2) for future discussion:

(PD). System (5.2) is point dissipative.

In the remainder of this section, we will concentrate on discussing in detail under which conditions (PD) could be realized. For this purpose, we further assume:

(H1). There exists a constant $K > 0$ such that $[0, K]$ is globally attractive for the subsystem:

$$\dot{x}(t) = x(t)g(t, x(t), x(t-\tau(t))) \tag{5.3}$$

with respect to $C^+ = C([-\tau_0, 0], R^+)$.

Theorem 5.1. *Suppose that there exists a Lipschitz function $g_1(x)$ such that*

$$\sup\{g(t, x, y) : 0 \le t \le \omega, y \ge 0\} \le g_1(x)$$

for all $x \ge 0$, and for some $K > 0$,

$$g_1(x) < 0 \qquad \text{if } x > K.$$

If $x(t, \phi)$ is a solution of (5.3) with initial function $\phi \in C^+$, then $0 \le x(t, \phi) \le z(t)$, where $z(t)$ satisfies

$$\dot{z} = z g_1(z) \tag{5.4}$$

with initial value $z(0) = \sup\{\phi(\theta) : -\tau_0 \le \theta \le 0\}$. Moreover, $x(t, \phi) \le K$ for t sufficiently large, and if $0 \le \phi(\theta) \le K$ for all $\theta \in [-\tau_0, 0]$ then $0 \le x(t, \phi) \le K$ for all $t \ge 0$.

Proof. We observe that C^+ is positively invariant with respect to (5.3). Therefore, the periodicity of $g(t, x(t), x(t-\tau(t)))$ in t implies that

$$g(t, x(t), x(t-\tau(t))) \leq g_1(x(t))$$

which gives

$$x(t)g(t, x(t), x(t-\tau(t))) \leq x(t)g_1(x(t))$$

whenever $x(t) \geq 0$. Hence a standard comparison argument shows that

$$x(t, \phi) \leq z(t) \qquad \text{for all } t \geq 0.$$

Furthermore, it is well-known that $[0, K]$ is globally attractive with respect to (5.4) under the assumption that $g_1(x) < 0$ whenever $x > K$. Hence $x(t, \phi) \leq K$ for t sufficiently large, that is, $x(t, \phi)$ is ultimately bounded. If $0 \leq \phi(\theta) \leq K$ for all $\theta \in [-\tau_0, 0]$, then $0 \leq z(0) \leq K$ which implies that $0 \leq z(t) \leq K$ holds for all $t \geq 0$. So $0 \leq x(t, \phi) \leq K$ for all $t \geq 0$.

□

Remark 5.1. The hypothesis on function g given in the above theorem could be met by any functions of the form

$$g(t, x(t), x(t-\tau(t))) = a(t) - b(t)x(t) - c(t)x(t-\tau(t))$$

where $a(.), b(.), c(.), \tau(.)$ are ω-periodic functions and $b(t) \geq b_0 > 0$ for all $t \geq 0$.

In applications, there is another class of models in which the specific growth functions have positive a feedback like $a(t)+c(t)x(t-\tau(t))$ and a self-inhibition, that is,

$$g(t, x(t), x(t-\tau(t))) = a(t) - b(t)x(t) + c(t)x(t-\tau(t)).$$

In [FrWu], Freedman and Wu discussed the following model

$$\dot{x}(t) = x(t)(a(t) - b(t)x(t) + c(t)x(t - \tau(t))) \tag{5.5}$$

where $a(.), b(.), c(.), \tau(.)$ are continuously differentiable, nonnegative ω-periodic functions and $a(t) > 0$, $b(t) > 0$. We state one of their main results here. The main tools used there are Horn's fixed-point theorem and Lyapunov-Razumikhim stability arguments. For details, we refer to [FrWu].

Proposition 5.5. *Suppose that the equation*

$$a(t) - b(t)k(t) + c(t)k(t - \tau(t)) = 0$$

has a positive, ω-periodic, continuous differentiable solution $k(t)$. Then the model equation (5.5) has a positive ω-periodic solution $Q(t)$. Moreover, if $b(t) > c(t)Q(t-\tau(t))/Q(t)$ for all $t \in [0, \omega]$, then $Q(t)$ is globally asymptotically stable with respect to positive solutions of (5.5).

Based on proposition 5.5, we are able to write out immediately the following result.

Theorem 5.2. *Assume that the conditions of proposition 5.5 are satisfied. Then (H1) holds for system (5.5).*

□

Now let us return to system (5.2). We have already observed that X^+ is positively invariant with respect to (5.2). In what follows, we will only consider (5.2) in X^+. Since $P(t, 0) \equiv 0$ and $\partial p(t, x)/\partial x \geq 0$, for all $t \geq 0$, it follows that under (H1), $x(t, \phi, y_0)$ is ultimately bounded with K as an upper boundary. In order to confirm (PD), we will need to show that $y(t, \phi, y_0)$ is also ultimately bounded. However, the growth of species y has no logistic self-limitation. This makes the discussion of species y's dissipativity much more difficult. The following is our first result on the dissipativity of system (5.2) with some specificity.

