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UNIVERSITY OF ALBERTA

A STUDY OF MATHEMATICAL MODELS FOR A CHEMOSTAT WITH PERIODIC INPUT AND FOR A CYCLOSTAT

by

FENG YANG

A THESIS

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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 A STUDY OF MATHEMATICAL MODELS FOR A CHEMOSTATS WITH PERIODIC INPUT AND FOR A CYCLOSTAT submitted by FENG YANG in partial fulfillment of the degree of Doctor of Philosophy.

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TO MY PARENTS AND MY FIANCÉE JUN LI

ABSTRACT

In this thesis, three individual topics in mathematical biology are discussed. Two of the topics are on mathematical biology models while the other one is on a theorem called the Butler-McGehee lemma, a lemma which is often referred in the study of mathematical biology.

The main result in chapter 2 is to generalize one of the various formats of the Butler-McGehee lemma (Butler and Waltman, 1986). An application to the uniform persistence of a class of dynamical systems which are not necessarily dissipative is given. In addition, we also give some discussions on the mathematical tools which are useful to the analysis of the biological models.

In chapter 3, a system of ordinary differential equations is utilized in order to model the interactions of n competing predators on a single prey population in a chemostat environment with a periodic nutrient input. In the case of one or no predators, criteria for the existence of periodic solutions are given. In the general case, conditions for all populations to persist are derived.

A new system called a cyclostat is modeled in chapter 4. First a single species system is considered. The criteria for survival vs. extinction of the species are given. The competition between two species in the system is also considered. The one result shows that under certain conditions, we can not have coexistence of the both species while the other result gives the conditions for persistence. The existence of such a case can be obtained by utilizing bifurcation theory (see Smith, Tang and Waltman, 1991).

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CHAPTER 1

INTRODUCTION

1.1. Biological background.

The two mathematical models considered in this thesis are based on the continuous culture technique used in laboratory experiments which was mainly developed in order to study microbial growth under nutrient limitation in a controlled environment, see Monod (1942) and, Novick and Szilard (1950).

A good description of the continuous culture technique can be found in Kubitschek (1970). The first model in our research describes an environment of chemostat with periodic input. The chemostat is a laboratory apparatus used in the continuous culture technique. Figure 1 gives a schematic diagram of a chemostat. Basically one can think of a chemostat as a well-stirred culture vessel, with an input and an output, which is inoculated with microorganisms. All essentials for growth of the microorganisms are added in the nutrient which is supplied through the input into the vessel continuously at a certain (a constant or a periodic fluctuating) rate. The output of the culture vessel removes the contents of the vessel at a rate same as the input rate so that the volume in the culture vessel remains constant. The removed contents contain proportional amounts of microorganisms, byproducts, and other growth medium.

Later, a more complicated laboratory apparatus was developed. This apparatus is called "gradostat", see Jäger, So, Tang and Waltman (1987). It is similar

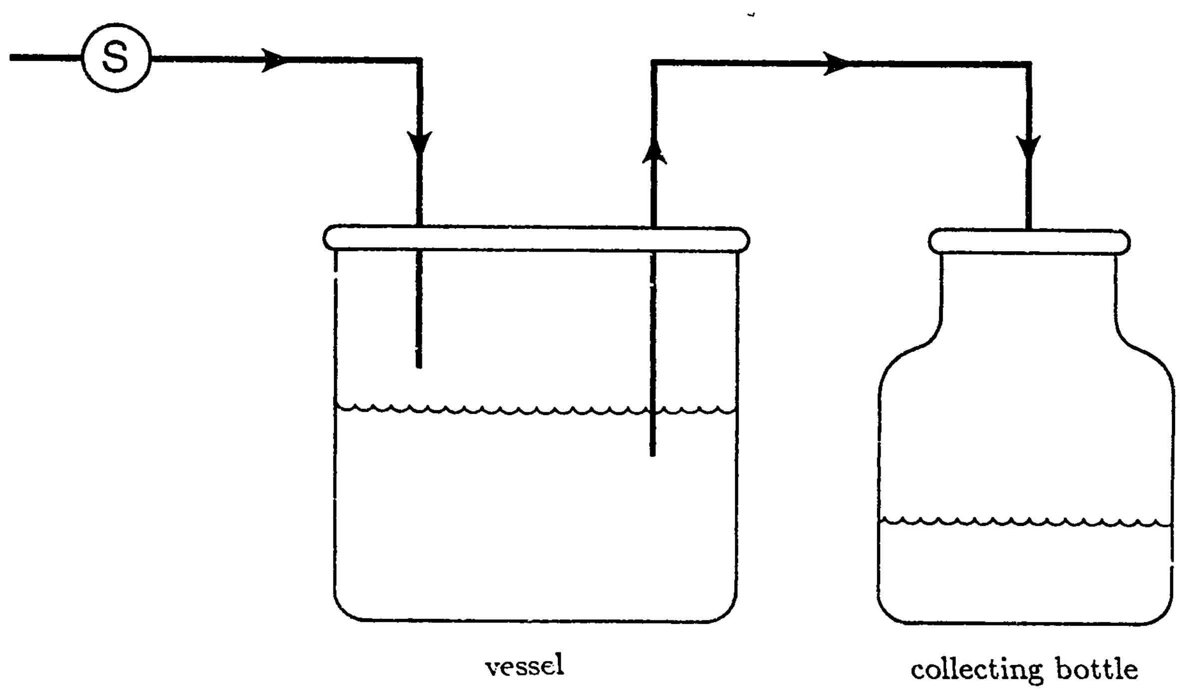


Fig. 1. Diagram of a chemostat.

to a chemostat with several culture vessels. The vessels are connected in a line. The input is attached to the first vessel while the output is attached to last one. Between the adjacent vessels is a two way flow. All the flows including the input and output are at a same rate so that the volume in each vessel is held constant. The second model in our research, however, describes another kind of multi-vessel system. This system, we call it "cyclostat", is almost the same as the gradostat system except in the way of connecting the vessels. In a cyclostat system, the vessels are connected in a circle with the input and the output inserted into a same vessel, and the flow is a one way flow. The term "cyclostat" comes from the way of connecting vessels. Figure 2 and Figure 3 illustrate the connection in gradostat and in cyclostat, respectively.

The continuous culture technique is used in industry for the economical production of useful microorganisms, see Herbert, Elsworth and Telling (1956) as well as for the simulation of biological waste decomposition or water purification by microorganisms, see Yang and Humphrey (1975).

In the first model, we shall be mainly interested in studying the competition between n species on a single prey which in turn feeds on the input nutrient. The whole system is put in a chemostat environment with a periodic input. This approach simply combines two previous settings: one is a system with two trophic levels in a chemostat environment with constant input, see Butler, Hsu and Waltman (1983), Butler and Waltman (1981), Butler and Wolkowicz (1986, 1987b), Wolkowicz (1989), and the other one is that with only one trophic level in a chemostat with periodic input, see Hale and Solominos (1983), Smith (1981), Hsu (1985).

The second model in this thesis has been set up by H.I. Freedman in discussion of this thesis. Most of the results has been obtained with one species living in a cyclostat environment with constant input. The case of two competitors in a

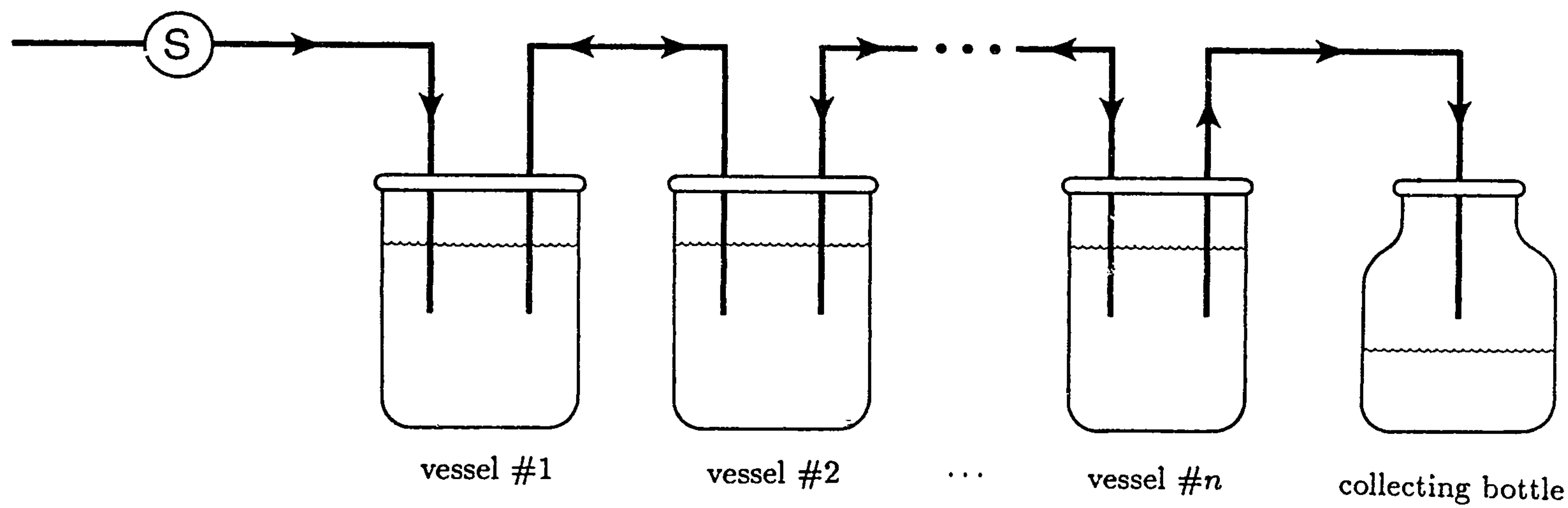


Fig. 2. Diagram of a gradostat.

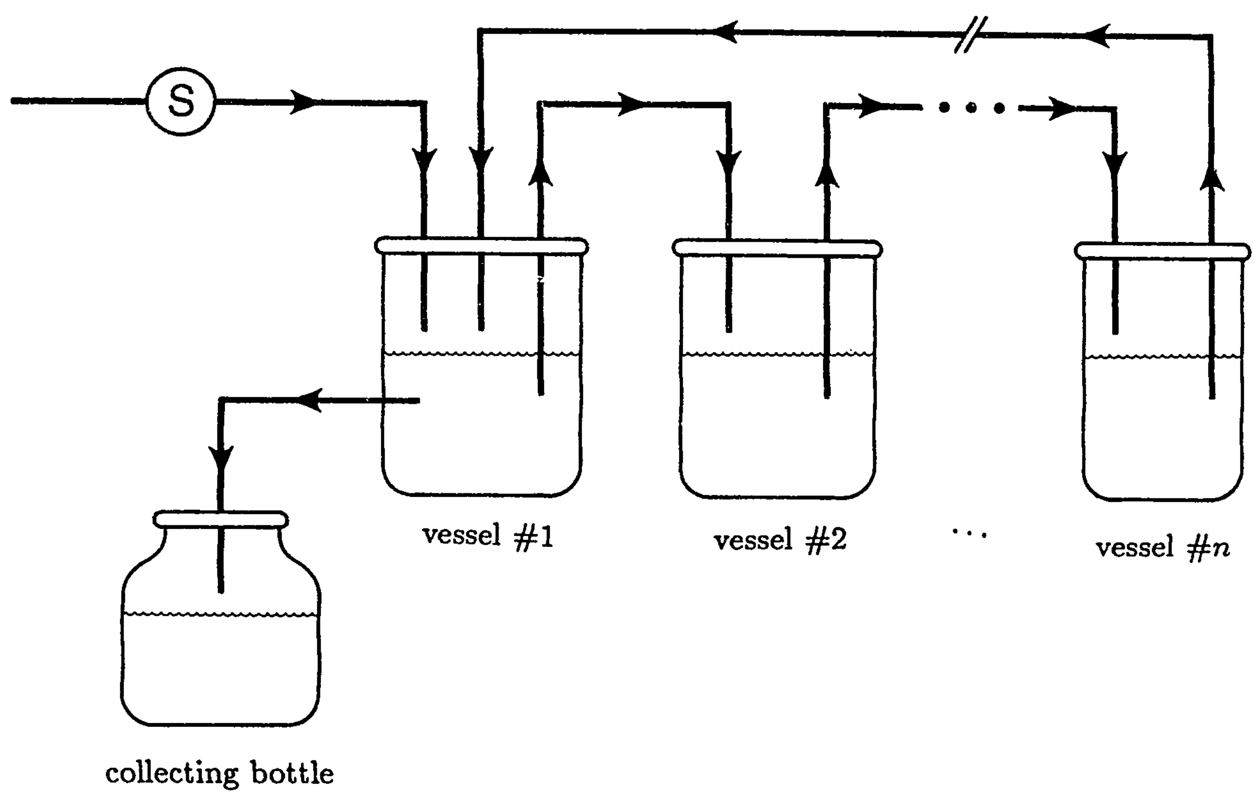


Fig. 3. Diagram of a cyclostat.

cyclostat with constant input is also considered. The result shows that under certain conditions, there is no coexistence. Up to the time of completion of this thesis, the author has not seen any research concerned about the so-called "cyclostat" or any similar system.

1.2. Mathematical definitions.

In this section, we give definitions needed for the study in this thesis. For the sake of convenience and efficiency, we also need some notations which simplify the statement of this thesis.

First, we define both $\dot{}$ and $'$ operators as $\frac{d}{dt}$.

Since both of the two models discussed in this thesis describes a dynamical systems in a certain way, most of the studies are carried out on the dynamical systems described by the models. So we start with the notations and definitions in the theory of dynamical systems.

Let X be a locally compact metric space with metric d. For any subset $K \subseteq X$, we shall use $\overset{\circ}{K}, \partial K, \overline{K}$ to denote its interior, boundary and closure, respectively. One example is $X = \mathbb{R}^n$, the n-dimensional Euclidean space in which we take $\mathbb{R}^n_+ = \{x \in \mathbb{R}^n \mid x_i \geq 0, i = 1, \ldots, n\}$ as K. Then $\overset{\circ}{K}$, ∂K, $\overline{K}$ represent the sets

$$\{x \in \mathbb{R}^n \mid x_i > 0, i = 1, \ldots, n\},$$
$$\{x \in \mathbb{R}^n \mid x_i = 0, \text{ for some } i = 1, \ldots, n\}, \qquad \text{and}$$
$$\mathbb{R}^n_+,$$

respectively. We denote by $\mathcal{F}$ a continuous flow $(X, \mathbb{R}, \pi)$ on X. The orbit, positive semi-orbit and negative semi-orbit of $\mathcal{F}$ through a point x of X will be denoted by $\gamma(x), \gamma^+(x), \gamma^-(x)$, respectively, and the ω- and α- limit sets of the orbit will be denoted by $\Lambda^+(x)$, $\Lambda^-(x)$, respectively. With these notations, we give the following definitions.

DEFINITION 1.1: A subset M of X is called *invariant* if for all $x \in M, \gamma(x) \subseteq M$. A *positively (negatively) invariant set* is a subset M of X such that for all $x \in M, \gamma^+(x)(\gamma^-(x)) \subseteq M$. M is called a *maximal invariant set* in a neighborhood of itself if it is an invariant set such that in the neighborhood there is no other invariant set containing M. A maximal invariant set is necessarily closed.

DEFINITION 1.2: The flow $\mathcal{F}$ is *dissipative* if for each $x \in X$, $\Lambda^+(x) \neq \phi$ and the invariant set $\Omega(\mathcal{F}) = \bigcup_{x \in X} \Lambda^+(x)$ has a compact closure.

DEFINITION 1.3: A nonempty subset M of X, invariant for $\mathcal{F}$, is called an *isolated invariant set* if it is the maximal invariant set in some neighborhood of itself. The neighborhood is called an isolating neighborhood. An isolated invariant set is necessarily closed, and if it is compact, a compact isolating neighborhood can be found.

DEFINITION 1.4: The *stable set* $W^+(M)$ of an isolated invariant set M is defined to be $\{x \in X : \Lambda^+(x) \neq \phi, \Lambda^+(x) \subseteq M\}$ and the *unstable set* is defined to be $\{x \in X : \Lambda^-(x) \neq \phi, \Lambda^-(x) \subseteq M\}$.

DEFINITION 1.5: The *weakly stable set* $W_w^+(M)$ of an isolated invariant set M is defined to be $\{x \in X : \Lambda^+(x) \cap M \neq \phi\}$, and the *weakly unstable set* $W_w^-(M)$ is defined to be $\{x \in X : \Lambda^-(x) \cap M \neq \phi\}$.

DEFINITION 1.6: Let M, N be isolated invariant sets (not necessarily distinct). We shall say that M *is chained to* N, written $M \to N$, if there exists $x \notin M \cup N$ such that $x \in W^-(M) \cap W^+(N)$.

DEFINITION 1.7: A finite sequence $M_1, M_2, \ldots, M_k$ of isolated invariant sets will be called a *chain* if $M_1 \to M_2 \to \cdots \to M_k (M_1 \to M_1$, if $k = 1)$. The chain will be called a *cycle* if $M_k = M_1$.

Persistence is a popular topic in the study of mathematical ecology. Persistence for dynamical system can defined in several different ways. The following are three of those primative definitions. In the definitions, we always assume that E is a positively invariant set for the system.

DEFINITION 1.8: $\mathcal{F}$ will be called *weakly persistent in a subset* E of X if for all $x \in \overset{\circ}{E}, \limsup_{t\to\infty} d(\pi(x,t), \partial E) > 0$.

DEFINITION 1.9: $\mathcal{F}$ will be called *persistent in a subset* E of X if for all $x \in \overset{\circ}{E}$, $\liminf_{t\to\infty} d(\pi(x,t), \partial E) > 0$.

DEFINITION 1.10: $\mathcal{F}$ will be called *uniformly persistent in a subset* E of X if there exists $\zeta > 0$ such that for all $x \in \overset{\circ}{E}$, $\liminf_{t\to\infty} d(\pi(x,t), \partial E) > \zeta$.

For a system of differential equations $\dot{x} = f(x)$ defined in $\mathbb{R}^n$, we can take $\mathbb{R}^n$ as X, $\mathbb{R}^n_+$ as E. Then the system is said to be (weakly) persistent if for all solutions $x(t)$ with $x(0) \in \overset{\circ}{E}$, then $x_i(t) > 0$ for $t > 0$ and $\liminf_{t\to\infty} x_i(t) > 0$, $i = 1, \ldots, n$ (replace liminf with limsup for weak persistence). Further if there exists $\zeta > 0$ such that $\liminf\limits_{t\to\infty} x_i(t) \geq \zeta$ for all such $x(t)$, then the system is said to be uniformly persistent.

It is well-known that for an invariant set E, its boundary ∂E is also invariant. Then we shall denote by $\partial_E \mathcal{F}$ the boundary flow of E, the flow restricted on the boundary of E. Without confusion, we shall use $\partial\mathcal{F}$ for $\partial_E\mathcal{F}$.

DEFINITION 1.11: $\partial\mathcal{F}$ is *isolated* if there exists a covering $\mathcal{M}$ of $\Omega(\partial\mathcal{F})$ by pairwise disjoint, compact, isolated invariant sets $M_1, M_2, \ldots, M_k$ for $\partial\mathcal{F}$ such that each M_i is also isolated for $\mathcal{F}$. $\mathcal{M}$ is then called an *isolated* covering.

DEFINITION 1.12: $\partial\mathcal{F}$ will be called *acyclic* if there exists some isolated covering $\mathcal{M} = \{M_i\}_{i=1}^k$ of $\Omega(\partial\mathcal{F})$ such that no subset of the $\{M_i\}$ forms a cycle (see

Definition 1.7). Otherwise, $\partial\mathcal{F}$ will be called *cyclic*. An isolated covering satisfying this condition will also be called acyclic.

DEFINITION 1.13: For any subset G of X, we define

$$L^+(G) \triangleq \bigcup_{x\in G} \Lambda^+(x) \quad \text{and} \quad L^-(G) \triangleq \bigcup_{x\in G} \Lambda^-(x).$$

In our discussion of the cyclostat model, we also need the concept of a cooperative system. To define such a system, we need to establish a partial order $\preceq$ on X. An example in $\mathbb{R}^n$ is that for any x and y in $\mathbb{R}^n$, we say $x \preceq y$ if $x_i \leq y_i$ for $i = 1, \ldots, n$.

DEFINITION 1.14: A (semi-)dynamical system $(X, \mathbb{R}, \pi)$ is called cooperative with respect to the partial order $\preceq$ on X if for any pair of $x, y \in X$ with $x \preceq y$, we have $\pi_t(x) \preceq \pi_t(y)$ for all $t \geq 0$.

Let $m = \{m_1, \ldots, m_n\}, m_i \in \{0,1\}, i = 1, \ldots, n$. We define a matrix

$$P_m = diag((-1)^{m_1}, \ldots, (-1)^{m_1}).$$

As another example of partial order in $\mathbb{R}^n$, for a pair of $x, y \in \mathbb{R}^n$, we say that $x \preceq y$ if and only if each component of $P_m(x-y)$ is nonnegative. In the study of our models, the partial order $\preceq$ on $\mathbb{R}^n$ is defined as in the above example by certain P_m. The cooperativity of a system on $\mathbb{R}^n$ is always with respect to this partial order. Therefore, for the sake of convenience, a system can be called cooperative without mentioning the partial order.

DEFINITION 1.15: A cylinder-like two-dimensional C^2-manifold with one boundary in $\mathbb{R}^k$, $k \geq 3$, is a two-dimensional manifold which is globally C^2-homeomorphic to the half cylinder,

$$\mathcal{C} = \left\{(z_1, \ldots, z_k) \in \mathbb{R}^k \mid z_1^2 + z_2^2 = 1, z_3 \geq 0, z_i = 0 \quad \text{for} \quad i > 3\right\}.$$

DEFINITION 1.16: Let $A, B \subset X$ be nonempty, we define the distance between them as

$$d(A, B) = inf\{d(x, y) \quad | \quad x \in A, y \in B\}.$$

Chapter 2

MATHEMATICAL PRELIMINARIES

2.1. Introduction.

Recently, there have appeared in the literature several papers dealing with persistence theory in dynamical systems, Butler, Freedman and Waltman (1986), Butler and Waltman (1986), Fonda (1988), Freedman and Moson (in press), Freedman and Waltman (1984, 1985), Gard (1987), Hofbauer and So (1989) and Hutson and Schmitt (preprint), semi-dynamical systems and related systems Butler and Waltman (1986), Dunbar, Rybakowsky and Schmitt (1986), Fonda (1988), Freedman and So (1987, 1989), Hale and Waltman (1989) and Hallam and Ma (1986) and their applications to ecological modeling Butler, Freedman and Waltman (1984), Freedman, Addicott and Rai (1987), Freedman and So (1987, 1989), Freedman and Waltman (1984, 1985), Kirlinger (1986, 1988). For a complete list of the various types of persistence for dynamical systems, their definitions and relations, see Freedman and Moson (in press).

When applying persistence theory to the question of survival versus extinction in models of interacting populations, a theorem known as the Butler-McGehee lemma is usually required. This lemma may take on various formats, depending on the nature of the dynamical or semi-dynamical system.

The original version of this lemma appears in Freedman and Waltman (1984), the setting for which is a hyperbolic restpoint of an autonomous ordinary differential equation. Since then, it has been extended to a compact isolated invariant set, instead of just a rest point, to a continuous flow on a locally compact metric space by Butler and Waltman (1986) and to continuous semi-flows by Dunbar, Rybakowsky, and Schmitt (1986). Later, Freedman and So (1989) have developed this lemma to a form utilizable for discrete semi-dynamical systems. The latest form for locally compact metric space has been given a new proof by Hofbauer and So (1989). We also mention that Hale and Waltman (1989) have obtained results for a complete metric space, not necessarily locally compact. This result, which is in the setting of an asymptotically smooth C^0-semigroup, is useful in studying the persistence of population models whose dynamics involve such concepts as delays or diffusions in functional differential equations or partial differential equations, respectively.