Theorem 5.3. *Assume that (H1) is satisfied and* $c(t) \equiv c, \quad \sigma(t) \equiv 0$ *for all* $t \in [0, \omega]$. *Then system (5.2) is point dissipative with a globally attractive region*

$$\mathcal{A} = \{(\phi, y) \in X^+ : \phi \le K, \quad c\phi + y \le M\}$$

where

$$M = \sup\{cx(1 + g(t, x, y)/r(t)) : 0 \le t \le \omega, \quad 0 \le x, y \le K\}.$$

Proof. Since $c(t) \equiv c, \quad \sigma(t) \equiv 0$ for all $t \in [0, \omega]$, system (5.2) becomes

$$\begin{aligned} \dot{x}(t) &= x(t)g(t, x(t), x(t - \tau(t))) - y(t)p(t, x(t)) \\ \dot{y}(t) &= y(t)(-r(t) + cp(t, x(t))). \end{aligned}$$

Denote $v(t) = cx(t) + y(t)$. Then we have

$$\begin{aligned} \dot{v}(t) = c\dot{x}(t) + \dot{y}(t) &= cx(t)g(t, x(t), x(t - \tau(t))) - r(t)y(t) \\ &= r(t)[cx(t)(1 + g(t, x(t), x(t - \tau(t)))/r(t)) - v(t)] \\ &\le r(t)(M - v(t)) \qquad \text{for t large.} \end{aligned}$$

Hence $\limsup_{t\to\infty} v(t) \le M$, that is, $\limsup_{t\to\infty}(cx(t) + y(t)) \le M$. This completes the proof.

□

The proof of theorem 5.3 is analogous to that for the autonomous case. For the more general case, we have the following assertion. Comparing their proofs, one can easily find some difference between autonomous and periodic cases.

Theorem 5.4. *Assume that (H1) is satisfied. Then system (5.2) is point dissipative provided that*

$$\int_0^\omega \min\{\partial p(t,x)/\partial x : 0 \le x \le K\}dt > 0. \tag{*1}$$

Proof. We divide the lengthy proof into several steps.

Step 1. It follows from assumption (H1) and proposition 5.1 that there exists a compact subset $\mathcal{A} \subset [0, K]$ such that $\mathcal{A}$ is positively invariant and attracts all solutions of subsystem (5.3) with respect to C^+. Actually, $\mathcal{A}$ could further be chosen as the global attractor of system (5.3) with respect to C^+, whose existence is guaranteed by theorem 2.2 in [HaWa]. Note that if we view y as a parameter in $(5.2)_a$, then for any $y \ge 0$, the compact set $\mathcal{A}$ is still positively invariant and globally attractive for $(5.2)_a$ with respect to C^+. So without loss of generality, we first suppose that $x \in \mathcal{A}$. Specifically, we have that $0 \le x \le K$.

Step 2. We consider the case first where

$$\int_0^\omega [-r(t) + c(t)p(t, K)]dt < 0.$$

Since X^+ is positively invariant, from $(5.2)_b$ we have

$$\dot{y}(t) \le y(t)[-r(t) + c(t)p(t, K)].$$

Then a standard comparison argument and Floquet theory on periodic linear systems imply that $\lim_{t\to\infty} y(t) = 0$. Hence system (5.2) is point dissipative.

Now suppose

$$\int_0^\omega [-r(t) + c(t)p(t, K)]dt \ge 0.$$

Step 3. We show the following argument.

Claim 1:. *There exists a constant* $\mu^* > 0$ *such that for any* $\mu \geq \mu^*$ *and for the following induced system*

$$\dot{x}(t) = x(t)g(t, x(t), x(t-\tau(t))) - \mu p(t, x(t)). \tag{5.6}$$

$x = 0$ *is globally asymptotically stable.*

Indeed, it is clear that $C^+([-\tau^*, 0], R)$, where $\tau^* = \max\{\tau(t) : 0 \leq t \leq \omega\}$, is positively invariant with respect to system (5.6) and $x = 0$ is a steady state of system (5.6). The linear variational equation of system (5.6) with respect to $x = 0$ is

$$\dot{u}(t) = [g(t, 0, 0) - \mu \partial p(t, 0)/\partial x]u(t).$$

Therefore if $\mu > \int_0^\omega g(t, 0, 0)dt / \int_0^\omega [\partial p(t, 0)/\partial x]dt \triangleq \mu_0$, then $x = 0$ is locally asymptotically stable with respect to $C^+([-\tau^*, 0], R)$. Denote $g^* = \max\{g(t, x, y) : 0 \leq t \leq \omega, \quad 0 \leq x, y \leq K\}$. It follows from $(5.2)_a$ that

$$\dot{x}(t) \leq g^* x(t) - \mu p(t, x(t)) \leq g^* x(t)$$

which implies that if $g^* < 0$, then the claim is done. Suppose $g^* \geq 0$. By the well-known mean value theorem, for any given $x \in [0, K]$, there exists a $\xi \in [0, x] \subset [0, K]$ such that

$$p(t, x) = p(t, 0) + x\partial p(t, \xi)/\partial x = x\partial p(t, \xi)/\partial x \geq x \min\{\partial p(t, x)/\partial x : 0 \leq x \leq K\},$$

from which, if we denote $a(t) = \min\{\partial p(t, x)/\partial x : 0 \leq x \leq K\}$, it follows that

$$\dot{x}(t) \leq [g^* - \mu a(t)]x(t).$$

Hence when $\mu > \omega g^* / \int_0^\omega a(t)dt \triangleq \mu_1$, where one can see why we require condition(*1), a standard comparison argument again implies that $x = 0$ is globally attractive with respect to system (5.6). Let $\mu^* = \max\{\mu_0, \mu_1\}$. Then for any $\mu \geq \mu^*$, $x = 0$ is globally asymptotically stable with respect to (5.6).

Step 4. We show another argument.

Claim 2:. $\liminf_{t\to\infty} y(t) < \mu^*$.

Otherwise. assume that there exists certain $T > 0$ such that $y(t) \geq \mu^*$ for all $t \geq T$. Then for all $t \geq T$, it follows from $(5.2)_a$ that

$$\dot{x}(t) \leq x(t)g(t, x(t), x(t - \tau(t))) - \mu^* p(t, x(t)).$$

Then Claim 1 in step 3 tells us that $\lim_{t\to\infty} x(t) = 0$. Hence for such a fixed constant $\varepsilon > 0$ satisfying

$$\int_0^\omega [-r(t) + c(t)p(t, \varepsilon)]dt < 0 \tag{*2}$$

there exists a $T_1 > 0$ such that $0 \leq x(t) \leq \varepsilon$ for all $t \geq T_1 + T$. Therefore as we did in step 2. we have

$$\dot{y}(t) \leq [-r(t) + c(t)p(t, \varepsilon)]y(t)$$

for all $t \geq T_1 + \sigma^* + T$, where $\sigma^* = \max\{\sigma(t) : 0 \leq t \leq \omega\}$. which implies that $\lim_{t\to\infty} y(t) = 0$. This contradicts our assumption and thus $\liminf_{t\to\infty} y(t) < \mu^*$. Note that such an ε satisfying (*2) does exist since $p(t, 0) \equiv 0$. Furthermore. note that T_1 could be independent of initial conditions for all those solutions starting in the compact set $\mathcal{A}$. of system (5.6) where $\mu = \mu^*$.

Step 5. Let $\delta(l) = \max\{-r(t) + c(t)p(t, l) : 0 \leq t \leq \omega\}$ for all $l \geq 0$. Then $\delta(l)$ is nondecreasing with respect to l. It follows from the assumption $\int_0^\omega [-r(t) + c(t)p(t, K)]dt \geq 0$ that $\delta(K) \geq 0$. Consequently, if $\delta(K) = 0$. then $-r(t) + c(t)p(t, K) \equiv 0$ for all $t \in [0, \omega]$ and hence

$$\dot{y}(t) \leq y(t)[-r(t) + c(t)p(t, K)] \equiv 0. \quad i.e. \quad \dot{y}(t) \leq 0.$$

From the above, together with Claim 2, that is $\liminf_{t\to\infty} y(t) < \mu^*$, we get that

$$\limsup_{t\to\infty} y(t) = \liminf_{t\to\infty} y(t) < \mu^*.$$

This means that system (5.2) is point dissipative.

Step 6. If $\delta(K) > 0$, denote $\delta_0 = \delta(K)$. Recall that functions $r(t)$ and $p(t,x)$ satisfy the following properties:

$$\int_0^\omega r(t)dt > 0,$$

$$p(t,0) \equiv 0 \quad \text{and} \quad \partial p(t,x)/\partial x \geq 0.$$

Hence, there exists an $\varepsilon_0 > 0$ such that

$$\int_\xi^{\xi+\omega} [-r(t) + c(t)p(t,\varepsilon_0)]dt < 0 \quad \text{for all } \xi > 0. \tag{*3}$$

Fix $\varepsilon_0 > 0$ satisfying (*3) and consider

$$\begin{aligned} \dot{x}(t) &= x(t)g(t,x(t),x(t-\tau(t))) - \mu^* p(t,x(t)) \\ x(\theta) &\in \mathcal{A} \quad \text{for all } \theta \in [-\tau^*,0]. \end{aligned} \tag{5.7}$$

From Claim 1, there exists a $T^* > 0$ such that $0 \leq x(t) \leq \varepsilon_0$ for all $t \geq T^*$ uniformly for all $x(t)$ satisfying (5.7). Let $M = \max\{K, \mu^* \exp[\delta_0(T^* + \sigma^* + \omega)]\}$, which is obviously a constant independent of initial data. Evidently, (H1) implies that

$$\limsup_{t\to\infty} x(t) \leq M.$$

We are going to show that $\limsup_{t\to\infty} y(t) \leq M$. Assume conversely that

$$\limsup_{t\to\infty} y(t) > \mu^* \exp[\delta_0(T^* + \sigma^* + \omega)] > \mu^*.$$