All the above theorems deal with a point x and its limit set $\Lambda^+(x)$ or $\Lambda^-(x)$ in phase space (see Chapter 1 for definitions). The object of this chapter is to generalize the Butler-McGehee lemma in such a way as to encompass orbits from a set G rather than from a single point and to consider the closure of the union of ω-limit (α-limit) set of all points in G. Obviously, if we take $G = \{x\}$, our result will reduce to one of the various known forms of the Butler-McGehee lemma. With this generalization, we can directly show the uniform persistence of certain systems by taking $G = E \backslash D$ (see Theorem 2.6).

In addition to the generalization of Butler-McGehee lemma, we shall also develop some useful tools for the study of the cyclostat model.

This chapter is organized as follows: In Section 2.2, the generalization of Butler-McGehee lemma is given together with a variation for discrete systems. Several corollaries are also given. Section 2.3 considers an application of the main theorem in Section 2.2 to uniformly persistent systems. Section 2.4 gives some results on a class of polynomials related to the cyclostat models in Chapter 4;

and the section also gives a theorem on the ω-periodic solutions of an ω-periodic system of ordinary differential equations.

2.2. Generalization of Butler-McGehee lemma.

In this section, we shall generalize the so-called Butler-McGehee lemma. First, we give two lemmas which will be called in the proof of the main theorem in this section.

LEMMA 2.1. *$\overline{L^+(G)}$ and $\overline{L^-(G)}$ (see Definition 1.13) are invariant.*

PROOF: It is well-known that $\Lambda^+(x)$ is invariant. Then, as a closure of a union of invariant sets, $\overline{L^+(G)}$ is invariant (see Theorems 1.2 and 1.3 in Chapter II of Bhatia and Szegö (1970)). The proof is similar for the case of $L^-(G)$. □

LEMMA 2.2. *Let $M \subset X$ be a compact isolated set for $\mathcal{F}$. For any set $G \subset X \backslash W^+(M)$, if $\overline{L^+(G)} \cap M \neq \phi$, then there exist a compact isolating neighborhood V of M and a sequence $\{y_n\} \subset \mathring{V}$ satisfying the following:*

(i) $y_n \to M$ as $n \to \infty$;

(ii) there exists $\{t_n\} \subset \mathbb{R}_+$ such that for all n, $\pi(y_n, -t_n) \in \partial V$ and $\pi(y_n, t) \in \mathring{V}$ if $t \in [0, t_n)$;

(iii) $\{\pi(y_n, -t_n)\}$ converges to a point $p \in \overline{L^+(G)}$.

PROOF: With the assumption of $\overline{L^+(G)} \cap M \neq \phi$, we may pick a compact isolating neighborhood V_1 of M and a sequence $\{z_n\} \subset L^+(G) \cap \mathring{V}_1$ so that $z_n \to M$ as $n \to \infty$. If $\gamma^-(z_n) \backslash \mathring{V}_1 \neq \phi$ for all n, then define $y_n \triangleq z_n$ and $V \triangleq V_1$. It is easy to see that so-defined $\{y_n\}$ and V satisfy (i) and (ii). In the other case, if $\gamma^-(z_n) \subset \mathring{V}_1$ for some n, then $\Lambda^-(z_n) \neq \phi$ and $\Lambda^-(z_n) \subset M$. It follows that there exists $x \in G \subset X \backslash W^+(M)$ such that $\Lambda^+(x) \cap M \neq \phi$ since $z_n \in L^+(G)$. A compact isolating neighborhood V of M can be found so that $x \notin V$. Since $x \in W_w^+(M) \backslash W^+(M)$, there exists a sequence $\{s_n\} \subset \mathbb{R}_+$ satisfying: (a) $s_n \to \infty$

as $n \to \infty$ while $s_n < s_{n+1}$; (b) $\pi(x, [s_n, s_{n+1}])\backslash V \neq \phi$; and (c) $\pi(x, s_n) \to M$ as $n \to \infty$ while $\pi(x, s_n) \in \overset{\circ}{V}$ for all n. Now, we define $y_n \triangleq \pi(x, s_n)$. By property (b), there exists $\{t_n\} \subset \mathbb{R}_+$ such that $\pi(x, s_n - t_n) \in \partial V$ while $\pi(x, s_n - t) \in \overset{\circ}{V}$ for all $t \in (0, t_n)$. The V and $\{y_n\}$ thus defined also satisfy (i) and (ii).

Since ∂V is compact, there exists a convergent subsequence $\{\pi(y_{n,} - t_n)\}$. Correspondently to this subsequence, we obtain subsequences of $\{y_n\}$ and $\{t_n\}$. These two subsequences of $\{y_n\}$ and $\{t_n\}$ are what we really want for (iii), and thus for the lemma. □

Following is the main theorem, a generalization of Butler-McGehee lemma, of this section (see Definition 1.13 for $L^+(G)$ and lmg).

THEOREM 2.3. *Let $M \subset X$ be a compact isolated invariant set for $\mathcal{F}$. For any set $G \subset X\backslash W^+(M)$, if $\overline{L^+(G)} \cap M \neq \phi$, then $\overline{L^+(G)} \cap W^+(M)\backslash M \neq \phi$ and $\overline{L^+(G)} \cap W^-(M)\backslash M \neq \phi$.*

PROOF: We utilize arguments similar to those in the proof of Lemma 2.1 and Theorem 4.1 of Butler and Waltman (1986).

By the Lemma 2.2, it suffices to show that $t_n \to \infty$ as $n \to \infty$. In fact, if it is true, then for any $t > 0$, there exists N such that $t_n > t$ for all $n \geq N$. It follows that for all $t > 0$,

$$\pi(p, t) = \lim_{n \to \infty} \pi\big(\pi(y_{n,} - t_n), t\big) = \lim_{n \to \infty} \pi\big(y_{n,} - (t_n - t)\big) \in V, \qquad (2.1)$$

since $\pi\big(y_{n,} - (t_n - t)\big) \in \overset{\circ}{V}$ for large n. (2.1) shows that $\gamma^+(p) \subset V$ and hence that $\Lambda^+(p) \neq \phi$ and $\Lambda^+(p) \subset M$ since V is compact and isolating M. It follows that $p \in \overline{L^+(G)} \cap W^+(M)\backslash M$, and so $\overline{L^+(G)} \cap W^+(M)\backslash M \neq \phi$.

However, the boundedness of any subsequence of $\{t_n\}$ violates the continuous dependence of orbits on initial points since M is compact and invariant. It follows that $t_n \to \infty$ as $n \to \infty$. This completes the proof of the theorem. □

REMARK: It is easy to see that the same result can be applied to the set $L^-(G)$ instead of $L^+(G)$. And if $W^+(M)$ is replaced by $W^-(M)$, the result still holds.

The following corollary is one of the various forms of the Butler-McGehee lemma (Theorem 4.1 of Butler and Waltman (1986)).

COROLLARY 2.4. *Let M be a compact isolated invariant set for $\mathcal{F}$. Then for any $x \in W_w^+(M)\backslash W^+(M)$, it follows that*

$$\Lambda^+(x) \cap W^+(M)\backslash M \neq \phi, \ \Lambda^+(x) \cap W^-(M)\backslash M \neq \phi.$$

A simlilar result holds for $\Lambda^-(x)$.

PROOF: The corollary follows by applying Theorem 2.3 to $G = \{x\}$. In this case, $L^+(G) = \Lambda^+(x)$. □

REMARK: Here, we can demonstrate by an example the fact that Theorem 2.3 is not a trivial extension of the Butler-McGehee lemma (i.e., the conditions in Theorem 2.3 do not imply those in the Butler-McGehee lemma). This example is given by the Lotka-Volterra equations

$$\begin{cases} \dot{x} = x(\alpha - \beta y), \\ \dot{y} = y(-\gamma + \delta x), \quad x(0),\ y(0) \geq 0, \quad \alpha, \beta, \gamma, \delta > 0. \end{cases} \tag{2.2}$$

Consider $X = \mathbb{R}^2_+$, $M = \{(0,0)\}$. Then $W^+(M) = \{(0,y) \mid y \geq 0\}$. Let $G = \mathring{\mathbb{R}}^2_+$. Then $\overline{L^+(G)} = X$ while $W_w^+(M) = W^+(M)$.

We now give a variant of Theorem 2.3 which is valid for discrete dynamical systems. All notations are adopted from Freedman and So (1989) except that $f : X \to X$ is a bijection which defines a discrete dynamical system on X. Further $L^+(G)$ is defined analogously as in Definition 1.13 in the sense of discrete systems.

THEOREM 2.5. *Let M be a compact isolated invariant set in X. For any $G \subset X\backslash W^+(M)$, if $\overline{L^+(G)} \cap M \neq \phi$, then $\overline{L^+(G)} \cap W^+(M)\backslash M \neq \phi$ and $\overline{L^+(G)} \cap W^-(M)\backslash M \neq \phi$.*

PROOF: The proof follows analogous to the proof of Theorem 2.3, noting that f maps a compact set into a compact set. □

2.3. Application to uniform persistence.

In this section, we consider only continuous flows. Let $E \subset X$ be a positively invariant set for $\mathcal{F}$ and let D be a nonempty closed set in E. Suppose B is a maximal invariant set in D for $\mathcal{F}$. Denote by $\mathcal{F}_B$ the flow $\mathcal{F}$ restricted to B. Then we have $\Omega(\mathcal{F}_B) \triangleq \bigcup_{x\in B} \Lambda^+(x) = L^+(B)$.

THEOREM 2.6. *Let E, D and $B \neq \phi$ be defined as above. Further, assume that $E\backslash D$ is positively invariant and $\mathcal{F}_B$ is dissipative, isolated and acyclic with acyclic covering $\mathcal{M}$. Denote $M = \bigcup_{M_i \in \mathcal{M}} M_i$. If there exist a compact neighborhood N of M in D and $\alpha_0 > 0$ such that for all $x \in E\backslash D$,*

$$\liminf_{t\to\infty} d\big(\pi(x,t), D\backslash N\big) \geq \alpha_0, \tag{2.3}$$

then $\mathcal{F}$ is uniformly persistent if and only if

(H) for each $M_i \in \mathcal{M}, W^+(M_i) \cap (E\backslash D) = \phi$.

PROOF: The necessity of (H) for the uniform persistence of $\mathcal{F}$ is obvious. Now suppose (H) holds. We divide $E\backslash D$ into two sets:

$$G = \{x \in E\backslash D \mid \Lambda^+(x) \neq \phi\} \quad \text{and}$$
$$Q = \{x \in E\backslash D \mid \Lambda^+(x) = \phi\} = (E\backslash D)\backslash G.$$

Since X is locally compact, there exists a compact neighborhood N_1 of N with $d(N, \partial N_1) = \alpha_1 > 0$. If $Q \neq \phi$, then we claim that $\liminf_{t\to\infty} d(\pi(x,t), N) \geq \alpha_1$

for any $x \in Q$. In fact, $\liminf_{t\to\infty} d(\pi(x,t), N) < \alpha_1$ implies that $\Lambda^+(x) \neq \phi$, since N_1 is compact, which contradicts the definition of Q. Therefore, it follows from (2.3) that $\liminf_{t\to\infty} d(\pi(x,t), D) \geq \min\{\alpha_0, \alpha_1\} > 0$ for each $x \in Q$.

With the above conclusion on Q, if $G = \phi$, we are done. Otherwise, if $G \neq \phi$, then $L^+(G) \neq \phi$ and $L^+(G) \subset E$ by the positive invariance of $E \backslash D$. Moreover, by (2.3), we have

$$d(L^+(G),\ D \backslash N) \geq \alpha_0 > 0. \tag{2.4}$$

It follows that to complete the proof, it suffices to show that $d(L^+(G), N) > 0$. Suppose, otherwise, that $d(L^+(G), N) = 0$. Then there exists $y \in N \cap \overline{L^+(G)}$ since N is compact. Lemma 2.1 shows that $\gamma(y) \subset \overline{L^+(G)}$. Therefore, it follows from (2.4) and the positive invariance of $E \backslash D$, $\gamma^-(y) \subset N \subset D$. Henceforth, $\Lambda^-(y)$ is a nonempty, compact and connected set contained in N. Since B is maximal in D, $\Lambda^-(y) \subset B$. It follows from the invariance of $\Lambda^-(y)$ that $\Lambda^-(y) \cap M_i \neq \phi$ for some $M_i \in \mathcal{M}$. We relabel $\{M_i\}_{i=1}^k$ so that M_i becomes M_1. Lemma 2.1 implies that $\Lambda^-(y) \subset \overline{L^+(G)}$ and hence $\overline{L^+(G)} \cap M_1 \neq \phi$. By Theorem 2.3, $\overline{L^+(G)} \cap W^+(M_1) \backslash M_1 \neq \phi$. Since $\mathcal{M}$ is pairwise disjoint, we may choose $y_1 \in \overline{L^+(G)} \cap W^+(M_1) \backslash M$, where M is as defined in the theorem. Since all arguments utilized to y are applicable to y_1, we end up with that $\Lambda^-(y_1) \cap M_j \neq \phi$ for some $M_j \in \mathcal{M}$. There are two cases: (i) $\Lambda^-(y_1) \backslash M_\ell \neq \phi$ for each $M_\ell \in \mathcal{M}$; or (ii) $\Lambda^-(y_1) \subset M_\ell$ for some $M_\ell \in \mathcal{M}$. Actually, in case (ii), $\ell = j$ since $\mathcal{M}$ is pairwise disjoint.

Consider case (i) first. Since $y_1 \in W_w^-(M_j) \backslash W^-(M_j)$ in this case, applying Theorm 2.3 to $\{y_1\}$, we can find $z \in \Lambda^-(y_1) \cap W^-(M_j) \backslash M_j$, where z can also be chosen so that $z \notin M$. As we mentioned above, all results we obtained for y are also true for y_1. It follows that $z \in \Lambda^-(y_1) \subset B \cap N$ and hence there exists $M_p \in \mathcal{M}$ such that $\Lambda^+(z) \subset M_p$, which implies that $M_j \to M_p$. If $M_j = M_p$, we obtain a cycle in $\mathcal{M}$, a contradiction to the fact that $\mathcal{M}$ is acyclic. Therefore assume $M_j \neq M_p$. Then we have $\Lambda^-(y_1) \cap M_p \neq \phi$ since $z \in \Lambda^-(y_1)$ implies that $\Lambda^+(z) \subset \Lambda^-(y)$. By the assumption of this case, $\Lambda^-(y_1) \backslash M_p \neq \phi$, which implies $y_1 \in W_w^+(M_p) \backslash W^+(M_p)$. Applying the above argument to M_p, we can find an $M_q \in \mathcal{M}$ such that $M_p \rightarrow M_q$. Repeating this procedure, we shall end up with a cycle in $\mathcal{M}$ since $\mathcal{M}$ is finite, which contradicts the assumption on $\mathcal{M}$, completing the proof in this case.

In case (ii), $M_j \rightarrow M_1$ in B. If $M_j = M_1$, we are done. Otherwise, we relabel M_j as M_2. Lemma 2.1 implies that $\overline{L^+(G)} \cap M_2 \neq \phi$. Then we repeat the argument from the very beginning on M_1. We shall end up with a cycle in $\mathcal{M}$ by the same reason as in case (i), completing the proof. □

REMARK: The above theorem assumes a nonempty B. In the case of that $B = \phi$, if condition (2.3) is changed to that there exists a nonempty compact neighborhood N in D such that (2.3) holds for all $x \in E \backslash D$, then $\mathcal{F}$ is uniformly persistent. As a matter of fact, in this case, $Q \triangleq \overline{L^+(E \backslash D)} \cap D \subset N$ by (2.3). If there exists a $q \in Q$, then by the positive invariance of $E \backslash D$ and compactness of N, $\gamma^-(q) \cap (E \backslash D) = \phi$ and $\gamma^-(q) \backslash N \neq \phi$. It follows that $L^+(E \backslash D) \backslash [(E \backslash D) \cup (D \backslash N)] \neq \phi$. This is a contradition either to the positive invariance of E or to (2.3). Therefore we must have $d(N, \overline{L^+(E \backslash D)}) > 0$ which combined with (2.3) completes the proof for our assertion.

Theorem 2.6 can be applied to a system which is not dissipative (the dissipativeness is needed only on a subset of the "boundary" D) while most of these kinds of theorems in current papers deal with a dissipative system only. The following is an example which fits Theorem 2.6 but not any other of the theorems which have appeared to the best of my knowledge since it is not a dissipative system.

EXAMPLE: Consider in the $\mathbb{R}^2$ space the differential equations:

$$\begin{cases} \dot{x} = f(x, y) \\ \dot{y} = g(x, y), \end{cases} \tag{2.5}$$

where the functions f and g are defined as

$$f(x, y) = \begin{cases} 0, & \text{if } x = -1 \text{ or } x \geq 1 \\ -\frac{(1+x)(2+x)y}{ln(-1-x)}, & \text{if } x < -1 \text{ and } x \neq -2 \\ -y, & \text{if } x = -2 \\ -\frac{y(1-x^2)}{(1+y^2)(1-p(x)q(y))}, & \text{if } |x| < 1, \end{cases}$$

and

$$g(x, y) = \begin{cases} 1, & \text{if } x \geq 1 \\ -(2+x), & \text{if } x \leq -1 \\ x, & \text{if } |x| < 1, \end{cases}$$

where $p(x), q(y)$ are any continuously differentiable functions satisfying,

$$\begin{aligned} 0 < & p(x) < \tfrac{1}{2}, && \text{if } 0 < x < 1 \\ & p(x) = 0, && \text{if } x \leq 0 \\ & p(x) = \tfrac{1}{2}, && \text{if } x \geq 1 \\ 0 < & q(y) < \tfrac{1}{2}, && \text{if } y < 0 \\ & q(y) = 0, && \text{if } y \geq 0. \end{aligned}$$

It is easily verified that such a system describes a dynamical system as shown in Fig. 4. We take

$$\begin{cases} E = \{ \ (x, y) \mid -2 \leq x < -1, y \leq ln(-1-x) \ \} \cup \{ \ (x, y) \mid x \geq -1 \ \}, \\ D = \partial E. \end{cases}$$

Then we have $B = \{ \ (x, ln(-1-x)) \mid \ -2 \leq x < -1 \ \}$ and $M = \{(-2, 0)\}$. By

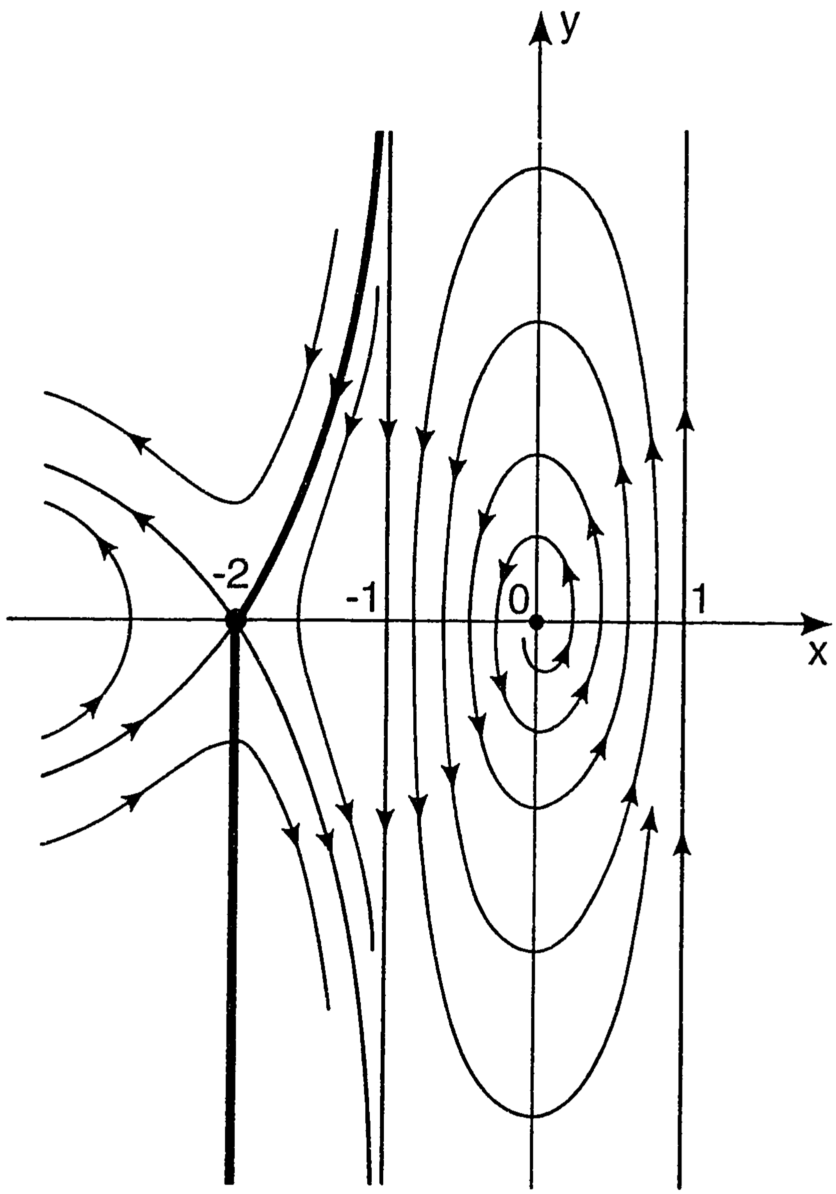


Fig. 4. An example for the application of Theorem 2.6.

some manipulations, we obtain the linear variational matrix of (2.5) at M as

$$\begin{pmatrix} 0 & -1 \\ -1 & 0 \end{pmatrix}.$$

It follows that M is a saddle point. From the definition of g, we can see that in the area between D and $x = -1$, $\dot{y}$ is always negative. It follows that all the orbits are apart from M with a certain distance as $t \to \infty$. And the stable set $W^+(M)$ of M in E is the curve $y = -ln(-1-x)$ with $-2 \le x < -1$, a part of D. By Theorem 2.6, the flow defined by (2.5) is uniformly persistent in E relative to D. On the other hand, since it is not a dissipative system as we can see, the result can not be obtained by other theorems which require the dissipativeness.

2.4. Results on a class of polynomials and on periodic ODEs.

In this section, we give theorems about the properties of the roots of the following polynomial which is related to the models which we will study in Chapter 4,

$$P_n(x) = x^n + x^{n-1} - 1. \tag{2.6}$$

In addition, we conclude this section with a theorem on the ω-periodic solutions of a ω-periodic system of ordinary differential equations in $\mathbb{R}^n$.

THEOREM 2.7. *$P_n(x) = 0$ has one and only one positive root α_n, which lies in the domain $(1 - \frac{2}{2n+1}, 1 - \frac{1}{2n-1})$, for $n \ge 2$. Moreover, the real parts of all other roots are strictly less than α_n.*

PROOF: Since $P_n(0) = -1 < 0$ and $P_n(1) = 1 > 0$, $P_n(x) = 0$ has a positive root in $(0,1)$. On the other hand $P_n'(x) = nx^{n-1} + (n-1)x^{n-2} > 0$ for $x > 0$ and $n \ge 2$. It follows that $P_n(x) = 0$ has a unique positive root α_n. For $n \ge 2$, it is always true that $P_n''(x) > 0$ for $x > 0$. Hence, we have

$$\alpha_n < 1 - \frac{P_n(1)}{P_n'(1)} = 1 - \frac{1}{2n-1},$$

which completes half of our estimate for α_n. To show the other part of the estimation, note that

$$\alpha_n^{n-1} = 1 - \alpha_n^n = (1-\alpha_n)(1 + \alpha_n + \cdots + \alpha_n^{n-1}).$$

Dividing the above equation by α_n^{n-2} and noting that $\alpha_n \in (0,1)$, we obtain

$$\alpha_n = (1-\alpha_n)(\frac{1}{\alpha_n^{n-2}} + \cdots + \frac{1}{\alpha_n} + 1 + \alpha_n) > (1-\alpha_n)((n-1) + \alpha_n).$$

The above inequality is equivalent to the following one

$$(1-\alpha_n)^2 - (n+1)(1-\alpha_n) + 1 > 0.$$

Solving this inequality for $1 - \alpha_n \in (0,1)$, we obtain

$$1 - \alpha_n < \frac{2}{n+1+\sqrt{n^2+2n-3}} < \frac{2}{2n+1}, \qquad \text{for} \quad n \geq 2.$$

This inequality completes the estimation of α_n.

Now, suppose $x_0 = A(\cos\theta + i\sin\theta)$ is any root of $P_n(x) = 0$ other than α_n, where $A > 0$ is the norm of x_0. Since $x_0^{n-1}(1 + x_0) = 1$, we have

$$A^{n-1}\sqrt{A^2 + 2A\cos\theta + 1} = 1$$

by taking the norm of both sides of the previous equation. If the real part $A\cos\theta$ of x_0 is greater than α_n, then A must be greater than α_n since $\cos\theta$ is always smaller than 1. If $A\cos\theta = \alpha_n$, we cannot have $\cos\theta = 1$, otherwise $x_0 = A = \alpha_n$, a contradiction to the assumption. It follows that A is always greater than α_n if the real part of x_0 is greater than or equal to α_n. However, then we have $1 = A^{n-1}\sqrt{A^2 + 2A\cos\theta + 1} > \alpha_n^{n-1}(1+\alpha_n) = 1$, a contradiction. This completes the proof. □

REMARK: For large n, say $n \geq 5$, we obtain a better estimation for α_n, which is $\left(1 - \frac{ln2}{n-1}, 1 - \frac{ln2}{n+ln2}\right)$. To show this, note that

$$\alpha_n^{-(n-1)} = 1 + \alpha_n < 2 \quad \text{and} \quad \alpha_n^{-n} = 1 + \alpha_n^{-1} > 2, \tag{2.7}$$

since $\alpha_n \in (0,1)$. On the other hand, we have

$$\begin{aligned} \alpha_n^{-(n-1)} &= \left[\left(1 - (1-\alpha_n)\right)^{-\frac{1}{1-\alpha_n}}\right]^{(n-1)(1-\alpha_n)} > e^{(n-1)(1-\alpha_n)}, \quad \text{and} \\ \alpha_n^{-n} &= \left[\left(1 + \frac{1-\alpha_n}{\alpha_n}\right)^{\frac{\alpha_n}{1-\alpha_n}}\right]^{\frac{n(1-\alpha_n)}{\alpha_n}} < e^{\frac{n(1-\alpha_n)}{\alpha_n}}, \end{aligned} \tag{2.8}$$

by the estimation of exponential functions. Combining (2.7) and (2.8), we obtain

$$\begin{aligned} &e^{(n-1)(1-\alpha_n)} < 2, \quad \text{i.e.,} \quad \alpha_n > 1 - \frac{ln2}{n-1}, \quad \text{and} \\ &e^{\frac{n(1-\alpha_n)}{\alpha_n}} > 2, \quad \text{i.e.,} \quad \alpha_n < 1 - \frac{ln2}{n+ln2}. \end{aligned}$$

It is not difficult to calculate that $\frac{ln2}{n-1} < \frac{2}{2n+1}$ for $n \geq 5$ while $\frac{ln2}{n+ln2} > \frac{1}{2n-1}$ for $n \geq 4$.

THEOREM 2.8. *$P_n(x) = 0$ has only one real root α_n when n is odd. When n is even, $P_n(x)$ has two real roots, one is α_n and the other, α_n^-, is a negative root which is less than -1.*

PROOF: Taking the first derivative of $P_n(x)$, we obtain

$$P_n'(x) = x^{n-2}(nx + (n-1)).$$

It is easy to show that $P_n(x)$ has only two critical points, 0 and $\frac{1-n}{n}$ for $n > 2$. Theorem 2.7 shows that $P_n(x)$ has only one positive root α_n. Now we consider $P_n(x)$ on $(-\infty, 0]$. First we calculate the value of P_n at $\frac{1-n}{n}$,the only critical point in $(-\infty, 0)$. Since $\left|\frac{n-1}{n}\right| < 1$ and the sign of $\left(\frac{1-n}{n}\right)^n$ is opposite to that of $\left(\frac{1-n}{n}\right)^{n-1}$ for any $n \geq 2$, $\left(\frac{1-n}{n}\right)^n + \left(\frac{1-n}{n}\right)^{n-1} < 1$ for any $n \geq 2$. It follows that $P_n\left(\frac{1-n}{n}\right) < 0$ for any $n > 2$. Actually, with the same argument, one can show that for any $x \in (-1, 0]$, $P_n(x) < 0$. Now suppose n is odd. Then $P_n(x) \to -\infty$ as $x \to -\infty$. By the above analysis, we know that P_n has only one critical point in $(-\infty, 0]$ at which P_n is less than zero. It follows that P_n has no root in $(-\infty, 0]$. For even n, $P_n(x) \to \infty$ as $x \to -\infty$. With a similar argument to the odd n, one can show that P_n has only one root α_n^- in $(-\infty, -1)$, completing the proof. □

THEOREM 2.9. *All roots of P_n are of single multiplicity. Furthermore, if two roots have the same real part, they are conjugate, and for any root α, we have $\alpha_n^- \leq Re(\alpha) \leq \alpha_n$ for n being even and $Re(\alpha) \leq \alpha_n$ for n being odd.*

PROOF: In the proof of Theorem 2.8, we have shown that the roots of $P_n'(x)$, 0 and $\frac{1-n}{n}$, are not roots of $P_n(x)$. It follows that the roots of P_n are of single multiplicity. Now suppose $\alpha = \beta + \gamma i$ is a root of P_n. Then we have

$$\|\alpha\|^{n-1}\|\alpha + 1\| = 1. \tag{2.9}$$

Suppose $\theta = \beta + \eta i$ is also a root of P_n, where $\eta \neq \gamma$ and $-\gamma$. Then if $|\eta| < |\gamma|$, the norms of θ and $\theta + 1$ are smaller than those of α and $\alpha + 1$, respectively. It follows that $1 = \|\theta\|^{n-1}\|\theta + 1\| < \|\alpha\|^{n-1}\|\alpha + 1\| = 1$, a contradiction. Similarly one can show the case of $|\eta| > |\gamma|$. It follows that if θ is a root of P_n other than

α, then $\eta = -\gamma$. Finally, by arguments similar to the above, we can show that $\beta > \alpha_n^-$ if $\gamma \neq 0$. This completes the proof. □

Besides the above theorems concerning the roots of (2.6), we also need the following theorem in Section 4.6. We define a function $U : I \to \mathbb{R}$ as follows,

$$U(x) \triangleq (f(1-x_1)-(1-\alpha_n))x_1+(1+\alpha_n)\sum_{i=2}^{n}\alpha_n^{i-2}(f(1-x_i)-(1-\alpha_n))x_i, \quad (2.10)$$

for $x = (x_1, \ldots, x_n) \in I$, where $I = \{x \in \mathbb{R}^n \mid 0 \leq x_i \leq 1, i = 1, \ldots, n\}$ is the unit cube in $\mathbb{R}^n$, α_n is as given in Theorem 2.7 and f satisfies that $f(0) = 0, f'(0) > 0$ for all $u \geq 0$.

THEOREM 2.10. *If further $f''(u) < 0$ for $u \geq 0$ and $f(1) > 1-\alpha_n$, then $U(x) = 0$ is an $(n-1)$-dimensional manifold through the point $x_\lambda = (1-\lambda, \ldots, 1-\lambda) \in I$, where λ is such that $f(\lambda) = 1-\alpha_n$. Further, $U(x) \geq 0$ is a convex set and hence is simply connected.*

PROOF: Since $U(x_\lambda) = 0$ and

$$\begin{aligned}\frac{\partial U(x_\lambda)}{\partial x_i} &= (1+\alpha_n)\alpha_n^{i-2}(f(1-x_i)-(1-\alpha_n)-f'(1-x_i)x_i)\big|_{x=x_\lambda} \\ &= -(1+\alpha_n)\alpha_n^{i-2}f'(\lambda)(1-\lambda) < 0, i = 2, \ldots, n+1,\end{aligned}$$

where we regard x_{n+1} as x_1. By the implicit function theorem, there exists an $(n-1)$-dimensional manifold M_{x_λ} in a neighborhood of x_λ. Let M be the maximal extension of the $(n-1)$-dimensional manifold M_{x_λ} on which $U(x) = 0$ in I.

We consider a function $h : [0, 1] \to \mathbb{R}$ defined by $h(u) = f(1-u)-1+\alpha_n - f'(1-u)u$ for $0 \leq u \leq 1$. It is easy to show that $h'(u) = -2f'(u)+f''(1-u)u < 0$ for $0 \leq u \leq 1$. It follows that $h(u)$ is monotonically decreasing in [0,1]. Since

$\frac{\partial U(x)}{\partial x_i} = (1+\alpha_n)\alpha_n^{i-2}h(x_i)$, $\frac{\partial U(x)}{\partial x_i} \neq 0$ for at least one i at any point $x \in I$ with $U(x) = 0$.

Let $\bar{x}$ and $\tilde{x}$ be such that $U(\bar{x}) \geq 0$ and $U(\tilde{x}) \geq 0$. Then for any $t \in (0,1)$, $x = t\bar{x} + (1-t)\tilde{x} \in I$, we have $h(x_i) \geq th(\bar{x}_i) + (1-t)h(\tilde{x}_i)$ for all $i = 1, \ldots, n$ since $h''(u) < 0$. However, $U(x) = (1+\alpha_n)\sum_{i=1}^{n} \alpha^{i-1}h(x_{i+1})$ is linear in h. It follows that $U(x) \geq tU(\bar{x}) + (1-t)U(\tilde{x}) \geq 0$, which completes the proof. □

The next theorem is valid for any polynomial.

LEMMA 2.11. *If a polynomial $P(\sigma)$ has k real roots counting multiplicity, then its derivative $P'(\sigma)$ has at least $k-1$ real roots.*

PROOF: Suppose $\sigma_1, \ldots, \sigma_\ell$ are the ℓ different real roots of $P(\sigma) = 0$, of multiplicity $k_1, \ldots, k_\ell$ respectively. Then, we have that $\sum_{j=1}^{\ell} k_j = k$. By the mean value theorem, we have $\ell - 1$ different roots $\zeta_1, \ldots, \zeta_{\ell-1}$ for P' between $\sigma_1, \ldots, \sigma_\ell$. On the other hand, σ_j is of multiplicity $k_j - 1$ for P', $j = 1, \ldots, \ell$ (0 multiplicity means that it is not a root). Thus, we have found

$$(\ell - 1) + \sum_{j=1}^{\ell}(k_j - 1) = k - 1$$

real roots for P', completing the proof. □

COROLLARY 2.12. *All roots of $P(\sigma) = -1 + \prod_{i=1}^{n}(\sigma - \sigma_i)$ with non-zero imaginary parts are of single multiplicity if all σ_i are real numbers.*

PROOF: We note that P' is the derivative of a polynomial of n real roots. By Lemma 2.11, there exists no complex root of P' with non-zero imaginary part. This completes the proof. □

Next theorem locates one of the ω-periodic solutions for a class of ω-periodic ordinary differential equations.

Let X be a closed convex subset of R^n with $\overset{\circ}{X} \neq \pi$ and

$$\dot{x} = f(t,x), \tag{2.11}$$

be an ω-periodic system in X, where $f(t,x)$ is smooth enough so that the existence and uniqueness of the initial value problem of (2.11) are satisfied. We adopt as our definition of uniform persistence in this setting that there exists $\delta > 0$ such that $\liminf_{t\to\infty} d(x(t), \partial X) \geq \delta > 0$ for all solutions of (2.11) such that $x_0 \in \overset{\circ}{X}$; and as our definition of dissipativity that there exists a $B > 0$ such that for any $x \in X$, $\|x(t)\| \leq B$ for sufficient large t.

THEOREM 2.13. *If (2.11) is dissipative and uniformly persistent in X, a positively invariant convex set in $\mathbb{R}^n$, then there exists an ω-periodic solution $x(t)$ lying in the interior of X.*

PROOF: In this proof we utilize the notation of Horn (1970). Consider the Poincaré map T derived by (2.11). Let $M = \overline{\bigcup_{x\in \text{ int } X} \Lambda^+(x)}$. Then by the positive invariance of $X, M \subset X$ and by dissipativity and uniform persistence, M is compact and $d(M, \partial X) \geq \eta > 0$. Denote $\varepsilon = \frac{\eta}{2} > 0$. Then for any $x \in$ int X there exists $N(x) > 0$ such that $T^n(x) \subset \mathcal{B}(M, \varepsilon)$, the ε-neighborhood of M, for all $n > N(x)$.

In the next part of the proof, we modify a method utilized by Hale (1977) to construct a compact positively invariant set K in $\overset{\circ}{X}$.

Define $B^* = \overline{\mathcal{B}(M,\varepsilon)}$. By continuity, for any $x \in \overset{\circ}{X}$, there exists a neighborhood Q_x of x such that $T^{N(x)}Q_x \subset B^*$. Since B^* is compact, we choose a finite subcover $\{Q_{x_j} \mid j = 1, \ldots, k\} \subset \{Q_x \mid x \in B^*\}$ such that $B^* \subset \bigcup_{j=1}^{k} Q_{x_j}$.

We denote $N = \max\{N(x_j) \mid j = 1, \ldots, k\}$ and define $K = \bigcup_{n=0}^{N} T^n B^*$. It is easy to see that $d(K, \partial X) > 0$ because K is compact.

We now claim that K is positively invariant. To prove this, it suffices to show that

$$T^{N+1}B^* \subset K. \tag{2.12}$$

As a matter of fact, for any $x \in K$, there exists $n \in \{0, 1, \ldots, N\}$ such that $x \in T^n B^*$. It follows from (2.12) that $T(x) \in T^{n+1}B^* \subset K$ since $1 \leq n+1 \leq N+1$. This shows that K is positively invariant. Now we prove (2.12). For any $x \in B^*$, there exists $j \in \{1, \ldots, k\}$ such that $x \in Q_{x_j}$. Since $N+1 > N(x_j) \geq 1, T^{N(x_j)}Q_{x_j} \subset B^*$. Therefore, we have

$$T^{N+1}(x) \in T^{N+1}Q_{(}x_j) = T^{N+1-N(x_j)}(T^{N(x_j)}Q_{x_j}) \subset T^{N+1-N(x_j)}B^* \subset K,$$

since $0 \leq N+1-N(x_j) \leq N$. This completes our proof of (2.12).

Let $S_0 = \overline{co}\, K$, the closure of the convex hull of K. By definition,

$$S_0 = \overline{\{y \mid y = at + b(1-t); a, b \in K, 0 \leq t \leq 1\}}.$$

If $d(S_0, \partial X) = 0$, there exists $y \in (S_0 \backslash K) \cap \partial X$ since S_0 is compact (see Lemma A.9 in Appendix) and $d(K, \partial X) > 0$. We can find $a, b \in K$ and $t \in (0,1)$ such that $y = at + b(1-t)$. Since $a, b \in K \subset \overset{\circ}{X}$, there exists $\epsilon > 0$ such that both $\mathcal{B}(a, \epsilon)$ and $\mathcal{B}(b, \epsilon)$ lie in the interior of X. However, there exists a $x \in \mathcal{B}(y, \epsilon) \backslash X$ since $y \in \partial X$. Then we have that both $a + (x-y)$ and $b + (x-y)$ are in $\overset{\circ}{X}$ since $\|x - y\| < \epsilon$. It follows that

$$[a + (x-y)]t + [b + (x-y)](1-t) = at + b(1-t) + (x-y) = x \notin X,$$

a contradiction to the convexity of X. It follows that $d(S_0, \partial X) = \delta_1 > 0$. Let $S_1 = \mathcal{B}(S_0, \frac{\delta_1}{2})$. Since $\bar{S}_1$ is compact, there exists $m = N(\bar{S}_1)$ such that $T^n(\bar{S}_1) \subset$

$K \subset S_0$ for all $n > m$. Let $S_2 = \overline{co}\left\{ \bigcup_{i=0}^{m} T^i(\bar{S}_1) \right\}$. Then $S_0 \subset S_1 \subset S_2$ are convex sets with S_1 open and $T^i(\bar{S}_1) \subset S_2$ for $i \leq m$, and $T^i(\bar{S}_1) \subset S_0$ for $i > m$. By Horn's Theorem (Horn, 1970) (see Theorem A.7 in Appendix), there exists a fixed point of T in $S_0 \subset$ int X. □

2.5. Discussion.

In the previous section, by applying Theorem 2.3, we established Theorem 2.6 which gives a criterion for a dynamical system to be uniformly persistent. As seen in the example for that theorem, the set G defined in the proof of the theorem, which is the strip defined by $-1 < x < 1$ in the example case, is usually not compact. This shows that the theorem is applicable to a nondissipative system. However, as we all know, most of the systems in the study of biological population theory are dissipative because it is hard to imagine that the population of a species could become unbounded in an environment with limited resources. Hence, Theorem 2.6 may be more useful in some other categary of applications.

Further improvement can be done to Theorem 2.6. We notice that the condition (2.3) is not easy to verify for many systems, while it is easy to verify for others. Hence one can either reconstruct the theorem or find an easy criterion for condition (2.3). Both approaches could be of interest for future investigation.

CHAPTER 3

COMPETITIONS FOR A PREY IN A CHEMOSTAT WITH PERIODIC INPUT

3.1. Introduction.

This chapter is concerned with a mathematical model of competing predators on a single prey population which grows in a chemostat environment.

The chemostat is a device used for growing microorganisms in a continuous cultured environment. Arguments indicating the degree to which the chemostat is an appropriate laboratory approximation of nature are cited in Hsu, Hubbell and Waltman (1977). These authors also describe the extensive use of the chemostat in such laboratory work.

The paper of Hsu, Hubbell and Waltman (1977) was the first to give a mathematical analysis of such a model. This paper dealt with n competing microorganisms for a single nutrient. Since that time, many papers have been written about various aspects of competition in a chemostat of populations on a single nutrient described by systems of autonomous ordinary differential equations, Butler and Wolkowicz (1985), Cushing (1989), Hsu (1978). Also see Hsu, Hubbell and Waltman (1978a,b) and Keener (1983) for related systems. The case of two complementary nutrients has also been considered by Butler and Wolkowicz (1987a).

Models of microorganic predators feeding on microorganic prey populations which in turn feed on a nutrient in a chemostat environment have also been of recent interest and have received extensive study, Butler, Hsu and Waltman (1983), Butler and Waltman (1981), Butler and Wolkowicz (1986, 1987b), Wolkowicz (1989). Here we are also interested in studying such a model.

The papers cited to this point have utilized autonomous systems as models. However, there is reason to consider nonautonomous models, particularly with periodic input, since nutrient may be added to the chemostat in a periodic mode rather than in a constant fashion. In the case of competing populations at a single trophic level for nutrient with periodic influx, there has been some work done, Hale and Solominos (1983), Smith (1981), Hsu (1980). The case of periodic washout has also been considered in Butler, Hsu and Waltman (1985). However, no analysis has yet been attempted in the case of periodic nutrient input in models with two trophic levels.

It is therefore the main purpose of this chapter to consider a model of n predators feeding on a prey population which in turn feeds on a nutrient in a chemostat environment with periodic input. In the submodel with no predators we establish the existence of a globally asymptotically stable periodic solution. In the case of one predator, we show that a positive solution can exist, but are unable to determine its stability. However we are able to show that subject to certain constraints, the system exhibits uniform persistence (see Definition 1.9 in Chapter 1). In the general case we obtain criteria for persistence (and hence coexistence of all populations).

Most papers dealing with persistence have considered dynamical systems which can be represented by autonomous ordinary differential equations. In our setting, however, we have a nonautonomous system which is a continuous semi-dynamical system. It is important to note that the results in Butler and Waltman (1986) are valid for such systems. Other papers which have considered persistence criteria for specific nonautonomous systems are Hallam (1987), Hallam and Ma

(1986, 1987).

In proving our theorems throughout this chapter we will be utilizing two different notations, that of cylinder spaces and that of Poincaré maps. Although this may add some confusion for the reader, it is compensated for by virtue of the fact that certain of the proofs are considerably simplified in the cylinder space notation and others require the Poincaré mapping notation in order to utilize some known results.

This chapter is organized as follows. In the next section we describe our model and obtain some preliminary results. In section 3.3 we consider the sub-model of no predators. In section 3.4 we analyze the general model. We conclude the chapter with a brief discussion in section 3.5.

3.2. The model.

We take as a model of n predators competing for a prey in a chemostat with periodic nutrient input, the system

$$\begin{cases} \dot{S} = D(S^0(t) - S) - \frac{m_0}{\gamma_0} f_0(S)x \\ \dot{x} = \big(m_0 f_0(S) - D_0\big)x - \sum\limits_{i=1}^{n} \frac{m_i}{\gamma_i} f_i(x) y_i \\ \dot{y}_i = \big(m_i f_i(x) - D_i\big) y_i \end{cases} \tag{3.1}$$

$$S(0) = S_0 \geq 0,\ x(0) = x_0 \geq 0,\ y_i(0) = y_{i0} \geq 0,\ i = 1, \dots, n$$

where $S^0(t)$ represents the input nutrient concentration rate of S at time t, D is the dilution (or wash-out) rate, D_0 and D_i are the sums of dilution rate D and the natural death rate of x and y_i respectively, m_0 and m_i are the maximal growth rates of x and y_i respectively, and γ_i are the yield factors.

Moreover, we assume

(A1) $S^0(t)$ is a nontrivial positive ω-periodic C^1 function.

(A2) $f_i : \mathbb{R}_+ \to [0, 1]$, $i = 1, \dots, n$, $f_i \in C^k(\mathbb{R}_+, [0, 1])$, is increasing, where k is an integer as required, and $f_i(0) = 0$, $f_i(+\infty) = 1$.

For some of our results we also require

(A3) $f_i'(r) > 0$ for $r \geq 0, \quad i = 1, \ldots, n.$

REMARK 3.1: Suppose

$$\ell_1 = \min\{S^0(t) \mid 0 \leq t \leq \omega\}, \quad \ell_2 = \max\{S^0(t) \mid 0 \leq t \leq \omega\},$$

and $\hat{S} = \frac{1}{\omega}\int_0^\omega S^0(t)dt$. Then clearly $0 < \ell_1 < \hat{S} < \ell_2$. As in Butler, Hsu and Waltman (1983), we can rescale S, x and y_i and relabel them as S, x and y_i, respectively so that (3.1) becomes

$$\begin{cases} \dot{S} = D(S^0(t) - S) - m_0 f_0(S)x \\ \dot{x} = (m_0 f_0(S) - D_0)x - \sum_{i=1}^{n} m_i f_i(x) y_i \\ \dot{y}_i = (m_i f_i(x) - D_i) y_i, \end{cases} \tag{3.2}$$
$$S(0) = S_0 \geq 0, \; x(0) = x_0 \geq 0, \; y_i(0) = y_{i0} \geq 0, \quad i = 1, \ldots, n.$$

System (3.2) is then our model to be analyzed.

REMARK 3.2: It is easy to verify that

$$S^*(t) = \frac{D}{e^{D\omega} - 1}\int_0^\omega e^{Dr} S^0(t + r)dr \tag{3.3}$$

is a globally exponentially stable ω-periodic solution of

$$\dot{S} = D(S^0(t) - S), \tag{3.4}$$

and moreover, every solution $S(t)$ of (3.4) can be written as $S(t) = S^*(t) + Ce^{-Dt}$ with $C = S(0) - S^*(0)$. Since $\ell_1 \leq S^0(t) \leq \ell_2$, all solutions $S(t)$ eventually enter the interval $I = [\ell_1, \ell_2]$, and remain there for all future time. The following lemma describes the behavior of $S^*(t)$.

LEMMA 3.3. *(i) There exists $b > 0$ such that*

$$\ell_1 + b \leq S^*(t) \leq \ell_2 - b \quad \text{for all} \quad t \in R;$$

(ii) $\frac{1}{\omega}\int_0^{\omega} S^*(t)dt = \hat{S}$.