Together with Claim 2, i.e, $\liminf_{t\to\infty} y(t) < \mu^*$, there exist large $t_2 > t_1 > 0$ such that $y(t_1) = \mu^*$, $y(t_2) = \mu^* \exp[\delta_0(T^*+\sigma^*+\omega)]$ and $y(t_1) \leq y(t) \leq y(t_2)$ for all $t \in [t_1,t_2]$. Recall that

$$\dot{y}(t) \leq y(t)[-r(t) + c(t)p(t,K)]$$

which implies that

$$y(t_2) \le y(t_1)\exp\{\int_{t_1}^{t_2}[-r(t)+c(t)p(t,K)]dt\} \le y(t_1)\exp[\delta_0(t_2-t_1)].$$

Hence $t_2 - t_1 \ge \frac{1}{\delta_0}\ln\frac{y(t_2)}{y(t_1)} = T^* + \sigma^* + \omega$, i.e. $t_1 + T^* + \sigma^* + \omega \le t_2$. Then it follows that

$$0 \le x(t) \le \varepsilon_0 \qquad \text{for all } t_1 + T^* \le t \le t_2$$

and

$$\dot{y}(t) \le y(t)[-r(t) + c(t)p(t,\varepsilon_0)] \qquad \text{for all } t_1 + T^* + \sigma^* \le t \le t_2.$$

Specifically, we have

$$y(t_2) \le y(t_2-\omega)\exp\{\int_{t_2-\omega}^{t_2}[-r(t)+c(t)p(t,\varepsilon_0)]dt\} < y(t_2)$$

since $y(t_1) \le y(t_2-\omega) \le y(t_2)$, $t_2 - (t_1 + T^* + \sigma^*) \ge \omega$ and the last inequality is from (*3). This contradiction shows that

$$\limsup_{t\to\infty} y(t) \le \mu^* \exp[\delta_0(T^* + \sigma^* + \omega)].$$

and therefore $\limsup_{t\to\infty} y(t) \le M$.

Step 7. We remark that if we didn't require $x \in \mathcal{A}$, the conclusion is still true and our idea of the above proof still works. Indeed for any $(\phi, y_0) \in X^+$, denote by $(x(t), y(t))$ the corresponding solution of system (5.2) with initial values (ϕ, y_0). Then there exists a $T_2 = T_2(\phi, y_0)$ such that $x(t) \in \mathcal{A}$ for all $t \ge T_2$. In step 6, since we were discussing the long term behavior of $y(t)$, without loss of generality, we could suppose that $t_2 > t_1 \ge T_2 + \sigma^*$. Then the proof we did in the above steps is still valid. Except for a T_2 shift delay of time, every step is exactly the same.

□

Remark 5.2. Biologically, the predator response function $p(t,x)$ always satisfies $\partial p(t,x)/\partial x > 0$, and so condition (*1) is automatically satisfied.

Remark 5.3. This result is an improvement of those in the related literature (see, for example [CCH], [ZhHu], [Zh1] and related references therein).

5.4. Uniform Persistence

In this section, we are going to prove that system (5.2) is uniformly persistent under certain conditions in terms of the behavior of the flow on ∂X^0.

Since the period $\omega > 0$, there exists an integer $m > 0$ such that $m\omega \geq \tau^0$. Therefore if we denote $U = T(m\omega)$, it is well-known that U is completely continuous. As an immediate result of proposition 5.1, we then have the following.

Theorem 5.5. *Under (PD), there is a connected global attractor $\mathcal{A}$ for U in X^+.*

□

Clearly, $(0,0)$ is a trivial solution of system (5.2). If system (5.2) is uniformly persistent, then the trivial solution $(0,0)$ must be unstable. The linearized variational system of (5.2) about $(0,0)$ is

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} g(t,0,0) & 0 \\ 0 & -r(t) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}.$$

We see that the following condition could be imposed on system (5.2) in order that it be uniformly persistent.

(H2). $\int_0^\omega g(t,0,0)dt > 0$.

For system (5.2) to be uniformly persistent, we further require the following assumptions:

(H3). System (5.3) has finite isolated and acyclic $m\omega$-periodic solutions $\{x_i^*\}_{i=1}^n \subset C^+$ which is the global attractor of (5.3) with respect to $C^+ \setminus \{O\}$.

(H4). For each x_i^*, $\int_0^{m\omega}[-r(t)+c(t)p(t,x_i^*(t-\sigma(t)))]dt > 0$, $i = 1, 2, \ldots, n$.

Theorem 5.6. *Under (PD), (H2), (H3), and (H4), U is uniformly persistent with respect to $(X^0, \partial X^0)$.*

Proof. In order to apply proposition 5.2, we first need to know the structure of $\tilde{A}_\partial = \bigcup_{(o,y)\in\partial X^0}\omega(o,y)$. Let $y = 0$. Then $(5.2)_a$ becomes (5.3). By the assumption (H3), $\{(0,0)\}\bigcup\{(x_i^*,0)\}_{i=1}^n$ is the ω-limit set of (5.2) on $C^+ \times \{0\}$. If $x_t \equiv 0$, then $(5.2)_b$ becomes

$$\dot{y}(t) = -r(t)y(t). \tag{5.8}$$

Clearly, for system (5.8) the trivial solution $y = 0$ is globally asymptotically stable with respect to R^+ provided $\int_0^\omega r(t)dt > 0$ holds. Hence we get

$$\tilde{A}_\partial = \{(0,0),(x_1^*,0),\ldots,(x_n^*,0)\}$$

which is disjoint, compact, isolated and acyclic for U on ∂X^0.