PROOF: (i) By Remarks 3.1 and 3.2, $\ell_1 \le S^*(t) \le \ell_2$ since it is periodic. Suppose $\max\{S^*(t) \mid 0 \le t \le \omega\} = \ell_2$ (or $\min_{0\le t\le\omega}\{S^*(t)\} = \ell_1$), then there exists $t^* \in (0,\omega]$ such that $S^*(t^*) = \ell_2$ (or $= \ell_1$). Now (3.4) has no constant solution since $S^0(t)$ is not constant, hence there exists $t_0 \in (0,t^*)$ such that $S^*(t_0) < \ell_2$ (or $> \ell_1$). Hence we can choose a solution $S(t)$ with

$$S^*(t_0) < S(t_0) < \ell_2 \text{ (or } \quad \ell_1 < S(t_0) < S^*(t_0)).$$

Then by the intermediate value theorem, there exists $t_1 \in (t_0, t^*]$ such that $S(t_1) = S^*(t_1)$ since $S(t_0) > S^*(t_0)$ (or $S(t_0) < S^*(t_0)$) while $S(t^*) \le S^*(t^*)$ (or $S(t^*) \ge S^*(t^*)$). This is a contradiction to the uniqueness of solutions of initial value problems.

(ii) The proof follows by substituting $S^*(t)$ into (3.4) and then integrating both sides of (3.4) from 0 to ω. □

Denote $\ell_1^* = \min\{S^*(t) \mid 0 \le t \le \omega\}$, $\ell_2^* = \max\{S^*(t) \mid 0 \le t \le \omega\}$. Then (i) implies $\ell_1 < \ell_1^* < \ell_2^* < \ell_2$. Also denote $y = (y_1, y_2, \ldots, y_n)$. The following lemma gives some properties of the solutions in $\mathbb{R}_+^{n+2}$.

LEMMA 3.4. *Suppose (A2) holds. Then each solution* $(S(t),\ x(t),\ y(t))$ *of (3.2) with its initial value in* $\mathbb{R}_+^{n+2}$ *will remain in* $\mathbb{R}_+^{n+2}$ *for all* $t \ge 0$. *Further if we denote* $u(t) = S^*(t) - S(t)$ *for solutions* $S(t)$, *then the following are true:*

(i) $u(0)e^{-Dt} \le u(t)$;

(ii) Either there exists $t_1 \ge 0$ *such that* $u(t) \ge 0$ *for all* $t \ge t_1$, *or* $u(t) < 0$ *for all* $t \ge 0$ *in which case* $u(t)$, $x(t)$ *and* $y_i(t)$ *all tend to zero exponentially as* $t \to +\infty$.

PROOF: Since $\dot{u}(t) = -Du(t) + m_0 f_0(S(t))x(t) \ge -Du(t)$, by standard comparison theory it follows that $u(0)e^{-Dt} \le u(t)$. On the other hand, by variation of constants, $u(t) = e^{-Dt}\big(u(0) + F(t)\big)$, where $F(t) = m_0 \int_0^t e^{Dr} f(S(r))x(r)dr$ is an increasing nonnegative function for $t \geq 0$ since the integrand is positive. Therefore, the first case of (ii) occurs if $u(0) \geq 0$ or $u(0) < 0$ but $F(+\infty) > -u(0)$. Otherwise, $u(t) < 0$ for all $t \geq 0$. In the latter case, let

$$w(t) = x(t) + \sum_{i=1}^{n} y_i(t) - u(t).$$

Since $u(t) < 0$, we have that $\dot{w}(t) = -D_0 x(t) - \sum_{i=1}^{n} D_i y_i(t) + Du(t) \leq -\delta w(t)$, where $\delta = \min\{D, D_0, D_1, \ldots, D_n\} > 0$. It follows that $w(t) \leq w(0)e^{-\delta t} \to 0$ as $t \to \infty$. Therefore, since $x(t)$, $y_i(t)$ and $-u(t)$ are all nonnegative, the assertion (ii) is true. □

With the above lemmas, we can now prove the following theorem.

THEOREM 3.5. *System (3.2) with (A2) satisfied is dissipative (see Definition 1.2 in Chapter 1) and all its solutions initiating in* $\mathbb{R}_+^{n+2}$ *satisfy*

(i) $0 \leq \liminf_{t\to\infty} u(t)$;

(ii) $\limsup_{t\to\infty} \left[S(t) + x(t) + \sum_{i=1}^{n} y_i(t)\right] \leq \frac{D\ell_2^*}{\delta}$, *where* δ *is given in the proof of Lemma 3.4;*

(iii) *there exists* $t_1 \geq 0$ *and* $\xi = \xi(S_0, x_0, y_0) > 0$ *such that* $S(t) \geq \xi$ *for* $t \geq t_1$.

PROOF: (i) follows directly from Lemma 3.3. To prove (ii), note that $\dot{w}(t) \leq -\delta w(t) + (D-\delta)u(t) \leq -\delta w(t) + (D-\delta)\ell_2^*$, since $u(t) \leq S^*(t) \leq \ell_2^*$ and $D - \delta \geq 0$. By variation of constants, $w(t) \leq e^{-\delta t}\left(w(0) - \frac{D-\delta}{\delta}\ell_2^*\right) + \frac{D-\delta}{\delta}\ell_2^*$. On the other hand, $S(t) + x(t) + \sum_{i=1}^{n} y_i(t) = w(t) + S^*(t)$, which combined with the previous inequality proves (ii). The dissipativeness of (3.2) follows from (ii).

Finally, (iii) follows from the dissipativeness of (3.2) and the fact that $\dot{S}(t) \geq D\ell_1 > 0$ on $\{(0, x, y) \in \mathbb{R}^{n+2} \mid x \in \mathbb{R}_+ \text{ and } y \in \mathbb{R}_+^n\}$. □

Since $f_i(r) < 1$ for all $r \in \mathbb{R}$, if $m_i \leq D_i$, then $m_i f_i(r) - D_i < 0$ for all r, in which case y_i (or x corresponding to $i = 0$) goes to zero. Therefore, we will consider only $m_i > D_i$ for all $i = 0, 1, \ldots, n$ throughout the remainder of this chapter.

3.3. Analysis of prey growth.

Here we emphasize the prey population, x, in the case where there are no predators and in certain cases where there are. As we will see in the following discussions, lack of nutrient is the only cause of prey extinction, i.e., consuming of the prey by predators can not lead to a prey extinction if there is a sufficient supply of nutrient for prey to survive. This is a natural phenomenon of a simple food chain.

3.3.1. Extinction of the prey.

The conditions given in the next theorem describe an environment which provides insufficient nutrient for prey survival and consequently x together with the y_i's will tend to extinction.

THEOREM 3.6. *Suppose (A2) holds. If* $\sigma_0 = \frac{1}{\omega}\int_0^{\omega}(m_0 f_0(S^*(t)) - D_0)dt < 0$, *then for every solution* $(S(t),\ x(t),\ y(t))$ *of (3.2),* $x(t)$ *and* $y_i(t),\ i = 1, \ldots, n$, *tend to zero exponentially.*

PROOF: Because of conclusion (ii) of Lemma 3.4, it suffices to show the theorem is valid with the assumption that $u(t) \geq 0$ for $t \geq t_1$ for some $t_1 \geq 0$ where $u(t) = S^*(t) - S(t)$. In this case, $f_0(S(t)) \leq f_0(S^*(t))$ for $t \geq t_1$ since f_i is increasing for any $i = 0, 1, \ldots, n$. With some elementary manipulations and analysis, we obtain

$$0 \leq x(t) \leq K\ e^{\sigma_0(t-t_1)} \quad \text{for} \quad t \geq t_1, \tag{3.4}$$

where $K = x(t_1)e^{(M+\omega\sigma_0)}$ and $M = \max\limits_{0 \leq t < \omega} \int_0^t (m_0 f_0(S^*(r)) - D_0)dr$. Furthermore, because of (A2) and (3.4), $m_i f_i(x(t)) - D_i \leq -\frac{D_i}{2}$ for $t \geq t_2$ for some $t_2 \geq t_1,\ i =$

$1,\ldots,n$. It follows that $y_i(t) \le y_i(t_2)e^{-\frac{D_i}{2}(t-t_2)}$ for $t \ge t_2$, which together with (3.4) completes the proof. □

With $m_i > D_i$, (A2) implies that there exists a unique λ_i for each $i = 0,1,\ldots,n$ such that $f_i(\lambda_i) = \frac{D_i}{m_i}$. The next result generalizes Corollary 2.3 of Hale and Solominos (1983).

THEOREM 3.7. *Suppose (A3) holds and the derivative f_0' of f_0 is strictly decreasing. If $\lambda_0 \ge \hat{S}$, then $x(t)$ and $y_i(t)$, $i = 1,\ldots,n$, tend to zero exponentially as $t \to \infty$.*

PROOF: Denote $I_+ = \{t \in [0,\omega] \mid S^*(t) \ge \lambda_0\}$ and $I_- = \{t \in [0,\omega] \mid S^*(t) < \lambda_0\}$, the complement of I_+ in $[0,\omega]$. It is easy to see from (A3) that I_- is a nonempty open set in $[0,\omega]$. By the mean value theorem

$$f_0(S^*(t)) - f_0(\lambda_0) = f_0'(\theta(t))(S^*(t) - \lambda_0) \le f_0'(\lambda_0)(S^*(t) - \lambda_0), \qquad (3.5)$$

where $\theta(t)$ lies between λ_0 and $S^*(t)$. In fact, if $t \in I_+$, $\theta(t) \ge \lambda_0$ then $f_0'(\theta(t)) \le f_0'(\lambda_0)$ and if $\theta(t) < \lambda_0$ then $f_0'(\theta(t)) > f_0'(\lambda_0)$ if $t \in I_-$. Hence in both cases (3.5) holds. The strict inequality $\int_0^\omega [f_0(S^*(t)) - f_0(\lambda_0)]dt < \omega f_0'(\lambda_0)(\hat{S} - \lambda_0)$ holds because of (3.5) and the nonemptiness of I_-. Therefore, we have

$$\sigma_0 = \frac{m_0}{\omega}\int_0^\omega (f_0(S^*(t)) - f_0(\lambda_0))dt < m_0 f_0'(\lambda_0)(\hat{S} - \lambda_0) \le 0.$$

By Theorem 3.6, the conclusion of this theorem is true. □

Note that since a functional response of the form $f(x) = \frac{x}{a+x}$ for some $a > 0$ satisfies all conditions of Theorem 3.7, x and y_i, $i = 1,\ldots,n$, tend to extinction exponentially when $\lambda_0 = \frac{a_0 D_0}{m_0 - D_0} \ge \hat{S}$, which is the assertion of Corollary 2.3 of Hale and Solominos (1983).

3.3.2. Nutrient threshold for the prey.

By the properties of a periodic ordinary differential system $\mathcal{P}$ in an Euclidean space $\mathcal{E}$, $\mathcal{P}$ is equivalent to a dynamical system $\pi(e,t)$ on a cylinder $E = \mathcal{E} \times \mathcal{Z}$

with a flow $\mathcal{F}$, where $\mathcal{Z} = [0,\omega]/\{0,\omega\}$, a quotient space of $[0,\omega]$ by identifying 0 and ω, (Sansone and Conti, 1964), or we may regard $\mathcal{Z}$ as a nontrivial circle on the plane. Here, we regard E as a subset of $\mathcal{E} \times \mathbb{R}^2$. Therefore, studying the asymptotic behavior of solutions of (3.2) is equivalent to studying the Ω-limit sets of trajectories of a dynamical system π with flow $\mathcal{F}$ on E, with $\mathcal{E} = \mathbb{R} \times \mathbb{R}_+^{n+1}$. For those notations and terminologies in the theory of dynamical systems, we have given the definitions in Chapter 1. In addition, we utilize the following notations specifically for this chapter:

For each point $e \in E$, we denote it by $e = (S, x, y, z)$, where S, x are scalars, y is an n-vector and $z \in \mathcal{Z}$,

$\mathcal{D} = \{x, y_1, \dots, y_n\}$ is the set of the enclosed $n+1$ symbols,

$v \subset \mathcal{D}$ is a subset of these symbols,

$\partial E_v = \{(S,x,y,z) \in E\}\big|_{v=0}$, i.e. ∂E_v is that boundary component of E, where all symbols contained in v are set equal to zero,

$\partial E_{\hat{v}} = \{(S, x, y_1, \dots, y_n, z) \in E\}\big|_{\mathcal{D}\setminus v=0}$,

If we define $M \triangleq \{(S^*(z), 0, 0, z) \in E \mid z \in \mathcal{Z}\}$, where S^* is given in Section 3.2, then M is a compact invariant set for $\mathcal{F}$. Furthermore, we have the following lemma describing a property on ∂E, utilizing $v = \{x\}$ and $v = \{y_i\}$.

LEMMA 3.8. *∂E_x and ∂E_{y_i}, $i = 1, \dots, n$, are invariant for $\mathcal{F}$. Moreover, $\partial E_x \subset W^+(M)$ such that if $e \in \partial E_x \setminus M$, then $\|\pi(e,t)\| \to \infty$ as $t \to -\infty$.*

PROOF: From (3.2), it is easy to see that ∂E_x and ∂E_{y_i} are invariant and $\pi(e,t) = (S(t), 0, y(t),\ t \mod(\omega)) \to (S^*(z(t)), 0, 0, z(t))$ as $t \to \infty$, $z \in [0, w]$, since $y_i(t) = y_i(0)\exp(-D_i t)$ whenever $e = (S_0, 0, y_0, 0) \in \partial E_x$. It follows that $\partial E_x \subset W^+(M)$. On the other hand, for $e \in \partial E_x \setminus M$, $S(t) \neq S^*(t)$ since $S(t) = S^*(t) +$

ce^{-Dt} for some constant $c \neq 0$ whenever $S(t_0) \neq S^*(t_0)$ for any $t_0 \in [0, \omega]$ (see Section 3.2). Therefore, $\|\pi(e,t)\| \to \infty$ as $t \to -\infty$. □

Note that from the above $\partial E = \partial E_x \cup \left(\bigcup_{i=1}^{n} \partial E_{y_i} \right)$ and hence ∂E is invariant.

THEOREM 3.9. *Suppose (A2) holds. If $\sigma_0 > 0$, then $\liminf_{t\to\infty} x(t) > 0$ for any $x(0) > 0$, or even stronger, for all $(S_0, x_0, y_0) \in \mathbb{R}_+^{n+2}$ with $x_0 > 0$, there exists $\zeta = \zeta(S_0, x_0, y_0) > 0$ such that $x(t) \geq \zeta$ for all $t \geq 0$.*

PROOF: First we assume that M is isolated. For any $e \in E$ and $\pi(e,t) = (S_e(t), x_e(t), y_e(t), t \mod (\omega))$, if $\liminf_{t\to\infty} x_e(t) = 0$, then $\Lambda^+(e) \cap \partial E_x \neq \phi$, and hence $M \subset \Lambda^+(e)$. It follows that $W_w^+(M) = \{e \in E \mid \liminf_{t\to\infty} x_e(t) = 0\}$. We claim that for any $e \in E \backslash \partial E_x$, if $\Lambda^+(e) \subset M$, then there exists $\alpha > 0$ such that $|S_e(t) - S^*(t+\alpha)| \to 0$ as $t \to \infty$. Actually, in the case that $\Lambda^+(e) \subset M$, then $x_e(t)$ and $y_{e,i}(t)$, $i = 1, \ldots, n$, tend to zero as $t \to \infty$, which implies $S_e(t) - S^*(t+\alpha)$ tends to zero for some $\alpha > 0$. It follows that

$$\lim_{t\to\infty} \frac{1}{\omega} \int_t^{t+\omega} \left(m_0 f_0(S_e(r)) - D_0\right) dr = \sigma_0 > 0, \tag{3.6}$$

and hence $\liminf_{t\to\infty} x_e(t) > 0$, a contradiction to $\Lambda^+(e) \cap \partial E_x \neq \phi$. So, $\Lambda^+(e) \backslash M \neq \phi$, or equivalently, $e \notin W^+(M)$, which together with Lemma 3.8 implies $W^+(M) = \partial E_x$. Therefore, by our assumption, $e \in W_w^+(M) \backslash W^+(M)$. Hence by Theorem 4.1 of Butler and Waltman (1986), there exists $\bar{e} \in \Lambda^+(e) \cap (W^+(M) \backslash M)$. Then it follows from Lemma 3.8 that $\Lambda^+(e)$ is unbounded, a contradiction to the dissipativeness of $\mathcal{F}$. This shows that $\Lambda^+(e) \cap \partial E_x = \phi$. Since $\Lambda^+(e)$ is compact, the distance $d(\Lambda^+(e), \partial E_x) = \zeta > 0$.

Therefore, with the above conclusion, it suffices to show that M is isolated for $\mathcal{F}$. Since $\sigma_0 > 0$, by the continuity of f_0, there exists $\Delta_0 > 0$ such that

$$\frac{1}{\omega} \int_0^{\omega} \left[m_0 f_0(S^*(r+\alpha) - \Delta_0) - (D_0 + \Delta_0) \right] dr \geq \frac{\sigma_0}{2} > 0. \tag{3.7}$$

From the dissipativeness of $\mathcal{F}$, we can find $\xi > 0$ (independent of $x_0 \in \mathbb{R}_+$) and $t_0 = t_0(x_0) \geq 0$ such that $0 \leq x(t) \leq \xi$ for all $t \geq t_0$. Define

$$K = \max_{1 \leq i \leq n} \{m_i(\max_{0 \leq x \leq \xi} f_i'(x))\} > 0 \quad \text{and} \quad \Delta = \frac{\Delta_0}{K} > 0.$$

Then $Q_\Delta \triangleq \{e \in E \mid d(e, M) < \Delta\}$ is an isolating neighborhood of M, where d is the metric on E. Otherwise, there exists an invariant set V containing M in Q_Δ with $V \backslash M \neq \phi$. By Lemma 3.8, $(V \backslash M) \cap \partial E_x = \phi$. Therefore for any $e \in V \backslash M$, $e \notin \partial E_x$, i.e., $x_0 > 0$. Since V is invariant, $\gamma^+(e) \subset V \subset Q_\Delta$, where $\gamma^+(e)$ is the positive semiorbit through e. In Q_Δ, however, we have

$$\frac{d}{dt}[\ln x(t)] \geq m_0 f_0(S^*(t) - \Delta_0) - (D_0 + \Delta_0).$$

Hence it follows from (3.7) that $x(n\omega) \geq x_0 \exp\left(\frac{\sigma_0}{2} n\omega\right) \to \infty$ as $n \to \infty$, a contradiction to $\pi(e, n\omega) \in V$ for all $n \geq 0$. This completes the proof. □

REMARK 3.10: (i) With the assumptions of Theorem 3.9, there exist for each $e \in E \backslash \partial E_x$ a $T \geq 0$ and a $\bar{\zeta} > 0$ such that $S^*(t) \geq S(t) + \bar{\zeta}$ for $t \geq T$. In fact, as shown in the previous discussion, there exists $T_1 > 0$ such that $u(t) \geq 0$ for $t \geq T_1$. Therefore $\Lambda^+(e) \subset \{(S, x, y, z) \mid S \leq S^*(z),\ \zeta \leq x \leq B,\ 0 \leq y \leq B,\ z \in \mathcal{Z}\}$ for some $B > 0$. Since $\Lambda^+(e)$ is compact and on $\{S = S^*(z)\}$, $u'(t) \geq m_0 f_0(\ell_1)\zeta > 0$, then $\Lambda^+(e) \cap \{S = S^*(z)\} = \phi$.

(ii) In the submodel where $y_i = 0,\ i = 1, \ldots, n$, Smith (1981) and Hale and Solominos (1983) gave some results on the persistence of x. However, due to the type of models they studied, the case with the y_i's consuming x is not discussed in their papers.

Denote $\partial_v \mathcal{F}$ as the flow on the boundary ∂E_v, where v is as before.

THEOREM 3.11. *Let the hypotheses of Theorem 3.9 hold. Then $\partial_y \mathcal{F}$ is uniformly persistent and there exists a nontrivial ω-periodic orbit* $(\bar{S}(t),\ \bar{x}(t), 0,\ t \mod (\omega))$ *on* ∂E_y.

PROOF: Note that $\Omega(\partial(\partial_y\mathcal{F})) = \{(S,x,y,z) \mid S = S^*(z), x = 0\} = M, \quad z \in [0,\omega]$ and $W^+(M) = \partial E_{xy}$. Then by Theorem 3.1 of Butler and Waltman (1986), $\partial_y\mathcal{F}$ is uniformly persistent. Now construct a Poincaré map T from the $S-x$ plane into itself by defining $T(S_0,x_0) = (S(\omega),x(\omega))$. It follows from Theorem 3.9 and the dissipativity that $\{T^n(S_0,x_0\}$ has a convergent subsequence for each (S_0,x_0) in the interior of $\mathbb{R}^2_+$. Then, by Massera's fixed point theorem (Theorem A.10 in appedix), there exists a fixed point $(\bar{S},\bar{x})$ of T in the interior of $\mathbb{R}^2_+$, which gives a nontrivial periodic orbit. □

Note that Smith (1981) and Hale and Somolinos (1983) proved the existence of a periodic solution in the $S-x$ plane using different techniques, but did not give any information on uniform persistence.

3.3.3. The stability and uniqueness of the periodic solution.

In the previous section we showed that in the case that $\sigma_0 > 0$, there exists a "nontrivial" periodic solution $(\bar{S}(t),\ \bar{x}(t),\ 0)$ in the $S-x$ plane while in the case that $\sigma_0 < 0,\ x(t) \to 0$. Hence for the remainder of this chapter, we always assume $\sigma_0 > 0$. Recall that $M = \{(S,0,0,z) \in E \mid S = S^*(z)\}$.

Before further disscusion, we give a clear picture of ∂E_y. ∂E_y is a 3-dimensional manifold with boundary which can be pictured simply by considering it's image under the homeomorphism $\mathcal{H} : (S,x,0,z) \mapsto (1+x,z,S) \equiv (r,\theta,w)$, where the latter are viewed as cylindrical coordinates in $\mathbb{R}^3$. This maps ∂E_y onto the exterior component of the cylinder $r=1$ in $\mathbb{R}^3$. Then

$$M = \{(S^*(\theta),0,0,\theta) \mid \theta \in \mathcal{Z}\}$$

has the image of a closed curve on the boundary of ∂E_y, which is the cylinder $r=1$.

Now that we know that a periodic solution exists, we are interested in establishing criteria guaranteeing that it is unique and globally asymptotically stable.

This is done in the next three theorems. Theorem 3.12 below deals with a general cylinder-like two-dimensional C^2-manifold with one boundary (Definition 1.15). The results obtained in this theorem are then applied to a specific manifold defined by solutions of a given partial differential equation in Theorem 3.13.

THEOREM 3.12. *Let the following hypotheses hold. (i) If the ω-limit set $\Omega(\partial E_y)$ of ∂E_y for $\partial \mathcal{F}_y$ lies on an invariant cylinder-like two-dimensional C^2-manifold with one boundary, $\mathcal{M}$, with M as its boundary. (ii) Each ω-periodic orbit except $(S^*(t), 0, 0, t \mod (\omega))$ is asymptotically stable on $\mathcal{M}$. Then $\partial \mathcal{F}_y$ has only one ω-periodic orbit $(\bar{S}(t),\ \bar{x}(t), 0, t \mod (\omega))$ which is globally asymptotically stable in the interior of ∂E_y.*

PROOF: Since $\Gamma \subset \Omega(\partial E_y)$ for any ω-periodic orbit Γ, all ω-periodic orbits lie on $\mathcal{M}$. Suppose $g : \mathcal{M} \to \mathcal{C}$ is the C^2-homeomorphism. Then for any solution $e(t) = (S(t), x(t), y(t), z(t))$ on $\mathcal{M}$, $g(e(t))$ is a curve on $\mathcal{C}$ which by (i), winds arround $\mathcal{C}$ as t increases. Therefore for any ω-periodic orbit Γ, $g(\Gamma)$ is a closed curve on $\mathcal{C}$ which winds arround $\mathcal{C}$. If an ω-periodic orbit Γ_1 is not unique, then by (ii), we can find another ω-periodic orbit Γ_2 such that $g(\Gamma_1)$ and $g(\Gamma_2)$, and both wind arround $\mathcal{C}$, and are adjacent to each other on $\mathcal{C}$. In this case, we call Γ_1 and Γ_2 adjacent on $\mathcal{M}$. Then the portion P of $\mathcal{M}$ between Γ_1 and Γ_2 with them as its boundary is a compact and connected C^2-manifold which is homeomorphic to the portion of $\mathcal{C}$ between $g(\Gamma_1)$ and $g(\Gamma_2)$. Let p be an interior point of P. The α-limit set A_p of p contains a minimal set $Z \subset P$. By the theorem in Schwartz (1963) (which requires hypothesis (i)), Z is a closed orbit in P (with respect to $\mathcal{M}$) since $\partial \mathcal{F}_y$ has no critical points and P is not homeomorphic to T^2, the two-torus. Moreover by (ii), Z does not coincide with either of Γ_1 or Γ_2 since $Z \subset A_p$. This contradicts the adjacency of Γ_1 and Γ_2.