Denote $M_0 = (0,0)$, $M_i = (x_i^*,0)$, $i = 1,\ldots,n$. We prove that

$$W^s(M_i)\bigcap X^0 = \varnothing \qquad \text{for all } i = 0,1,\ldots,n.$$

Recall the definition of the stable set of a compact invariant set $\mathcal{A}$.

$$W^s(\mathcal{A}) = \{x \in X : \omega(x) \neq \varnothing \quad \text{and } \omega(x) \subset \mathcal{A}\}.$$

Here each M_i consists of a single point $(x_i^*,0)$ and U is completely continuous which implies that for every $v \in X^+$, $\{U^n(v)\}_{n=0}^\infty$ is precompact. Hence for any $v \in W^s(M_i)$, it follows that $\lim_{n\to\infty} U^n(v) = (x_i^*,0)$. Thus to prove $W^s(M_i)\bigcap X^0 = \varnothing$, it suffices to show that for each M_i, $i = 0,1,\ldots,n$, there exists a $\delta_i > 0$ such that

$$\limsup_{n\to\infty} d(U^n(v), M_i) \geq \delta_i \qquad \text{for all } v \in X^0$$

which is equivalent to proving that there exists a $\delta_i > 0$, such that for any $v \in N(M_i, \delta_i) \bigcap X^0$, where $N(M_i, \delta_i)$ is the δ_i-neighborhood of M_i in X^+, there exists an $n_i = n_i(v) \geq 1$ such that $U^{n_i}(v) \notin N(M_i, \delta_i)$. We first consider M_1. Since

$$\int_0^{m\omega} [-r(t) + c(t)p(t, x_1^*(t - \sigma(t)))]dt > 0,$$

there exists an $\varepsilon_0 > 0$, such that for any $\varepsilon \in (0, \varepsilon_0)$, we have

$$\int_0^{m\omega} [-r(t) + c(t)p(t, x_1^*(t - \sigma(t))) - \varepsilon]dt > 0.$$

Denote $a = \max_{0 \leq t \leq m\omega} x_1^*(t) + 1$. For any fixed $\varepsilon \in (0, \varepsilon_0)$, by the uniform continuity of $G(t, x(t - \sigma(t)), y(t))$ on the compact set $[0, m\omega] \times [\hat{0}, \hat{a}] \times [0, a]$, there exists a constant $\delta_\varepsilon \in (0, 1)$ such that for any (x_1, y_1) and (x_2, y_2) in $[\hat{0}, \hat{a}] \times [0, a]$ with $|x_1 - x_2|_{sup} < \delta_\varepsilon$, $|y_1 - y_2| < \delta_\varepsilon$ and $t \in [0, m\omega]$, we have

$$|G(t, x_1(t - \sigma(t)), y_1(t)) - G(t, x_2(t - \sigma(t)), y_2(t))| < \varepsilon,$$

where $\hat{\cdot} \in C^+$ is a constant function and $|\cdot|_{sup}$ is the sup-norm in C^+. Since

$$\lim_{v \to M_1} T(\cdot)(v) = (x_1^*(\cdot), 0)$$

uniformly for all $t \in [0, m\omega]$, there exists a constant $\delta_1 > 0$ such that for any $v \in N(M_1, \delta_1)$, it follows that

$$|x(t + \cdot, v) - x_1^*(t + \cdot)|_{sup} < \delta_\varepsilon$$

$$\text{and} \qquad |y(t, v)| < \delta_\varepsilon \quad \text{for all } t \in [0, m\omega].$$

Assume, by contradiction, that there exists a $v_0 \in N(M_1, \delta_1) \bigcap X^0$ such that for all $n \geq 1$, $U^n(v_0) \in N(M_1, \delta_1)$. For any $t \geq 0$, decompose t into

$t = nm\omega + t_1$, where $t_1 \in [0, m\omega)$ and $n = [t/m\omega]$, the greatest integer less than or equal to $t/m\omega$. Then it follows that

$$|x(t+\cdot, v_0) - x_1^*(t+\cdot)|_{sup} = |x(t_1+\cdot, U^n(v_0)) - x_1^*(t_1+\cdot)|_{sup} < \delta_\varepsilon$$

and

$$|y(t, v_0)| = |y(t_1, U^n(v_0))| < \delta_\varepsilon$$

for all $t \geq 0$. Denote $(x(t), y(t)) = (x(t, v_0), y(t, v_0))$. Then by the periodicity of $G(t, x, y)$ in t, it follows that

$$|G(t, x(t-\sigma(t)), y(t)) - G(t, x_1^*(t-\sigma(t)), 0)| < \varepsilon \quad \text{for all } t \geq 0.$$

which implies

$$G(t, x(t-\sigma(t)), y(t)) > G(t, x_1^*(t-\sigma(t)), 0) - \varepsilon \quad \text{for all } t \geq 0.$$