We can use the same argument to show the global stability of the ω-periodic orbit Γ utilizing the dissipativity of the system. This time we consider $(S^*(z), 0, 0, z)$ as Γ_1, and to form Γ_2, we first define $\hat{\Gamma}$ as follows,

$$\hat{\Gamma} = \overline{\mathcal{M}} \backslash \mathcal{M},$$

where $\overline{\mathcal{M}}$ is the closure of $\mathcal{M}$ in ∂E_y. Then it is easy to see that $\hat{\Gamma}$ is either a closed curve (including the case of a single point) or an empty set. In the latter case, the intersection of $\mathcal{M}$ and $\{(S, x, 0, z) \in \partial E_y \mid S = 0\}$ is a closed curve $\tilde{\Gamma}$ (see Fig. 5). As Γ_2, we consider $\hat{\Gamma}$ if it is not empty and consider $\tilde{\Gamma}$ if $\hat{\Gamma}$ is empty. Then all orbits approach to that portion of G bounded by Γ_1 and Γ_2. If Γ is not globally stable, then there exists one orbit $\gamma(e)$, $e \in \partial E_y$, such that $\Lambda^+(e) \backslash \Gamma \neq \phi$. However, since Γ is asymptotically stable, we have

$$d(\Lambda^+(e), \Gamma) > 0.$$

As stated above, $\Lambda^+(e) \subset G$. Applying the theorem in Schwartz (1963) again, we obtain a closed orbit other than Γ, a contradiction to the uniqueness of Γ. This completes the proof. □

The above theorem establishes the global stability provided it can be shown that the manifold $\mathcal{M}$ exists and all positive periodic solutions are stable. The next theorem gives a criterion in terms of a related partial differential equation for this to be true. Although the application of the next theorem is not simple in many of the cases, because of the complexity of (3.8), we believe that it is worthwhile to state it here since for some specific cases, it may not be difficult for one to find a solution of (3.8), hence the theorem can be applied.

THEOREM 3.13. *Consider the initial-boundary value problem*

$$\begin{cases} u_t + \left[D(S^0(t) - S) - m_0 f_0(S)x\right]u_S + \left[(m_0 f_0(S) - D_0)x\right]u_x + Du = DS^0(t) \\ u(S, 0, t) = S^*(t), \quad u(S, x, 0) = u(S, x, \omega), \end{cases} \tag{3.8}$$
$$t \in [0, \omega] \quad S \geq 0, \;\; x \geq 0.$$

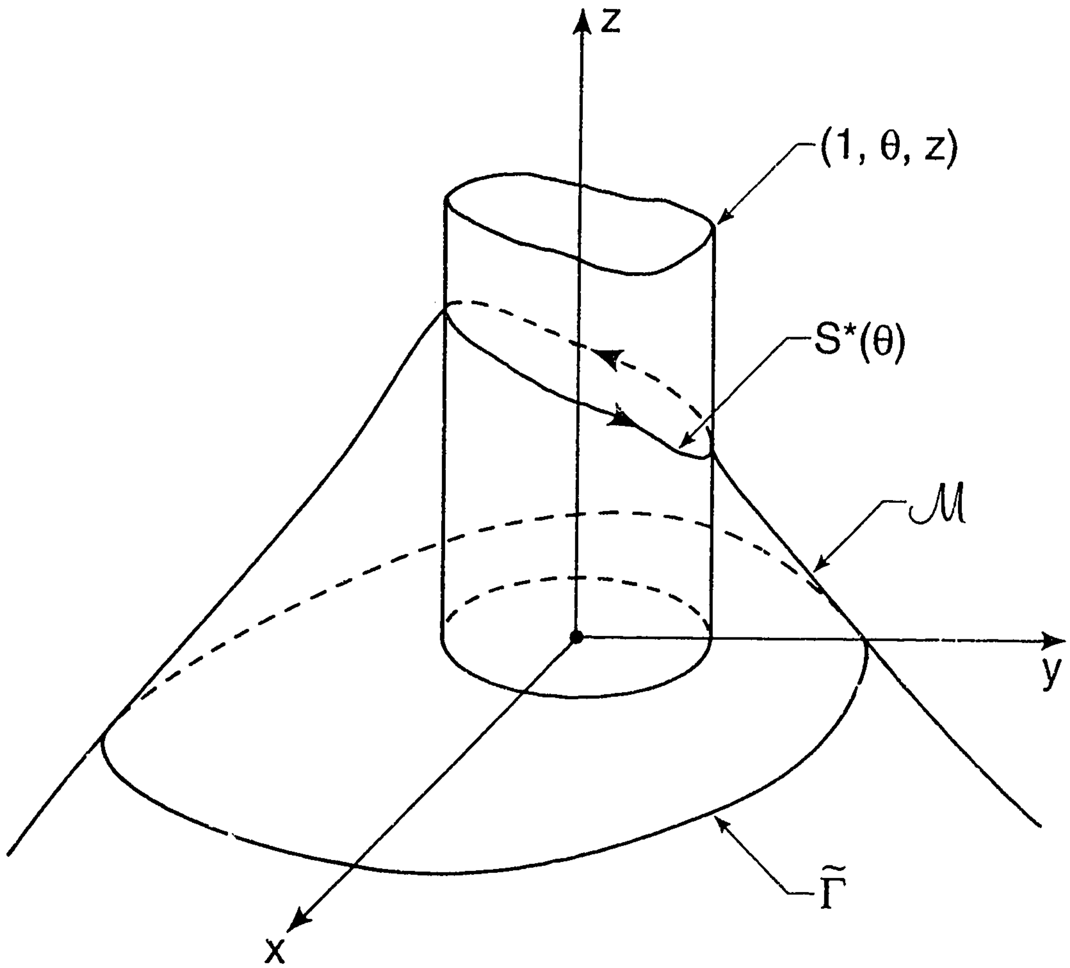


Fig. 5. A description for the proof of Theorem 3.12.

Suppose $\tilde{u}(S,x,t)$ is a C^2-solution of (3.8) which satisfies:

$$\frac{\partial \tilde{u}}{\partial x} \neq 0 \quad \text{and} \quad \Gamma_t = \{(S,x) \mid \tilde{u}(S,x,t) = S^*(t)\} \cong [0,1].$$

Then if $\frac{\partial \tilde{u}}{\partial S} \Big/ \frac{\partial \tilde{u}}{\partial x} \leq \frac{D}{D_0}$ on Γ_t for all $t \in [0,\omega]$ the conclusion of Theorem 3.12 is true.

PROOF: If the hypotheses are satisfied, then $\mathcal{M} = \{(S,x,z) \mid \tilde{u}(S,x,z) = S^*(z), z \in \mathcal{Z}\}$. It is easy to see that $\mathcal{M}$ is an invariant and global attractor in E_y utilizing

$$\tilde{u}(t) = \tilde{u}(S(t), x(t), t \mod \omega)$$

for an orbit in E_y. Since $\frac{\partial \tilde{u}}{\partial x} \neq 0$, by the implicit function theorem, there exists $h : \mathbb{R} \times \mathcal{Z} \to \mathbb{R}^+$ such that $\tilde{u}(S, h(S,z), z) = S^*(z)$. For an ω-periodic orbit $(\bar{S}(t), \bar{x}(t), t \mod \omega)$ of $\mathcal{F}_y$, it follows that $\bar{x}(t) = h(\bar{S}(t), t)$. Since $\mathcal{M}$ is invariant, $\bar{S}(t)$ is a solution of

$$\dot{v} = D(S^0(t) - v) - m_0 f_0(v) h(v,t) \tag{3.9}$$

whose linear variational equation about $\bar{S}(t)$ is

$$\dot{v} = \big[-D - m_0 f_0(\bar{S}(t)) \frac{\partial h}{\partial v}(\bar{S}(t), t) - m_0 f_0'(\bar{S}(t))\bar{x}(t)\big] v. \tag{3.10}$$

But $-\frac{\partial h}{\partial v}(\bar{S}(t), t) = \frac{\partial \tilde{u}}{\partial x} / \frac{\partial \tilde{u}}{\partial x}\big|_{S=\bar{S}(t)} \leq \frac{D}{D_0}$. Hence it follows from (3.10) that

$$\dot{v} \leq \frac{D}{D_0}\big[m_0 f_0(\bar{S}(t)) - D_0 - \frac{D_0}{D} m_0 f_0'(\bar{S}(t))\bar{x}(t)\big] v,$$

which implies $\bar{S}(t)$ is asymptotically stable for (3.9) since $\int_0^\omega (m_0 f_0(\bar{S}(t)) - D_0) dt = 0$. Obviously, $\mathcal{F}_y|_{\mathcal{M}}$ can be generated by the solution $v(t)$ of (3.9) by defining the orbit $(v(t), h(v(t), t), t \mod \omega)$ on $\mathcal{M}$. Then Theorem 3.12 gives the uniqueness and global stability. □

In the case that $D = D_0$, we observe that $\tilde{u}(S, x, t) = S + x$ is a solution of (3.8), which satisfies all the conditions of the above theorem. This solution was obtained by observation, not by solving system (3.8). With this solution, Theorem 3.13 can be applied to the next theorem.

THEOREM 3.14. *If $D = D_0$, system (3.2) has a globally asymptotically stable ω-periodic solution in the interior of E_y.*

PROOF: Let $\tilde{u}(S, x, t) = S + x$. Then by Theorem 3.13, the conclusion is true.□

Finally, we note that Smith (1981) proved that if $D_0 \leq D$, system (3.2) has only one nontrivial ω-periodic solution $(\bar{S}(t), \bar{x}(t))$ on E_y which is asymptotically stable. However, he gave no information on the global stability of $(\bar{S}(t), \bar{x}(t))$. For $D = D_0$, Hale and Solominos (1983) gave the same result as Theorem 3.14.

3.4. The population growth of predators.

In order to discuss (3.2) further, we need a globally stable ω-periodic solution $(\bar{S}(t), \bar{x}(t), t \mod \omega)$ on E_y. Therefore, in addition to $\sigma_0 > 0$, we assume $D = D_0$ throughout the remainder of this chapter. Denote by $(\bar{S}(t), \bar{x}(t))$ the solution described in Theorem 3.14. Our discussions are divided into the following three circumstances.

3.4.1. Extinction of y_i due to the lack of prey.

In a chemostat environment with competition, the extinction of a species of competitors can be caused either by the lack of resources or by the lack of competition ability. In this section, we consentrate ourselves on the criteria for the first case and leave the second one to the next section.

THEOREM 3.15. *Suppose (A2) holds. If $\sigma_i \triangleq \frac{1}{\omega}\int_0^{\omega}(m_i f_i(\bar{x}(t)) - D_i)dt < 0$, then $y_i(t) \to 0$ exponentially as $t \to \infty$.*

PROOF: Let $(S(t), x(t), y(t))$ be a solution of (3.2). Note that if we replace $S(t)$ by $S(t) + x(t)$ in Lemma 3.4, the assertions (i) and (ii) are still valid (the arguments are precisely the same). Therefore, it suffices to show this theorem with the assumption $S(t) + x(t) \leq S^*(t)$ for $t \geq t_1$ for some $t_1 \geq 0$. Since f_0 is increasing and $x(t) \geq 0$,

$$\dot{x}(t) \leq \big(m_0 f_0(S^*(t) - x(t)) - D\big)x(t). \tag{3.11}$$

By Theorem 3.14, all solutions of

$$\dot{u} = \big(m_0 f_0(S^*(t) - u) - D\big)u \tag{3.12}$$

tend to $\bar{x}(t)$ as $t \to \infty$. It follows from (3.11) and (3.12) that

$$\liminf_{t\to\infty} |\bar{x}(t) - x(t)| \geq 0. \tag{3.13}$$

On the other hand, $y_i(t) = y_i(t_2)\exp\left[\int_{t_2}^{t}(m_i f_i(x(r)) - D_i)dr\right]$ for any $t_2 \geq 0$ and $t \geq t_2$. By (3.13), we can choose t_2 so large that $\frac{1}{\omega}\int_t^{t+\omega}(m_i f_i(x(r)) - D_i)dr < \frac{\sigma_i}{2} < 0$ for $t \geq t_2$. It follows that $0 \leq y_i(t) \leq K\ e^{-\delta t}$ for some $K > 0$, $\delta > 0$ and $t \geq t_2$. This completes the proof. □

COROLLARY 3.16. *Suppose (A3) holds and $f_i'(x)$ is strictly decreasing. If $\lambda_i \geq \frac{1}{\omega}\int_0^\omega \bar{x}(t)dt$, then $y_i(t) \to 0$ exponentially as $t \to \infty$.*

PROOF: We can prove this corollary using the same argument as in the proof of Theorem 3.7 by replacing $\lambda_0, f_0, m_0, \sigma_0$ and S^* with $\lambda_i, f_i, m_i, \sigma_i$ and $\bar{x}$, respectively. □

Usually it is hard to construct the solution $(\bar{S}(t), \bar{x}(t))$, and hence to compute $\int_0^\omega \bar{x}(t)dt$. The next corollary gives a criterion for extinction utilizing only the right hand sides of the equations.

COROLLARY 3.17. *Under the hypotheses of Corollary 3.16, if* $\lambda_i \geq \frac{\sigma_0}{m_0 L}$, *then* $y_i(t) \to 0$ *exponentially as* $t \to \infty$, *where* $L = \min_{\ell_1 \leq x \leq \ell_2} f_0'(x)$.

PROOF: This follows directly from Corollary 3.16 and the following lemma. □

LEMMA 3.18. *Under the hypotheses of Corollary 3.16,* $\frac{1}{\omega}\int_0^\omega \bar{x}(t)dt \leq \frac{\sigma_0}{m_0 L}$.

PROOF: Clearly, $\frac{1}{\omega}\int_0^\omega f_0(\bar{S}(t))dt = \frac{D}{m_0}$. It follows that

$$\begin{aligned}\frac{\sigma_0}{m_0} &= \frac{1}{\omega}\int_0^\omega [f_0(S^*(t)) - f_0(\bar{S}(t))]dt = \frac{1}{\omega}\int_0^\omega f_0'(\theta(t))(S^*(t) - \bar{S}(t))dt \\ &\geq \frac{L}{\omega}\int_0^\omega \bar{x}(t)dt,\end{aligned} \tag{3.14}$$

where $\theta(t)$ is the mean value of $S^*(t)$ and $\bar{S}(t)$. The lemma follows. □

3.4.2. Extinction of y_i due to competition.

Now we discuss some situations in which y_k, for some k, tends to extinction no matter how abundant the prey is, because it is outcompeted by other predators.

Denote $g_i(z) = m_i f_i(z) - D_i$ and $G_{ik}(z, r) = g_i(z) - r g_k(z)$.

THEOREM 3.19. *Suppose (A2) holds. If there exists a positive* r *such that* $G_{ik}(z, r) > 0$ *for all* $z \in (0, \ell_2)$, *then* $y_{i0} > 0$ *implies that* $y_k(t) \to 0$ *exponentially as* $t \to \infty$.

PROOF: The theorem can be shown using the same arguments as in the proof of Theorem 2.4 of Hale and Solominos (1983) and utilizing the conclusion of Theorem 3.9 in this chapter. □

Note that the assumption that $G_{ik}(z, r) > 0$ for all $z \in (0, \ell_2)$ and some $r > 0$ implies that $\lambda_i < \lambda_k$.

THEOREM 3.20. *Suppose (A3) holds. If* $\frac{\sigma_i}{\sigma_k} > r^* \triangleq \max_{0 \leq z \leq \ell_2} \left\{\frac{m_i f_i'(z)}{m_k f_k'(z)}\right\}$, *then* $y_{i0} > 0$ *implies* $y_k(t) \to 0$ *exponentially as* $t \to \infty$.

PROOF: As stated in the beginning of the proof of Theorem 3.15, it suffices to show the validity of the theorem with $S(t) + x(t) \le S^*(t)$ for $t \ge t_1$ for some $t_1 \ge 0$. Also, we have shown in that proof that $x(t) \le \bar{x}(t) + \theta(t)$ with $\theta(t) \to 0$ as $t \to \infty$. Define $Y(t) = \ln \frac{y_k^{r^*}(t)}{y_i(t)}$ since $y_i(t) > 0$ for all $t \ge 0$. Then $Y(t)$ satisfies

$$Y' = -G_{ik}(x(t), r^*). \tag{3.15}$$

Some calculations yield

$$\frac{\partial G_{ik}(z, r^*)}{\partial z} = m_i f_i'(z) - r^* m_k f_k'(z) < 0 \quad \text{for} \quad z \in [0, \ell_2].$$

It follows that G_{ik} is decreasing in z. By (3.15)

$$Y(t) \le Y(0) - \int_0^t G_{ik}(\bar{x}(v) + \theta(v), r^*) dv. \tag{3.16}$$

Since $\theta(t) \to 0$ as $t \to \infty$ and f_i and f_k are continuous,

$$\mathcal{E}(t) \triangleq \int_t^{t+\omega} [G_{ik}(\bar{x}(v) + \theta(v), r^*) - G_{ik}(\bar{x}(v), r^*)] dv \to 0 \quad \text{as} \quad t \to +\infty. \tag{3.17}$$

It follows from (3.16), (3.17) and $\sigma_i > r^* \sigma_k$ that $Y(t) \to -\infty$ as $t \to \infty$, which implies that $y_k(t) \to 0$ exponentially as $t \to \infty$. □

We now note that we can have a corollary of Theorem 3.19 for Michaelis-Menten systems which is similar to Theorem 2.5 of Hale and Solominos (1983). As in that paper, we define $\mu_i = \frac{m_i}{D_i}$, $i = 0, 1, \ldots, n$, and we obtain the following result:

THEOREM 3.21. *Consider system (3.2) with*

$$f_i(z) = \frac{z}{a_i + z}, \; i = 0, 1, \ldots, n.$$

If $\lambda_1 < \lambda_2 \le \cdots \le \lambda_n < \frac{1}{\omega} \int_0^\omega \bar{x}(v) dv$ and $\mu_1 \le \mu_k$ for some k such that $2 \le k \le n$, then $\frac{\sigma_1}{\sigma_k} > \frac{m_1 a_k}{m_k a_1}$ and $y_{10} > 0$ imply $y_k(t) \to 0$ exponentially as $t \to \infty$.

PROOF: In this case, $\lambda_i = \frac{a_i D_i}{m_i - D_i}$, $\mu_i = \frac{m_i}{D_i}$, $i = 1, \ldots, n$. Hence

$$a_1 = \lambda_1(\mu_1 - 1) \le \lambda_1(\mu_k - 1) = \frac{\lambda_1}{\lambda_k} a_k < a_k. \tag{3.18}$$

On the other hand,

$$\frac{m_1 f_1'(z)}{m_k f_k'(z)} = \frac{m_1 a_1 (a_k + z)^2}{m_k a_k (a_1 + z)^2}. \tag{3.19}$$

Define $h(z) = \left(\frac{a_k+z}{a_1+z}\right)^2$. Then

$$\frac{dh(z)}{dz} = 2\left(\frac{a_k + z}{a_1 + z}\right) \cdot \frac{(a_1 - a_k)}{(a_1 + z)^2}$$

$$= \frac{2(a_1 - a_k)(a_k + z)}{(a_1 + z)^3} < 0 \quad \text{for} \quad z \geq 0.$$

It follows that $h(z)$ is decreasing and so is $\frac{m_1 f_1'(z)}{m_k f_k'(z)}$. Therefore, from (3.19),

$$\frac{m_1 f_1'(z)}{m_k f_k'(z)} \leq \frac{m_1 f_1'(0)}{m_k f_k'(0)} = \frac{m_1 a_k}{m_k a_1} \quad \text{for} \quad z \geq 0.$$

If we define $r^* = \frac{m_1 a_k}{m_k a_1}$, then the conditions in Theorem 3.20 hold. This completes the proof. □

3.4.3. Survival and coexistence of the predators.

In the previous sections, we have shown that $\sigma_i < 0$ is a sufficient condition for y_i to tend to extinction whereas $\sigma_i > 0$ is not sufficient for y_i to survive, as shown in Theorems 3.19 and 3.20. In this section, we give several sufficient conditions for the y_i to be persistent. We utilize the notations developed in Chapter 1 and Section 3.3.2.

THEOREM 3.22. *Suppose (A2) holds. If $\sigma_i > 0$, then $\partial_{\widehat{xy_i}}\mathcal{F}$ is uniformly persistent on $\partial E_{\widehat{xy_i}}$.*

PROOF: In this case we only need consider $y \in \mathbb{R}_+$, i.e. $\mathcal{E} = \mathbb{R} \times \mathbb{R}^2_+$. Then we denote $\mathcal{F} = \partial_{\widehat{xy_i}}\mathcal{F}$, $\partial E_{\widehat{xy_i}} = E$. As we proved earlier, $\Omega(\partial\mathcal{F}) = \{M_0, M_1\}$, where $M_0 = \{(S^*(z), 0, 0, z) \mid z \in \mathcal{Z}\}$ and $M_1 = \{(\bar{S}(z), \bar{x}(z), 0, z) \mid z \in \mathcal{Z}\}$. Using results obtained in sections 3.3.1 and 3.3.2, it can be shown that M_0 is isolated for both $\partial\mathcal{F}$ and $\mathcal{F}$ while M_1 is also isolated for $\partial\mathcal{F}$. Now utilizing the assumption $\sigma_i > 0$ and the technique used in the proof of isolatedness of M_0 for $\mathcal{F}$ in Theorem 3.9, we can prove that M_1 is also isolated for $\mathcal{F}$. Hence, $\mathcal{M} = \Omega(\partial\mathcal{F})$ is an isolated covering of itself. On the other hand, $\mathcal{M}$ is acyclic since M_1 is globally stable on ∂E_y.

In the proof of Theorem 3.9, we proved that $W^+(M_0) = \partial E_x$. And

$$W^+(M_1) \cap \text{ int } E = \phi$$

will lead to a contradiction to $\sigma_i > 0$. Therefore, the uniform persistence follows from Theorem 3.1 of Butler and Waltman (1986). □

REMARK 3.23: Note that if $\sigma_i > 0$, and $y_k(t) \to 0$ as $t \to \infty$ for $k \neq i$, then $x_0 > 0$, $y_{i0} > 0$, implies $\liminf_{t\to\infty} y_i(t) > 0$. This follows from the uniform persistence established by Theorem 3.22.

Remark 3.23 requires that other predators go to extinction for y_i to survive. The next theorem gives conditions which guarantee that y_i survives independent of the growth of the other predators.

THEOREM 3.24. *Suppose (A2) holds. Let $\sigma_i > 0$ and $\lambda_i = \lambda$ for all $i = 1, \ldots, n$. Then $y_{i0} > 0$ and $x_0 > 0$ imply that $\limsup_{t\to\infty} y_i(t) > 0$.*

PROOF: Suppose the conclusion is false, i.e., $\lim_{t\to\infty} y_i(t) = 0$. Define $Y_k(t) = \ln y_k(t)$ for those k such that $y_{k0} > 0$. Then

$$\frac{dY_i}{dY_k} = \frac{g_i(x)}{g_k(x)} \triangleq g_{ik}(x). \tag{3.20}$$

By the assumption on λ, there exists $r > 0$ such that $g_{ik}(x) \geq r$ for all $x \geq 0$ except $x = \lambda$. It follows from (3.20) that

$$Y_i(t) \geq r\ Y_k(t) + C, \quad \text{where} \quad C \quad \text{is a constant,}$$

which shows that $Y_k(t) \to -\infty$ whenever $Y_i(t) \to -\infty$. Therefore $y_k(t) \to 0$ as $t \to \infty$ for $k \neq i$. By Remark 3.23, $\liminf_{t\to\infty} y_i(t) > 0$, a contradiction, completing the proof. □

Next, we discuss the existence of an ω-periodic orbit on $\partial E_{\widehat{xy_i}}$. By Theorems 2.13, the following is a direct corollary of Theorem 3.22

COROLLARY 3.25. *Suppose (A2) holds. If $\sigma_i > 0$, then $\partial_{\widehat{xy_i}}\mathcal{F}$ has a nontrivial ω-periodic solution on $\partial E_{\widehat{xy_i}}$.*

For the remainder of this section, we assume that $\lambda_i = \lambda, \quad i = 1, \ldots, n$. Although this seems restrictive we note that this case has been of interest to previous authors (Hsu, 1978; Hsu *et al.*, 1977). As well, any generic results obtained in this case may also be valid for values of λ_i sufficiently close to λ.

THEOREM 3.26. *Suppose (A2) holds. If for all $i = 1, \ldots, n$, $\sigma_i > 0$ and $\lambda_i = \lambda$, then $\limsup_{t\to\infty} y_i(t) > 0$ for those i such that $y_{i0} > 0$.*

PROOF: This follows directly from Theorem 3.24. □

This theorem gives a sufficient condition for all y_i's to coexist. The following results concern a class of systems with additional conditions on the f_i's, but still includes Michaelis-Menten nutrient uptakes.

THEOREM 3.27. *Suppose (A3) holds and f_i' is strictly decreasing for $i = 1, \ldots, n$. If $\lambda_i = \lambda \leq \frac{\sigma_0 f_i'(\ell_2)}{m_0 G f_i'(\ell_1)}$ for all $i = 1, \ldots, n$ and $G = \max_{0 \leq x \leq \ell_2} f_0'(x)$, then $\limsup_{t\to\infty} y_i(t) > 0$ for those i such that $y_{i0} > 0$.*

PROOF: The proof follows from Theorem 3.26 and the following Lemma 3.28. Note that (A3) implies λ is of multiplicity 1 for each g_i. □

LEMMA 3.28. *Under the assumption of Theorem 3.27, $\sigma_i > 0$ for all $i = 1, \ldots, n$.*

PROOF: As in the proof of Theorem 3.6, we have

$$\sigma_i \geq \frac{m_i}{\omega} \int_0^\omega f'(\bar{x}(t))(\bar{x}(t) - \lambda)dt, \quad i = 1, \ldots, n. \tag{3.21}$$

Since f_i' is decreasing,

$$\int_0^\omega f'(\bar{x}(t))(\bar{x}(t) - \lambda)dt > \int_0^\omega f_i'(\ell_2)\bar{x}(t)dt - \omega f_i'(\ell_1)\lambda. \tag{3.22}$$

On the other hand, similarly to Lemma 3.18, it can be shown that

$$\frac{\sigma_0}{m_0 G} \leq \frac{1}{\omega} \int_0^\omega \bar{x}(t)dt. \tag{3.23}$$

Combining (3.23) with $\lambda \leq \frac{\sigma_0}{m_0 G} \cdot \frac{f_i'(\ell_2)}{f_i'(\ell_1)}$, we obtain

$$\lambda \leq \frac{f_i'(\ell_2)}{f_i'(\ell_1)} \cdot \frac{1}{\omega} \int_0^\omega \bar{x}(t)dt,$$

which, by (3.21) and (3.22), implies that $\sigma_i > 0$, completing the proof. □

COROLLARY 3.29. *For the Michaelis-Menten system, if*

$$\frac{a_i D_i}{m_i - D_i} = \lambda \leq \frac{\sigma_0 (a_0 + \ell_1)^2 (a_i + \ell_1)^2}{m_0 a_0 (a_i + \ell_2)^2}$$

for $i = 1, \ldots, n$, *then* $\limsup_{t \to \infty} y_i(t) > 0$ *for all such* i *that* $y_{i0} > 0$.

3.5. Discussion.

This chapter is concerned with predator competition for a microorganism growing in a chemostat environment with a periodic nutrient input. In particular we considered interactions among the consumers at various trophic levels.

In the first instance we considered the case where the chemostat dynamics involved the nutrient and one primary consumer. It was found that extinction or survival of the consumer depended on the time average (over one period) of an expression involving the periodic fluctuation of nutrient in the absence of that consumer. In the case of survival, it was shown that both the nutrient and consumer concentrations approached a unique periodic solution.

We then considered the case of a nutrient, one primary consumer, and several secondary consumers feeding on, and competing for, the primary consumer. We showed, not unsurprisingly, that if the primary consumer was not in sufficient supply, then all secondary consumers went extinct. We were then able to identify several parameters which determined the survival or extinction of the secondary consumers as a consequence of competition.

Further if only one secondary consumer survives, we showed that a periodic solution (not necessarily unique) exists.

In the case where certain of the parameters, termed λ_i, are equal, we were able to obtain criteria which led to survival of all consumers. It is still an open question in the case of different λ_i's whether one can again find such criteria, although we suspect that such is the case.

A second problem of interest for future investigation would be to modify the model of Wolkowicz (1989) by introducing a periodic nutrient input. Finally, it would be of great interest to consider the question of coupled chemostats (gradostat) with periodic nutrient input.

Chapter 4

A CYCLOSTAT MODEL

4.1. Introduction.

In last two decades, many authors have devoted themselves to the study of chemostat systems. They achieved a lot of interesting results on the topic. A varied laboratory apparatus called a gradostat and its mathematical model subsequently has been set up and studied. Untill today, there are still many authors interested in these two topics in various settings.

In this chapter, we modify the notion of a gradostat to that of a cyclostat which can also be implemented as a laboratory apparatus shown as in Figure 3. The idea is to modify the gradostat in such a way that the flows between the culture vessels are in one direction only, and that the output of the last culture vessels flows back to the first one, which itself has an additional output to a collecting vessel in order to keep the volume in the culture vessels constant. This model can be considered as an emulation of some recycleable environment. Hence this chapter will contain to the best of our knowledge the first work on such systems. The model is described by the equations (4.1) in next section.

4.2. The model.

The biological model we consider in this chapter consists of n vessels connected in a cycle by one-way flows, in which one species of microorganism is fed up by the input nutrient (see Fig. 3).

As a model of this system, we take

$$\begin{cases} \dot{S}_1 = D(S_0 + S_n - 2S_1) - \frac{m}{\gamma} f(S_1) x_1 \\ \dot{S}_i = D(S_{i-1} - S_i) - \frac{m}{\gamma} f(S_i) x_i \\ \dot{x}_1 = D(x_n - 2x_1) + m f(S_1) x_1 \\ \dot{x}_i = D(x_{i-1} - x_i) + m f(S_i) x_i \end{cases} \tag{4.1}$$

$$S_1(0), S_i(0), x_1(0), x_i(0) \geq 0; \; i = 2, \ldots, n,$$

where $S_0 > 0$ represents the input nutrient concentration rate of S, $D > 0$ is the dilution (or wash-out) rate, S_i and x_{ij} represent the populations of the nutrient and the microorganism in ith vessel respectively, m is the maximal growth rate of the species, and γ is the yield factor of the nutrient S corresponding to the species. As a consequence of the biological reality, that any population can not have negative numbers, we consider system (4.1) in $\mathbb{R}_+^{2n}$ only. As to the nutrient uptake functions f, we assume

(A01) $f(0) = 0$, $f(u) > 0$ for $u > 0$, $f(u)$ monotonically increases to 1 as u tends to ∞, and $f \in C^r$ where r is as required; or

(A02) in addition to (A01), $f'(u) > 0$ for $u \geq 0$.

The positivity and the monotone behavior of f are based on the known facts that the nutrient uptake rates are always positive and that increasing the nutrient input increases the nutrient uptake rates, which are of limit 1 as the input tends to infinity, on the competitors. The rest of the above assumptions are made just for mathematical convenience.

We make the following change of variables,

$$\bar{S}_i = \frac{S_i}{S_0}, \bar{x}_i = \frac{x_i}{\gamma S_0}, \bar{f}(u) = \frac{m}{D} f(S_0 u), i = 1, \ldots, n.$$

And we rescale the time t by $\bar{t} = Dt$ and take all the derivatives with respect to $\bar{t}$. For convenience, we drop the bar and denote the new variables as in (4.1). Then system (4.1) becomes,

$$\begin{cases} \dot{S}_1 = (1 + S_n - 2S_1) - f(S_1)x_1 \\ \dot{S}_i = (S_{i-1} - S_i) - f(S_i)x_i \\ \dot{x}_1 = (x_n - 2x_1) + f(S_1)x_1 \\ \dot{x}_i = (x_{i-1} - x_i) + f(S_i)x_i \end{cases} \tag{4.2}$$

$$S_1(0), S_i(0), x_1(0), x_i(0) \geq 0; \; i = 2, \ldots, n.$$

Here f, satisfies one of the following assumptions,

(A1) $f(0) = 0$, $f(u) > 0$ for $u > 0$, $f(u)$ approaches increasingly to $\frac{m}{D}$ as u tends to ∞, and $f \in C^r$ where r is as required; or

(A2) in addition to (A1), $f'(u) > 0$ for $u \geq 0$.

If $n = 1$ or 2, system (4.2) describes a chemostat or a gradostat model respectively, for which many authors have done a lot of work. Therefore we only consider system (4.2) with $n \geq 3$ throughout this chapter.

As a matter of fact, we can describe (4.2) as a dynamical system π on $\mathbb{R}^{2n}$ by extending f to $\mathbb{R}$ continuously, say $f(u) = 0$ for all $u < 0$. Even further, with a well-known theorem in the theory of functional analysis, we can extend f C^r-differentiably to $\mathbb{R}$ if f is C^r-differentiable. By doing so, we can bring the theory of dynamical systems into our study of the cyclostat model. Hence we consider system (4.2) to be defined on $\mathbb{R}^{2n}$.

4.3. General aspects of the system.

In this chapter, we devote ourselves to the study of the persistence of the microorganism in system (4.2). But before paying attention specifically to the microorganism, we will give some results on the system.

We denote $(S_1, \ldots, S_n, x_1, \ldots, x_n) \in \mathbb{R}_+^{2n}$ by (S, x), where $S, x \in \mathbb{R}_+^n$, and

$$\begin{aligned} H_x &\triangleq \{(S,x) \in \mathbb{R}^{2n} \mid x_i = 0 \quad \text{for} \quad i = 1, \ldots, n\}, \\ H_x^+ &\triangleq \{(S,0) \in \mathbb{R}^{2n} \mid S_i \geq 0 \quad \text{for} \quad i = 1, \ldots, n\}. \end{aligned} \tag{4.3}$$

The following lemma guarantees that we concentrate ourselves in $\mathbb{R}_+^{2n}$ for our purpose of study of system (4.2). From now on throughout this chapter, we always mean $\mathbb{R}_+^{2n}$ whenever an area is concerned without spicification.

LEMMA 4.1. *H_x is invariant for π while H_x^+ is positively invariant for the subsystem of π in H_x, and consequently, $\mathbb{R}_+^{2n}$ is positively invariant for π.*

PROOF: For any $e = (S, x) \in H_x$, $x_i = 0$ for all $i = 1, \ldots, n$. It follows that $x_i(t) = 0$ for all $t > 0$ since $\dot{x}_i = 0$ for all i. If H_x^+ is not invariant in H_x, then we can find an orbit $\pi(t, 0, e)$ of (4.2) such that $e \in \partial H_x^+$, the boundary of H_x^+ in H_x, and there exists $T > 0$ such that $\pi(t, 0, e) \notin H_x^+$ for $t \in (0, T]$. Here the T can be chosen as small as we want. Then we can find an $i \in \{1, \ldots, n\}$ such that $S_i(t) \geq 0$ while $S_{i+1}(t) < 0$ for $t \in (0, T]$ and $S_{i+1}(0) = 0$ (if $i = n$, $S_{n+1} = S_1$) since for $e = 0$ we have $\dot{S}_1 = 1 > 0$ at e. By the mean value theorem, there exists $c \in (0, T)$ such that $\dot{S}_{i+1}(c) < 0$. However, by the definition of (4.2), $\dot{S}_{i+1}(c) \geq -S_{i+1}(c) > 0$. The contradiction leads to our assertion on H_x^+.

To show the positive invariance of $\mathbb{R}_+^{2n}$, assume that there exists such an orbit $\pi(t, 0, e)$ that $e \in \mathbb{R}_+^{2n}$ while $\pi(\tau, 0, e) \notin \mathbb{R}_+^{2n}$. Then there exist $\tau_0 > 0$ such that $e_0 = \pi(\tau_0, 0, e) \in \partial\mathbb{R}_+^{2n}$. By the first part of the theorem, e_0 can not be in

H_x^+. Therefore we can find some $i \in \{1, \ldots, n\}$ such that $x_i > 0$ while $x_{i+1} = 0$ (if $i = n, x_{n+1} = x_1$) where x_i and x_{i+1} are components of $e_0 = (S, x)$ in x. Then utilizing arguments similar to showing the positive invariance of H_x^+, we are led to a contradiction, completing the proof. □

By the above lemma, we can consider a subsystem of (4.2), which represents a cyclostat with nutrient flow only,

$$\begin{cases} \dot{S}_1 = (1 + S_n - 2S_1) \\ \dot{S}_i = (S_{i-1} - S_i) \end{cases} \tag{4.4}$$

$$S_1(0), S_i(0) \geq 0; \ i = 2, \ldots, n.$$

System (4.4) is a linear autonomous system whose Jacobian is as follows

$$A = \begin{pmatrix} -2 & 0 & 0 & \ldots & 0 & 1 \\ 1 & -1 & 0 & \ldots & 0 & 0 \\ 0 & 1 & -1 & \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ldots & -1 & 0 \\ 0 & 0 & 0 & \ldots & 1 & -1 \end{pmatrix}.$$

After some algebraic manipulations, we obtain the characteristic function of A as follows:

$$E(\sigma) = (\sigma + 2)(\sigma + 1)^{n-1} - 1. \tag{4.5}$$

Then by Theorem 2.7, we have the following theorem.

THEOREM 4.2. *All solutions of system (4.4) tend to the only equilibrium $\hat{E} = (1, \ldots, 1) \in \mathbb{R}_+^n$ exponentially.*

PROOF: In (4.5), let $\alpha = \sigma + 1$. Then $E(\sigma)$ becomes a polynomial in α which is same as $P(\alpha)$ defined in (2.6). By Theorem 2.7, the real parts of all roots of

$P(\alpha) = 0$ are smaller than $1 - \frac{1}{2n-1}$. It follows that the real parts of all roots of $E(\sigma) = 0$ are negative. Therefore, the trivial solution of the homogeneous linear system of (4.4) is globally exponentially stable and hence so is $\hat{E}$ for (4.4). This completes the proof. □

The above theorem gives the following corollary.

COROLLARY 4.3. *Under assumption (A1), system (4.2) is dissipative and all solutions in $\mathbb{R}_+^{2n}$ tend to the invariant manifold*

$$H \triangleq \{(S,x) \in \mathbb{R}_+^{2n} \mid S_i + x_i = 1, i = 1, \ldots, n\}.$$

PROOF: For each solution $(S(t), x(t))$ of (4.2), define $W_i(t) = S_i(t) + x_i(t)$. Then $(W_1(t), \ldots, W_n(t))$ satisfies system (4.4). By Theorem 4.2, $W_i(t)$ tends to 1 for all $i = 1, \ldots, n$. It is easy to see that H is compact, completing the proof. □

REMARK: By Theorem 4.2, we can see that without the existence of the microorganism x_i, system (4.2) shall eventually approach a state where the nutrient concentrations in each vessel are equal. Also, we can see from the theorem that the point $\tilde{E} = (1, \ldots, 1, 0, \ldots, 0) \in \mathbb{R}_+^{2n}$ is an equilibrium of system (4.2).

Let K be any subset of a set of numbers $\{1, \ldots, n\}$. Then we define

$$G_K \triangleq \{(S,x) \in \mathbb{R}_+^{2n} \mid S_i = 0, i \in K\}.$$

$$H_K \triangleq \{(S,x) \in \mathbb{R}_+^{2n} \mid x_i = 0, i \in K\}. \tag{4.6}$$

The following lemma is required in order to prove some of the succeeding theorems.

LEMMA 4.4. *For a nonempty K, any $y \in G_K$ or any $y \in H_K \backslash \{\tilde{E}\}$ (in case of H_K, $K \neq \{1, \ldots, n\}$) can not be an ω-limit point of any point $p \in \mathbb{R}_+^{2n}$.*

PROOF: For the given K and $y \in G_K$, if $K = \{1, \ldots, n\}$, then we have that $\dot{S}_1 = 1 > 0$ at y. If $K \neq \{1, \ldots, n\}$, then there must exist some $i \in K$ such that $S_{i-1} > 0$ while $S_i = 0$. It follows that $\dot{S} = S_{i-1} > 0$ at y. With the same arguments, if $y \in H_K \backslash \{\tilde{E}\}$, there exits $i \in K$ such that $\dot{x}_i = x_{i-1} > 0$ at y. It follows that no matter whether $y \in G_K$ or $y \in H_K$, there always exists a component y_j of y such that $\dot{y}_j > 0$ while $y_j = 0$. Suppose y is an ω-limit of some point $p \in \mathbb{R}^{2n}_+$. Then by the uniqueness of the solutions and the continuous dependence of initial conditions of system (4.2), $\mathbb{R}^{2n}_+$ is not positively invariant, a contradition to Lemma 4.1. This completes the proof. □

The next theorem states that if the microorganism in some vessel goes to extinction, then those in all other vessels also go to extinction.

THEOREM 4.5. *For system (4.2),* $\lim_{t \to \infty} x_i(t) = 0$ *for some* $i \in \{1, \ldots, n\}$ *if and only if* $\lim_{t \to \infty} x_k = 0$ *for all* $k \in \{1, \ldots, n\}$.

PROOF: The sufficiency is obvious. Now we suppose $\lim_{t \to \infty} x_i = 0$ for some i while $\limsup_{t \to \infty} x_k > 0$ for some $k \neq i$. Then there exists some point $y \in H_K$ which is an ω-limit point of some point in $\mathbb{R}^{2n}_+$, where K is a subset of $\{1, \ldots, n\} \backslash \{k\}$ containing i. This is a contradiction of Lemma 4.4, which completes the proof. □

We all know that any species will go to extinction if it is out of the resources which it requires for life. Therefore, in the setting of a cyclostat device, we can imagine that the nutrient in each vessel will be bounded away from zero since we keep putting it into the device. The next theorem shows this fact, and even stronger that they are all bounded away from zero uniformly by an amount $\eta > 0$.

THEOREM 4.6. *There exists an* $\eta > 0$ *such that for any solution of (4.2),* $\liminf_{t \to \infty} S_i(t) \geq \eta$.

PROOF: As in the proof of Lemma 4.4, every point $y \in G_K$ lies on an orbit from outside of $\mathbb{R}_+^{2n}$. By the continuous dependence of the initial condition, there exists a neighborhood N_y of y in $\mathbb{R}_+^{2n}$ such that all points in N_y are not in any ω-limit set of all points in $\mathbb{R}_+^{2n}$. According to Corollary 4.3, all ω-limit sets of $e \in \mathbb{R}_+^{2n}$ are located in a compact set H. Since $C = H \bigcap (\bigcup_{K \neq \phi} G_K)$ is compact, where K runs through all nonempty subsets of $\{1, \ldots, n\}$, there exists a finite subcover $\{N_1, \ldots, N_p\}$ of $\{N_y \mid y \in C\}$ for C. It follows that there exists $\eta > 0$ such that $\liminf_{t \to \infty} d(C, \pi(t, 0, e)) \geq \eta$ for any $e \in \mathbb{R}_+^{2n}$, completing the proof. $\square$

By Corollary 4.3, we can study the asymptotic behavior of system (4.2) by the orbits on H only. Thus, we will confine ourselves to the following reduced n-dimensional system throughout the rest of this chapter,

$$\begin{cases} \dot{x}_1 = (x_n - 2x_1) + f(1 - x_1)x_1 \\ \dot{x}_i = (x_{i-1} - x_i) + f(1 - x_i)x_i \end{cases} \tag{4.7}$$

$$x_1(0), x_i(0) \geq 0, x_1, x_i \leq 1, \; i = 2, \ldots, n.$$

4.4. The extinction criterion of the species.

With the results in previous sections, we now can deal with the persistence of the species. First, it is easy to see $E_0 = (0, \ldots, 0) \in \mathbb{R}_+^n$ is an equilibrium on the boundary $\partial\mathbb{R}_+^n$, and by Lemma 4.4, system (4.7) has no other equilibrium on $\partial\mathbb{R}_+^n$. Then using a similar technique as in the proof of Lemma 4.1, we can show that I is positively invariant for the system generated by (4.7), where I is the unit cube in $\mathbb{R}_+^{2n}$.

By straightforward manipulations, we obtain the Jacobian at E_0 for (4.7),

$$J(E_0) = \begin{pmatrix} -2+f(1) & 0 & 0 & \dots & 0 & 1 \\ 1 & -1+f(1) & 0 & \dots & 0 & 0 \\ 0 & 1 & -1+f(1) & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & -1+f(1) & 0 \\ 0 & 0 & 0 & \dots & 1 & -1+f(1) \end{pmatrix}.$$

Its characteristic function is as follows,

$$E(\nu) = (\nu + 2 - f(1))(\nu + 1 - f(1))^{n-1} - 1. \tag{4.8}$$

LEMMA 4.7. *System (4.7) is a cooperative system (see Definition 1.14).*

PROOF: Let $F_i(x)$ be equal to the right hand side function of the ith equation in (4.7). Then we have $\frac{\partial F_i}{\partial x_j} = 1 > 0$ if $j = i - 1$ (if $i = 1, x_0 = x_n$), and $\frac{\partial F_i}{\partial x_j} = 0$ for all other $j \neq i$. This completes the proof. □

By Theorem 2.7 and (4.8), we can show the next theorem.

THEOREM 4.8. *Under assumption (A1), if $f(1) < (1 - \alpha_n)$, where α_n is given as in Theorem 2.7, then all solutions of (4.7) tend to E_0 exponentially, i.e., we say that system (4.7) goes to extinction.*

PROOF: By Theorem 2.7 and (4.8), the eigenvalues ν of $J(E_0)$ satisfy $Re(\nu) \leq f(1) - (1 - \alpha_n) < 0$ under the assumptions of this theorem. It follows that all solutions of the linear system $\dot{x} = J(E_0)x$ tend to E_0 exponentially. Under (A1), $F_i(x)$ is less than the ith row of $J(E_0)x$ in the interior of $\mathbb{R}^n_+$ for all i since $F_i(x)$ is decreasing. Therefore, for each solution $x(t) = (x_1(t), \dots, x_n(t))$ of (4.7), we have $\dot{x}(t) < J(E_0)x(t)$. By Theorem 1.7.1 of Ladde and Lakshmikantham (1980) (see Theorem A.8 in Appendix), $x(t) \to 0$ exponentially as $t \to \infty$, since (4.8) is coorperative. This proves the theorem. □

Now we define λ as the value at which $f(\lambda) = (1 - \alpha_n)$. Then the above theorem states that if $\lambda > 1$, then x goes to extinction. In the next section, we will prove a theorem which shows that system (4.7) is uniformly persistent if $\lambda < 1$. It follows that $\lambda = 1$ is a threshold for survival vs. extinction for x. So, another interesting question is how the solutions of (4.7) behave when $\lambda = 1$. The next theorem addresses this question,

THEOREM 4.9. *Under assumption (A2), if $\lambda = 1$, i.e.,$f(1) = (1 - \alpha_n)$, then E_0 is globally asymptotically stable.*

PROOF: First we define a Liapunov function on the compact set $I \subset \mathbb{R}^n_+$ as follows

$$V(x) = x_1 + (1 + \alpha_n) \sum_{i=2}^{n} \alpha^{i-2} x_i \tag{4.9}$$

.