Consider

$$\dot{z}(t) = z(t)(G(t, x_1^*(t-\sigma(t)), 0) - \varepsilon)$$

$$z(0) = y(0) > 0 \quad \text{since } v_0 \in X^0.$$

Then a standard comparison argument implies that

$$y(t) \geq z(t) \qquad \text{for all } t \geq 0,$$

where $z(t) = z(0)\exp[\int_0^t (G(s, x_1^*(s-\sigma(s)), 0) - \varepsilon)ds]$. However $\lim_{t\to\infty} z(t) = +\infty$ since $z(0) > 0$ and $\int_0^{m\omega}(G(t, x_1^*(t-\sigma(t)), o) - \varepsilon)dt = \int_0^{m\omega}[-r(t) - c(t)p(t, x_1^*(t-\sigma(t))) - \varepsilon]dt > 0$. Hence $\limsup_{t\to\infty} y(t) = +\infty$. This contradicts our assumption that $U^n(v_0) \in N(M_1, \delta_1)$ for all $n \geq 1$. Thus for all $v \in X^0$, we have

$$\limsup_{n\to\infty} d(U^n(v), M_1) \geq \delta_1.$$

In the same way, from $\int_0^{m\omega}[-r(t) + c(t)p(t, x_i^*(t-\sigma(t)))]dt > 0$, we can prove that there exists a $\delta_i > 0$ such that for all $v \in X^0$, it follows that

$$\limsup_{n\to\infty} d(U^n(v), M_i) \geq \delta_i \quad \text{for all } i = 2, \ldots, n.$$

There is some difference in discussing M_0 since intuitively the growth of species x is not of Kolmogorov-type. Fortunately, this shortage will not result in causing our idea not to work. Indeed the properties of the function $p(t, x)$, namely that $p(t, 0) \equiv 0$, $\partial p(t, x)/\partial x \geq 0$ imply that $|yp(t, x)| \leq \varepsilon x$ for arbitrarily small $\varepsilon > 0$ whenever x and y are both sufficiently small but positive. Then the remaining discussion is analogous provided $\int_0^\omega g(t, 0, 0)dt > 0$. We omit the details. Thus $W^s(M_i) \bigcap X^0 = \varnothing$ for all $i = 0, 1, \ldots, n$.

Note that in the above, we actually have also proved that $\{M_i : i = 0, 1, \ldots, n\}$ is isolated and acyclic for U in X^+. Then the uniform persistence of U with respect to $(X^0, \partial X^0)$ follows from theorem 5.5 and proposition 5.2.

□

Now we are in a position to prove that system (5.2) is uniformly persistent.

Theorem 5.7. *System (5.2) is uniformly persistent provided (PD), (H2), (H3) and (H4) hold.*

Proof. $T(t)$ is an ω-periodic semiflow on X^+ with $T(t)X^0 \subset X^0$ for all $t \geq 0$. Then $T(t)$ is certainly also an $m\omega$-periodic semiflow on X^+, where we choose integer m such that $m\omega \geq \tau_0$. Let $U = T(m\omega)$. Then we know that

(i) U is point dissipative in X^+ since $T(t)$ is point dissipative in X^+ by assumption (PD);

(ii) U is compact since $m\omega \geq \tau_0$ and the fact that $T(t)$ is compact for all $t \geq \tau_0$.

From theorem 5.6, U is uniformly persistent. Then the uniform persistence of $T(t)$ follows from proposition 5.3. That is, system (5.2) is uniformly persistent.

□

It is clear that compactness or certain weak compactness, such as asymptotic smoothness or α-contraction of the semiflow, is very important in discussing either continuous or discrete dynamical systems. However, it is well-known that the semiflow $T(t)$, $t \geq 0$ generated by a functional differential system is compact only when the time t is no less than the maximum of all delays appearing in the system. As a complement to this shortage, a significant result due to Hale([Hale2], theorem 4.1.1) asserts that in an equivalent norm in $C = C([-\delta, 0], R^n)$, the semiflow $T(t) : C \to C$, $t \geq 0$ is an α-contraction for all $t \geq 0$. With this argument and some newly developed fixed point theorems, one could show the existence of ω-periodic orbits in ω-periodic systems without the requirement that $\omega \geq \delta$. This is a significant improvement. Furthermore, there are many recent papers which really depend on this argument. Nevertheless, we found some minor mistakes in Hale's proof([Hale2], theorem 4.1.1, pages 61-62). First, the defined mapping $S(t) : C \to C$, $t \geq 0$ is not really an easily-shown semigroup on C since $S(0) \neq I(identity)$. Secondly, the newly defined "$* - norm$" is not equivalent to the supernorm in C. For example, choose $\phi \in C$ to be a nonzero constant function, denoted by $\phi = \hat{a}$, then $|\phi|_{sup} = |a| > 0$ while $|\phi|^* = 0$. They are not equivalent to each other. The reason is that $S(t)$ is not a semigroup on C at all, whereas in the verification of the equivalence between the $* - norm$ and the super-norm, the property of $S(t)$ being a semigroup on C was assumed. Unfortunately, at the present stage we can neither give a corrected proof nor give a counterexample. We leave the discussion on the existence and uniqueness of ω-periodic coexistence states with least period ω to future research in terms of topological degree theory and global bifurcation theory.