For this function, we have $V(E_0) = 0, V(x) > 0$ for $x \in I \backslash E_0$. Taking the derivative of (4.9) along the solutions of (4.7), we obtain

$$\begin{aligned}
\dot{V}(x) &= (x_n - 2x_1) + f(1)x_1 + (1 + \alpha_n) \sum_{i=2}^{n} \alpha^{i-2} \left[(x_{i-1} - x_i) + f(1)x_i \right] \\
&= \left(f(1 - x_1) - (1 - \alpha_n) \right) x_1 + (1 + \alpha_n) \sum_{i=2}^{n} \alpha^{i-2} \left(f(1 - x_i) - (1 - \alpha_n) \right) x_i \\
&= U(x) < 0,
\end{aligned}$$

for all $x \in I \backslash \{E_0\}$, since f is increasing, where $U(x)$ is given by (2.10) in section 2.4. This completes the proof. □

The above theorem tells us that the species goes to extinction even if $\lambda = 1$, which is the critical value for the species.

4.5. Persistence.

First, we require some lemmas which are essential to obtain criteria for persistence.

LEMMA 4.10. *If n is even and $f(1) = (1 - \alpha_n^-)$, where α_n^- is defined in Theorem 2.8, then there exists a neighborhood N of E_0 such that there exists no equilibrium in $N \bigcap \mathring{\mathbb{R}}_+^n$.*

PROOF: For $x = (x_1, \ldots, x_n) \in \mathring{\mathbb{R}}_+^n$ to be an equilibrium, one must have,

$$G(x) \triangleq \big(2 - f(1 - x_1)\big) \prod_{i=2}^{n} \big(1 - f(1 - x_i)\big) = 1. \tag{4.10}$$

Since $f(1) = 1 - \alpha_n^- > 2$ by Theorem 2.8, we can choose N so small that each factor of $G(x)$ is still negative when $x \in N \cap \mathring{\mathbb{R}}_+^n$. It follows that

$$G(x) < \big(2 - f(1)\big) \prod_{i=2}^{n} \big(1 - f(1)\big) = 1$$

since n is even, which is a contradiction to (4.10). This shows that there exists no equilibrium in $N \cap \mathring{\mathbb{R}}_+^n$. □

Consider an autonomous system in $\mathbb{R}^n$,

$$\dot{x} = g(x).$$

We may always split $\mathbb{R}^n$ into three subspaces $E^s \oplus E^c \oplus E^u$, where E^s, E^c, and E^u are the generalized eigenspaces corresponding to eigenvalues of $Dg(E_0)$ of real part less than zero, equal to zero, and greater than zero, respectively. Then according to Theorem III.7 in Shub (1987) (see Theorem A.3), to each of the three $Dg(E_0)$ invariant subspaces E^s, E^c, and E^u there are associated local g invariant C^r embedded discs W_{loc}^s, W_{loc}^c, and W_{loc}^u tangent to the linear subspace at E_0.

LEMMA 4.11. *If $f(1) > (1-\alpha_n)$, then $W^s_{loc} \bigcap \mathbb{R}^n_+ = \{E_0\}$ and $W^c_{loc} \bigcap \mathbb{R}^n_+ = \{E_0\}$ for those discs, which are sufficiently small.*

PROOF: Before proving the lemma, we introduce a partial order in $\mathbb{R}^n$, with which system (4.7) generates an order preserving flow by the definition in Smith (1988) (see Definition A.1 in Appendix). We say that, for x and $y \in \mathbb{R}^n$, $x \preceq y$ if $y-x \in \mathbb{R}^n_+$, i.e., $y_i - x_i \geq 0$ for all $i = 1, \ldots, n$. It is easy to see that $\preceq$ so defined is a partial order in $\mathbb{R}^n$. By Lemma 2.1 in Smith (1988) (see Lemma A.1 in Appendix), system (4.7) preserves the order $\preceq$ if we extend (4.7) to $\mathbb{R}^n$ as was done at the beginning of Section 4.3. Since in the model described by $\dot{x} = J(E_0)x$, the ith vessel gets input from the previous one while it sends output to the next one (we consider the first vessel is next to the nth), the system leaves no proper invariant nontrivial subspace. It follows that $J(E_0)$ is irreducible (see Definition A.3). We also note that $s(J(E_0)) = f(1) - (1 - \alpha_n) > 0$ (see Definition A.2 for $s(A)$, where A is a $n \times n$ matrix).

Therefore, by Lemma 2.10 in Smith (1988) (see Lemma A.2 in Appendix), $W^s_{loc} \bigcap \mathbb{R}^n_+ = \{E_0\}$. Otherwise, suppose $x \in W^s_{loc} \bigcap \mathbb{R}^n_+ \backslash \{E_0\}$. Then the orbit through x will stay in the interior of $\mathbb{R}^n_+$ for all future time by Lemmas 4.1 and 4.4, and it will approache E_0 since it is in the stable manifold of E_0. In this case, we can find $t_1 > t_2 > 0$ such that $\pi(t_2, 0, x) \preceq \pi(t_1, 0, x)$, which contradicts Lemma 2.10 in Smith (1988) (see Lemma A.2). This completes the proof of first part of the lemma.

For W^c_{loc}, we notice, by Theorem 2.8, that the manifold is at most two dimensional, and W^c_{loc} is one dimensional if and only if n is even and $f(1) = (1 - \alpha_n^-)$. We first consider the linear subspace E^c generated by the only zero eigenvalue of $J(E_0)$. Since E^c is one dimensional, all solutions of $\dot{x} = J(E_0)x$ on E^c are rest points. If $E^c \cap \mathbb{R}^n_+ \backslash \{E_0\} \neq \phi$, then there exists a rest point x in the interior of $\mathbb{R}^n_+$. However, by the setting of $\dot{x} = J(E_0)x$, $x_{i-1} = (1-f(1))x_i$ for $i = 2, \ldots, n$. It follows that x_{i-1} and x_i have alternative signs since $1 - f(1) = \alpha_n^- < 0$. This contradiction to Lemma 4.4 shows that E^c is attached to $\mathbb{R}^n_+$ at only one point E_0, and so does W^c_{loc} if it is small enough since W^c_{loc} is tangent to E^c at E_0. Now we consider the case of two dimensions. In this case, all solutions of $\dot{x} = J(E_0)x$ are loops on E^c, one inside another with E_0 in the 'center'. Therefore, for small enough W^c_{loc}, solutions of (4.9) on W^c_{loc} wind around E_0 (see Fig. 6). It is easy to see that the nonemptiness of $W^c_{loc} \cap \mathbb{R}^n_+ \backslash \{E_0\}$ violates the positive invariance of $\mathbb{R}^n_+$. The proof is completed. □

LEMMA 4.12. *Under the same hypotheses of Lemma 4.11, $\{E_0\}$ is an isolated invariant set in $\mathbb{R}^n_+$ for $\mathcal{F}$ generated by (4.7).*

PROOF: With $f(1) > (1 - \alpha_n^-)$, we have one of the following four cases: (a) all eigenvalues are positive, (b) same as case (a) except that one eigenvalue is equal to zero, i.e., $f(1) = (1 - \alpha_n^-)$, (c) some eigenvalues are positive while others are negative, or (d) some are positive, some are negative and some eigenvalues are zero. In cases (a) and (c), E_0 is a hyperbolic rest point, hence it is an isolated invariant set. For cases (b) and (d), by Theorem III.7 in Shub (1987) (see Theorem A.3), all invariant sets in a small enough neighborhood of E_0 lie on W^c_{loc}. By Lemma 4.11, $W^c_{loc} \cap \mathbb{R}^n_+ = \{E_0\}$. It follows that E_0 is isolated in $\mathbb{R}^n_+$. This completes the proof. □

THEOREM 4.13. *Under assumption (A2), if $f(1) > (1 - \alpha_n)$, i.e., $\lambda < 1$, then system (4.7) is uniformly persistent.*

PROOF: Here, we want to utilize Theorem 2.6 in Chapter 2. We define E as $\mathbb{R}^n_+$, D as $\partial\mathbb{R}^n_+$, B as E_0. As shown in the proof of Lemma 4.4, all points on $D \backslash B$ enter the interior of E, which is the set of $E \backslash D$, for all the succeeding time. It

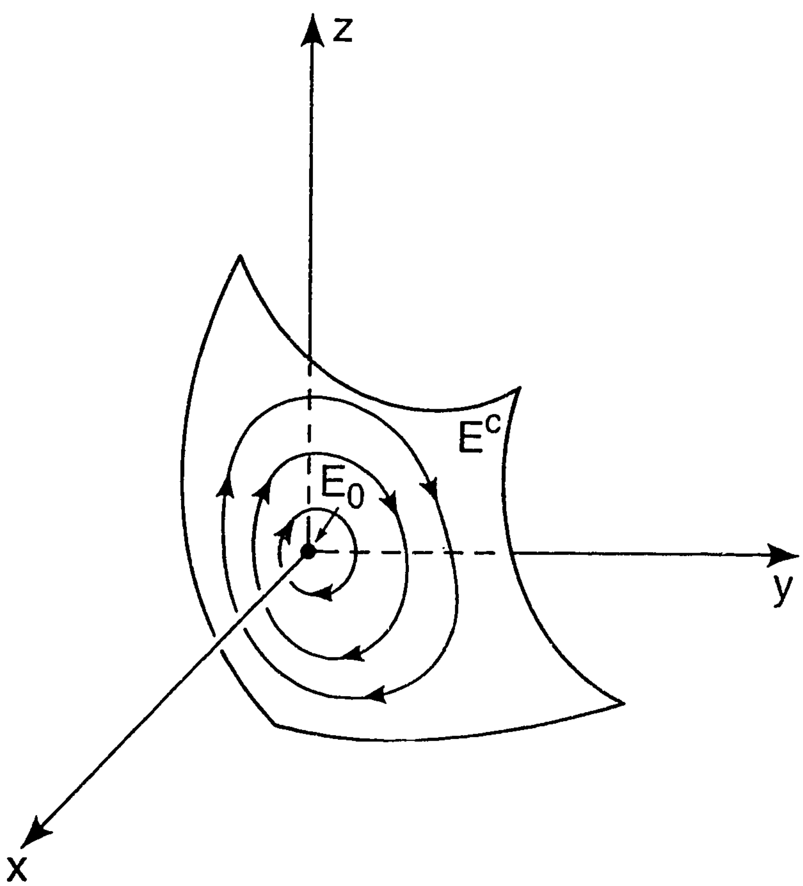


Fig. 6. Illustration of a case in the proof of Theorem 4.11.

follows that B is the only invariant set on D. Since B is compact, the flow $\mathcal{F}_B$ on it is dissipative. Since (4.7) is deduced from (4.2), by Lemma 4.1, $E \backslash D$ is positively invariant. We take B itself as the covering $\mathcal{M}$. By Theorem 2.6 in Chapter 2, if we can show that $\mathcal{F}_B$ is isolated in E and acyclic with $\mathcal{M}$, and condition (H) holds, then we are done.

Lemma 4.12 shows the isolatedness of $\mathcal{F}_B$. Now suppose $\mathcal{F}_B$ is cyclic. Then there exits such an orbit in $E \backslash B$ that has B as its ω-limit set. Therefore, this orbit is on the stable manifold of B, which is a contradiction to Theorem 2.10 in Smith (1988) (see Lemma A.2) since there exist distinct points x and y on the orbit with $x \preceq y$. This contradiction shows that $\mathcal{F}_B$ is acyclic. By Lemma 4.11, for any $x \in E \backslash D$, x cannot be in $W^s(B)$. It follows that (H) holds. This completes the proof. □

REMARK: By Theorem 2.7, we know that $\alpha_n \to 1$ as $n \to \infty$. This shows, with the above theorem, that the larger the number of vessels in system (4.7), the easier for the species to survive.

Next, we give more details about the ω-limit sets of system (4.7).

THEOREM 4.14. *Under (A2), if $\lambda < 1$ and $f''(u) < 0$ for $u \geq 0$, then there exist a unique interior equilibrium $\bar{x}$ for system (4.7).*

PROOF: First by Theorem 2.13 in Chapter 2, for any $\omega > 0$, there exists an ω-periodic solution in the interior of I for system (4.7) which is dissipative and persistent by Theorem 4.13. We pick a point p_n from the $\frac{1}{n}$-periodic orbit. Then a limit point $\bar{x}$ of the sequence $\{p_n\}$ will be an interior equilibrium. In fact, by the persistence of (4.7), E_0 is isolated, i.e., there exists a neighborhood of E_0 in which there exists no periodic orbit. It follows that $\bar{x} \neq E_0$, the only equilibrium on the boundary ∂I.

Assume $\tilde{x}$ is another interior equilibrium. Then there exists at least one $i \in \{1, \ldots, n\}$ such that $\tilde{x}_i \neq \bar{x}_i$, say $\tilde{x}_i > \bar{x}_i$ or vise versa. However, it is easy to verify that the function $g(u) = (1 - f(1 - u))u$ is increasing for $u \geq u_0$ for some $u_0 \in (0, 1 - \lambda)$. Since $g(x_i) = x_{i-1} > 0$ for an equilibrium $x = (x_1, \ldots, x_n)$, $0 < 1 - f(1 - x_i) < 1$ for $i = 2, \ldots, n$. It follows that $x_1 < x_2 < \cdots < x_n$ and $x_i > 1 - \lambda$ for $i = 2, \ldots, n$. It turns out that $g(x_1) = x_n - x_1 > 0$ and hence $x_1 > 1 - \lambda$. Therefore $\tilde{x}_{i-1} = g(\tilde{x}_i) > g(\bar{x}_i) = \bar{x}_{i-1}$ if $\tilde{x}_i > \bar{x}_i$, here we regard x_0 as x_n and in this case $x_n = x_1 + g(x_1)$. It follows that $\tilde{x}_i > \bar{x}_i$ for any $i = 1, \ldots, n$. Then it is not difficult to verify that $1 = G(\tilde{x}) > G(\bar{x}) = 1$, where G is defined as in (4.10). The contradiction leads to the uniqueness of the interior equilibrium. □

THEOREM 4.15. *Under (A1), if $1 > \lambda$ and $f''(u) < 0$, then the interior equilibrium $\bar{x}$ is globally asymptoticall stable.*

PROOF: By staightforward manipulations, we obtain the Jacobian of the linear variational system of (4.9) at $\bar{x}$ as follows,

$$J(\bar{x}) = \begin{pmatrix} \delta_1 & 0 & 0 & \ldots & 0 & 1 \\ 1 & \delta_2 & 0 & \ldots & 0 & 0 \\ 0 & 1 & \delta_3 & \ldots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ldots & \delta_{n-1} & 0 \\ 0 & 0 & 0 & \ldots & 1 & \delta_n \end{pmatrix}.$$

where $\delta_1 = -2 + f(1 - \bar{x}_1) - f'(1 - \bar{x}_1)\bar{x}_1 < 0, \delta_i = -1 + f(1 - \bar{x}_i) - f'(1 - \bar{x}_i)\bar{x}_i < 0$ for $i = 2, \ldots, n$. Then we can find the eigenfunction for $J(\bar{x})$ as follows,

$$E(\sigma) = -1 + \prod_{i=1}^{n} (\sigma - \delta_i)$$

We consider an auxiliary function

$$F(\sigma) = \prod_{i=1}^{n}(\sigma - \delta_i) = E(\sigma) + 1.$$

Since $f''(u) < 0$ for $u \geq 0, 1 - f(1-u) + f'(1-u)u$ is increasing. It is easy to see that $\bar{x}_1 < \bar{x}_2 < \cdots < \bar{x}_n < 2\bar{x}_1$ for the equilibrium $\bar{x}$. Therefore, we have $\delta_1 + 1 > \delta_2 > \cdots > \delta_n$. It follows that $F(\sigma)$ has at least $n-1$ different roots $\delta_2, \ldots, \delta_n$ of n real roots, and has at most one root δ_1 of double multiplicity. There exist only two cases: (a) $\delta_1 = \delta_2$, or (b) $\delta_1 \neq \delta_2$ (see Fig. 7).

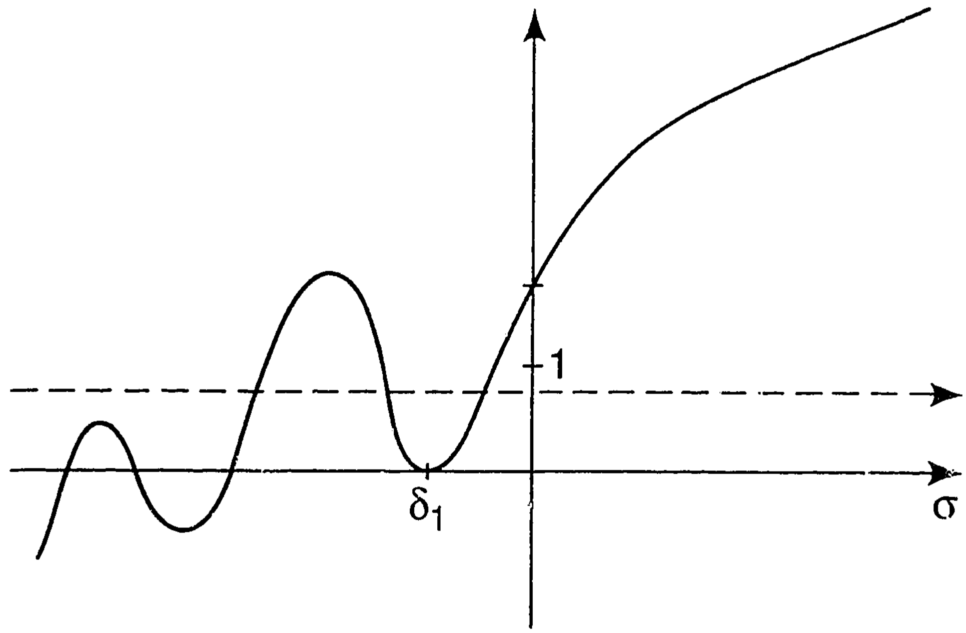
First, we have $F(0) = \prod_{i-1}^{n}(-\delta_i) > G(\bar{x}) = 1$ since $f' > 0$. We establish a parametric function related to $E(\sigma)$ and $F(\sigma)$ as follows

$$E_\beta(\sigma) = F(\sigma) - \beta, \qquad \beta \in [0,1]$$

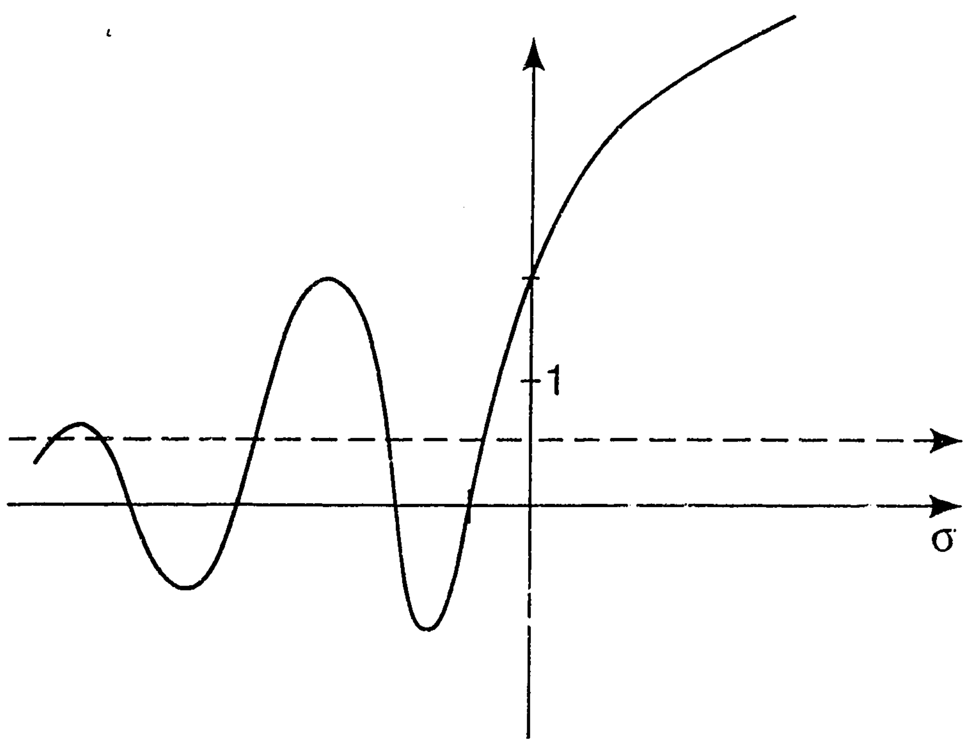
It is easy to see that $E_0(\sigma) = F(\sigma)$ and $E_1(\sigma) = E(\sigma)$. Since $E'_\beta(\sigma) = F'(\sigma) > 0$ for all $\sigma \geq 0, \beta \in [0,1]$, and $E_\beta(0) = F(0) - \beta > 0$ for all $\beta \in [0,1]$, the largest real root σ_β of $E_\beta(\sigma)$ is negative for all $\beta \in [0,1]$. With the graphs of all possible polynomials $F(\sigma)$ (see Fig. 7), we know that for any $\beta \in (0,1], \sigma_\beta$ is of single multiplicity for $E_\beta(\sigma) = 0$. It follows that all real roots of $E_\beta(\sigma)$ are less than σ_β.

Now, we prove that all the real parts of other roots of $E_\beta(\sigma)$ are less than σ_β. If it is not true, then there exist $\beta \in (0,1]$ and a root $\eta_\beta = a_\beta + b_\beta i$ of $E_\beta(\sigma)$ such that $a_\beta \geq \sigma_\beta$ and $b_\beta \neq 0$. Then we have

$$\begin{aligned}\beta^2 = \left|F(\eta_\beta)\right|^2 = \prod_{i=1}^{n}\left|\eta_\beta - \delta_i\right|^2 = \prod_{i=1}^{n}\left[(a_\beta - \delta_i)^2 + b_\beta^2\right] \\ > \prod_{i=1}^{n}(\sigma_\beta - \delta_i)^2 = \left|F(\sigma_\beta)\right|^2 = \beta^2,\end{aligned}$$



(a)



(b)

Fig. 7. Graphs of $F(\sigma)$ in the proof of Theorem 4.15.

a contradiction which leads to the conclusion that $a_\beta < \sigma_\beta$ for all β, especially for $\beta = 1$. It follows that $\bar{x}$ is asymptotically stable.

To show the global stability of $\bar{x}$, we notice that by Theorem 4.1 in Hirsch (1985) (see Theorem A.4), the stable set $W_s(\bar{x})$ of $\bar{x}$ has Lebesgue measure 1 in I since the equilibrium set $E = \{E_0, \bar{x}\}$ with E_0 being totally unstable in I. Assume that there exists $x \in \overset{\circ}{I} \backslash W_s(\bar{x})$. Then it is easy to see that both $O_+(x) = \{y \in I \mid y > x\}$ and $O_-(x) = \{y \in I \mid y < x\}$ have their Lebesgue measure greater than 0. Therefore, there exist $y_1 \in O_+(x) \cap W_s(\bar{x})$ and $y_2 \in O_-(x) \cap W_s(\bar{x})$. Since $\bar{x}$ is asymptotically stable and $x \notin W_s(\bar{x})$, we have $\omega(x) \cap \{\bar{x}\} = \phi$. Hence by Theorem 3.8 in Hirsch (1985) (see Theorem A.7), we have

$$\{\bar{x}\} = \omega(y_2) < \omega(x) < \omega(y_1) = \{\bar{x}\},$$

a contradiction leading to that $W_s(\bar{x}) = int I$, completing the proof. □

COROLLARY 4.16. *For system (4.7) with Michaelis-Menten uptakes, i.e.,* $f(u) = \frac{mu}{a+u}$ *with* $m, a > 0$, *if* $\frac{a(1-\alpha_n)}{m-(1-\alpha_n)} < 1$, *then the system has a globally stable interior equilibrium* $\bar{x}$.