From proposition 5.4, theorem 5.6 or theorem 5.7, it easily follows that there exist $m\omega$-periodic coexistence states for all integers $m > 0$ such that $m\omega \geq \tau_0$. In this sense periodic coexistence states still exist. To show the existence of ω-periodic coexistence states with least period ω, our idea is to show first the uniqueness of $m\omega$-periodic coexistence states for all such m, then to suppose that there exist at least two integers, say m_1 and m_2, such that $m_i\omega \geq \tau_0$, $i = 1, 2$ and m_1 and m_2 are coprime, so we can claim the existence and uniqueness of an ω-periodic coexistence state with $m = 1$. To do this, topological degree theory will play a key role.

It is well-known that both delay systems(FDEs) and reaction-diffusion systems(PDEs) generate infinite-dimensional dynamical systems, which we denote by $T(t)$, $t \geq 0$. The significant difference between these two is that the semiflow generated by a reaction-diffusion system is compact whenever $t > 0$, whereas in the case of FDEs, only when t is no less than the delays does compactness occur. In this sense, one will see that it is easier to deal with an infinite-dimensional dynamical system resulting from spatial heterogeneity than one arising from time delays. For example, in [Zh1] a two-species periodic Kolmogorov reaction-diffusion system with spatial heterogeneity was discussed. For more details on periodic-parabolic boundary value problems, we refer to [Hes]. In this area, one of the interesting and challengable problems is the Turing instability problem, i.e. how diffusion changes the stability of an ODE or FDE system [Con], [CGS], [Dan6].

5.5. Biological Implication

In this chapter, we discussed a very general Gause-type predator-prey system with periodic delays and answered a fundamental question of biological interest concerning model (5.1), that is, how the periodic delays in both predator and prey dynamics affects the long-term survival of both species. We derived criteria for the coexistence of both the predator and the prey. Furthermore, since the growth of the predator has no logistic self-limitation, we developed a very techanical discussion on the dissipativity of system (5.1). We actually have shown the so-called permanence(dissipativity and uniform persistence) of both the predator and the prey. Biologically, dissipativity means the species will not grow beyond all bounds, and uniform persistence means the species' survival for all time. The criteria derived here are natural in that in theorem 5.7, condition (PD) implies that the growth of either species cannot become unbounded, and condition (H2) implies that the prey, as the food sourse for predator, cannot become extinct, since in our system the predator is assumed to die out in the absence of prey. Conditions (H3)-(H4) imply that the predator response cannot be too small. Under these natural hypotheses, the predator-prey system exhibits permanence(long-term survival of the system).

CHAPTER 6

FURTHER DISCUSSION AND REMARKS

In this thesis, we have carried out a detailed discussion for the long term dynamical behaviors of periodic systems (2.1), (3.1) and (5.1). Throughout this thesis, our emphasis centred around the global asymptotical stabilities for monotone periodic systems (chapters 2, 3 and 4) and permanence (dissipativity and uniform persistence) for a non-monotone Gause-type predator-prey periodic system(chapter 5).

On the basis of what we did in this thesis, it is possible to extend some of our ideas to more general cases in applications. Specifically, those results derived in chapter 4 on discrete monotone dynamical systems should have very good applications in periodic differential delay systems if we could analogously set up a Floquet theory for linear periodic differential delay systems. Furthermore, in this thesis we did not consider spatial heterogeneity and randomness. Hence the following three topics, i.e. Floquet theory for delay periodic systems, the Turing instability problem(spatial heterogeneity) and stochastic differential systems(randomness), will be very important for further discussion.

6.1. Floquet Theory for Delay Equations

For ordinary differential equations, Floquet theory has been well established. The Floquet theorem asserts that for linear periodic ordinary differential equations, there exists a linear invertible periodic transformation that will transform the equation to an autonomous one. One might expect to establish a Floquet theorem for differential delay equations in an analogous way. However, differential delay equations have many different features from ordinary differential equations. First of all, they are infinite dimensional systems. As a result, their Floquet theorem might be much more complicated. Secondly, there may exist a nontrivial solution that goes to zero faster than any exponential. Such solutions are called *small solutions.* Thus, an invertible periodic transformation, in general, does not exist and the analog of the Floquet theorem may not hold anymore. Examples can be found in Hale's book [Hale1].

Floquet theory would play a very important role in the study of linear periodic differential delay equations. However, a general Floquet theorem for linear periodic differential delay equations is still under investigation. At present, we only can *almost* prove the following conjecture [PeFr3]:

Conjecture 6.1. *Consider*

$$\dot{x}(t) = a(t)x(t) + b(t)x(t - \tau(t)), \tag{6.1}$$

where $a(t)$, $b(t)$, $\tau(t)$ *are supposed to be T-periodic and* $b(t) \geq 0$, $\tau(t) \geq 0$ *in* $[0, T]$. *Then* $x = O$ *in equation (6.1) is asymptotically stable if*

$$\int_0^T [a(t) + b(t)]dt < 0.$$

This conjecture is analogous to a result in the autonomous case where the linear stability of all equilibra could be determined by the associated cooperative and irreducible system of ordinary differential equations since they have exactly same equilibra([Sm8] pages 92-93).