PROOF: The system satisfies all the conditions in Theorem 4.15. □

4.6. The compitition among two species in a cyclostat model.

By adding one more species $y = (y_1, \ldots, y_n) \in \mathbb{R}^n_+$ which also consumes the input nutrient to system (4.1), we obtain a system as follows in which two species, x and y, compete for the only input resource S,

$$\begin{cases} \dot{S}_1 = D(S_0 + S_n - 2S_1) - \frac{m_x}{\gamma_x} f(S_1)x_1 - \frac{m_y}{\gamma_y} g(S_1)y_1 \\ \dot{S}_i = D(S_{i-1} - S_i) - \frac{m_x}{\gamma_x} f(S_i)x_i - \frac{m_y}{\gamma_y} g(S_i)y_i \\ \dot{x}_1 = D(x_n - 2x_1) + m_x f(S_1)x_1 \\ \dot{x}_i = D(x_{i-1} - x_i) + m_x f(S_i)x_i \\ \dot{y}_1 = D(y_n - 2y_1) + m_y g(S_1)y_1 \\ \dot{y}_i = D(y_{i-1} - y_i) + m_y g(S_i)y_i \end{cases} \tag{4.11}$$

$$S_1(0), S_i(0), x_1(0), x_i(0), y_1(0), y_i(0) \geq 0; \; i = 2, \ldots, n.$$

All the descriptions about the variables, parameters, constants and functions are the same as those given right after (4.1). Further after a similar analysis as done in sections 4.2 and 4.3, we can reach that $S_i + x_i + y_i$ tends to S_0 eventually; and then, instead of (4.11), we can study the following system,

$$\begin{cases} \dot{x}_i = (x_{i-1} - p_i x_i) + f(1 - x_i - y_i)x_i \\ \dot{y}_i = (y_{i-1} - p_i y_i) + g(1 - x_i - y_i)y_i \end{cases} \tag{4.12}$$

$$x_i(0), y_i(0) \geq 0, x_i, y_i \leq 1, \; i = 1, \ldots, n,$$

where $p_i = 2$ if $i = 1$, otherwise $p_i = 1$, and f and g satisfy (A1) or (A2). Here we identify $x_0 = x_n$ and $y_0 = y_n$. We define

$$\mathcal{P} = \{(x, y) \in \mathrm{IR}^{2n} \mid x_i, y_i \geq 0 \quad and \qquad x_i + y_i \leq 1, i = 1, \ldots, n\}.$$

Then it is not difficult to show that (4.12) is a semi-dynamical system defined in $\mathcal{P}$ since all forward solutions of (4.12) exist for all $t \geq 0$ in $\mathcal{P}$.

In section 4.4, we have shown that if $1 \leq \lambda_1$ (or $1 \leq \lambda_2$), then x (or y) goes to extinction, where λ_1 and λ_2 are the values at which the functions f and

g are equal to $1-\alpha_n$ respectively. Therefore, the results on $\lambda_j \geq 1$ for $j=1$ or 2 are obvious. On the other hand, we also showed that if $\lambda_1 < 1$ (or $\lambda_2 < 1$), then there exists $\bar{x}$ (or $\bar{y}$) $\in \mathring{\mathbb{R}}^n_+$ such that with $y=0$ (or $x=0$), all x tend to $\bar{x}$ (or y tend to $\bar{y}$) eventually. In this section, we shall study the behavior of x and y in the interior of $\mathcal{P}$ under the assumptions that $\lambda_j < 1$ for $j=1,2$.

First, we give a result whenever x and y have the same functional response to the input nutrient S, i.e., $f(u)=g(u)$ for all $u \in [0,1]$.

THEOREM 4.17. *Assuming (A1), if $f(u)=g(u)$ for all $u \in [0,1]$, then the set of equilibria consists of*

$$L=\{(x,y)\in \mathbb{R}^{2n}_+ \mid x_i+y_i=\bar{x}_i, i=1,\ldots,n\}$$

and $\{E_0\}$, where $\bar{x}_i$ is the ith component of $\bar{x}$ given in Theorem 4.14. And almost every solution of (4.12) approaches to one of the points on this segment.

PROOF: It is easy to see that in this case, for any solution (x,y) of (4.12), $x+y$ satisfies system (4.7). Therefore, by the previous result, any equilibrium $(\hat{x},\hat{y})$ of (4.12) satisfies the equalities $\hat{x}_i+\hat{y}_i=\bar{x}_i$. It follows that if $\hat{x}_i=q\bar{x}_i$ for some i and $q\in[0,1]$, then

$$\hat{x}_{i-1}=(p_i-f(1-\hat{x}_i-\hat{y}_i))\hat{x}_i=q\bar{x}_{i-1}.$$

This shows that $\hat{x}=q\bar{x}$ and hence $\hat{y}=(1-q)\bar{x}$, which is the case that $(\hat{x},\hat{y})\in L$.

Now, by reversing the sign of y, we obtain a cooperative system from (4.12). Then by Theorem 4.1 in Hirsch (1985) (see Theorem A.4), almost every solution tends to an equilibrium. This completes the proof. □

To proceed further into this section, we assume that $f(u) > g(u)$ for all $u \in (0,1)$. Otherwise, we could end up in a situation which is too sophisticated to study. This assumption means that species x always has a stronger functional response to the resource than y does. It seems that x can definitely survive under our assumption $\lambda_j < 1$. The question is whether or not y is able to survive itself in the competition for a single resource. The following theorem answers this question.

THEOREM 4.18. *Under (A1), if $f''(u)$ and $g''(u)$ are continuous and $f(u) > g(u)$ for all $u \in (0,1)$, the the equilibrium $E_x = (\bar{x}, 0)$ of (4.12) is globally stable. In other words, y goes to extinction while x survives.*

Before giving the proof of this theorem, we show two lemmas which helps in proving the theorem.

LEMMA 4.19. *Under the conditions of Theorem 4.18, there exists no interior equilibria for system (4.12).*

PROOF: As (4.10), we define

$$G_1(x,y) \triangleq \prod_{i=1}^{n} (p_i - f(1 - x_i - y_i))$$

and,

$$G_2(x,y) \triangleq \prod_{i=1}^{n} (p_i - g(1 - x_i - y_i)).$$

By the assumption that $f > g$, we have that $G_1(x,y) < G_2(x,y)$ for all $(x,y) \in \mathcal{P}$. However, for any interior equilibrium $(\hat{x}, \hat{y})$, we have $G_1(\hat{x}, \hat{y}) = 1 = G_2(\hat{x}, \hat{y})$, a contradiction, completing the proof. □

LEMMA 4.20. *All of the equilibria, namely (0,0), $(\bar{x}, 0)$ and $(0, \bar{y})$ of system (4.12) are simple according to the definition in Hirsch (1985), i.e., there exists no eigenvalue of those three equilibria having 0 real part. And further, $(\bar{x}, 0)$ is a sink,* *i.e., all its eigenvalues are of negative real parts, while $(0, \bar{y})$ has some eigenvalues with positive real parts.*

PROOF: We define a matrix $A_h(x,y)$, where h is a function satisfying (A1) or (A2) and $(x,y) \in \mathbb{R}_+^{2n}$, as follows

$$A_h(x,y) = \begin{pmatrix} \delta_1 & 0 & 0 & \dots & 0 & 1 \\ 1 & \delta_2 & 0 & \dots & 0 & 0 \\ 0 & 1 & \delta_3 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & \delta_{n-1} & 0 \\ 0 & 0 & 0 & \dots & 1 & \delta_n \end{pmatrix},$$

where $\delta_i = -p_i + h(1 - x_i - y_i) - h'(1 - x_i - y_i)z_i$, $z_i = x_i$ or y_i, depending on $h = f$ or g respectively. Then, by some straightforward manipulations, we obtain the Jacobians at those three equilibria as follows

$$J(0,0) = \begin{pmatrix} A_f(0,0) & 0 \\ 0 & A_g(0,0) \end{pmatrix},$$

$$J(\bar{x},0) = \begin{pmatrix} A_f(\bar{x},0) & * \\ 0 & A_g(\bar{x},0) \end{pmatrix},$$

and,

$$J(0,\bar{y}) = \begin{pmatrix} A_f(0,\bar{y}) & 0 \\ * & A_g(0,\bar{y}) \end{pmatrix},$$

where * represents an $n \times n$ matrix. It is not too difficult to see that $A_f(0,0)$ and $A_g(0,0)$ are of the same form as the matrices in the beginning of section 4.4. It follows that the origin (0,0) is totally unstable, i.e., all its eigenvalues are of positive real parts. Using a similar argument, we obtain that the eigenvalues of $A_f(\bar{x},0)$ and $A_g(0,\bar{y})$ are of negative real parts since the two matrices are similar to those in the proof of Theorem 4.15. For $A_f(0,\bar{y})$ and $A_g(\bar{x},0)$, we obtain their eigenfunctions as follows,

$$P_h(\sigma) = -1 + \prod_{i=1}^{n}(\sigma + p_i - h(1-\bar{z})),$$

where h equals f or g and z is x or y depending upon whether $h = g$ or $h = f$ respectively. Utilizing a similar technique in the proof of Theorem 4.15, we can prove that the roots of P_g all have negative real parts since $P_g(0) = -1+\prod_{i=1}^{n}(p_i - g(1-\bar{x}_i)) > 0$. It follows that all eigenvalues of $J(\bar{x},0)$ have negative real parts. On the other hand, at least one root of P_f has a positive real part since $P_f(0) < 0$ while $P_f(\sigma)$ tends to infinity as $\sigma \to \infty$. Therefore, to complete the proof, it suffices to show that P_f has no 0 real part solutions. By Theorem 2.12, P_f has no pure imaginary roots of greater than one multiplicity. Suppose βi and $-\beta i$ is a pair of conjugate eigenvalues of $J(0,\bar{y})$. Then the corresponding eigenvectors will span a 2-dimensional plane $\mathcal{H}$ which passes through the equilibrium $(0,\bar{y})$ and is transversal to the part of boundary $\{(0,y) \mid 0 \leq y_i \leq 1, i = 1,\ldots,n\}$. This violates the positive invariance of $\mathcal{P}$ since the closed trajectories surrounding the equilibrium winds arround it on a 2-dimensional manifold tangent to $\mathcal{H}$. It follows that of the equilibrium set of (4.12) in $\mathcal{P}$, $(\bar{x},0)$ is the only sink, while the other two are simple equilibria with eigenvalues whose real parts are positive. This completes the proof. □

Now, we turn to the proof of Theorem 4.18 to conclude this section.

PROOF OF THEOREM 4.18: As stated in the proof of Theorem 4.17, system (4.12) becomes a cooperative system by reversing the sign of y. Then by Theorem 4.4 in Hirsch (1985) (see Theorem A.6), almost every trajectory of (4.12) in $\mathcal{P}$ converges to a sink which is $(\bar{x},0)$ in this case by Lemma 4.20. Also by Lemma 4.20, $(\bar{x},0)$

is asymptotically stable. It follows that the stable set $W^s(\bar{x}, 0)$ of the equilibrium is an open set which contains the interior of $\mathcal{P}$. This completes the proof. □

Theorem 4.18 tells us that only if $f > g$, species y will go to extinction while x survives no matter how close the two functions are. It shows that the system (4.12) follows the competitive exclusive law in population theory.

4.7. Discussion.

As we mentioned in the introduction chapter, the cyclostat model is a mod-[illegible] of the gradostat model. Up to the time of completion of this thesis, we [illegible] not found any system in the real world which a cyclostat model emulates. However, it is possible to implement this model as a laboratory apparatus (see Fig. 3). On the other hand, this model still has a lot of interesting problems. The first one is whether or not the two species model can have persistence. If the answer is yes, what is the criteria for the persistence. For other problems, we consider a cyclostat model of more than one trophic level.

Just after the completion of this thesis, the author is brought to the attention to the research developed by Smith, Tang and Waltman (1991). Their results in the paper cover the results in the cyclostat model of this thesis in some way (saying so is because that the models in their paper are set with a specific type of uptake functions, so-called Michaelis-Menten function). However, most of the results in the paper need only assumption (A.1) or (A.2) (see section 4.2) for the uptake functions to satisfy. For the results obtained by bifurcation theory, if we take f_u satisfying (A.2) with $f_u''(x) < 0$ for $x \geq 0$ and $s(A + F_u(z)) > 0$ (see Smith, Tang and Waltman (1991)), then we can obtain the same results by setting $f_v(x) = m\tilde{f}_v(x)$ where $\tilde{f}_v$ is any function satisfying (A.2) with $\tilde{f}_v''(x) < 0$ for $x \geq 0$ and m is set to be the bifurcation parameter.

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Appendix

Here we list some definitions and theorems of other authors that we used in our study.

We begin by considering

$$x' = f(x) \tag{A.1}$$

where $x \in \mathbb{R}^n$ and f is a continuously differentiable function defined on a convex, open set $U \subset \mathbb{R}^n$. We also consider a partial ordering on $\mathbb{R}^n$ generated by an orthant. More precisely, let $m = (m_1, \ldots, m_n), m_i \in \{0,1\}, 1 \leq i \leq n$, and $K_m = \{x \in \mathbb{R}^n \mid (-1)^{m_i} x_i \geq 0, 1 \leq i \leq n\}$. For $x, y \in \mathbb{R}^n$, we say $x \preceq_{K_m} y$ if only if $y - x \in K_m$. For the sake of convenience, we drop the subscription of K_m from $\preceq_{K_m}$ without any confusion.

DEFINITION A.1: We say that the solution operator ϕ_t of (A.1) *preserves the partial ordering* $\preceq$ *(for* $t \geq 0$*)* and (A.1) *is type* K_m *monotone* if whenever $x, y \in U$ with $x \preceq y$ then $\phi_t(x) \preceq \phi_t(y)$ for all $t \geq 0$ for which both $\phi_t(x)$ and $\phi_t(y)$ are defined.

LEMMA A.1. *(Smith (1988)) If* $f \in C^1(U)$ *where* U *is open and convex in* $\mathbb{R}^n$ *then* ϕ_t *preserves the partial ordering* $\preceq$ *for* $t \geq 0$ *if and only if* $P_m Df(x) P_m$ *has nonnegative off-diagonal elements for every* $x \in U$*, where* $P_m = diag((-1)^{m_1}, \ldots, (-1)^{m_n})$.

DEFINITION A.2: We write $s(A)$ for the stability modulus of an $n \times n$ matrix, $s(A) = \max\{Re(\nu) \mid \nu$ is an eigenvalue of $A\}$.

DEFINITION A.3: A matrix A is called *irreducible* if it does not leave invariant any proper nontrivial subspace generated by a subset of the standard basis vectors for $\mathbb{R}^n$ or, equivalently, if one cannot put the matrix in the following form:

$$A = \begin{pmatrix} M_1 & M_2 \\ 0 & M_3 \end{pmatrix}.$$

where M_1 and M_3 are square matrices, by a reordering of the standard basis.

LEMMA A.2. *(Smith (1988)) Let (A.1) be a type K_m monotone system. Suppose x_0 is a hyperbolic steady state of (A.1) where $s(Df(x_0)) > 0$ and $Df(x_0)$ is irreducible. Then $W^+(x_0)$ does not contain distinct points x and y with $x \preceq y$.*

THEOREM A.3. *(Shub (1987)) Let 0 be a fixed point for the C^r local differomorphism $f : U \to \mathbb{R}^n$ where U is a neighborhood of zero in $\mathbb{R}^n$ and $1 \le r \le \infty$. Let $E^s \oplus E^c \oplus E^u$ be the invariant splitting of $\mathbb{R}^n$ into the generalized eigenspaces of $Df(0)$ corresponding to eigenvalues of absolute value less than one, equal to one, and greater than one. To each of the five $Df(0)$ invariant subspaces E^s, $E^s \oplus E^c$, $E^c, E^c \oplus E^u$, and E^u there is associated a local f invariant C^r embedded disc $W^s_{loc}, W^{sc}_{loc}, W^c_{loc}, W^{cu}_{loc}$, and W^u_{loc} tangent to the linear subspace at 0 and a ball B around zero in an adapted norm such that:*

(1) $W^s_{loc} = \{x \in B \mid f^n(x) \in B, n \ge 0; d(f^n(x), 0) \to 0$ exponentially$\}$. and $f : W^s_{loc} \to W^s_{loc}$ is a contraction mapping.

(2) $f(W^{cs}_{loc}) \cap B \subset W^{cs}_{loc}$. If $f^n(x) \in B$ for all $n \ge 0$, then $x \in W^{cs}_{loc}$.

(3) $f(W^c_{loc}) \cap B \subset W^c_{loc}$. If $f^n(x) \in B$ for all $n \in Z$, then $x \in W^c_{loc}$.

(4) $f(W^{cu}_{loc}) \cap B \subset W^{cu}_{loc}$. *If* $f^n(x) \in B$ *for all* $n \leq 0$, *then* $x \in W^{cu}_{loc}$.

(5) $W^u_{loc} = \{x \in B \mid f^n(x) \in B, n \leq 0; d(f^n(x), 0) \to 0$ *exponentially*$\}$. *and* $f_{-1} : W^u_{loc} \to W^u_{loc}$ *is a contraction mapping.*

DEFINITION A.4: Give a partial order $\preceq$ in X. We call (A.1) a monotone system if for any $x \preceq y$ in X, we have

$$\pi(x,t) \preceq \pi(y,t) \quad \text{for} \quad t \geq 0,$$

where $\pi(u,t)$ is the trajectory of (A.1) through $u \in X$.

For the next three theorems, (A.1) need to be a monotone system. $W^c \subset \mathbb{R}^n$ is the set of points which have compact closures for their positive trajectories.

THEOREM A.4. *(Hirsch (1985)) There is a set* $Q \subset W^c$ *having Lebesgue measure zero, such that* $x(t) = \phi_t(x)$ *approaches the equilibrium set* E *as* $t \to \infty$, *for all* $x \in W^c \backslash Q$.

We say $M \preceq N$ for $M, N \subset \mathbb{R}^n$ if $x \preceq y$ for all $x \in M$ and $y \in N$. Then we have,

THEOREM A.5. *(Hirsch (1985)) Exactly one of the following conditions holds for* $x \preceq y$:

(1) $\Omega(x) \preceq \Omega(y)$, *or*

(2) $\Omega(x) = \Omega(y) \subset E$,

where E is the set of equilibria.

DEFINITION A.5: An equilibrium p is called ***simple*** if $0 \notin \mathrm{Spec}Df(p)$, ***hyperbolic*** if $\mathrm{Re}\lambda \neq 0$ for all $\lambda \in\mathrm{Spec}Df(p)$, a ***sink*** if $\mathrm{Re}\lambda < 0$, a ***trap*** if there exists some open set N, not necessarily containing p, such that $\phi_t(x) \to p$ uniformly in N as $t \to \infty$.

THEOREM A.6. *(Hirsch (1985)) (a) Assume E is countable. Then $x(t)$ converges to a trap as $t \to \infty$, for almost all $x \in W^c$.*
(b)

Assume all equilibria are simple. Then $x(t)$ converges to a sink as $t \to \infty$, for almost all $x \in W^c$.

THEOREM A.7. *(Horn (1970)) Let $S_0 \subset S_1 \subset S_2$ be convex subsets of the Banach space X, with S_0 and S_2 compact and S_1 open relative to S_2. Let $f : S_2 \to X$ be a continuous mapping such that, for some integer $m > 0$,*

$$f^j(S_1) \subset S_2 \quad \text{for} \quad 1 \leq j \leq m-1, \quad \text{and} \quad f^j(S_1) \subset S_0 \quad \text{for} \quad m \leq j \leq 2m-1.$$

Then f has a fixed point in S_0.

DEFINITION A.6: The function $g(t,u)$ is said to possess a ***quasi-monotone nondecreasing property*** if for $u, v \in \mathbb{R}^n$ such that $u \preceq v$ and $u_i \leq v_i$, then $g_i(t,u) \preceq g_i(t,v)$ for any $i = 1, \ldots, n$ and fixed t.

THEOREM A.8. *(Ladde and Lakshmikantham (1980)) Assume that*

(i) $g \in C[E, \mathbb{R}^n]$ and that $g(t,u)$ is quasi-monotone nondecreasing in u for each t, where E is an open (t,u)-set in $\mathbb{R}^{n+1}$;

(ii) $[t_0, t_0 + a)$ *is the largest interval of existence of the maximal solution* $r(t) \triangleq r(t, t_0, u_0)$ *of*

$$\dot{x} = g(t, x);$$

(iii) $m \in C\big[[t_0, t_0 + a), \mathbb{R}^n\big], (t, m(t)) \in E, t \in [t_0, t_0 + a)$, *and for a fixed Dini derivative* (D), *the inequality*

$$Dm(t) \leq g(t, m(t))$$

holds for $t \in [t_0, t_0 + a)$.

Then $m(t_0) \leq u_0$ *implies that* $m(t) \leq r(t), t \in [t_0, t_0 + a)$.

Next we prove a lemma showing that the convex hull of a compact set is compact.

LEMMA A.9. *For any compact set* K *in a linear space* X, *its convex hull*

$$coK \triangleq \{y \mid y = at + b(1 - t); a, b \in K, 0 \leq t \leq 1\}$$

is compact.

PROOF: For any open cover C_λ of coK, if we can find a finite subcover of C_λ, then we are done. First, for any $a, b \in K$, since the segment $L(a, b) \triangleq \{at + b(1-t) \mid 0 \leq t \leq 1\}$ is compact, we can have a finite subcover $C(a, b) = \{C_{\lambda_i}\}_{i=1}^{k(a,b)}$. On the other hand, we can find an "$\epsilon(a, b)$-tube" $T(a, b) \triangleq \{y \in X \mid d(y, L(a, b)) < \epsilon(a, b)\}$ such that $L(a, b) \subset T(a, b) \subset \cup_{i=1}^{k(a,b)} C_{\lambda_i}$. Denote by $N_b(a), N_a(b)$ the ϵ-neiborhood of a, b respectively. Then we consider $K \times K$ in the product space $X \times X$. It is well-known that $K \times K$ is compact in $X \times X$ since K is so in X. Define

$D(a,b) \triangleq N_b(a) \times N_a(b)$ for each $(a,b) \in K \times K$. Then the set $\{D(a,b)\}$ forms an open cover of $K \times K$. By the compactness of $K \times K$, there exists a finite subcover $\{D(a_j,b_j)\}_{j=1}^{\ell}$ of $\{D(a,b)\}$. Then we claim that $\mathcal{C} = \cup_{j=1}^{\ell} \mathcal{C}(a_j,b_j)$ is a finite subcover of $\{C_\lambda\}$. It is obvious that $\mathcal{C}$ is finite since it is a finite union set of finite sets. For any $y \in coK$, there exist $a,b \in K$ and $t \in [0,1]$, such that $y = at + b(1-t)$. On the other hand, there exists $j \in \{1,\ldots,\ell\}$ such that $(a,b) \in D(a_j,b_j)$. It follows that

$$d(y, L(a_j,b_j)) \le d(y, a_j t + b_j(1-t)) \le td(a,a_j) + (1-t)d(b,b_j) \le \epsilon(a_j,b_j),$$

i.e., $y \in T(a_j,b_j) \subset \cup_{C \in \mathcal{C}(a_j,b_j)} C$. This shows that $\mathcal{C}$ is a cover of K, completing the proof. □

THEOREM A.10. *(J.L. Massera, 1950) Let G be a simply connected plane open domain and T a topological mapping of G into itself, $TG \subset G$. If T is sense-preserving and there exists a point $x_0 \in G$ and a subsequence of its successive images $x_1 = Tx_0, x_2 = Tx_1, \ldots$ which converges to a point in G, then T has a fixed point in G.*