6.2. Turing Instability Problem

In 1952, Turing [Tur] found that in some systems, when diffusions were considered, the stability of the corresponding ODE systems may be changed. The Turing instability problem is to fully understand just what features of reaction-diffusion systems are necessary and sufficient for Turing instability [Con], [Dan6], [FrPe2], [Tur]. In the past decades, the Turing instability problem has attracted more and more mathematicians and became a very hard and challenging problem.

In [Dan6], Dancer considered

$$\begin{aligned} \frac{\partial u}{\partial t} &= r_1(t)\Delta u + u(a(t) - b(t)u + c(t)v) \quad in \Omega \times [0, \infty) \\ \frac{\partial v}{\partial t} &= r_2(t)\Delta v + v(d(t) + e(t)u - f(t)v) \\ \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 \quad on \quad \partial\Omega \times [0, \infty). \end{aligned} \tag{6.2}$$

and

$$\begin{aligned} \frac{du}{dt} &= u(a(t) - b(t)u + c(t)v) \\ \frac{dv}{dt} &= v(d(t) + e(t)u - f(t)v). \end{aligned} \tag{6.3}$$

where Δ is the Laplacian operator, Ω is a bounded open set in $\mathbb{R}^m$ with smooth boundary and $a, b, c, d, e, f, r_1, r_2$ are T-periodic and $r_1(t), r_2(t) > 0$. Suppose that (u_0, v_0) is a strictly positive T-periodic solution of (6.3) which is stable (as a solution of (6.3)). We say that a Turing instability occurs if (u_0, v_0) is unstable as a solution of the partial differential equations (6.2). In the autonomous case and with u_0 and v_0 independent of time, this problem has been studied extensively [Con] and it is found that Turing instabilities do not occur for the standard ecological models (standard predator-prey, competing species or cooperating species) but sometimes do occur in general. For these three classes of models, one can also easily show that there are no non-constant periodic solutions in the antonomous case. Thus the interesting case is where the equations are not autonomous. Dancer proved in [Dan6] that Turing instabilities do not occur for the competing species or cooperating species models in the time dependent case. His proof depends on the order structure. More surprisingly, it was shown that for predator-prey models, Turing instabilities sometimes occur. These even occur if r_1 and r_2 are constant although Turing instabilities do not occur if $r_1(t) \equiv r_2(t)$. As pointed out by Dancer [Dan6], this has significant implications for the partial differential equation in the predator-prey case because it implies that the solution of (6.2) that one sees need not be the simplest solution and that bifurcations of solutions with x dependence occur. Dancer's methods also imply that uniqueness of strictly positive periodic solutions may fail for a periodic predator-prey model. As pointed out by Dancer [Dan6] once again, the time periodic problem may be significantly more complicated than the autonomous problem.

In [FrPe2], the following initial boundary value problem was discussed:

$$\begin{aligned}
&\frac{\partial I(x,t)}{\partial t} = d_1(x)\Delta I(x,t) + \alpha m(x,t-\sigma) - \gamma I(x,t) - \alpha e^{-\gamma\tau} m(x,t-\tau)\\
&\frac{\partial m(x,t)}{\partial t} = d_2(x)\Delta m(x,t) + \alpha e^{-\gamma\tau} m(x,t-\tau) - \beta m^2(x,t)\\
&\qquad \text{in} \quad \Omega \times [0,\infty) \qquad\qquad (6.4)\\
&\qquad \frac{\partial I}{\partial n} = 0, \quad \frac{\partial m}{\partial n} = 0 \qquad \text{on} \quad \partial\Omega \times [0,\infty)\\
&\qquad I(x,\theta) = \varphi(x,\theta) \geq 0, \quad m(x,\theta) = \psi(x,\theta) \geq 0, \quad x \in \Omega, \quad \theta \in [-\tau, 0],
\end{aligned}$$

where α, β, τ are positive constants and $\sigma \geq 0$. the diffusive coefficients $d_1(x)$ and $d_2(x)$ are non-negative. It was shown that Turing instability does not occur in (6.4). However diffusions benefit the population survival.

As indicated by those few published works, it is very interesting and challenging to investigate the Turing instability problem.

6.3. Stochastic Models

If we allow for some randomness in some of the coefficients of a differential equation, we often obtain a more realistic mathematical model of the situation.

As pointed out by Oksendal [Ok], there are several reasons why one should learn more about stochastic differential equations: they have a wide range of applications outside mathematics, there are many fruitful connections to other mathematical disciplines and the subject has a rapidly developing life of its own as a fascinating research field with many interesting unanswered questions. To consider stochastic models is one of our future research interests.

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IMAGE EVALUATION TEST TARGET (QA-3)

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